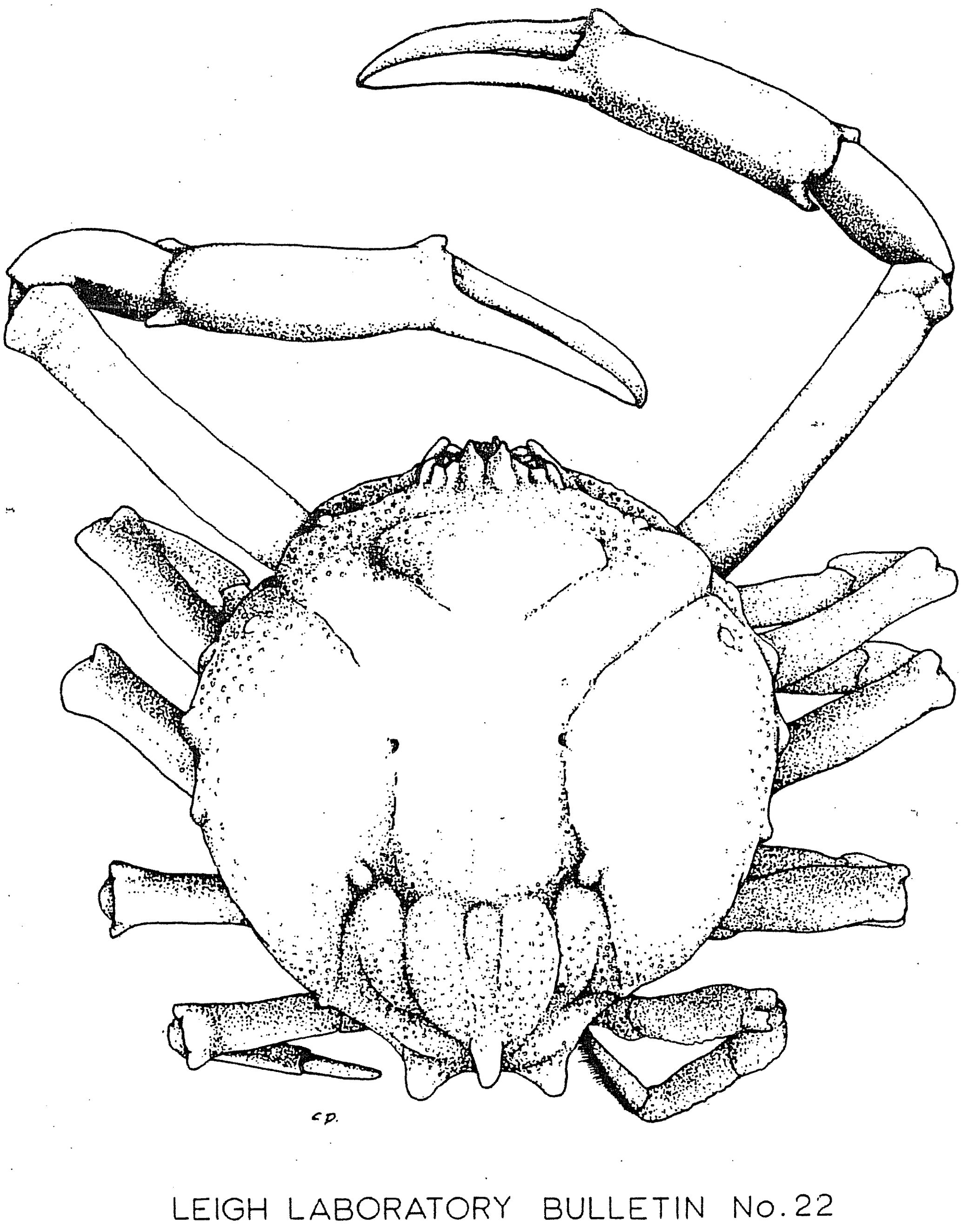
CRABS OF NEW ZEALAND

C.L.McLay



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BRACHYURA AND CRAB-LIKE ANOMURA OF NEW ZEALAND

by

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PREFACE

The Leigh Laboratory Bulletins began in 1978 with a report on the biological and physical survey of New Zealand's first marine reserve. In 1981 a compilation of existing knowledge on the fish of the marine reserve was printed and proved so useful that further accounts of the local fauna were encouraged. Two groups of molluscs and the common sponges have already been treated in this way.

This volume, on crabs, by Dr McLay is the latest in the series of descriptions of local fauna and sets new standards of coverage and detail.

Colin McLay spent most of 1984 on sabbatical at Leigh, working mainly on hermit crabs and predation, but he also spent considerable time compiling this review of existing knowledge from the scattered literature and from his own extensive knowledge. All students and other workers will be appreciative of a single volume giving the available information and showing clearly where further work would be useful.

W.J. Ballantine

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My thanks also to my colleagues in the Zoology Department, University of Canterbury. To Malcolm Jones (now in Plymouth), to Malcolm Forster and Harry Taylor who helped me to grasp something about crab physiology, and to Bob Pilgrim, Islay Marsden and Graham Fenwick for many valuable discussions. I should also acknowledge the stimulus provided by Baughan Wisely who in 1972 suggested that I might like to go up to Kaikoura and have a look at' a spider crab (*Notomithrax ursus*) which decorates itself with seaweed. This casual suggestion began my interest in crabs. Finally, I must thank all my graduate students of recent years who have provided information and have read parts of the manuscript at various stages. In particular Louise Clark, Paul Creswell, Rob Davidson, Rohan Dewa, Clinton Duffy, Helen Menzies, Tracey Osborne and Julie Pringle.

Helen Spinks and Peter McLay helped to type the manuscript into the wordprocessor and coped wonderfully well with the attempt to eliminate inconsistencies in style and elimination of errors. Any errors which remain must be blamed on the author! I also wish to thank John Black and Clinton Duffy who prepared many of the illustrations and page layouts.

I am grateful to editors of the following publications for permission to reproduce previously published illustrations:

> Records of the National Museum, Wellington; Transactions, Proceedings and Journal, Royal Society of New Zealand; Memoirs of the New Zealand Oceanographic Institute, Wellington; New Zealand Journal of Zoology, DSIR; Proceedings of the United States National Museum, Smithsonian Institution Press, Washington; Memoirs of the Queensland Museum, Brisbane; Bulletin Museum National d'Histoire Naturelle, Paris; Researches on Crustacea, Carcinological Society of Japan, Odawara Carcinological Museum; A.H. & A.W. Reed (Octopus Publishing Group (NZ) Ltd), Auckland; Siboga Expedition Monographs, E.J. Brill, Leiden.

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INTRODUCTION

Crab-like marine arthropods are among the most advanced forms of crustaceans. They have a well developed carapace, usually wider than long, short bodies with the abdomen folded underneath as a segmented flap and the first pair of pereiopods chelate. These sometimes fearsome-looking appendages often deter people from handling them but in fact most crabs are easily manipulated once you overcome the initial fear of being bitten. Perhaps this aversion is the reason why there still remains much to be discovered about crabs. Most crabs cannot inflict any sort of damage to a human but those which can are easily handled after a bit of trial and error. The words of Thomson (1932) are probably equally applicable today: '...the sea, which teems with animal and vegetable life, and with unrealized sources of national wealth, has hitherto received very little attention. ... In this general neglect of marine biology the Crustacea have shared. The number of workers who have added to our knowledge of this group is very small...'

The predatory, commensal and mutualistic relationships of crabs with other marine animals, their reproductive and population dynamics and their importance as members of marine communities are fascinating to the marine ecologist. Various aspects of crab behaviour, burrowing, sound production, masking and foraging are intriguing to the animal behaviourist. Physiological adaptations of their osmotic balance, respiration and ventilation, hormonal control of moulting, autotomy and regeneration of lost limbs, and their highly organised nervous systems are exciting to physiologists. The reasons for the apparently low genetic diversity of crustaceans provides a challenge to geneticists. For the great majority of New Zealand crabs we have barely even begun to scratch the surface of the wide range of studies that are possible.

The main habitats and places in which crabs can be found are:

1) Under stones and boulders, sandy and rocky intertidal areas. In addition to daytime low tides, collecting at night in these areas can be especially rewarding.

2) In similar areas to those in above but sub-tidally, using SCUBA gear.

3) In deep water on all types of bottoms (rocky, sandy and muddy) using dredges,nets or pots from boats.

4) Among seaweeds and seagrass.

5) Among shells of mussel beds and inside these and other shellfish.

6) At higher levels on the shore exposed to waves and sun.

7) In estuaries, brackish lagoons, tidal rivers, under stones or in burrows.

8) In freshwater lakes and rivers.

9) In stomachs of fish, birds or marine mammals.

10) Along the drift line on beaches, among seaweed cast up on the shore (dead adults or moults).

11) In the open sea as plankton (larval stages), swimming adults or clinging to drifting weed.

12) Cretaceous or Tertiary fossil beds.

The first crabs to be described from New Zealand may have been the hymenosomatid Halicarcinus planatus (Fabricius 1775) and the majid Notomithrax ursus (Herbst 1788) collected during one of Cook's voyages (Andrews 1986). The first fossil crab described from New Zealand was the xanthid Tumidocarcinus tumidus (Woodward 1876). Early contributors to the study of our crab fauna were H.Milne Edwards (1834-1853), White (1843-1847), Dana (1851-1852), A.Milne Edwards (1860 -1876) and Heller (1868). The first attempt to list the New Zealand fauna was by Miers (1876b) followed by Filhol (1886) and Hutton (1904) but these authors included many incorrect records and contributed to a great deal of early confusion. One of the early, longer term and most valuable contributions to the study of New Zealand crabs was made by Charles Chilton in his papers from 1882 to 1919. An important amateur contribution was made by G.M.Thomson (1898-1922) who taught biology at Otago Boys' High School and was also a member of parliament. A significant attempt to sort out the confusion was made by Chilton & Bennett (1929) although they did not deal with the entire fauna. (E.W.Bennett was a student of Chilton's before going to Perth, W.A..) In 1932 G.M.Thomson announced that he was in the process of preparing a natural history of the whole group of New Zealand Crustacea, having listed over 750 species and prepared over 400 line drawings, but to my knowledge this was never completed or published (see Thomson 1932). Later, Richardson (1949a, 1949b, 1949c) provided keys to some families. Bennett completed a more thorough review in 1936 but this was not published until 1964, although it was annotated up to 1962 by Elliot Dawson, Richard Dell and John Yaldwyn. The popular little book 'Native Crabs' by Dell (1963a) brought together much of this early work. Two brachyuran families were a source of continued difficulties, Hymenosomatidae and Pinnotheridae, and it was not until Mary Gordon (1968, published as Melrose 1975) and Roderic Page (1983) completed their work that this problem was solved. The most significant modern contributions came from Des Griffin's papers (1963-1973) and Richard Dell (1963-1972). The work Bill Stephenson (1968-1972), Takeda & Miyake (1969), John Lucas (1980) and papers by Elliot Dawson and John Yaldwyn helped to clarify and expand our knowledge of the crab fauna. The extensive and valuable work on larval stages by Robert Wear (1964-1985) has relied upon earlier taxonomic work and has greatly contributed to our understanding of crab larval stages. Biogeographic analysis of the fauna has been most recently done by Yaldwyn (1965), Dell (1968b) and Knox (1975) although this is based on only part of the fauna. The most significant contribution to the study of brachyuran ecology and physiological adaptations was made by Malcom Jones(1976-1983) and his students at the University of Canterbury.

Although fossil crabs of New Zealand are not dealt with separately in this book the interested reader can consult Feldman (1986), Fleming (1979,1981), Glaessner (1960,1969,1980) and Jenkins (1974). Where there are extinct, fossil species in genera with modern representatives these have been mentioned at the end of each section, but all known fossil species have been included in the Checklist.

The modern New Zealand fauna of crab-like crustaceans consists of 10 species of Anomura (3 Porcellanidae, 6 Lithodidae, 1 Paguridae) and 77 species of Brachyura (1 Dromiidae, 4 Homolidae, 2 Tymolidae, 1 Raninidae, 3 Leucosiidae, 22 Majidae, 14 Hymenosomatidae, 2 Atelecyclidae, 1 Cancridae, 7 Portunidae, 4 Xanthidae, 1 Belliidae, 2 Goneplacidae, 10 Grapsidae, 2 Pinnotheridae and 1 Ocypodidae) giving a total of 87 species. With the declaration of the 320km Exclusive Economic Zone the Kermadec Islands naturally become part of the New Zealand region although in the past they have been considered part of the Australian region. Our knowledge of the crab fauna of these islands is incomplete and has not been reviewed since the work of Chilton (1910) but eventually they should be included in the New Zealand fauna. Inclusion of the Kermadec crabs will bring a distinctly tropical element to our fauna and may add a further 20-30 species. Undoubtedly, there remain many unrecorded or even undescribed species from deep water to be added to the N.Z. fauna. Thus the total modern fauna may well be around 120-130 species.

There are no known anomuran fossils from New Zealand but there are 24 fossil brachyurans (2 Torynommidae, 5 Raninidae, 4 Majidae, 1 Atelecyclidae, 3 Portunidae, 5 Xanthidae, 2 Goneplacidae, 1 Grapsidae and 1 Ocyopodidae). There are many undescribed fossil crabs from New Zealand. Thus the total known fossil and modern fauna is 111 species in 72 genera and 20 families.

The information in this book is presented under each species and is based upon both published papers and unpublished theses as well as my own research. Each crab is given its scientific name and author as well as a common name, where this is appropriate. A more or less complete synonymy lists older names and is followed by the type locality where this is known. World-wide distribution is expanded into more detail for New Zealand and its offshore islands. Some species are so widespread that it is no use listing specific localities around New Zealand but for less well known species details of the few known sites are listed. For some species my own records are used to expand the known range, otherwise I have relied upon previous authors, especially Dell (1968a). However, statements that 'species occur throughout New Zealand' really only conceal the fact that we know very little about the precise fauna that is likely to be found at a point on the coastline. Given two widely separated occurrences it has been assumed that the species occurs everywhere in between those limits. There is still a need for exact faunal records, especially from the west coasts of both main islands.

A diagnostic description of each species follows a standard format, dealing with the carapace, chelipeds, walking legs and abdomen in that order. Accompanying each description are one or more illustrations of the whole crab and enlargements of various critical morphological features. I have provided a key to identify post-larval stages of the modern crab-like crustaceans from the New Zealand region. Remember that if you cannot get anywhere using the key, you can always resort to the tactic of matching your specimen with an illustration. For larval stages the reader is referred to Wear & Fielder (1985) who provide an identification key along with excellent illustrations.

Colour notes are given for each species but it must be remembered that crustacean colours are notoriously variable and it is unlikely that all possible variations have been included. Maximum sizes are given for each species, separately for males and females when known, and the abbreviations of CW for carapace width and CL for carapace length, in mm, have been used. The habitat and depth information for each species should be useful for confirming an identification and also for suggesting where to look for a particular species.

Under breeding all the information about the times when ovigerous females are found, their egg numbers, egg size, egg development, egg colour and any latitudinal variations are given. Also size at maturity, relationships between egg numbers and female size and the likely maximum number of broods per year or per maximum lifetime are suggested. This is followed by development and growth in which the number of larval stages and their occurrence in the plankton are recorded. When known growth, moulting and relative growth of the benthic phase are discussed.

The section on behaviour covers feeding, burrowing, mating, territoriality, social interactions, sound production, masking, swimming and other behaviours characteristic of each species. Where no information is available, I have relied upon information about related overseas species. This at least suggests what kinds of behaviours we might expect to find for New Zealand species.

Under ecology I have dealt with population dynamics, abundance, life history and longevity, factors affecting distribution within the crab's habitat, (including such information about physiological adaptations of osmoregulation and respiration that seem relevant), diet, dispersal, predators (including fish, birds, mammals, other crabs, starfish, sea anemones, etc) and commercial exploitation. In this section I have drawn upon studies often done outside the region and therefore predators, diet and details of life history may be different. After all, New Zealand is approx. 1600km long and covers 13^{o} of latitude. Where nothing is known I have presented results of studies of related overseas species.

Finally at the end of each species' section I have listed the major references which were used and which might provide additional information for those who want to know more. But I would like to suggest that you might be better advised to embark on your own study and add to what little is known about many species. Most of the information is presented here! I have tried to indicate where the major gaps in our knowledge are but undoubtedly others will think of equally interesting questions to answer. I have made extensive use of overseas studies in the belief that these can be used to fill in many of these gaps or at least indicate what we should look for. If we ignore this work we will simply spend most of our time 'reinventing the wheel' rather than making significant progress.

BRACHYURA AND CRAB-LIKE ANOMURA OF NEW ZEALAND

Checklist of Recent and Fossil Species
Order: Decapoda
Sub Order: Pleocyemata
Infra Order: Anomura

Family Lithodidae (6 spp, 1 undescribed)
- Lithodes murrayi Henderson, 1888
- Lithodes longispina Sakai, 1971
- Neolithodes brodiei Dawson & Yaldwyn, 1970
- Paralomis zelandica Dawson & Yaldwyn, 1971
- Paralomis hystrix (De Haan, 1849)
- Paralomis n.sp.

Family Paguridae (1 sp.)
- Porcellanopagurus edwardsi Filhol, 1885

Family Porcellanidae (3 spp.)
- Petrolisthes elongatus (H. Milne Edwards, 1837)
- Petrolisthes novaezelandiae Filhol, 1886
- Petrocheles spinosus Miers, 1876

Infra Order: Brachyura
Section: Podotremata

Family Dromiidae (1 sp.)
- Petalomera wilsoni (Fulton & Grant, 1902)

Family Homolidae (4 spp.)
- Homola orientalis Henderson, 1888
- Latreillia australiensis Henderson, 1888
- Paromola petterdi (Grant, 1905)
- Paromola spinimana Griffin, 1965

Family Raninidae (1 sp. + 5 fossil spp.)
- Hemioon novozelandicum Glaessner, 1980 (fossil)
- Laeviranina perarmata Glaessner, 1960 (fossil)
- Lyreidus elegans Glaessner, 1960 (fossil)
- Lyreidus tridentatus De Haan 1841
- Lyreidus waitakiensis Glaessner, 1980 (fossil)
- Ranilia pororariensis Glaessner, 1980 (fossil)

Family Tymolidae (2 spp.)
- Cymonomus bathamae Dell, 1971
- Cymonomus aequilonius Dell, 1971

Family Torynommidae (2 fossil spp.)
- Torynomma (Torynomma) flemingi Glaessner, 1980 (fossil)
- ?Eodorippe spedeni Glaessner, 1980 (fossil)

Section: Heterotremata

Family Leucosiidae (3 spp.)
- Ebalia laevis (Bell, 1855)
- Merocryptus lambriformis A. Milne Edwards, 1873
- Randallia pustulosa Wood-Mason, 1891

Family Majidae (22 spp., 1 undescribed + 4 fossil spp.)
Actinotocarcinus chidgeyi Jenkins, 1974 (fossil)
Eurynome bituberculata Griffin, 1964
Cyrtomaia lamellata Rathbun, 1906
Platymaia maoria Dell, 1963
Platymaia n.sp.
Pyromaia tuberculata (Lockington, 1877)
Achaeopsis ramusculus (Baker, 1906)
Acheus curvirostris (A. Milne Edwards, 1873)
Rochinia riversandersoni (Alcock, 1895)
Eurynolambrus australis H. Milne Edwards & Lucas, 1841
Leptomaia tuberculata Griffin & Tranter, 1986
Trichoplatus huttoni A. Milne Edwards, 1876
Notomithrax minor (Filhol, 1885)
Notomithrax peronii (H. Milne Edwards, 1834)
Notomithrax ursus (Herbst, 1788)
Leptomithrax atavus Glaessner, 1960 (fossil)
Leptomithrax australis (Jacquinot, 1853)
Leptomithrax garricki Griffin, 1966
Leptomithrax irirangi Glaessner, 1960 (fossil)
Leptomithrax longimanus Miers, 1876
Leptomithrax longipes (Thomson, 1902)
Leptomithrax tuberculatus mortenseni Bennett, 1964
Leptomithrax uruti Glaessner, 1960 (fossil)
Teratomaia richardsoni (Dell, 1960)
Thacanophrys filholi (A. Milne Edwards, 1876)
Jacquinotia edwardsi (Jacquinot, 1853)

Family Atelecyclidae (2 spp., + 1 fossil sp.)
Pteropeltarion novaezelandiae Dell, 1972
Trichopeltarion fantasticum Richardson & Dell, 1964
Trichopeltarion greggi Dell, 1969 (fossil)

Family Cancridae (1 sp.)
Cancer novaezelandiae (Jacquinot, 1853)

Family Portunidae (7 spp., + 3 fossil spp.)
Ovalipes catharus (White, 1843)
Ovalipes molleri (Ward, 1933)
Ovalipes sp A. Glaessner, 1960 (fossil)
Portunus pelagicus (Linnaeus, 1766)
Liocarcinus corrugatus (Pennant, 1777)
Nectocarcinus antarcticus (Jacquinot, 1853)
Nectocarcinus bennetti Takeda & Miyake, 1969
Pororaria eocenica Glaessner, 1980 (fossil)
Rhachiosoma granulifera (Glaessner, 1960) (fossil)
Scylla serrata (Forskal, 1775)

Family Xanthidae (4 spp., + 5 fossil spp.)
Menippe sp. Glaessner, 1960 (fossil)
Ozius truncatus H. Milne Edwards, 1834
Pilumnopeus serratifrons (Kinahan, 1856)
Pilumnus lumpinus Bennett, 1964
Pilumnus novaezelandiae Filhol, 1886
Pseudocarcinus sp. Glaessner, 1960 (fossil)
Tumidocarcinus dentatus Glaessner, 1960 (fossil)
Tumidocarcinus giganteus Glaessner, 1960 (fossil)
Tumidocarcinus tumidus (Woodward, 1876) (fossil)

Family Belliidae (1 sp.)
- Heterozius rotundifrons A. Milne Edwards, 1867

Family Goneplacidae (2 spp., + 2 fossil spp.)
- Carcinoplax victoriensis Rathbun, 1923
- Galene proavita Glaessner, 1960 (fossil)
- Glaessneria arenicola (Glaessner, 1960) (fossil)
- Neommatocarcinus huttoni (Filhol, 1886)

Section: Thoracotremata

Family Grapsidae (10 spp. + 1 fossil sp.)
- Leptograpsus variegatus (Fabricius, 1793)
- Plagusia chabrus (Linnaeus, 1758)
- Plagusia tuberculata Lamarck, 1818
- Hemigrapsus crenulatus (H. Milne Edwards, 1837)
- Hemigrapsus edwardsi (Hilgendorf, 1882)
- Miograpsus papaka Fleming, 1981 (fossil)
- Helice crassa Dana, 1851
- Cyclograpsus insularum Campbell & Griffin, 1966
- Cyclograpsus lavauxii H. Milne Edwards, 1853
- Planes cyaneus Dana, 1852
- Planes marinus Rathbun, 1914

Family Pinnotheridae (2 spp.)
- Pinnotheres atrinicola Page, 1983
- Pinnotheres novaezelandiae Filhol, 1885

Family Ocypodidae (1 sp., + 1 fossil sp.)
- Macrophthalmus hirtipes (Heller, 1862)
- Macrophthalmus ?major (Glaessner, 1960) (fossil)

Family Hymenosomatidae (14 spp.)
- Amarinus lacustris (Chilton, 1882)
- Elamena longirostris Filhol, 1885
- Elamena momona Melrose, 1975
- Elamena producta Kirk, 1878
- Halicarcinus cookii (Filhol, 1885)
- Halicarcinus innominatus Richardson, 1949
- Halicarcinus ovatus Stimpson, 1858
- Halicarcinus planatus (Fabricius, 1775)
- Halicarcinus tongi Melrose, 1975
- Halicarcinus varius (Dana, 1851)
- Halicarcinus whitei (Miers, 1876)
- Halimena aoteoroa Melrose, 1975
- Hymenosoma depressum Jacquinot, 1853
- Neohymenicus pubescens (Dana, 1851)

TOTALS: 87 recent species (2 undescribed), in 58 genera, in 19 families.
24 fossil species, in 19 genera, in 9 families.
Overall 111 species, in 72 genera, in 20 families.

IDENTIFICATION KEY FOR NEW ZEALAND CRAB-LIKE CRUSTACEA

1. Last two pairs of legs reduced, abdomen not folded underneath the thorax.
Fig. 6 - Porcellanopagurus edwardsi Filhol, 1885

At least the first three pairs of legs well developed, abdomen folded underneath the thorax
. . . . 2

2. Carapace oval-shaped, chelipeds well developed, eyes median to antennae, only 3 pairs of walking legs visible dorsally, fourth pair reduced and concealed.
. . . . 7

Four pairs of walking legs visible dorsally, chelipeds not excessively flattened, eyes usually lateral to antennae, abdomen somewhat reduced and not used in locomotion.
. . . . 3

3. Last two pairs of walking legs reduced and dorsally placed.
. 14

Last two pairs of walking legs may be reduced but they are not sub-chelate. First segment of antennal peduncle not freely movable.
. . . . 4

4. Carapace granulate and orbits minute. Disto-lateral margin of epistome prolonged forward or channelled. Third maxilliped narrowing anteriorly.
. 20

Disto-lateral margin of epistome not prolonged forward or channelled. Third maxilliped not narrowing anteriorly.
. . . . 5

5. Carapace oblong or rounded, not narrowed anteriorly. Orbits formed, usually complete, in which the eyes can be concealed.
. 55

Carapace narrowed anteriorly and produced as a rostrum between the eyes.
. . . . 6

6. Orbits generally more or less incomplete, chelipeds especially mobile, rarely much larger than walking legs. Hooked hairs almost always present. Male genital openings coxal.
. 22

Small crabs, CW <20mm, carapace thin and flat, chelipeds not long or especially mobile. Male genital openings sternal. No orbits, hooked hairs usually absent.
. 42

7. Carapace flattened, rostrum blunt, chelipeds elongate, broad and depressed.
. . . . 8

Carapace convex, rostrum well developed, chelipeds elongate, massive.

. 10

8. Antero-lateral margins of carapace bearing 10-12 spines, rostrum extending past eyes and 6 small spines on each side.

Fig. 9 - Petrocheles spinosus Miers, 1876

Antero-lateral margins of carapace without spines.

. . . . 9

9. Antero-lateral margins of carapace convex but interrupted by 2 oblique notches in hepatic and branchial regions. Cheliped carpus flattened, inner margin with 2 small spines, outer margin with 4 small spines.

Fig.8 - Petrolisthes novaezelandiae Filhol, 1886

Antero-lateral margins of carapace convex, without teeth or interruptions. Cheliped carpus flattened, inner margin with a single small proximal spine, outer margin with 3 small distal spines.

Fig. 7 - Petrolisthes elongatus (H.Milne Edwards, 1837)

10. Second abdominal segment divided by sutures into five plates.

Fig. 3 - Neolithodes brodiei Dawson & Yaldwyn, 1970

Second abdominal segment not divided into five plates.

. 11

11. Median area of third to fifth abdominal segments membranous with calcified nodules (but not median plates)

. 12

Median area of third to fifth abdominal segments not membranous, entire.

. 13

12. Carapace bearing about 18 long spines, carpi of first three pairs of walking legs each bearing a pair of long spines, rostrum elongate but slender and with widely divergent, long terminal bifurcation.

Fig. 2 - Lithodes longispina Sakai, 1971

Carapace bearing more than 18 prominent spines, carpi of first three pairs of walking legs without a pair of long spines, rostral spines short.

Fig. 1 - Lithodes murrayi Henderson, 1888

13. Whole crab covered in acute spines.

Fig. 5 - Paralomis hystrix (De Haan, 1849)

Whole crab covered in short, blunt spines.

Fig. 4 - Paralomis zelandica Dawson & Yaldwyn, 1971

14. Carapace quadrate, rostrum short and triangular, first three abdominal segments visible dorsally, last two pairs of legs reduced and placed sub-dorsally.

. 15

The previous combination of characters do not apply.
. 16

15\. Carapace surface finely granular, rostrum about one-twelfth of total carapace length.
Fig. 16 - <u>Cymonomus</u> <u>bathamae</u> Dell, 1971

Carapace surface with few, fine, rounded granules, rostrum about one-quarter of total carapace length.
Fig. 17 - <u>Cymonomus</u> <u>aequilonius</u> Dell, 1971

16\. Last 2 pairs walking legs with propodal spines opposing the dactyls (i.e. sub-chelate). Carapace much wider than long and covered with a sculptured layer of short hairs.
Fig. 10 - <u>Petalomera</u> <u>wilsoni</u> (Fulton & Grant, 1902)

Last pair of legs may be sub-chelate but the penultimate pair are not.
. 17

17\. Carapace pyriform (pear-shaped) with anterior part narrowed like a neck, ocular peduncles very long and bearing bulbous eyes.
Fig. 12 - <u>Latreillia</u> <u>australiensis</u> (Henderson, 1888)

Carapace quadrangular, urn-shaped or longitudinally oval without its anterior part conspicuously narrowed like a neck.
. 18

18\. Rostrum without lateral spine, carapace dorsally convex with high lateral sides, rostrum distally bifurcate, supra-orbital spine short and acute. Neither of last 2 pairs of walking legs sub-chelate.
Fig. 11 - <u>Homola</u> <u>orientalis</u> (Henderson, 1888)

Dactyls of last pair of legs expanded, flattened and triangular. Carapace smooth, antero-lateral margins with a single prominent, forwardly-directed spine, third pair of walking legs shortest.
Fig. 15 - <u>Lyreidus</u> <u>tridentatus</u> (De Haan, 1841)

Last pair of walking legs sub-chelate.
. 19

19\. Supra-orbital spines acute and long, projecting forward like a pair of antlers.
Fig. 13 - <u>Paramola</u> <u>petterdi</u> (Grant, 1905)

Anterior half of carapace armed with many long, sharp spines. Chelipeds also armed with many acute spines.
Fig. 14 - <u>Paramola</u> <u>spinimana</u> Griffin, 1965

20\. Carapace globular, posterior margin has a pair of lobes on either side of a conspicuous intestinal spine.
Fig. 20 - <u>Randallia</u> <u>pustulosa</u> Wood-Mason, 1891

Carapace rhomboidal and/or sculptured.
. 21

21. Carapace much wider than long, with a stout laterally-directed process on the branchial region.
Fig. 19 - Merocryptus lambriformis A.Milne Edwards, 1873

Carapace as wide as long, antero-lateral margin with 2 concavities, posterior margin with 3 short blunt processes.
Fig. 18 - Ebalia laevis (Bell, 1855)

22. Carapace much wider than long, broadly triangular, alate (winged), produced as flanges overhanging the legs. Rostrum very short and faintly notched.
Fig. 28 - Eurynolambrus australis H.Milne Edwards & Lucas, 1841

Carapace oval or broadly pyriform (pear-shaped).
. 23

23. Carapace pyriform, narrowed and neck-like anteriorly, rostrum consisting of 2 very short spines. No post-orbital spines. Legs very long and spindly.
Fig. 26 - Achaeus curvirostris (A. Milne Edwards, 1873)

Carapace oval or pyriform, post-orbital spines present.
. 24

24. Rostrum consisting of 3 spines, median spine longest.
. 25

Rostrum consisting of either a single spine or a pair of stout spines.
. 26

25. Carapace oval, legs long and spindly, rostral spines acute, branchial region not armed with a stout spine.
Fig. 23 - Platymaia maoria Dell, 1963

Carapace oval, legs long and spindly, rostral spines blunt, branchial region armed with a stout spine.
Fig. 22 - Cyrtomaia lamellata Rathbun, 1906

26. Carapace broadly pyriform, rostrum consisting of a single acute spine, 3 median tubercles, 1 gastric, 1 cardiac and 1 intestinal.
Fig. 24 - Pyromaia tuberculata (Lockington, 1877)

Rostrum consisting of 2 prominent or blunt spines.
. 27

27. Legs very long and spindly, much longer than chelipeds, rostrum of 2 long spines (about one third of carapace length), orbit flanked by short acute spines.
Fig. 25 - Achaeopsis ramusculus (Baker, 1906)

Legs and chelipeds of similar length, chelipeds may be longer.
. 28

28. Rostrum of 2 very long, acute, widely divergent spines.
. 29

Rostrum of 2 short spines which may be acute or blunt and divergent or sub-parallel.
. 32

29. Carapace covered in small nodules, no marginal spines.
Fig. 29 - Leptomaia tuberculata Griffin & Tranter, 1986

Carapace with well developed marginal spines.
. 30

30. Chelipeds long and crested, carapace with a lamellate, marginal hepatic process.
Fig. 40 - Thacanophrys filholi (A. Milne Edwards, 1876)

Chelipeds not crested, no lamellate, marginal hepatic process.
. 31

31. Carapace margins with 2 spines, 1 hepatic and 1 (longest) branchial.
Fig. 27 - Rochinia riversandersoni (Alcock, 1895)

Carapace margins with 6 or 7 spines increasing in length posteriorly.
Fig. 39 - Teratomaia richardsoni (Dell, 1960)

32. Walking legs with sub-chelate dactyls.
Fig. 30 - Trichoplatus huttoni A. Milne Edwards, 1876

Walking legs normal, not sub-chelate.
. 33

33. Carapace bearing flat-topped tubercles, flattened lobes and short conical spines.
Fig. 21 - Eurynome bituberculata Griffin, 1964

Tubercles on carapace not flattened.
. 34

34. Rostrum short, consisting of two blunt lobes, floor of orbit formed by expanded basal antennal article.
Fig. 41 - Jacquinotia edwardsi (Jacquinot, 1853)

Rostrum well developed, consisting of two well developed spines.
. 35

35. Supra-orbital eave, intercalated spine and post-orbital spine widely separated from each other, post-orbital spine simple. Eyestalks short, slender, cornea small. Carpus of cheliped with 2 longitudinal ridges converging proximally.
. 36

Supra-orbital eave, intercalated spine and post-orbital lobe closely approximated, post-orbital lobe excavated anteriorly. Eyestalks stout, cornea very large. Carpus of cheliped lacking prominent ridges.
. 38

36. Carapace with both spines and tubercles dorsally. Two hepatic spines. More than 3 marginal branchial spines extending on to dorsum of carapace posteriorly.
. 37

Carapace hairy and covered by tubercles only. Three hepatic spines. Merus of cheliped with dorsal row of laterally compressed spines, carpus with dorsal ridge serrate.
Fig. 33 - Notomithrax ursus (Herbst, 1788)

37. Protogastric regions smooth or only faintly tuberculate. Seven marginal branchial spines. Merus of cheliped smooth dorsally, carpus with dorsal ridge poorly developed, tuberculate, lateral ridge well developed.
Fig. 31 - Notomithrax minor (Filhol, 1885)

Entire surface of carapace covered by tubercles and spines, 5 marginal branchial spines. A pair of short spines at the posterior carapace margin. Merus of cheliped with a few spines and tubercles dorsally, carpus with dorsal and lateral ridges entire.
Fig. 32 - Notomithrax peronii (H.Milne Edwards, 1834)

38. Intercalated spine in orbit markedly shorter than antorbital, almost excluded from outer rim of supraorbital margin by distal approximation of antorbital spine and postorbital spine.
. 39

Intercalated spine as long as antorbital, reaching outer rim of supraorbital margin.
. 40

39. Antorbital spine separated from postorbital spine, two marginal hepatic spines.
Fig. 38 - Leptomithrax tuberculatus mortenseni Bennett, 1964

Antorbital and postorbital spines closely approximated, one marginal hepatic spine.
Fig. 39 - Leptomithrax longipes (Thomson, 1902)

40. Postorbital lobe with a prominent spinule or tubercle on upper anterior edge.
. 41

Postorbital lobe lacking a spinule on upper anterior edge.
Fig. 36 - Leptomithrax longimanus Miers, 1876

41. Carapace in both male and female covered by a few spines.
Fig. 35 - Leptomithrax garricki Griffin, 1966

Carapace in male densely covered by spines, in female by numerous tubercles.
Fig. 34 - Leptomithrax australis (Jacquinot, 1853)

42. Carapace with distinct gastrocardiac groove and cervical grooves.
. 47

Carapace without distinct gastrocardiac groove.
. . . . 43

43. Eyestalks entirely visible dorsally, folded antennules similarly visible. Epistome absent. Dactyls of each walking leg devoid of teeth.
Fig. 84 - Hymenosoma depressum Jacquinot, 1853

Cornea of eye, but not eyestalks visible dorsally, folded antennules completely hidden. Epistome large and rectangular. Dactylus of each walking leg sparsely dentate.
. . . . 44

44. Distinct suture between carapace and rostrum. Rostrum without keel or ridge ventrally. Dactylus of each walking leg with a single large tooth adjacent to claw, lacking other dentation.
Fig. 83 - Halimena aoteoroa Melrose, 1975

Rostrum and carapace completely fused, no suture between them. Rostrum with a keel ventrally. Dactylus of each walking leg with 2 large teeth adjacent to claw, lacking other dentation.
. . . . 45

45. Rostrum narrow, produced, sub-rostral keel with strong spine extending from it. Carapace triangular. Legs with many sturdy teeth.
Fig. 73 - Elamena longirostris Filhol, 1885

Rostrum broad, rounded, sub-rostral keel blunt. Carapace rounded, legs without teeth except for 1 on merus.
. . . . 46

46. Length of rostrum at least half width. Keel deepest anteriorly, tapering behind. Prominent upwardly curved tooth on the distal end of merus of walking legs. Antero-lateral carapace margins angular.
Fig. 75 - Elamena producta Kirk, 1878

Length of rostrum less than a third of width. Keel shallow, of equal depth throughout. Tooth on merus of each walking leg reduced, obtuse. Antero-lateral carapace margins without distinct angles.
Fig. 74 - Elamena momona Melrose 1975

47. Rostrum trilobate or tridentate, arising below level of carapace, carapace rim continuous above rostrum and concavities between lobules extending below this rim.
. . . . 48

Rostrum simple or, if trilobate, lobes arising from level of carapace, separated from it only by a suture.
. . . . 50

48. Three rostral lobes arising well below carapace rim, carapace rim being continuous above rostrum, with lateral rostral lobes at same level as median one and not set at an angle to it. Antero-lateral border of carapace convex. Dactylus of each walking leg with a single row of teeth or tubercles.
Fig. 77 - Halicarcinus innominatus Richardson, 1949

Three rostral lobes arising just below rim of carapace, with lateral lobes set at an oblique angle to median lobe. Anterolateral border of carapace straight or concave. Dactylus of each walking leg with double row of teeth.
. 49

49. Rostral lobes widely separated, median rostral tooth shortest, lateral lobes sloping downward and outward.
Fig. 79 - Halicarcinus planatus (Fabricius, 1775)

Rostral lobes close together, median lobe a little longer than laterals, all lobes projecting straight forward.
Fig. 78 - Halicarcinus ovatus Stimpson, 1858

50. Rostrum distinctly trilobate or tridentate, concavities between lobes reaching almost to suture between carapace and rostrum.
. 51

Rostrum simple or, trilobate only distally, any concavities between lobes not reaching near suture between rostrum and carapace.
. 52

51. Rostrum extending past eyes. Rostral lobes acute, subequal.
Fig. 80 - Halicarcinus tongi Melrose, 1975

Rostrum not projecting past eyes. Rostral lobes rounded apically, median one slightly longer than laterals.
Fig. 76 - Halicarcinus cooki (Filhol, 1885)

52. Rostrum not projecting past eyes, and forming a flat almost horizontal platform.
Fig. 81 - Halicarcinus varius (Dana, 1851)

Rostrum projecting past eyes, and downwardly deflexed anteriorly.
. 53

53. Rostrum distinctly trilobate on tip, projecting well past eyes. Dactylus of each walking leg with a single row of sharp recurved teeth.
Fig. 82 - Halicarcinus whitei (Miers, 1876)

Rostrum simple, just extending past eyes. Dactylus of each walking leg lacking teeth or sparsely dentate.
. 54

54. Rostrum deflexed only a little downwardly, convex from side to side above, narrowing to a blunt point anteriorly. Dactylus of each walking leg curved, with a single blunt tooth adjacent to claw. Covered with long feathery hairs.
Fig. 85 - Neohymenicus pubescens (Dana, 1851)

68. The pair of median frontal teeth closely set and produced further forwards than anterior orbital; no supra-orbital tooth. Chelipeds relatively long, carpus armed with small acute teeth.
Fig. 46 - Ovalipes molleri (Ward, 1933)

The pair of median frontal teeth closely set but not produced much further forwards than anterior orbital teeth, prominent supra-orbital tooth present. Chelipeds relatively short, carpus with a long, robust, distal inner spine.
Fig. 45 - Ovalipes catharus (White, 1843)

69. Last anterolateral tooth very long and directed laterally, chelipeds very long (3 times CL).
Fig. 47 - Portunus pelagicus (Linnaeus, 1766)

All anterolateral teeth of similar size and shape, chelipeds massive.
Fig. 51 - Scylla serrata (Forskal, 1775)

70. Symbiotic crabs with reduced eyes and orbits. Body swollen and smooth; sometimes taken at night free-swimming and attracted to light.
. 83

Free-living crabs with a more or less straight-sided body and well developed eyes.
. 71

71. Carapace surface smooth and with a single, long laterally directed, acute spine or two smaller anterolaterally directed spines (the second larger than the first).
. 82

Carapace surface smooth or tuberculated but without prominent, acute, lateral spines.
. 72

72. Front broad, eyestalks relatively short, less than one-third of CW, dactyls of walking legs often compressed and spinous. A narrow gap between external maxillipeds.
. 73

Front narrow, eyestalks relatively long, dactyls of walking legs styliform. External maxillipeds almost or fully closing across the mouth.
Fig. 71 - Macrophthalmus hirtipes (Heller, 1862)

73. Frontal margin of carapace bearing 10-14 broad spines.
. 74

Frontal margin of carapace may be tuberculated but without spines.
. 75

74. Dorsal carapace surface tuberculate, dorsal margins of meri of walking legs smooth except for a single distal spine.
Fig. 61 - Plagusia depressa tuberculata Lamarck, 1818

Dorsal carapace surface mostly smooth with blunt tubercle just behind each orbit, dorsal margins of meri of walking legs spinous.

Fig. 60 - Plagusia chabrus (Linnaeus, 1758)

75. Frontal margin tuberculated, 2 anterolateral teeth behind external orbital angle, branchial regions with 7-9 prominent, weakly curved transverse ridges.

Fig. 59 - Leptograpsus variegatus (Fabricius, 1793)

Frontal margin smooth.

. 76

76. Meri of legs flattened and transverse striations on at least the anterior half of the carapace.

. 81

Meri of legs not especially flattened, no striations on carapace.

. 77

77. Anterolateral carapace margins with 2 small teeth behind the orbital corner.

. 79

Anterolateral carapace margins without teeth.

. 78

78. Orbits small but well incised, outer corner raised, median frontal groove prominent.

Fig. 66 - Cyclograpsus lavauxi H.Milne Edwards, 1853

Orbits very small and shallow, outer corner not raised, eyes very small, median frontal groove absent.

Fig. 65 - Cyclograpsus insularum Campbell & Griffin, 1966

79. Eyestalk length much less than one-fifth of CW.

. 80

Eyestalk length approx. one-fifth of CW, lateral margins of carapace straight, sub-parallel.

Fig. 64 - Helice crassa Dana, 1851

80. A strong, broad frontal groove extending back from frontal margin and separating 2 protuberances. Fourth and fifth segments of male abdomen fused.

Fig. 62 - Hemigrapsus edwardsi (Hilgendorf, 1882)

A short, shallow groove extending back from frontal margin. Fourth and fifth segments of male abdomen faintly movable.

Fig. 63 - Hemigrapsus crenulatus (H.Milne Edwards, 1837)

81. Carapace varies from a little broader than long (ratio 0.86) to a little longer than broad (ratio 1.06). Legs relatively short (proportion of length of 3 distal segments of second leg to CL is 0.68 to 0.89).

Fig. 67 - Planes cyaneus Dana, 1852

Carapace distinctly wider than long (ratio 1.07 to 1.16). Legs relatively longer (proportion of length of 3 distal segments of second leg to CL is 0.77 to 0.99).
Fig. 68 - Planes marinus Rathbun, 1914

82. Eyestalks very long, almost half CW, lateral carapace margin produced into a single long, acute spine against which the eyes can rest.
Fig. 58 - Neommatocarcinus huttoni (Filhol, 1886)

Eyestalks short, lateral carapace margin armed with 2 short acute spines.
Fig. 57 - Carcinoplax victoriensis Rathbun, 1923

83. Chela with a continuous dorsal row of setae on propodus, terminal segment of abdomen quadrate. In the female the legs are noticeably asymmetrical.
Fig. 69 - Pinnotheres atrinocola Page, 1983

Chela without a continuous dorsal row of setae on propodus, terminal segment of abdomen trapeziform. Legs of female not markedly asymmetrical.
Fig. 70 - Pinnotheres novaezelandiae Filhol, 1885

Lithodes murrayi Henderson, 1888
Southern Stone Crab

Synonymy

Lithodes murrayi Henderson, 1888; Bouvier, 1896; Thompson, 1900; Hale, 1941; Dell, 1963a; Yaldwyn, 1965; Yaldwyn & Dawson, 1970; Arnaud, 1971; Pseudolithodes pyriformis Birshtein & Vinogradov, 1972; Lithodes murrayi Webb, 1972; Campodonico & Guzman, 1972; Arnaud, Do-Chi & Rannou, 1976; Arnaud & Do-Chi, 1977; (not of Kensley, 1977; 1980; Melville-Smith, 1982; MacPherson, 1983; = L.tropicalis A. Milne Edwards, 1883); Lithodes murrayi Takeda & Hatanaka, 1984; Lithodes unicornis Macpherson, 1984; Lithodes murrayi Dawson & Yaldwyn, 1985.

Type Locality

Off Prince Edward Is, southern Indian Ocean, 570m.

Distribution

Southern Ocean, circumpolar: Possession Is. (Ross Sea), Prince Edward Island, Crozet Is., Macquarie Is, southern New Zealand, southern Chile and off the Falkland Is. Within New Zealand, Kaikoura Peninsula, Solander Is., Foveaux Strait and west coast of Stewart Is. Reports of L.murrayi off the Durban coast of South Africa have been corrected to L.tropicalis by Melville-Smith & Louw (1987).

Diagnosis (Fig. 1a-e).

Carapace is broadly pyriform ('pear-shaped') with length (including the rostrum) greatly exceeding width, regions are well defined and surface armed with long, acute spines. Degree of development of spines is variable. The rostrum is five-spined, directed slightly upward, the base broad, and terminating in two prominent diverging spines which are directed forwards and upwards, the distal portion shorter and more slender with its apex bifurcate. On the lower surface of the rostrum is a large spine directed downwards and forwards. The gastric area, behind the rostrum, is swollen, with a few small scattered tubercles but armed with four acute, conical spines arranged in two rows, the anterior pair of larger size. The cardiac area is well-defined, separated from the gastric area by a deep transverse sulcus and bearing two acute spines. In front of these are two conspicuous tubercles. The branchial areas are moderately convex and each is armed with a pair of conspicuous spines and a smaller submedial spine with scattered tubercles. The eyes are close together freely movable, cornea well developed and oblique. On a lower level are the antennules with the antennae nearby. The second joint of the antennal peduncle has a conical spine on its outer distal border and the flagellum is about equal in length to the carapace. There is a strong spine external to the ocular peduncle and the antero-lateral border is armed with about six prominent spines of varying size. Postero-lateral border broadly convex, armed with about nine spines the last is submedial and largest. Chelipeds small compared to the walking legs, the right somewhat stouter, all segments armed with conical, acute spines especially on the upper surface. Fingers long, excavated internally, right fingers have many minute teeth, both have numerous tufts of bristle-like setae scattered over the inner

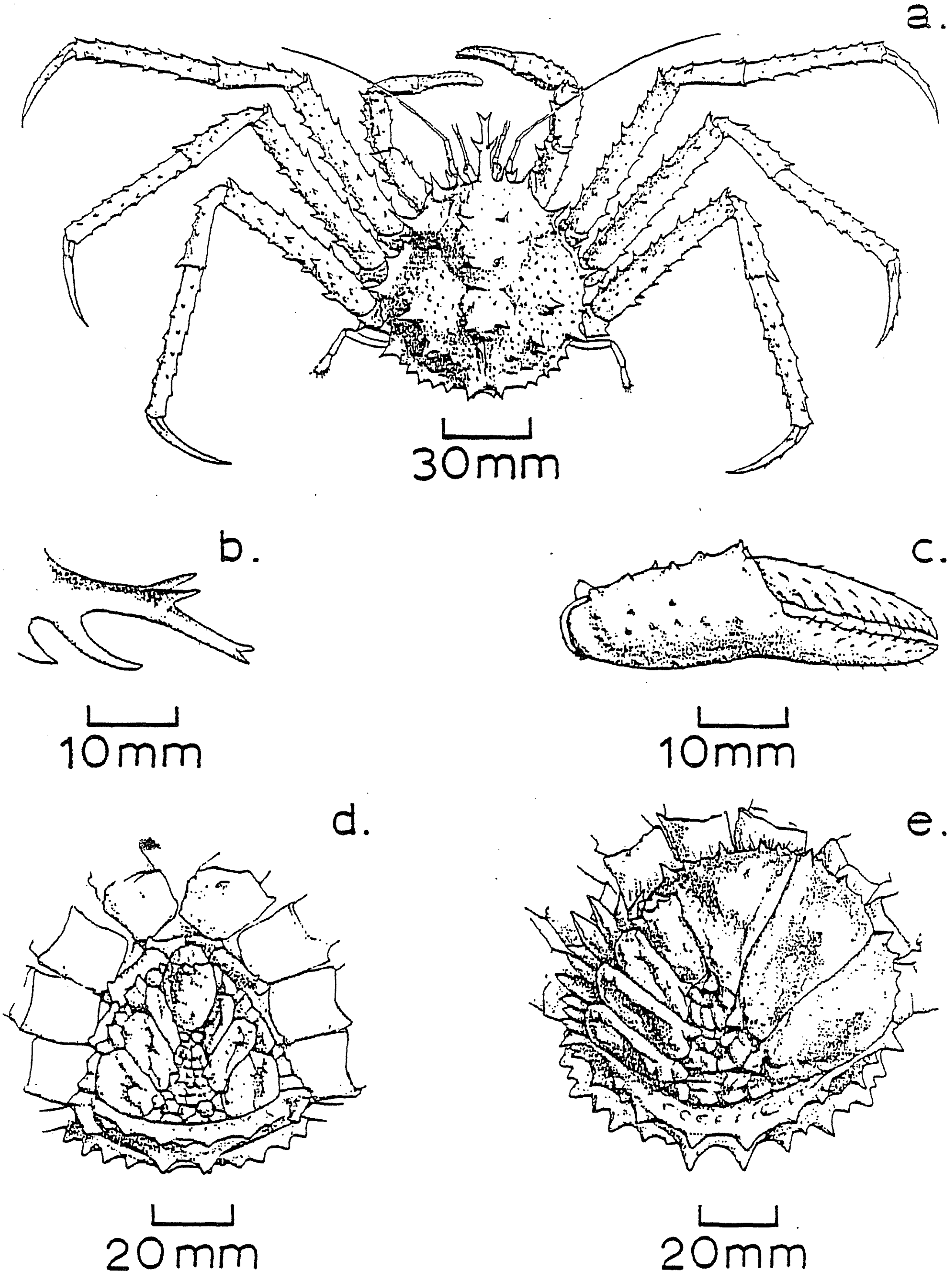


Fig. 1 - *Lithodes murrayi*: a - male, dorsal view; b - lateral view of rostrum; c - right chela, male, outer face; d - male abdomen, ventral view; e - female abdomen, ventral view (after Henderson, 1888).

surface. Walking legs very long, spinous with a prominent spine distally on the merus, and two spines at either end of the carpus. Dactyli long and armed, without spines on their inner margins. The reduced last pair of legs are smooth, flattened with the terminal portion densely pubescent and placed in gill chambers. Abdomen of six segments plus telson in both sexes, symmetrical in male, asymmetrical in female. First abdominal segment bears two small submedian spines, the second bears a large pair and has a raised posterior border, the penultimate segment has two small spines on its posterior border. Plates of third to fifth segments replaced by a median membranous portion which bears numerous sharp nodules. Uropods absent. Female has a pair of rudimentary pleopods on the first segment, and single pleopods on the left side of the next four segments. Right border of abdomen armed with a series of about 10 marginal plates in female, with plates on both sides in the male. Pleopods absent in male.

Colour

Dark purplish-red or brick-red with pale pinkish-white patches. Tips of dactyls of walking legs are black. Due to the attenuation of red light these crabs may be cryptically coloured.

Size

Male 172mm CW, 209mm CL (incl. rostrum). Female 138mm CL, female (ovigerous) 113mm CL. Smallest ovigerous female 71mm CW, 91mm CL. Distance between tips of second legs is approximately 110-120cm.

Habitat

Caught by potting and sometimes entangled in deep water set nets. Associated with suspension-feeding fauna e.g. sponges, gorgonians, polychaetes, brachiopods, bryozoans and ascidians.

Depth

120-700m.

Breeding

Ovigerous females of L.murrayi have been taken in December, February and April. Females collected in February by Webb had large numbers of unlaid eggs in their ovaries, suggesting that ovigerous females could be expected in later months. Arnaud & Do-Chi (1977) found that clutch size increased non-linearly from about 1000 eggs for a 55mm CW female to 2300 for an 84mm CW female. Webb (1972) estimated brood size of a 140mm CW female at approx. 8000 eggs. The eggs are yellow when newly laid, red when mature, measuring 2.56mm diameter and weighing 0.01gm each. Arnaud & Do-Chi (1977) found that L.murrayi eggs increase from 2.31mm to 2.45mm during development. These are very large eggs, larger than eggs of Lithodes maja (2.0 x 1.8mm) (Pike & Williamson 1959). In this species eggs are laid in autumn and are carried through the winter months (September to November), hatching in April or May. Females moult soon afterwards. Stuardo & Solis (1963) found that Lithodes antarcticus from the Straits of Magellan (53^{o}S) was also a seasonal spawner. It also has large eggs and after moulting, mating and spawning in shallow waters during the warm months (December-January) the incubating females and adult males disperse to depths around 200m in February (summary from Sloan 1985). This pattern may also be true for L.murrayi.

Sloan (1985) has argued that there are two distinct reproductive strategies among lithodid crabs: aseasonal spawners with small numbers (<40,000) of large (>2.1mm) eggs (e.g. Lithodes spp.) and seasonal spawners with large numbers (300,000) of small (<1.2mm) eggs (e.g. Paralithodes spp.). However there seems to be considerable variation in reproductive strategy among the Lithodes spp. While Sloan (1985) found L. aequispina in a British Columbia fjord was aseasonal, studies in Japan and Russia suggest that there it is seasonal (see Hiramoto & Sato 1970). While L.cousei is aseasonal in the Gulf of Alaska (Somerton 1981a), L.longispina from Japan is a seasonal spawner. Finally, L.antarcticus, L.maja and L.murrayi would be expected, on the basis of their large eggs, to be aseasonal but in fact they appear to be seasonal spawners. Therefore the hypothesis that large egg size is associated with aseasonal spawning may well be incorrect. The suggested mechanism behind this strategy - that seasonal spawners produce small eggs hatching larvae whose abundance is cued to pulses of suitable food produced in the plankton while aseasonal spawners produce large eggs which hatch well-provisioned larvae whose survival is less dependent on seasonally available food - needs further study.

The relationship between clutch size and CL in L.murrayi is non-linear (Arnaud & Do-Chi 1977) but a linear relationship is found in L.aequispina (Hiramoto and Sato 1970, also Jewett, Sloan & Somerton 1985) and L.antarctica (Guzman and Campodonico 1972). But in P.camtschatica (Haynes 1968, but see Somerton & MacIntosh 1985), P.platypus (Sasakawa 1975 also Somerton & MacIntosh 1985) and L.couesi (Somerton 1981) fecundity initially increases and then remains fairly constant giving a curvilinear relationship. Thus lithodid crabs exhibit a wide variety of fecundity/size relationships and in all species clutch size variability is high. As noted earlier there is an order of magnitude difference in clutch size between Lithodes spp. and Paralithodes spp. which have many small eggs. It is probable that lithodid females produce a maximum of only one clutch of eggs per year (maybe less) because of slow development at low temperatures. The pattern seems to be that eggs are laid soon after mating which follows every adult moult (Jewett, Sloan & Somerton 1985).

Comparison of regression line intercepts for fecundity data suggests that 8-13% of eggs are lost during incubation to the eyed stage in Lithodes aequispina (Jewett, Sloan & Somerton 1985). There are no comparative data for other lithodids.

In a detailed comparison of the reproductive strategies of two lithodid species Somerton & MacIntosh (1985) revealed some interesting differences between Paralithodes camtschatica and P.platypus. P.camtschatica produce smaller eggs (1.0mm long) and spawn annually while P.platypus produces larger eggs (1.2mm long) but spawn biennially. There is a two-year ovarian cycle and a development period of 14-15 months. These crabs expend more energy per spawning, produce larger larvae and have a longer (17yr) adult life-span than P.camtschatica (10yr). They point out that P.platypus conforms to the low frequency reproduction model (LFR) proposed by Bull & Shine (1979) i.e. a species in which populations reproduce annually but individuals reproduce biennially or less often. Greater expenditure of energy per spawning and longer life may be a consequence of moulting less often, thereby avoiding an energetically expensive and hazardous event. The management implication of these results is that percentage of adult females carrying embryos cannot be used for LFR species to determine whether or not a sufficient number of males remain in the population.

In an interesting study of the small, shallow water lithodid, Cryptolithodes typicus from British Comumbia, Hart (1965) found that eggs (about 1.0mm diam.) were laid in summer (May onwards), carried over winter (with little development until December) and hatched in March-April. Eggs did not hatch simultaneously but larvae emerged over a three-week period. This may be an offspring-investment strategy which enhances larval survival and may also occur in other lithodids.

In northern British Columbia 41% of male and female golden king crabs, Lithodes aequispina, were parasitized by the rhizocephalan barnacle Briarosaccus callosus and were therefore sterile. Parasitized crabs behave like unparasitized brooding females which migrate to deeper water to spawn. Parasitism did not inhibit moulting in host crabs or influence body size in females but male body size and right cheliped allometry were decreased. This high level of infection is probably the result of confinement of host and parasite to an area with restricted exchange with the surrounding sea (Sloan 1984). Infection levels in other crabs range from 1.0-15.0% (Hawkes et al. 1986). Arnaud & Do-Chi (1977) found 3.5% of L.murrayi from exposed islets in the southwestern Indian Ocean were parasitized by B. callosus. Lower levels have been reported for L.antarcticus from southern Chile (Stuardo & Solis 1963). B.callosus infects seven other lithodid species. Rhizocephalan parasites of anomurans do not inhibit moulting but similar parasites of brachyuran crabs suppress moulting after the externa is formed (Bower & Sloan 1985). The rather limited data of Hawkes et al. (1987) suggest that moult increments of parasitized Alaskan blue king crabs (Paralithodes platypus) are reduced compared to non-parasitized crabs. B.callosus effects on king crab haemolymph include inhibition of ion regulation, decrease in pH and increase in total protein, hemocyanin and glucose concentrations (Shirley, Shirley & Meyers 1986).

Development and Growth

Larval stages of Lithodes murrayi are unknown. The range of variation in lithodid larval development has been tabulated by Konishi (1986). Larvae of L.maja, L.aequispina and L.antarctica and their megalopae have been described by MacDonald et al. (1957), Hayes (1982) and Campodonico (1971) respectively. These species tend to have abbreviated development, 2-4 zoeal stages followed by the megalopa, which has many spines on the carapace like the adult crabs. Larval development may take 3-4 months depending upon water temperature.

Arnaud & Do-Chi (1977) have studied relative growth in L. murrayi from the Crozet Islands. Carapace width increases isometrically with carapace length in both sexes as do most female dimensions except for merus length (of first leg) which is negatively allometric and left cheliped height which is positively allometric. In males height and length of both cheliped propodi as well as merus length (of first leg) are all positively allometric with respect to carapace length. The smallest L.murrayi female carrying eggs was 60mm CL (excl. rostrum) and most females produce eggs by the time they reach 80mm CL.

Relative growth has also been studied in Lithodes antarcticus from southern Chile. For both males and females carapace length grows isometrically with carapace width. In males the length of the merus of the first legs and the length and height of the right cheliped propodus all grow positively allometrically. In females these show negative allometry (Stuardo & Solis 1963). Males reach sexual maturity between 90-102mm CL (not including spines) and females at about 75mm. In northern British Columbia 50% of female L.aquespina mature at 105.5mm CL while chela allometry suggests that males mature at 114mm (Jewett, Sloan & Somerton 1985). There is a trend of increasing size of maturity with decreasing latitude. In L.couesi males cheliped height can be used to detect maturity as there is a marked increase in cheliped size at a pubertal moult which can occur anywhere in the range 80-120mm CL. Estimated sizes of 50% maturity are 91.4mm CL for males and 80.2mm for females (determined by presence of eggs) (Somerton 1981). Weber (1967) has estimated that the red king crab, Paralithodes camtschatica from Alaska takes about 5 years to reach sexual maturity at a comparable size but there is considerable varation in growth rates between different areas of the North Pacific. Similarly, the blue king crab, P.platypus shows different sizes of 50% maturity in different areas of Alaska (Somerton & MacIntosh 1983).

Mature king-crabs may moult annually but large crabs may only moult every 2-3 years. Growth increments of both male and female immature P. camtschatica (10-50mm CL) from Alaska range from 23-27%, but larger crabs have smaller percentage growth of about 20% at 80mm. Analysis of size-frequency modes suggests that crabs over 60mm have nearly constant absolute increments of about 16mm (Weber 1967) which means that percentage increments would decline even further. Large male Lithodes aequispina also show average increments per moult of 16.2mm, moulting annually up to 145mm CL and gradually becoming biennial or less frequent thereafter (Jewett, Sloan and Somerton 1985).

Regeneration of lost limbs by P.camtschatica from the Bering Sea has been investigated by Edwards (1972). Almost 30% of juveniles and 15% adults had lost at least one limb. Limb loss increased in frequency from anterior to posterior limbs. It is suggested that full regeneration of a limb may require 4-5 moults. The right chela is normally larger but when it is lost dominance is transfered to the left chela. With lower moult frequency adult crabs have limited ability to regenerate lost limbs.

Behaviour

Nothing known about L.murrayi but it may share the aggregation behaviour peculiar to king crabs (e.g. Paralithodes camtschatica). Juveniles of Paralithodes form large 'pods' resembling hay stacks containing several thousand small crabs and this may confer some protection against fish predators (Powell & Nickerson 1965). In addition adult crabs may form 'pods' when migrating to shallow water for breeding and moulting. These aggregations may protect newly-moulted soft crabs. Lithodes aequispina seem to have a migratory pattern which consists of 1) juvenile recruitment in the shallows (50-100m); 2) moulting, mating and egg extrusion by adults slightly deeper; 3) downward migration by incubating females while males tend to remain in shallows; 4) hatching and larval release at depth (>200m); 5) post-spawning recovery in deep water; 6) upward migration by females for moulting and mating (Sloan 1985). If this crab is an aseasonal spawner, as Sloan (1985) suggests, then different parts of the population would be at different stages of the migratory cycle at any one time. The duration of this cycle is probably longer than a year. L.antarcticus from southern Chile behaves somewhat differently: males precede females into the shallows (<10m) to moult; then females arrive in the warm season (Nov.-Dec.), moult, copulate, extrude eggs and then disperse with males offshore to deeper water to incubate the eggs and release larvae. Juvenile L.antarcticus recruit and spend the first few years of life in very shallow (2-3m) water (Stuardo & Solis 1963). Some anecdotal observations suggest that L.murrayi may follow a similar pattern (Arnaud 1971, Arnaud et al. 1976, Arnaud & Do-Chi 1977).

Lithodid crabs may be caught using baited pots in deep water or alternatively by a coarse mesh set net with a weighted foot rope and floating head rope set across the migratory pathway of the crabs (Makarov 1938).

Mating behaviour of Paralithodes camtschatica, observed in captivity, consists of males using their chelipeds to grasp the female cheliped meri in a pre-copulatory face to face embrace that lasts for 3-7 days through the pre-moult and moult stages. This 'handshake', which is not essential for the submissive female to moult, may well last much longer in the wild. Males will retain a firm hold on their partners even when removed from the water. The size of grasping partners is not correlated (Makarov 1938, Powell & Nickerson 1965) but Powell et al. (1974) suggest that small males may not produce enough sperm to fertilize a full clutch of eggs. The male assists the female to moult and protects her while she is soft and swelling. Casting of the old exoskeleton requires about 9-10 min (Weber 1967). After the female has moulted the male reclasps her by the chelipeds and inverts her beneath his body, bringing their abdomens close together. The female begins to lay her eggs from the genital apertures at the base of the second legs and the male spreads bands of spermatophores, from the base of the reduced last pair of legs, over the eggs which become attached to the pleopod setae. Spreading of the spermatophores over the eggs is accomplished by vigorous movements of the last pair of legs. Female king crabs have no seminal receptacle and therefore require the presence of a male during ovulation. The soft female attains her full size about 2 hours after shedding of the old exoskeleton by which time fertilization is complete, and the male departs. Females which moult alone are still attractive to males up to 9 days after moulting and can produce a full clutch of fertilized eggs. After this time their success declines and by 13 days none were successful since males were repelled by female aggression (McMullen 1969). In captivity a male is polygamous and is capable of fertilizing about 5 females over a period of 10 days but the number of successful matings in the wild could well be somewhat lower because males must compete for females arriving on the spawning ground. In Alaska breeding P.camtschatica occupy the subtidal peripheries of kelp-covered reefs at 3-8m depth. It is interesting to note that although mating in this crab involves the male grasping the female by her chelipeds this does not seem to result in high levels of limb loss (Edwards 1972). This may be contrasted with the majid Jacquinotia edwardsi where many limbs are lost, especially by females, as a result of tug-of-wars between males contesting over females.

Ecology

Lithodid crabs seem to be omnivorous although animal food predominates. Adult guts contain remains of polychaetes, echiuroids, small molluscs, starfish, sea urchins, holothuroids, and fish (Markarov 1938). Post-larval Paralithodes camtschatica from Alaska feed on diatoms, foraminifera, ?sponges as well as polychaetes and small crustacea (harpacticoids, ostracods) found living in sediment (Feder, McCumby & Paul 1980). Adult P.camtschatica from Alaska eat mainly molluscs (bivalves, Nucula, Nuculana, Macoma), Crustacea (mainly barnacles) and fish but the dominant food can vary between areas (Jewett & Feder 1982). Guts of L.murrayi from the Crozet Islands contain sessile (algae, foraminifera, hydrozoans, bryozoa, sponges and polychaetes), sedentary (gastropods, bivalves, echinoids and pycnogonids) and mobile organisms (other Lithodes, isopods, amphipods, cephalopods and fish debris) indicating an omnivorous diet of wide diversity (Arnaud & Do-Chi 1977).

Besides humans, the principal predators of lithodid crabs are fish (Markarov 1938, Gray 1964). Recently moulted, soft crabs are especially vulnerable. Large adult male crabs may well gain refuge from predators by virtue of their size. Nemertean worms of the genus Carcinonemertes are found on Paralithodes camtschatica from Alaska. Planktonic larvae settle on crab hosts and remain on the exoskeleton as juvenile worms. Those which infest ovigerous hosts invade the egg mass where they feed on host eggs, grow and reproduce sexually. Worms lay their own eggs in the host brood and worm larvae hatch near the time the host eggs hatch. In some populations and seasons, nemertean density was high enough to cause mortality of nearly all of the host eggs. There may well be several nemertean species involved (Wickham 1986, Wickham & Kuris 1988).

An extensive king-crab fishery based on males only has developed in the north Pacific since about 1900 involving Japan, Korea, Russia and the United States. Historically the fishery has been based mainly on the red king crab, P.camtschatica. Production peaked in 1980 at about 200 million pounds but despite a minimum legal size which allows for three years of reproduction by males this has since crashed as a result of severe over-exploitation and the blue king crab, P.platypus is now the primary component of the catch. King-crabs are a gourmet sea food and very high prices (NZ $125.00 per kilogram) are paid for them. Attention is now shifting to other lithodid species such as Lithodes aequispina, L.couesi, L.tropicalis, L.antarcticus and L.murrayi to meet the demand. An extensive fishery based on L.antarcticus and Paralomis granulosa has developed in Chile in the last decade (Campodonico 1981). The discovery of significant stocks of king crabs associated with orange roughy in deep water off the Wairarapa Coast (see DSIR Annual Report to Parliament 1985) has aroused interest among New Zealand fishermen. Much more biological information is needed before exploitation of these stocks should be allowed to proceed. Special consideration needs to be given to setting a minimum legal size which allows sufficient reproductive contribution. Lithodes species are much less fecund and may be much longer lived than the Paralithodes species. Another significant factor that must be taken into account is the effect of rhizocephalan parasites, such as Briarosaccus callosus, which sterilize crabs and could severely depress recruitment to the population.

Lithodes aequispina in northern British Columbia can be heavily infested with cocoons of a sanguivorous piscicolid leech, Notostomum cyclostoma. Larger crabs, which moult less frequently, have higher numbers of cocoons, especially on the carapace but also on the limbs, but the leeches do not feed on the crab host, obtaining their blood meals from fish (Sloan, Bower & Robinson 1984). Parasitism of lithodids by rhizocephalans is discussed above under 'Breeding'.

An interesting commensal association between several lithodid crabs and liparid fish (Careproctus spp.) has been reported. The female fish has a long ovipositor which she uses to lay her large (approx. 4-5mm diam.) eggs in the gill chamber of the crab. North Pacific Careproctus ?sinensis lay their eggs in the king crab, Paralithodes camtschatica (Rass 1950, Vinogradov 1950, Hunter 1969), off California and British Comumbia C.melanurus use the box crab, Lopholithodes foraminatus (Parrish 1972, Peden & Corbett 1973), off Namibia C.griseldea use the stone crab Lithodes tropicalis (Melville-Smith & Louw 1987), and off Chile C.falklandica uses L.antarctica while Careproctus sp. uses Paralomis granulosa (Balbontin, Campodonico & Guzman 1979). In the crab's branchial cavity the fish eggs have ideal conditions for aeration and protection during their development. The association seems likely to be beneficial to only one party because the ability of half the crab's gills to carry out gaseous exchange would be impaired. The fish lay from 200-1500 eggs in only one gill chamber and these must displace and compress the gills. In the cases of P.camtschatica and L.tropicalis only large males carry the fish eggs. However, an L.forminatus female 120mm CW had over 400 eggs in its right gill chamber (Peden & Corbett 1973). It may be that the fish select large crabs and these are all males. Melville & Louw (1987) found that about 10% of male L.tropicalis CL>110mm carried fish eggs. There are no reports of fish eggs in Lithodes murrayi but this may simply be because no one has looked for them. A liparid, Careproctus kermadecensis Nielsen 1964 has been described from 6660-6770m in the Kermadec trench and the family is probably widespread in the New Zealand region (Chris Paulin pers. comm.).

References

Arnaud (1971), Arnaud & Do-Chi (1977), Arnaud, Do-Chi & Rannou (1976), Bower & Sloan (1985), Haynes (1968), Pike & Williamson (1965), Powell (1965), Powell & Nickerson (1965), Makarov (1938), McMullen (1969), Sloan (1985), Somerton (1981a), Stuardo & Solis (1963), Webb (1972), Weber (1967), Yaldwyn & Dawson (1969).

Lithodes longispina Sakai, 1971

Synonymy

Lithodes longispina Sakai, 1971a; Takeda, 1974; Dawson & Yaldwyn, 1985.

Type Locality

Off Matsushima, Japan, 600m.

Distribution

Japan, Guam, New Caledonia, south-east Australia, New Zealand. Within N.Z., off Wairarapa coast.

Diagnosis (Fig. 2a-e)

Carapace broadly pyriform ('pear-shaped') length (including rostrum) greatly exceeding width, regions well defined and armed with long acute spines. Rostrum five-spined, directed strongly upward in its proximal half but distal half is horizontal. At the junction of these two halves there is a pair of long accessory spines, the rostral tip is divided into two long, sharp, spines with an angle of about 30° and the sub-rostral spine is long and stout. Carapace spines are very long and sharp and eight in number. Four gastric spines, two long followed by two short, two cardiac spines, very long, and each branchial region has one extremely long sub-medial spine and one or two smaller posterior ones. The eyes are close together, freely movable, cornea well developed. On a lower level are the antennules with the antennae nearby. Second joint of antennal peduncle has a spine on its outer border, antennal flagellum long. There is a strong spine external to the ocular peduncle and the antero-lateral border is armed with 3 spines (second longest). Postero-lateral border broadly convex, armed with about 6 spines, the last is sub-medial and longest. Chelipeds, unequal, small compared to walking legs, merus armed with longitudinal series of short spines, terminal spine of anterior border prominent, carpus and propodus armed with 10-12 spinules on upper surface, fingers long, excavated internally. Walking legs, long, very thin, merus armed with 12-13 spines on anterior border, carpus has two very long spines, one proximal and the other distal, propodus markedly long and thin, armed with numerous spinules, dactyl has several spinules. Last pair of legs reduced and tucked into the gill chambers. Abdomen of six segments plus telson in both sexes, symmetrical in males asymmetrical in females. Second segment consists of three plates, third to fifth segments are replaced by a median membranous portion which is marked with 37-38 tubercles arranged in transverse lines. Female abdomen has about ten marginal plates on the right side while the male has about ten marginal plates on both sides. Uropods absent. Rudimentary pleopods on the first abdominal segment and single pleopods on the left side of the next four segments in females, but pleopods absent in males.

Colour

Deep red.

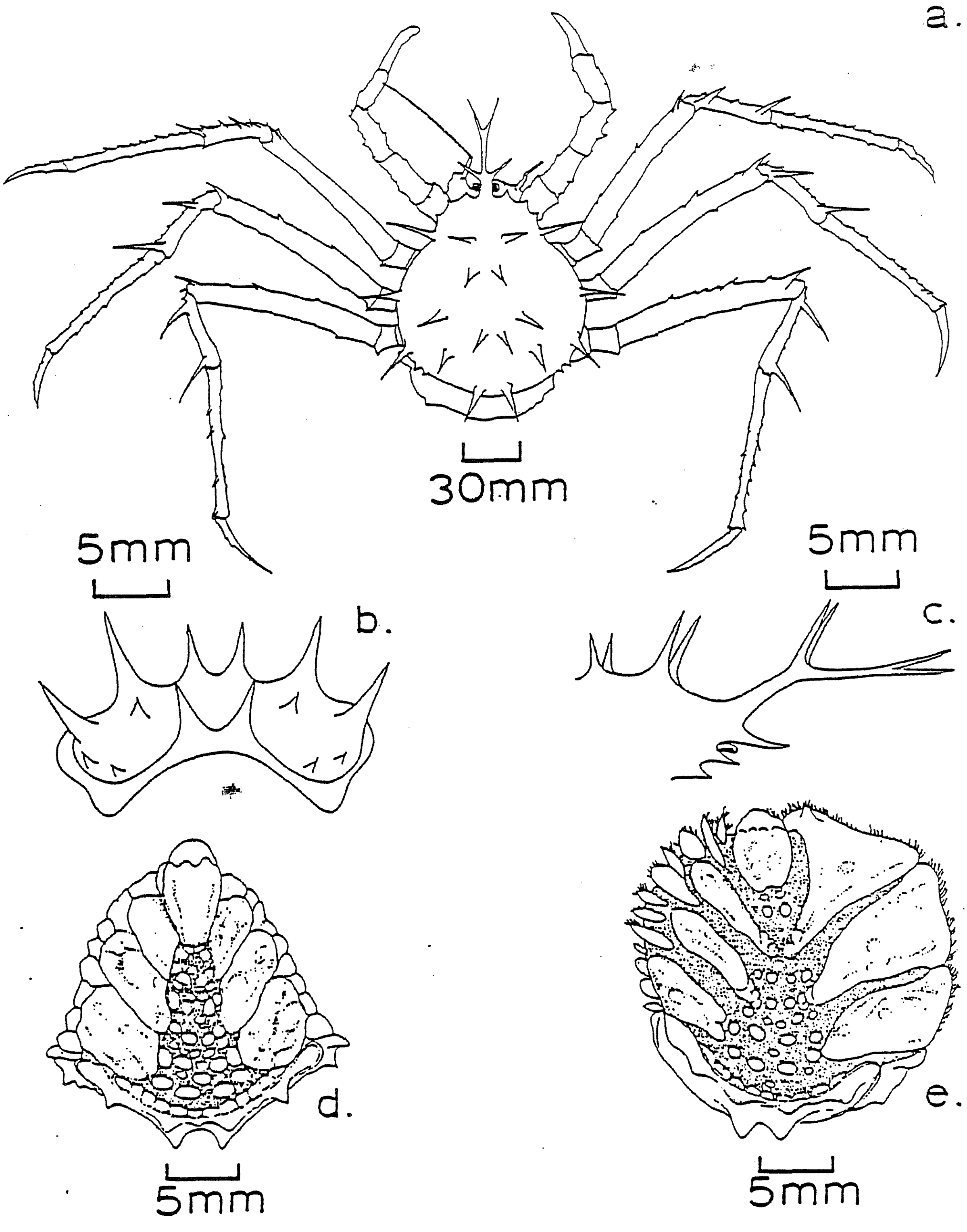


Fig. 2 - Lithodes longispina: a - female, dorsal view (by J. Black, based on a photo from Sakai, 1971); b - profile of carapace, posterior view; c - lateral view of rostrum; d - male abdomen, ventral view; e - female abdomen, ventral view (after Sakai, 1971).

Size

Male 98mm CW, 169mm CL (incl. rostrum).

Habitat

Deep water soft bottoms.

Depth

600-865m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown. Refer to L.murrayi where these aspects of lithodid biology are discussed.

References

Dawson & Yaldwyn (1985), Sakai (1971a), Takeda (1974).

Neolithodes brodiei Dawson & Yaldwyn, 1970

Synonymy

Neolithodes brodiei Dawson & Yaldwyn, 1970; Webb, 1972; Dawson & Yaldwyn, 1985.

Type Locality

Campbell Plateau, 50°58'S, 173°57'E, 832m.

Distribution

South-eastern Australia, New Zealand. Within N.Z., off Wairarapa coast, south of Solander Island, Campbell Plateau.

Diagnosis (Fig.3)

Carapace broadly pyriform ('pear shaped'), much longer (including rostrum) than wide, regions well defined and armed with many small spines. Rostrum simple, directed upward with a pair of small spines at its base immediately behind and to the side of the pair of strong, obliquely-projecting basal spines. Major spines on the carapace are four gastric, two cardiac and about ten branchial spines. The eyes are close together, freely movable, cornea ventral. On a lower level are the antennules with the long antennae nearby. Spine (i.e. acicle) on outer border of second joint of antennal peduncle is rudimentary. There is a strong spine external to the ocular peduncle and the antero-lateral border is armed with three spines. Postero-lateral border broadly convex, armed with about 15 marginal spines. Chelipeds unequal, small compared to walking legs, armed with numerous spines, fingers long, curved inward, excavated internally. Differences in dentition indicate that the chelipeds are clearly differentiated into a 'crusher' and 'cutter'. The larger right cheliped has three interlocking, stout, conical proximal teeth with scissor-like margins for the distal third. The left cheliped has minute proximal teeth but most of the margins form a scissor-like edge. Walking legs long, flattened and with numerous small spines on the dorsal surface. Dactyls without teeth on the ventral margin, long, narrowing and thorn-like with acute tips. Last pair of legs reduced and located in gill chambers. Abdomen of six segments plus telson in both sexes, symmetrical in males, asymmetrical in females. Covered with many small, strongly pointed, closely packed spines. First segment with a calcareous spinous plate, remaining segments defined but without calcareous plates. Second segment composed of five pieces separated by sutures. Third to fifth segments with calcified nodules and no membranous area. In female, lateral plates on left side enlarged. A pair of rudimentary pleopods on the first segment and single pleopods on the left side of the next four segments in females but pleopods absent in males. Uropods absent in both sexes.

Colour

Red.

Size

Female (ovigerous) 112mm CW, 131mm CL (incl. spines).

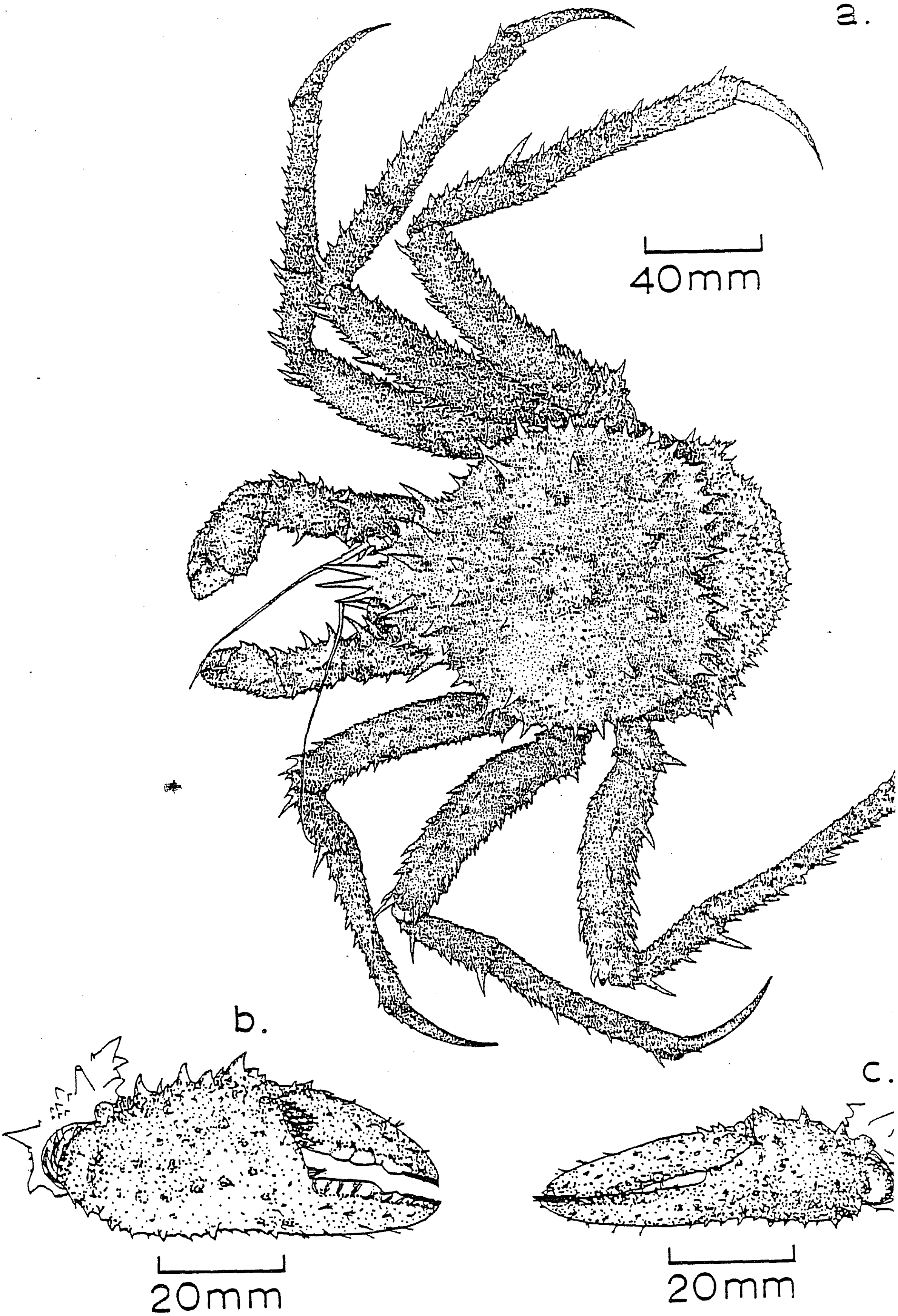


Fig. 3. - *Neolithodes brodiei*: a - dorsal view, female; b - outer face right cheliped, female; c - outer face left cheliped, female (by J. Black).

Habitat

Globigerina ooze, grey mud.

Depth

798-1120m.

Breeding

Webb (1972) collected an ovigerous female in February south of Solander Island but did not report any details except that the eggs were black. The ovigerous female reported by Dawson & Yaldwyn (1970) was collected in January from the Campbell Plateau. A female (CW = 107mm) collected from Hawke Bay in June was carrying a clutch of 4-5000 eggs with larval eye spots evident and the eggs had a diameter of 3.7mm. This would suggest that *Neolithodes brodiei* has large eggs and low fecundity to an even higher degree than *Lithodes murrayi*.

Development and Growth

According to Konishi (1986) larval development has not been studied in any *Neolithodes* spp. The large egg size reported above may indicate that *N.brodiei* has abbreviated development.

Behaviour, Ecology

Unknown. *N.brodiei* is the commonest lithodid found around New Zealand and may have considerable commercial possibilities (E. Dawson pers. comm.). Refer to *Lithodes murrayi* where lithodid behaviour and ecology is discussed.

References

Dawson & Yaldwyn (1970, 1985), Webb (1972).

Paralomis zelandica Dawson & Yaldwyn, 1971

Synonymy

Paralomis zelandica Dawson & Yaldwyn, 1971; 1985.

Type Locality

Chatham Rise, 44°18'S, 174°31'E, 640m.

Distribution

South and central eastern New Zealand.

Lithodid crabs are extraordinarily variable from place to place and adults often look very different from juveniles. I think that P.zelandica may well prove to be simply an adult P.hystrix but a full range of sizes of each supposed species needs to be examined.

Diagnosis (Fig. 4a)

Carapace broadly pyriform ('pear-shaped') width greatly exceeding length, numerous, subequal, conical, bluntly-pointed, short spines. Rostrum simple, acute, with two pairs of dorsolateral spines and an unpaired dorsal median spine at its base; ventral edge with a distinct swollen median lobe bearing several small flat tubercles laterally. The eyes are close together, freely movable, cornea ventral. On a lower level are the antennules with the antennae nearby. Outer border of second joint of antennal peduncle has an acicle which consists of two long lateral spines, a single, shorter, terminal spine and two still shorter median spines. External orbital spine strong, acute and larger than any other spine on hepatic margin. Postero-lateral border broadly rounded and armed with about 15 small marginal spines. Chelipeds unequal, similar in size to walking legs, armed with numerous spines, especially on inner margins of merus and carpus. Fingers short, stout and covered with numerous bunches of short setae. Walking legs stout, strongly-spined. Last pair of legs reduced and located in the gill chambers. Abdomen of six segments plus telson in both sexes, symmetrical in males, asymmetrical in females. Covered with many small, strongly pointed spines. Second segment entire, unpaired median plate and paired lateral and marginal plates fused together. Median plate of segments 3-5 entire, lateral plates distinct. Marginal plates present on right side only in females and on both sides in males. Females have a pair of rudimentary pleopods on the first segment and single pleopods on the left side of the next four segments. Pleopods absent in males, uropods absent in both sexes.

Colour

Creamy-white with pink spines.

Size

Male 127mm CW (incl. spines), 111mm CL (incl. rostrum).

Habitat

Fine sandy mud.

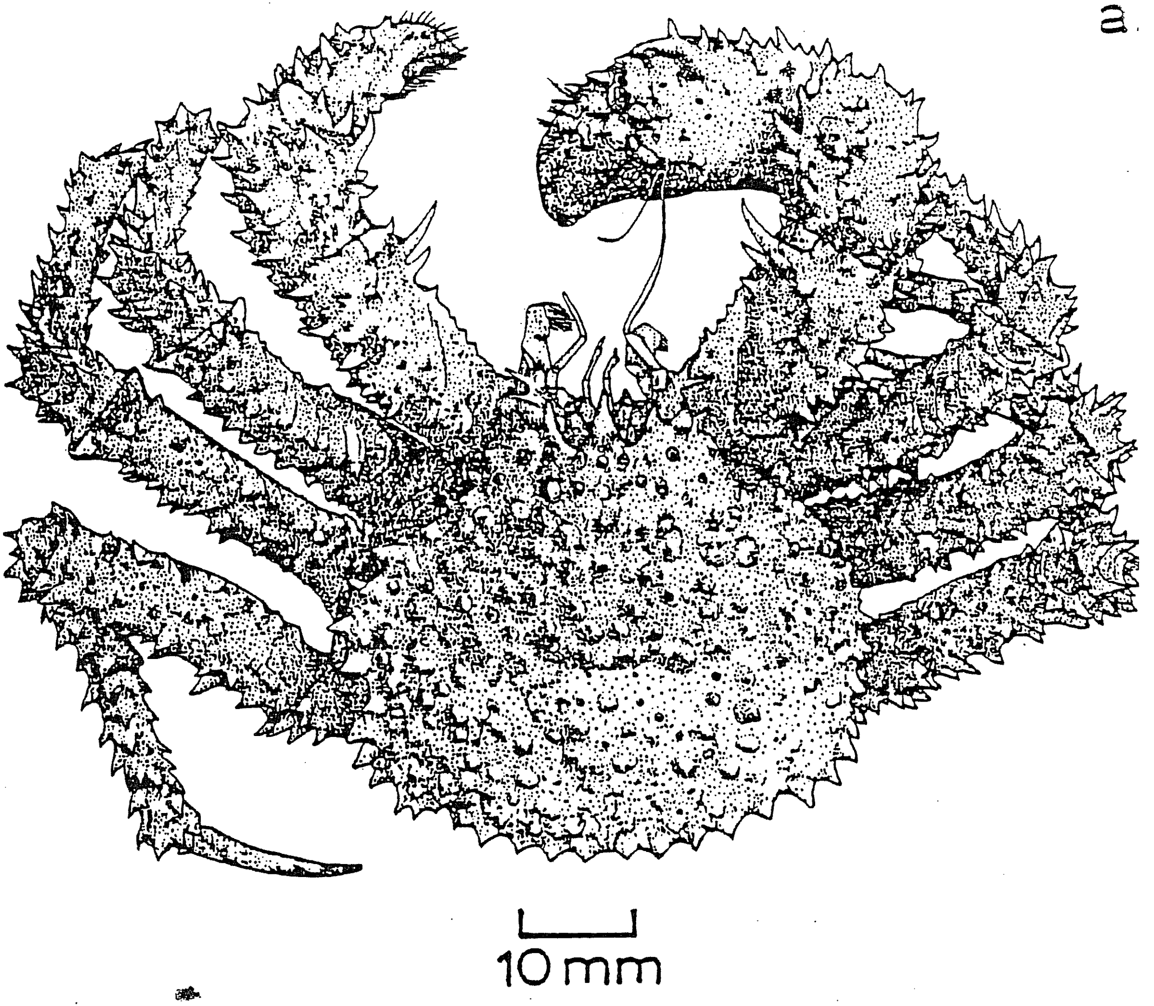


Fig. 4 - Paralomis zelandica: a - male, dorsal view (by J. Black, based on a photo from Dawson & Yalwyn, 1971).

Depth

640m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown. See *Lithodes murrayi* for discussion of these aspects of lithodid crabs.

References

Dawson & Yaldwyn (1971), Haig (1974), Sakai (1971a), Takeda (1974).

Note

A further undescribed species of *Paralomis* has been collected off East Cape (E. Dawson pers. comm.).

Paralomis hystrix (De Haan, 1849)

Synonymy

Lithodes hystrix De Haan, 1849; Acantholithus hystrix Stimpson, 1858; Paralomis hystrix Ortmann, 1892a; Acantholithus hystrix Bouvier, 1894; 1896; Doflein, 1902; 1906; Balss, 1913; Yokoya, 1933; Miyake, 1965; Paralomis hystrix Sakai, 1971a; Acantholithus hystrix Dawson & Yaldwyn, 1985.

Type Locality

Japan

Distribution

Japan and (?) New Zealand.

Diagnosis (Fig. 5a)

Carapace broadly pyriform ('pear shaped'), length slightly greater than width, covered with numerous long, sharply pointed spines. Rostrum simple, acute, curving upwards, two pairs of dorsolateral spines and an unpaired dorsal median spine at its base; ventral edge bearing a few spinules. The eyes are close together, freely movable, cornea ventral. On a lower level are the antennules withhe antennae nearby. Acicle of antenna (on second joint of peduncle) composed of four very long spines and one or two tiny spinules. Eye stalks armed with a few tiny spinules and a terminal spine. External orbital spine long, acute, hepatic margin bearing 6-7 acute spines of varying size. Postero-lateral border broadly rounded and armed with about 22-24 long, sharp spines. Chelipeds unequal, similar in size to walking legs, armed with numerous sharp spines, those on inner margins of merus and carpus are especially long. Fingers short, stout and covered with numerous bunches of short setae. Chelipeds clearly differentiated into a 'crusher' and 'cutter'. The larger right cheliped has three conical, interlocking proximal teeth and scissor-like cutting tips for one-fifth of length. Left cheliped has cutting edges. Walking legs, stout, bearing long, acute spines, last pair of legs reduced and tucked into the gill chambers. Dactyls of walking legs have a row of 7-8 tiny spines along the ventral margin. Abdomen of six segments plus telson in both sexes, symmetrical in males, asymmetrical females. Densely covered with many long, acute spines. First abdominal segment calcareous, rest soft. Second segment entire, plates fused. Median plate of segments 3-5 entire, lateral plates distinct. Marginal plates present on right side only in females and on both sides in males. Females have a pair of rudimentary pleopods on the first segment and single pleopods on the left side of the next four segments. Pleopods absent in males, uropods absent in both sexes.

Colour

Deep red-orange.

Size

Male 114mm CW, 126mm CL (incl. spines).

Habitat

Continental shelf.

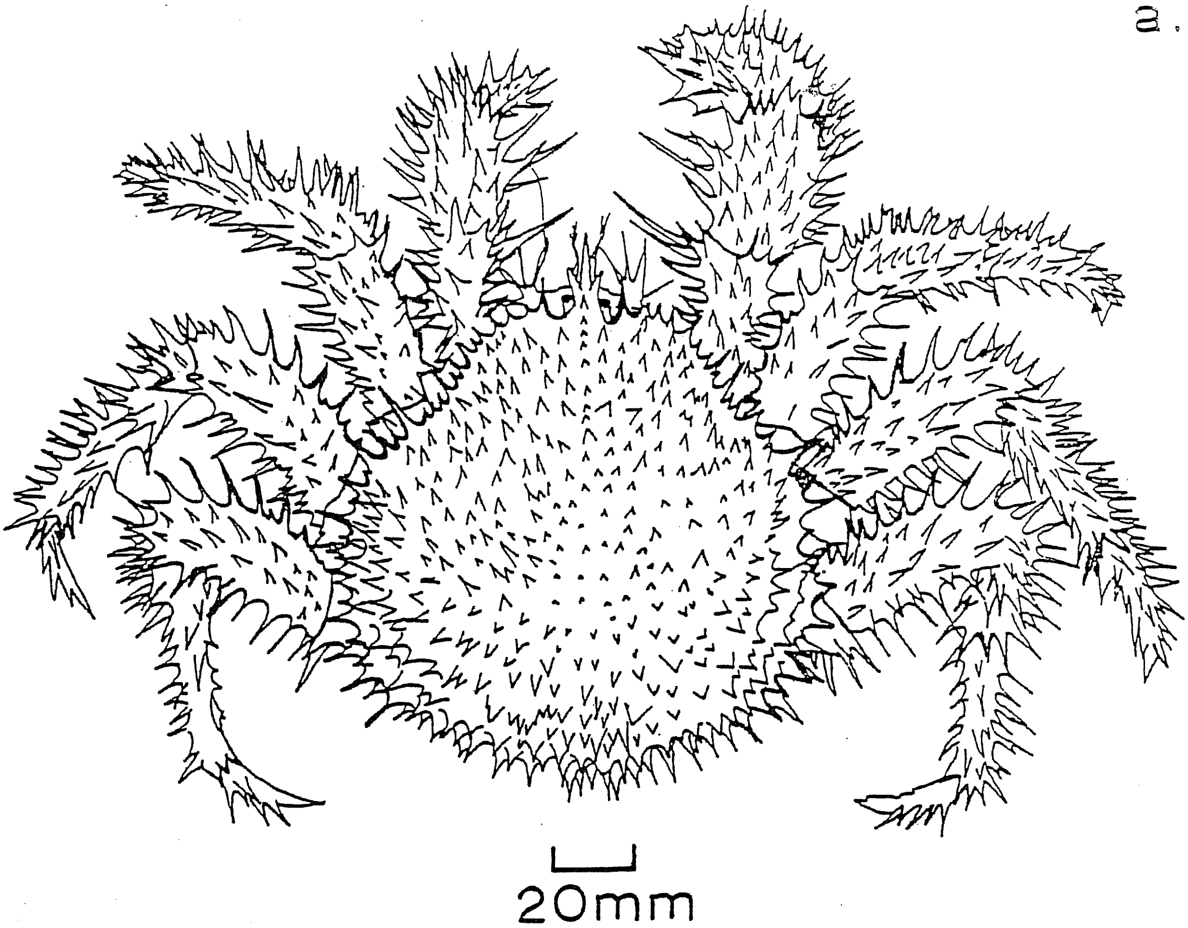


Fig. 5 - Paralomis hystrix: a - male, dorsal view (by C. Duffy, based on a photo from Sakai, 1971).

Depth

150-600m.

Breeding

Unknown. Ovigerous *Paralomis granulosa* from southern Chile have been collected in November, when the eggs also began to hatch (Campodonico & Guzman 1981).

Development and Growth

Unknown. Development of *Paralomis granulosa* is very abbreviated both in number of stages (two zoea plus megalopa) as well as duration (about 10-12 days at 11°C) (Campodonico & Guzman, 1981). *Lithodes maja* is the only other lithodid known to have only two zoeal stages (MacDonald et al. 1957). Campodonico & Guzman (1981) reared larvae of *P.granulosa* with and without *Artemia* as food and while larvae in both groups produced megalopae, survival was seriously reduced in the absence of food. The presence of yolk reserves in all larvae and its gradual decrease as development proceeds, indicates that both zoeae and megalopae are to some extent lecithotrophic but additional food is probably normally required.

Behaviour, Ecology

Unknown. Refer to *Lithodes murrayi* for discussion of the aspects of lithodid biology.

References

Campodonico (1977, 1980), Campodonico & Guzman (1981), Dawson & Yaldwyn (1985), Sakai (1971a).

Porcellanopagurus edwardsi Filhol, 1885

Synonymy

Porcellanopagurus edwardsi Filhol, 1885; Thomson, 1898; Alcock, 1905; Chilton, 1909; Stephensen, 1927; Thompson, 1930; Balss, 1930; Bennett, 1932; Forest, 1951; Roberts, 1972a; 1972b; Yaldwyn, 1975; Fenwick, 1978; Takeda, 1981; Wear, 1985.

Type Locality

Campbell Island.

Distribution

Kaikoura Peninsula, Stewart Island, Campbell Island, Auckland Island, Snares Island.

Diagnosis (Fig. 6a-d)

Carapace finely granulated produced anteriorly as a blunt rostrum wide at its base and slightly convex on the sides. Antennules about twice as long as eyestalks, antennae are very long and slender. Upper margin of orbit is smooth and the eyestalks extend a little beyond the tip of the rostrum. The eyestalks are of uniform width along their length and the cornea is not bulbous. Four antero-lateral teeth, including the post-orbital. A strong post-orbital tooth at the outer angle of the orbit, followed by two equidistant, blunt, antero-laterally directed teeth and a blunt, postero-laterally directed tooth at the posterior corner, marking the greatest width of the carapace. In addition there may be secondary teeth in front and behind the second antero-lateral tooth. In juveniles the secondary teeth are absent. Chelipeds well developed with the right one much larger than the left. Merus triangular, widening distally, carpus about as broad as long, marked on the upper surface with transverse lines of setae arranged in short curves, propodus flattened, about as long as the carapace is wide, considerably wider than carpus, margins spinose. Whole surface of propodus bears scattered tufts of short setae which also occur on the dactyl. Fingers of right cheliped with well developed blunt teeth, with tufts of setae between the bases of them. Propodus of left cheliped much smaller, narrower than carpus, fingers slender, inner margins straight and fitting close together without teeth. The right cheliped appears to be a "crusher" while the left is a "handler" of food. First two pairs of legs well developed, finely granulose, margins spinose, with well-developed dactyls ending in a hooked claw. Last two pairs of legs reduced, propodus of the sub-chelate third leg has a narrow band of pegs on its posterior margin. Fourth leg smaller, propodus has a broad band of pegs on its anterior border, extending on to the dactyl. The last two pairs of legs are probably used to support and manipulate the bivalve shell carried by the crab. Abdomen is straight, very short, soft and with well developed uropods which grasp the bivalve shell under its hinge-line. The uropods are symmetrical, flattened and bear well-developed rasps on the dorsal surface. The rasps consist of distally-directed, broad, over-lapping plate-like pegs. The telson is soft, rounded and with a small notch in the posterior margin. Female pleopods are sub-dorsal in position rather than lateral as in other hermit crabs.

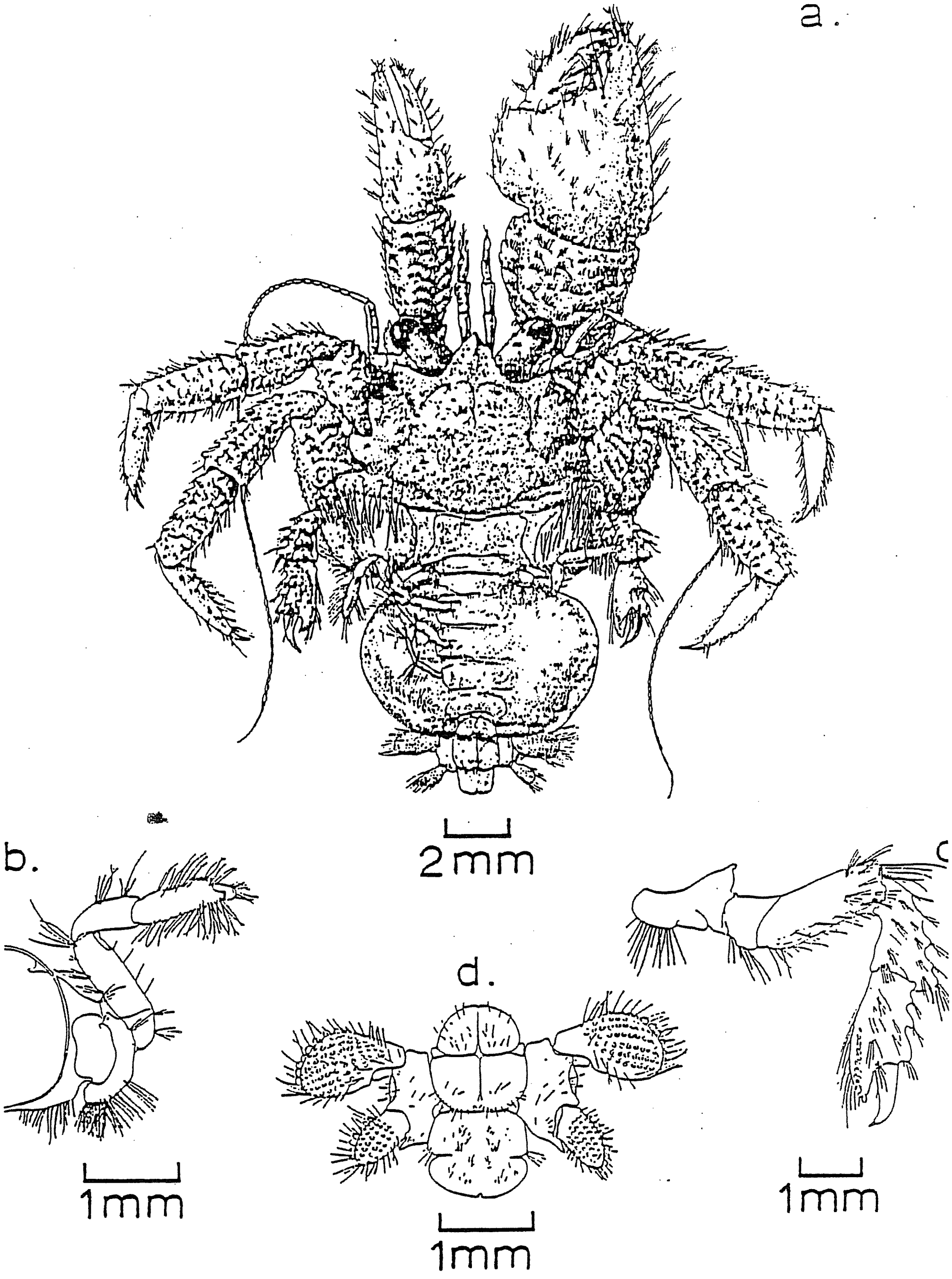


Fig. 6 - *Porcellanopagurus edwardsi*: a - male, dorsal view; b - right 4th leg, dorsal view; c - right 3rd leg, dorsal view; d - posterior region of abdomen, dorsal view (modified after Forest, 1951).

Colour

Body and limbs orange, cornea of eye green, antennules light purple, antennae barred orange and white. Distal half of propodal segments on first two pairs of legs white, proximal half orange.

Size

Male 24.8mm CW. Female 18.6mm CW.

Habitat

On sand and rocks, among algae and shells.

Depth

Shallow subtidal (in subantarctic waters) to 150m.

Breeding

Ovigerous females have been collected at Campbell Is. in March, April, May, July and October. Zoea larvae have been collected from plankton in October, November and February (Roberts 1972b). Roberts reared larvae from the female collected in April which had eggs ready to hatch so presumably larvae could be expected in the plankton much later than February. The female (16.8mm CW) collected in May had (?)2000 new eggs 0.75mm diameter. To have produced larvae in the summer months the crabs must have carried eggs through the winter and since the female collected in April had mature eggs it seems likely that ovigerous females probably occur in summer as well. It is likely that females may carry a brood of eggs for long periods because embryonic development would be slow in these cold waters. Therefore females may only produce a single large brood per year.

Development and Growth

Roberts (1972a) has thoroughly described the four zoeal stages of P.edwardsi but he did not indicate how long each stage of development required. Small numbers of larvae occurred in the plankton in October, November (peak) and February at Campbell Island.

Behaviour

P.edwardsi is unusual among hermit crabs in using single bivalve shells or shells of univalve gastropods for protection. These shells hardly protect the crab from predators because they usually only cover the rear half. When the female is carrying a brood of eggs these are concealed because the pleopods to which the eggs are attached are sub-dorsally positioned. However, males also carry shells and it is difficult to imagine what value the shell is apart from its obvious camouflage function. Bivalve shells such as Leptomya aucklandica, Genaximus otagoensis, Chlamys delicatula, Venerupis largillierti and Kidderia campbellica, are grasped by the rasp-like uropods which are inserted under the hinge-line and the third pair of legs are probably used to grasp the shell margin and prevent loss of the shell. Some gastropod shells such as Sigapatella novaezelandiae, Haliotis virginea and Margarella antipoda are also used.

Nothing is known about the behaviour of this hermit crab but it seems unlikely that shell-exchange behaviours common in gastropod-shell users would be well developed. Bivalve shells are unlikely to be in short supply and besides P.edwardsi often uses damaged shells. The only requirement seems to be that the hinge-line should be intact.

Ecology

Nothing is known about feeding behaviour but the dimorphic chelipeds suggest that P.edwardsi may well be a predator of hard-shelled prey with the right cheliped used to break them open.

References

Bennett (1932), Chilton (1909), Forest (1951), Roberts (1972a, 1972b).

Petrolisthes elongatus (H. Milne Edwards, 1837)
Blue False Crab

Synonymy

Porcellana elongata H.Milne Edwards, 1837; White, 1843; Petrolisthes (Petrolisthes) elongatus Miers 1874; 1876b; Porcellana rupicola Kirk, 1878; Petrolisthes elongatus Thomson, 1898; Oliver, 1923; Young, 1929; Bennett 1930; 1932; Trevarthen & Kulka, 1950; Trevarthen, 1951; Batham, 1956; 1958; Dell, 1963a; Bennett, 1964; Wear, 1964b; 1965b; Batham, 1965; Greenwood, 1965; Hayward, 1974; Jones M.B., 1976; 1977; Knox, Bolton & Hackwell, 1977; Marsden & Fenwick, 1978; Knox & Bolton, 1978; Knox & Fenwick, 1978a; Marsden, 1981; Jones, 1983; Knox, 1983b.

Type Locality

New Zealand

Distribution

Tasmania and New Zealand. Found very widely around the coasts of North, South and Stewart Island also Auckland Islands. P. elongatus may have been introduced by man to Tasmania in among oysters (see Halicarcinus inomminatus).

Diagnosis (Fig. 7a-c)

Carapace flattened, smooth, oval-shaped, truncated posteriorly, longer than wide (ratio approx. 1.1). Margins without teeth, regions not well defined. Posterior margin concave. Antennae longer than CL, rostrum short but extending beyond eyes, blunt, broad, deflexed, dorsal surface concave. Eyes large and prominent, cannot be withdrawn into orbits. Post-orbital corner a clear-cut right angle. Third maxillipeds very large, covering the whole buccal area and extending forward to the tip of rostrum. Maxilliped palps well developed and bearing long setae which are used for filter feeding. Outer margin of carpal segment not denticulate. Chelipeds very large, flattened, especially carpus and propodus. There are three small, sharp, distal spines on the outer margin of the carpus and a single, small proximal spine on the inner margin. Propodus broadest at the base of dactyl (movable finger), fingers tapering, without teeth but minutely granulate and occluding along their entire length. Tips of fingers strongly curved, blunt, crossing. Legs much shorter than chelipeds, only three pairs visible, meri laterally flattened, remaining segments setose, propodus with three or four short spines ventrally, dactyl short and strongly curved. Last pair of legs setose but without spines, reduced, folded and partially concealed under the abdominal flap. Abdomen of six segments, broadly developed, two or three segments visible dorsally, telson divided into seven plates and surrounded laterally by large uropods. Both telson and uropods setose. Spines on the chelipeds and legs are variable in development and position. They may be easily broken off by wear and tear.

Colour

Variable colouration from black, blue, greyish, greenish or even pinkish. Antennules dark brown proximally, bright red-orange tips, antennae dark brown. Dorsal surface of chelipeds and legs

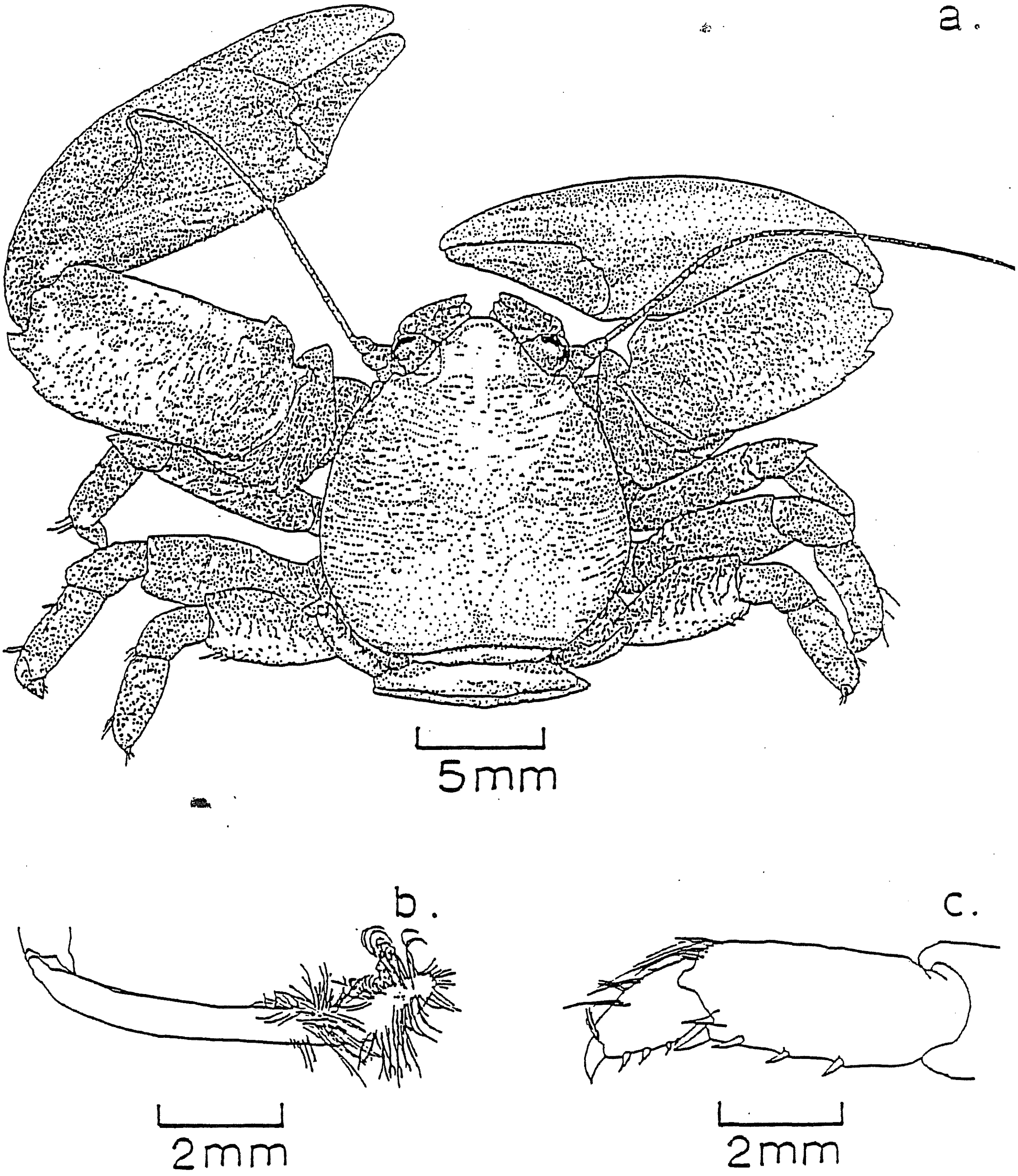


Fig. 7 - Petrolisthes elongatus: a - male, dorsal view; b - distal region, left 4th leg; c - distal segments left 2nd walking leg (by J. Black).

same as carapace, ventral surfaces lighter (white, yellow, blue-green).

Size
Female CL 16mm, male CL 16.5mm.

Habitat
An extremely gregarious crab found beneath boulders in the intertidal region, sheltering in beds of large mussels on rocky coasts and on wharf piles, and extending into estuaries.

Depth
Upper littoral down to just below low tide.

Breeding
Studies at Auckland, Wellington, Kaikoura and Christchurch suggest that the breeding biology of P.elongatus varies from north to south (Greenwood 1965, Wear 1965b, Jones 1977, Scott 1958).

At Auckland Greenwood (1965) found that ovigerous females were present throughout the year (2.3-17% of females) with the greatest proportion ovigerous in October. Planktonic zoeae are also found in all months. Females mature at 8.1mm CL and probably produce more than one brood per year although this has not been verified. Eggs are initially dark rust-red in colour, but fade during development as yolk is used. Later eggs are light brown with green and gold patches and measure 0.65 x 0.3mm. Egg numbers increase logarithmically with CL.

At Wellington Wear (1965b) found that the sex ratio is biased in favour of females in most months. Females are sexually mature at 8.5 mm CL when they carry approx. 200 eggs. The relationship between number of eggs and female CL is logarithmic and at 16 mm CL females carry from 1500-1750 eggs. Egg laying begins in July and by September about 90% of females are ovigerous. New eggs are reddish-purple and measure 0.65 x 0.4mm but close to hatching they are reddish, semi-transparent and measure 1.0 x .75mm. By February and March few females are ovigerous and all these have eye-pigmented eggs. In late September a few first-stage larvae appear in the plankton indicating that incubation is from 6-8 weeks. Females with late stage eggs have their ovaries gravid with the next batch of eggs and at least 2 broods are laid annually by each female. Larvae are most abundant in the plankton during January and February and are not found after March.

At Kaikoura Jones (1977) found that the sex ratio fluctuated widely with no seasonal pattern but females generally outnumbered males. Ovigerous females were first found in October (although Morgans 1967 recorded some in August), increasing until January (68%). At the start of breeding females were predominantly large (8-10mm CL) with smaller females breeding in December and January. Ovigerous females were absent after March. Indirect evidence of male sexual maturity (presence of spermatophore ribbons extending from the male genital opening near the base of the last walking leg) showed that 4.9mm - 16.5mm CL males extruded spermatophores in most months except June and July. Females with stage 1 eggs were found from October to January but females with stage 4 eggs did not appear until January suggesting that P.elongatus at Kaikoura has only 1 brood per year. Each female may have 2 or perhaps 3 broods over her lifespan. Brood size increased logarithmically with female CL, at 5.5mm they carried about 70 eggs and at 14mm, 930 eggs. Therefore each female may produce from 500 eggs (2 broods) to 1000 eggs (3 broods). During incubation there was a 15.2% mortality probably due to egg loss, failure to develop and disease.

At Christchurch Scott (1958) recorded ovigerous females at the end of August but some females have eggs developing in the ovaries as early as May. In August ovaries contain both mature eggs ready to be laid as well as immature eggs for the second brood. Egg-laying continued until mid-December and 1 female laid a second brood 3 weeks after the first brood hatched without an intervening moult. Other females moulted as soon as the first brood hatched. Newly laid eggs measured 0.6mm and were dark red. Ovigerous females were most frequent in November (41%) and were collected until February. Regular exposure to air during each low tide and higher air temperatures may be important in ensuring egg development since ovigerous females kept in aquaria do not successfully produce larvae. Egg hatching began about mid-November and continued until February. During March-August 1982, zoea of P.elongatus were rarely found in plankton from the Avon Heathcote Estuary (Roper, Simons and Jones 1983).

Further south at Stewart Island ovigerous females have been collected in November and December but no systematic sampling has been undertaken to define the breeding season (Jones 1977).

In summary the breeding season of P.elongatus decreases from 12 months at Auckland to 9 months at Wellington and 6 months at Kaikoura. Females seem to mature at a smaller size at Kaikoura than at Wellington or Auckland and larger (>12mm CL) females seem to have smaller numbers of eggs per brood. But small females are the reverse and have larger brood sizes. Egg size does not appear to be correlated with latitude but whereas incubation at Wellington was 6-8 weeks, at Kaikoura incubation was of the order of 3 months. It would appear that temperature differences from north to south are probably responsible for differences in life history between localities. However it is necessary to conduct a thorough experimental study of the effects of temperature on adult growth rates, gonad maturation, incubation and time of larval development to test this hypothesis.

Development and Growth

Porcellanid zoeae are elongate, characterized by very long, tapering rostral and posterior carapace spines. The telson is triangular with a convex posterior margin bearing several processes. There are 5 free abdominal somites and no uropods. Only first and second maxillipeds functional, pereiopods small, non-functional, 3 or 4 pairs of pleopods in later stages (Greenwood 1965).

Five zoeal stages are possible in P.elongatus but only 3 and occasionally 4 zoeal stages are passed through in reaching the megalopa stage. Wear (1964b, 1965b) and Greenwood (1965) have described the pre-zoea and larval development in this species. During the day zoeae are not found in surface plankton. The megalopae can survive for long periods but are probably only planktonic until suitable benthic habitat is found. Kingsford & Choat (1985) found large numbers of megalopae, attributed to the genus "Petrolisthes", associated with clumps of drifting algae off the coast of Leigh in December. The occurrence of floating algae and its pattern of movement will clearly have an effect on recruitment to shore populations.

Behaviour

P.elongatus has two distinct kinds of feeding mechanism, macrophagy and filter feeding. Scott (1958) found that pieces of Pomatoceros worms were conveyed to the mouth where they were shredded by the second maxilliped and sliced in a scissor-like fashion by the mandibles. However most food consists of fine organic particles filtered from the water by the long setae on the third maxillipeds. Right and left maxillipeds sweep alternately and as they approach the mouth the exhalent respiratory current aids in rejection of unwanted mud particles and sand grains. As the third maxilliped begins to unfold for the next stroke the terminal setae of the second maxillipeds are passed through them, combing out the particles which are passed on to the maxillae. The maxillae move from side to side in sympathy with movements of the scaphognathites. This results in food being passed back towards the mandibles. Water is drawn towards the crab and the antennules (chemoreceptive or tactile in function) are extended into the water current and flicked about. The third maxillipeds may also occasionally sweep the substrate and pick up pieces of algae and utilize bottom deposits.

Agonistic interactions of P.elongatus have not been studied but work by Molenock (1976) on 4 species of Californian Petrolisthes which also live in dense aggregations suggest some things to look for. In these species the long antennae and enlarged chelae are used extensively in agonistic (and also sexual) interactions which preserve individual space and serve a social bonding and exploratory function. Interactions of Petrolisthes involve little forceful physical contact and none of the agonistic acts seemed to be derived from filter feeding activities (cf. sexual behaviour, below).

When attempting to escape P.elongatus will readily autotomize their chelae and limbs. Scott (1958) found that the percentage of the population at Christchurch regenerating one or more limbs (chelae or legs) varied from 10% (sheltered sites) to 40% (exposed sites), mean 26%. Most of the limb losses involved chelipeds (48%) with first (15%), second (16%) and third (21%) walking leg losses being less frequent. Loss of limbs seems to have little effect upon locomotory efficiency. Escape is also aided by the use of the large abdominal flap which allows the crab to swim backwards (like a crayfish). The flattened body and legs allow P.elongatus to escape into crevices between rocks.

Mating behaviour of P.elongatus has not been observed but involves transfer of spermatophores from the male to the female. The female aerates her eggs by flexing the abdomen and thrusts the reduced last pair of legs into the egg mass to remove debris.

The study of 4 Californian species of Petrolisthes, (P.manimaculis, P.eriomerus, P.cinctipes, P.cabrilloi) by Molenock (1975) gives some clues about the nature of courtship and mating of New Zealand Petrolisthes. In the laboratory P.manimaculis defended a small territory (7cm diam.) within which the female moved freely, but protected by the male. The female frequently rested just in front of the male, making short excursions, during which she stretched her appendages and performed grooming movements, apparently in preparation for the moult. Courtship often lasted several hours and during this time the male often oscillated his bright blue third maxillipeds. This was not a part of feeding because they were not drawn into the mouth. About 30min. after moulting the soft female was tapped and manoeuvred by the male using his legs so that their sterna were juxtaposed with the male underneath. But copulations also occurred with the male on top or with the pair perpendicular. The male was usually larger than the female. Copulation was usually completed within 60sec. The females deposited eggs on their pleopods within a few hours of copulation. P.manimaculis males also copulated with hard females, without prior courtship, but these females did not deposit eggs. Courtship and copulation of P.eriomerus were extremely similar to that of P.manimaculis, but the remaining 2 species were quite different. P.cinctipes males only copulated with hard females and within the territory defended 1-4 female crabs. Territories were held for 2-21 days but sometimes small males were able to sneak in and mate with the females. Courtship interactions were brief. There were no maxilliped oscillations by males but approaches were made with chelae hunches, rocks and nudges. Females moved back and forth, turning and grooming in the vicinity of the male, resembling the pre-moult movements of P.manimaculis and P.eriomerus females even though no moult occurred before copulation. About an hour after copulation the female deposited her eggs. Courtship and mating by P.cabrilloi was similar to P.cinctipes but males copulated with both hard and soft females with little or no preliminary exchanges. Considering the need for reproductive isolation there is a surprising degree of similarity in the behavioural acts of some of these species. A comparison of the behaviour of the New Zealand species would be interesting because they are spatially separated.

Ecology

At Kaikoura juvenile (<4mm CL) P.elongatus were present in every month (Jones 1977), small juveniles (<2mm CL) began to appear in March (onset of recruitment) and from May to December juveniles were the dominant size class. Numbers of juveniles decreased from October to March as they continued to grow and become either males or females. Large males (>14mm CL) and females (>12mm CL) present from October to March disappeared during April to June probably as a result of mortality. The maximum life span ranged from 12-18 months depending upon season of recruitment. Therefore P. elongatus is comparatively short-lived producing only 2 or 3 broods of eggs.

At Leigh P.elongatus is preyed upon by the black-fingered crab, Ozius truncatus, suckerfish (Diplocrepis puniceus) and rockfish (Acanthoclinus quadridactylus). It is probably eaten by red- and black-billed gulls (Larus novaehollandiae, L.bulleri) and also kingfishers (Halcyon sanctus). Scott (1958) found the remains of a young *P. elongatus* in the sea anemone *Isocradactis magna*, and the wandering sea anemone (*Phlyctenactis tuberculosa*), the cephalopods *Robsonella australis* and *Octopus maorum* will readily attack and eat this crab in the laboratory. Habib (1977) found that the pufferfish (*Contusus richei*) in Lyttelton Harbour also eats this crab. Webb (1966,1973a,1973b) found that sand flounder (*Rhombosolea plebeia*), common sole (*Peltoramphus novaezelandiae*), spotty (*Pseudolabrus celidotus*), pufferfish, and short finned eels (*Anguilla australis*) in the Avon Heathcote Estuary ate varying amounts of *P.elongatus*. Zoeae of this crab are eaten by horse mackerel (*Trachurus novaezelandiae*), 0.7% of gut volume (Godfriaux 1970a) and also by kahawai (*Arripis trutta*) in Wellington harbour (Baker 1971). Graham (1939) found that 9 species of fish in Otago Harbour consumed small numbers of *Petrolisthes* spp. but unfortunately he did not distinguish *P.elongatus* from *P.novaezealandiae.*

In the Avon-Heathcote Estuary Jones (1976) found that *Petrolisthes elongatus* only occurred under silt-fee stones and was concentrated in areas with channels of free-flowing sea water. It made up 9.3% of the 6 species collected. Laboratory experiments showed that *P.elongatus* were photonegative (in both air and water) and preferred stones over both sand and mud. They survived 7 day exposure to 50% sea water, although activity was reduced, but died at 10% and 0%. This species is relatively stenohaline between 18.7-37.4 ppt. Hoskins (1966) found that this crab is an osmo-conformer and does not regulate its haemolymph sodium concentration as the external medium changes. In this estuary *P.elongatus* is absent from some areas (chiefly at higher levels) where suitable substrates occur. Jones and Greenwood (1982) found that the occurrence of small (mean dry body weight 0.12g) crabs may be controlled by intolerance to desiccation but larger crabs have a significantly slower rate of water loss and should be able to tolerate conditions at these higher shore levels. Absence from stony habitats at high-tidal levels may be related to the requirement of a minimum time of water coverage to feed. One factor that has not been considered is the possible impact of avian predators at these sites.

The relationship between volume and surface area for *P.elongatus* is given by Pellegrino (1984) who estimated that 70% of crab mass is contained in the pereiopods and only 30% in the body. Shanks (1982) compared the effects of aerial exposure on *P.elongatus* and *Cyclograpsus lavauxi* and found that *P.elongatus* has a much faster rate of water loss and a much lower lethal water loss level (25-31%). Time to reach the lethal percentage was 16.8 hours for small crabs and 30.7 hours for large crabs. In the field these crabs live well within these limits because they have only 6-8 hours exposure. Jones (1977) found large crabs higher up the shore than small crabs and Pellegrino (1984) suggested that retreat from higher shore levels in warmer months was due to desiccation stress. Shanks (1982) found that the osmotic concentration of fully hydrated crabs in 100% seawater was higher than the medium but chloride ion concentration was lower than the medium. During desiccation water was lost preferentially from the extracellular compartment. With increasing loss of body water during aerial exposure, the osmotic concentration of the haemolymph increased but changes in the individual ionic components were not the same. Sodium concentration increased in 2 stages: below 12% body water loss, sodium levels were significantly elevated but above 12% they were as expected, given the amount of water lost. But changes in magnesium ions showed the opposite pattern, suggesting that these changes may be linked to corresponding changes in sodium concentration. Potassium concentration was lower than expected and chloride concentration was higher than expected. Thus P.elongatus is capable of some degree of osmoregulation under aerial conditions. Water content seems to be related to habitat: Pellegrino (1984) estimated 67.6% in crabs from Island Bay, Wellington. Crabs collected from Governor's Bay (a marine site) had a total body water content of 64.3-66% but Jones and Greenwood (1982) found only 60.3% in crabs from the nearby Avon-Heathcote Estuary. However comparably sized crabs from both populations had a similar desiccation resistance.

References

Bennett (1932), Dell (1963a), Graham (1939), Greenwood (1965), Habib (1977), Hoskins (1966), Jones (1976, 1977,1983), Jones & Greenwood (1982), Molenock (1975,1976), Pellegrino (1984), Roper, Simons and Jones (1983), Scott (1958), Shanks (1982), Thomson (1898), Wear (1964b,1965b), Webb (1966,1973a, 1973b).

Petrolisthes novaezelandiae Filhol, 1886
Red False Crab

Synonymy

Petrolisthes novaezelandiae Filhol, 1886; Petrolisthes stewarti Filhol, 1886; Petrolisthes novaezelandiae Thomson, 1898; Chilton, 1906a; Bennett 1930; 1932; ?Petrolisthes elongatus Powell, 1937; Petrolisthes novaezelandiae Wear 1964a; 1965c; Fenwick, 1978; Marsden & Fenwick, 1978; Probert et al., 1979.

Type Locality

New Zealand

Distribution

Endemic to New Zealand. From Bay of Islands south to Stewart Island and Auckland Islands.

Diagnosis (Fig. 8a-b)

Carapace flattened, slightly wider than long, covered in fine, short hairs, surface uneven. Antennae much longer than CL. Rostrum, broad based, blunt, projecting well past eyes and with short, stout hairs on the margins. Dorsal surface of rostrum is concave and this depression extends back as a broad frontal groove separating a pair of protuberences on the carapace. These protuberences bear bunches of setae and extending obliquely towards the lateral carapace margin on each side are a further three raised areas, each bearing setae. Third maxillipeds large, with well developed setiferous palps, extending as far forward as the rostrum. Outer margin of carpal segment is denticulate. Eyes short, fat unable to be withdrawn into orbits and with the post-orbital corner produced as a short tooth. Anterolateral margins convex but interrupted by two oblique depressions or notches in the hepatic and branchial regions. Posterior carapace margin concave. Chelae small in female, larger in male, carpus flattened with a central ridge on the outer surface, inner margin with two spines (one proximal, the other midway), outer margin with four approximately equidistant spines, each bearing bunches of long hairs. Chela propodus also flattened, broadest at base of dactyl, strong central ridge, lower margin bearing numerous small spines and fringed with long hairs. Outer surface of fingers each with a central ridge, movable finger with a carinate dorsal border, inner margins of both fingers without teeth, movable finger fitting in behind fixed finger. Fingers variable in length, more slender and elongated than in P.elongatus and may have a narrow gape. Only three pairs of legs visible dorsally, meri laterally compressed. Other segments fringed with bunches of long hairs, dactyli curved and sharp. Fourth pair of legs shortest, sub-dorsal and folded against the posterolateral corner of the carapace and tips inserted under the broad abdominal flap. Telson divided into seven plates, setose and surrounded by well developed uropods.

Colour

Males reddish, females greyish with red spots. Preserved material has white carapace and legs and pale orange chelipeds.

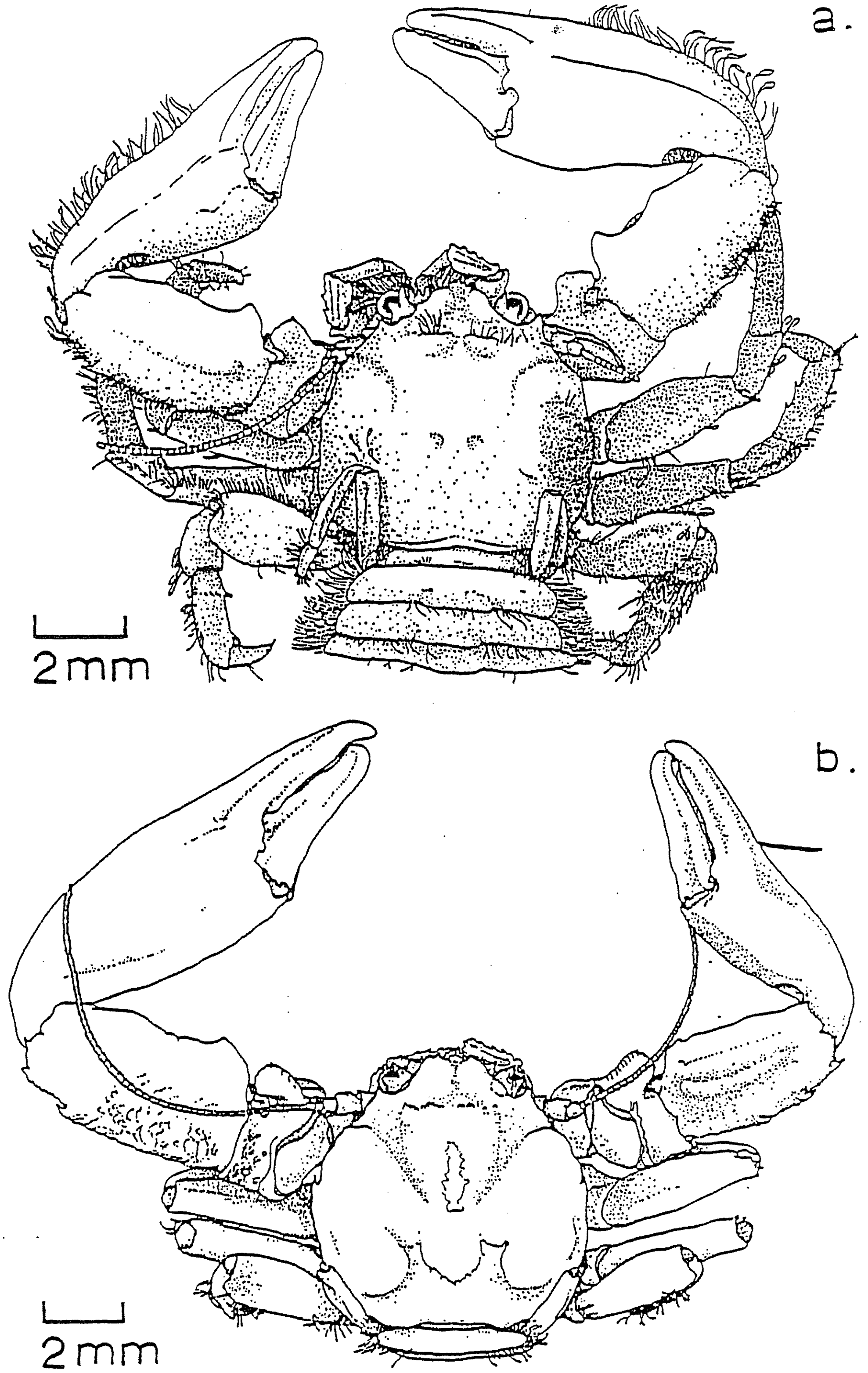


Fig. 8 - Petrolisthes novaezelandiae: a - female, dorsal view; b - male, dorsal view (by C. Duffy).

Size

Female 12mm CW, 12.5mm CL. Male size unknown.

Habitat

Intertidal (rarely), beneath boulders, *Macrocystis* holdfasts, among shell debris.

Depth

Intertidal (rarely), 3-75m.

Breeding

Ovigerous females have been collected in September, February and March. Eggs freshly laid are brick-red in colour and measure 0.6 x 0.4mm. When ready to hatch they are transparent with a pair of conspicuous black larval eyespots and measure 1.0 x 0.65mm. The smallest ovigerous female (3.2mm CW) carried 50-60 eggs and the largest females (12mm CW) carried about 300 eggs (Wear 1965c).

Development and Growth

Larval development of *P.novaezelandiae* has been described by Greenwood (1965) and Wear (1964a) who found that this species was the most abundant of the 3 types of porcellanid larvae found in the Wellington plankton especially during spring and summer. The pre-zoea stage which lasts only 3-4 hours has been described by Wear(1965c). Planktonic zoea larvae of this family are characterised by an enormously long rostrum and posterior carapace spines. Zoeae of *P.novaezelandiae* are found in the Wellington Harbour plankton throughout the year but are most abundant from November to January. During March-August 1982, zoeae of *P.novaezelandiae* were rarely found in plankton from the Avon-Heathcote Estuary (Roper, Simons and Jones 1983). Larvae may pass through a maximum of 5 stages but only 2 stages are essential for development.

Kingsford & Choat (1985) recorded large numbers of megalopae, attributed to the genus "*Petrolisthes*", beneath clumps of drifting algae off the coast of Leigh in December. The occurrence of floating algae and its pattern of movement will clearly have an effect on recruitment to local populations.

Behaviour

See *P.elongatus* for discussion of courtship and mating of related species.

Ecology

Snapper (*Chrysophrys auratus*) and trevally (*Caranx lutescens*) from Hauraki Gulf and NW Bay of Plenty eat *P.novaezelandiae* occasionally, 0.2-0.3% of gut volume (Godfriaux 1969,1970a) and red gurnard (*Chelidonichthys kumu*) eat it very rarely (Godfriaux 1970a). Zoeae larvae of *P.novaezelandiae* are eaten by kahawai (*Arripis trutta*) in Wellington harbour (Baker 1971).

References

Bennett (1930, 1932), Greenwood (1965), Roper,Simons and Jones (1983), Thomson (1898), Wear (1964a,1965c).

Petrocheles spinosus Miers, 1876
Spiny False Crab

Synonymy

Petrolisthes (Petrocheles) spinosus Miers, 1876a; *Petrocheles spinosus* Thomson, 1898; Chilton, 1911a; Bennett, 1930; 1932; Batham, 1956; Bennett, 1964; Wear, 1965a; 1966; Hayward, 1974; Fenwick, 1978; Marsden & Fenwick, 1978; Probert et al., 1979.

Type Locality

New Zealand

Distribution

Endemic to New Zealand. Hauraki Gulf, Bay of Plenty, Lyall Bay and southern half of the South Island. Also recorded from Kawerua, between Hokianga and Kaipara Harbours. Larvae have been collected from Spirits Bay, Northland.

Diagnosis (Fig. 9a-b)

Carapace flattened, as wide as long, densely covered with short hairs, lateral margins convex, posterior margin concave. Antero-lateral margins armed with two series of sharp spines curving upwards and forwards. First series of 4-5 small spines (including post-orbital corner) and after slight gap 6-7 more spines, with a larger, dorsally situated spine opposite the first of this second series. Antennae much longer than CL, rostrum strongly deflexed and extending well past eyes which are large and bulbous. Sides of rostrum fringed with about six short, sharp spines directed forwards and upwards, rostral tip narrowly rounded and bearing tiny spinules. Orbital margin first granular and then smooth. Post-orbital corner right-angled. Third maxillipeds large, well developed, setiferous palps and extending as far forward as rostrum. Exposed surfaces finely tomentose, outer margin of carpus with a distal spine. Chelipeds large, carpus, propodus and dactyl flattened and covered with small tubercles. Inner margin of carpus bearing four stout, equidistant spines, upper surface with sharply and irregular granular ridge, outer margin has eight spines. Propodus elongate, lower margin minutely spinulous to tip of fixed finger, outer surface with two rows of granules and another row of granules along upper margin and on to the movable finger. Fingers tapering, inner margins finely granulate, pilose within. First three pairs of legs much shorter than chelipeds, meri flattened; all segments covered with long, dense hairs. Meri with a close row of spines on the upper margin, carpi have four small spines on the upper margin, dactyli with four spines below. Fourth pair of legs shortest and folded against posterolateral corner of carapace and tips inserted under broad abdominal flap. Telson divided into five plates, margins setose.

Colour

Grey with bluish tinge, finger tips reddish, spines ochreous.

Size

Male 9mm CW, 9.5mm CL. Female 12mm CW, 11.5mm CL.

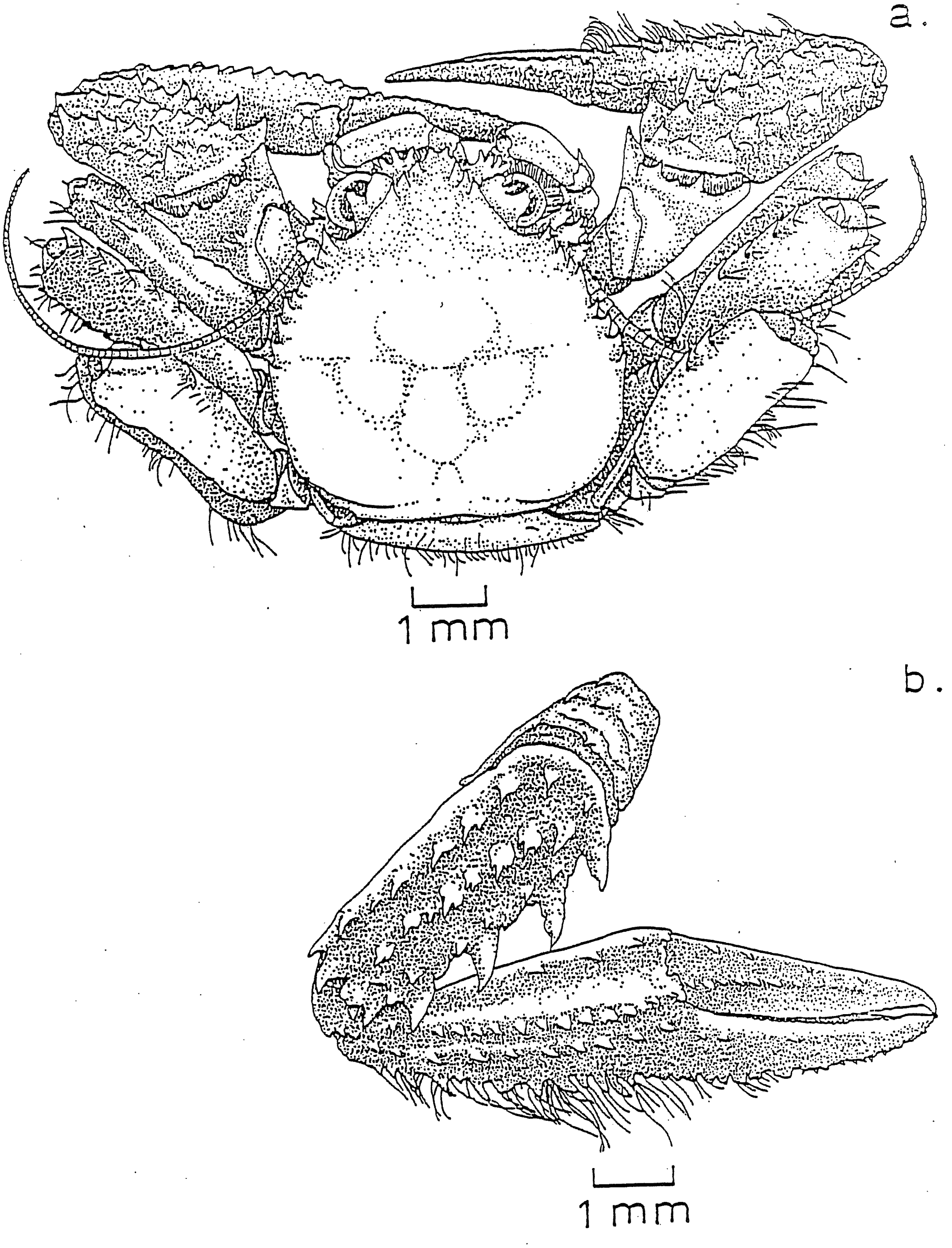


Fig. 9 - <u>Petrocheles</u> <u>spinosus</u>: a - female, dorsal view; b - right chela, female, outer face (by C. Duffy).

Habitat

Sub-littoral on mud, shingle or rock substrate also Lessonia holdfasts. The southern distribution and absence of littoral records from the North Island suggests that P.spinosus is a cold-temperate species restricted to colder water in the north.

Depth

Intertidal-100m.

Breeding

A single ovigerous female has been collected from Halfmoon Bay, Stewart Island in October. This crab (CW 12mm) carried 683 eggs near to hatching when they measured 0.69 x 0.56mm, coloured bright orange. Eggs about to hatch measure 0.78 x 0.63mm. After larval release the ovaries were gravid with immature eggs measuring 0.5 x 0.45mm. This suggests that females produce at least 2 batches of eggs per year. Early stage larva appear in Wellington plankton in late July and by September all 5 stages are present. Larvae persist in the plankton until January but are rare at all times (Wear 1965a).

Development and Growth

Larvae of P.spinosus pass through a prezoea and 5 planktonic stages which have been described by Wear (1965a,1966). The pre-zoeal stage only lasts 30-45 minutes at 16deg C. The zoeal larvae of P.spinosus suggest a close relationship between the Porcellanidae and Galatheidae. The possession of 5 zoeal stages is a galatheid feature and suggests that P.spinosus is closer to the ancestral stock than either of the two Petrolisthes species in New Zealand.

Behaviour

See P.elongatus for discussion of courtship and mating of related species.

Ecology

This crab has been recorded from blue cod (Parapercis colias) stomachs.

References

Bennett (1930,1932,1964), Miers (1876a), Thomson (1898), Wear (1965a,1966).

Petalomera wilsoni (Fulton & Grant, 1902)
Sponge Crab

Synonymy

Cryptodromia lateralis Heller, 1868; Miers, 1876b; Thomson, 1898; Cryptodromia wilsoni Fulton & Grant, 1902; Cryptodromia lateralis Chilton, 1911a; Dromia pseudogibbosa Ihle, 1913; Parisi, 1915; Balss, 1922; Petalomera wilsoni Rathbun, 1923; Hale, 1927; Dromia pseudogibbosa Yokoya, 1933; Petalomera wilsoni Sakai, 1935; 1936b; Barnard, 1946; Petalomera lateralis Richardson, 1949b; Petalomera wilsoni Barnard, 1950; Guiler, 1952; Dell, 1963a; Bennett, 1964; Sakai, 1965; Suzuki & Kurata, 1967; Dell, 1968a; Wear, 1970c; Kim, 1970; Griffin, 1972; Kim, 1973; Sakai, 1976; Wear, 1977; Kensley, 1978; 1981; Kim & Kim, 1982; Wear & Fielder, 1985.

Type Locality

Port Phillip Heads, Victoria, Australia.

Distribution

St. Helena (south Atlantic), South Africa, Australia, New Zealand and Japan. P.wilsoni has one of the widest distributions of any of the dromiid sponge crabs. Within Australia, southern Western Australia, South Australia, Victoria, New South Wales and Tasmania. Within New Zealand from Cape Kari Kari to Kaikoura, Wanganui to Tasman Bay.

Diagnosis (Fig. 10a-f)

Carapace much wider than long (ratio 1.3-1.4), moderately convex, thickly covered with soft, long, areolate pubescence. Rostral area projecting slightly in front of eyes, anterolateral margins rounded, posterolateral margins convergent, posterior margin concave. Median rostral tooth small, acute and projecting as far as lateral rostral teeth. Frontal groove extends backwards separating two protuberances. Lateral rostral teeth continuous with supra-orbital margin which has a strong tooth, external orbital angle not produced and a strong infraorbital tooth present beneath the eye. Three strong anterolateral teeth, last two upwardly directed, and a large posterolateral tooth behind the branchial groove. Chelipeds large, especially in male, merus triangular in cross section, all three borders have small rounded tubercles. Upper border of propodus with three rounded nodules (more evident in male), fingers armed with seven teeth. First pair of legs longer than second, carpi and propodi have nodules at distal end of anterior borders. Inner margins of dactyls have 4-5 small spines. Last two pairs of legs much reduced, fourth pair sub-dorsal. A single propodal spine opposes the dactyl on each of the legs. Telson wider than long, uropod plates visible externally. Female sternal grooves end wide apart between bases of first and second legs.

Colour

A shaggy covering of dark khaki hairs over the entire animal, although these are usually concealed under a piece of sponge or compound ascidian which may be brightly coloured.

Size

CW 70mm.

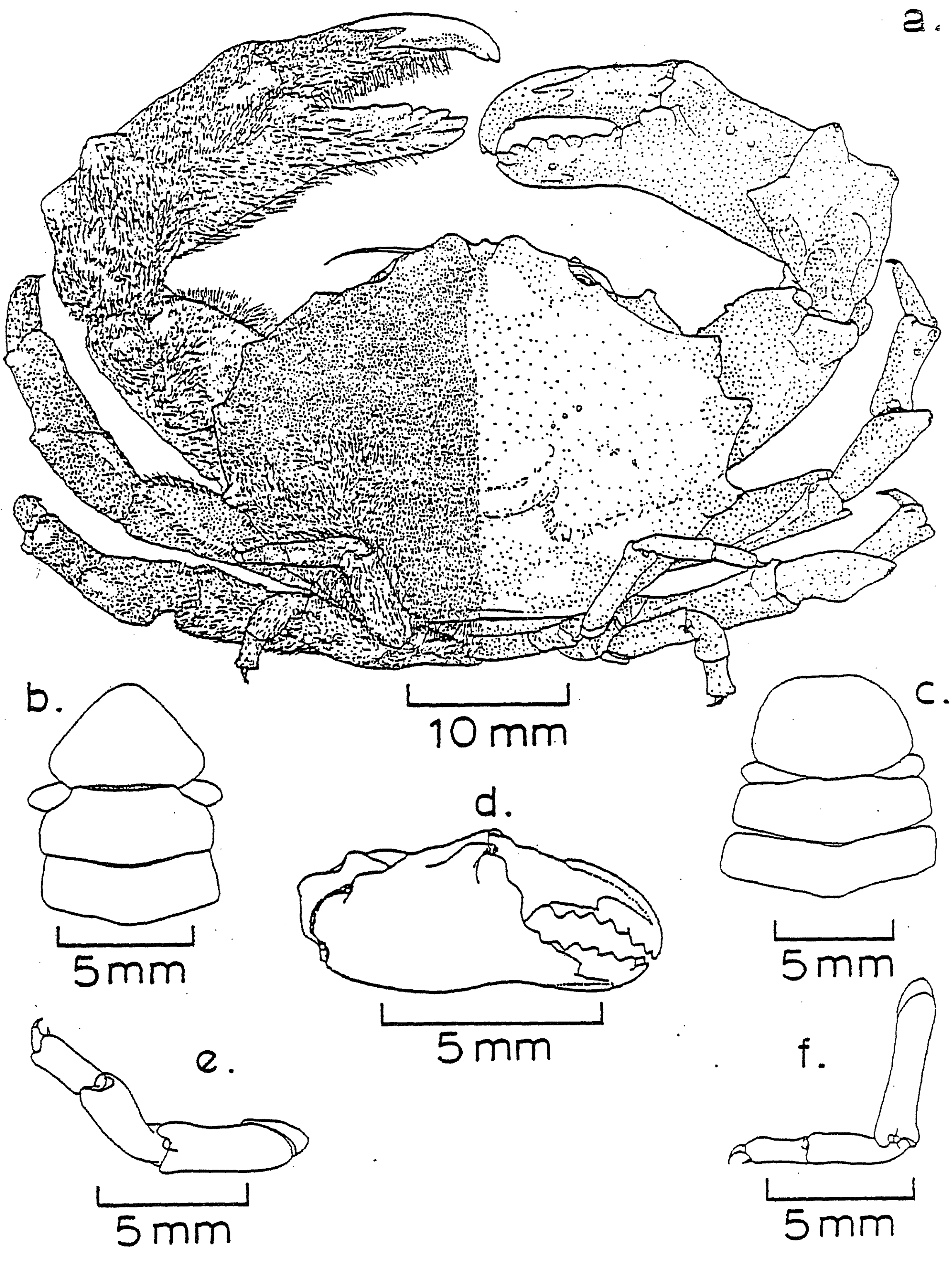


Fig. 10 - *Petalomera wilsoni*: a - male, dorsal view; b - distal segments of male abdomen, ventral view; c - distal segments of female abdomen, ventral view; d - right chela, male, outer face; e - 3rd walking leg; f - 4th walking leg (by J. Black).

Habitat

Low intertidal rock pools, under boulders but more commonly sub-tidal usually associated with sponges and ascidians encrusting hard substrates.

Depth

Intertidal and continental shelf, 0-190m.

Breeding

Ovigerous females have been collected in December to June although larvae occur in Wellington plankton throughout the year. New eggs measure 0.75mm diameter and are deep red in colour, while eggs ready to hatch measure 1.0mm diameter and are light orange.

Dromiid crabs tend to have large eggs but show a wide size range with large-egged species having direct development. Hines (1986) has reviewed the importance of egg size in brachyuran life histories.

Development and Growth

Larvae hatch as a prezoea, followed by 3 or possibly 4 zoeal stages before moulting to the megalopa (Wear 1970c,1977). First zoea hatched from eggs in the laboratory, zoea 2 and megalopa from plankton (Wear & Fielder 1985). Megalopae have been found in _Macrocystis_ holdfasts.

Behaviour

P.wilsoni, like most other dromiid crabs, is a slow-moving, secretive species. It is called a sponge crab because it camouflages itself with a piece of sponge or ascidian, which is carried above the crab by the last 2 pairs of legs. The dactyls of these legs are modified into long spines which grip the sponge or ascidian and 'stretch' it over the carapace. Because the crab lives in close association with these encrusting animals it is well camouflaged. The masking behaviour of _P.wilsoni_ has not been studied but is probably similar to the behaviour of _Cryptodromia hilgendorfi_ (see McLay 1982, 1983). This sponge crab is masked throughout its life (some larger _P.wilsoni_ do not carry a mask) and uses its chelae to cut out the piece of sponge or ascidian, crawls underneath discarding the old cap and then walks off with its new.camouflage. A wide variety of sponges and ascidians are used and these are constantly changed as the crab grows and moves from one 'host' to another. Camouflage changes are always made during the intermoult period and sometimes the same cap is used after moulting. The camouflage prevents visual detection by predators and may also protect the crab because some sponges and ascidians are distasteful to fish predators.

Wicksten (1986) has reviewed carrying behaviour of brachyuran crabs from different families: the Homolidae, Latreillidae, Tymolidae and Dorippidae as well as the Dromiidae all show this behaviour. A variety of objects are carried: shells, pieces of sponge, tunicates, algae, branches of gorgonians or antipatharians, or chips of rock. Except for the Dorippidae all the other families have been classified in the section Podotremata which contains the 'primitive' brachyurans. Wicksten suggests that carrying may well be a conservative behaviour pattern.

Ecology

Snapper (Chrysophrys auratus) from the Hauraki Gulf eat small numbers of P.wilsoni (Godfriaux 1969).

References

Bennett (1964), Dell (1963a,1968a), McLay (1982,1983), Wear (1970c,1977), Wear & Fielder (1985), Wicksten (1986).

Homola orientalis Henderson, 1888

Synonymy

Homola orientalis Henderson, 1888; Homola andamanica Alcock, 1899; Alcock & Anderson, 1899; Homola orientalis Whitelegge, 1900; Homola andamanica Alcock, 1901; Homola orientalis Doflein, 1902; Homola barbata orientalis Doflein, 1904; Balss, 1922; Homola orientalis Rathbun, 1923; Thelxiope orientalis Barnard, 1926; Homola orientalis Sakai, 1936b; Thelxiope orientalis Barnard, 1950; Gordon, 1950; Sakai, 1965; Homola orientalis Campbell, 1971; Serene & Lohavanijaya, 1973; Yaldwyn & Dawson, 1976; Sakai, 1976; Thelxiope orientalis Crosnier, 1976; Homola orientalis Sakai, 1979; Guinot & Richer de Forges, 1981; Wear & Fielder, 1985.

Type Locality

Philippines.

Distribution

Wide-spread Indo-west Pacific : off south-east Africa, Gulf of Aden, Andaman Sea, Indonesia, Philippines, Japan, Australia (southern Queensland to Victoria) and off north-east New Zealand (Bay of Plenty, 37°25.5′S, 176°28.5′E, south-east of Mayor Is.).

Diagnosis (Fig. 11a-d)

Carapace quadrangular, longer than broad, convex with a short bifid rostrum without lateral accessory spines. The eyes are on long stalks and the proximal segment is slender and visible dorsally. Eyes and antennules are not retractile, antennal flagellum is longer than the carapace. The carapace has high, upright lateral walls, anterolateral spines are distinct and at some distance behind the level of the supraorbital spines. Supraorbital spine is short and simple and there is an intermediate spine between rostral and each supraorbital spine. Mouthframe more or less quadrate in shape and there are no obliquely longitudinal grooves on the female sternum. Chelipeds small and pubescent. First three pairs of legs longer, posterior margins of meri armed with spines. Last pair of legs prehensile and subdorsal in position. The dactyl is about half the length of the propodus and is turned back against a series of spines on the propodus.

Colour

Unknown.

Size

A male of 15mm CW, 19mm CL, and female of 21mm CW, 27mm CL have been reported by Serene & Lohavanijaya (1973) but the specimen of Yaldwyn & Dawson (1976) was a female (ovigerous) 27.6mm CW, 35mm CL.

Habitat

The Bay of Plenty specimen was collected in a crayfish pot. Usually found on muddy bottoms.

Depth

Continental shelf and slope, 38-548m.

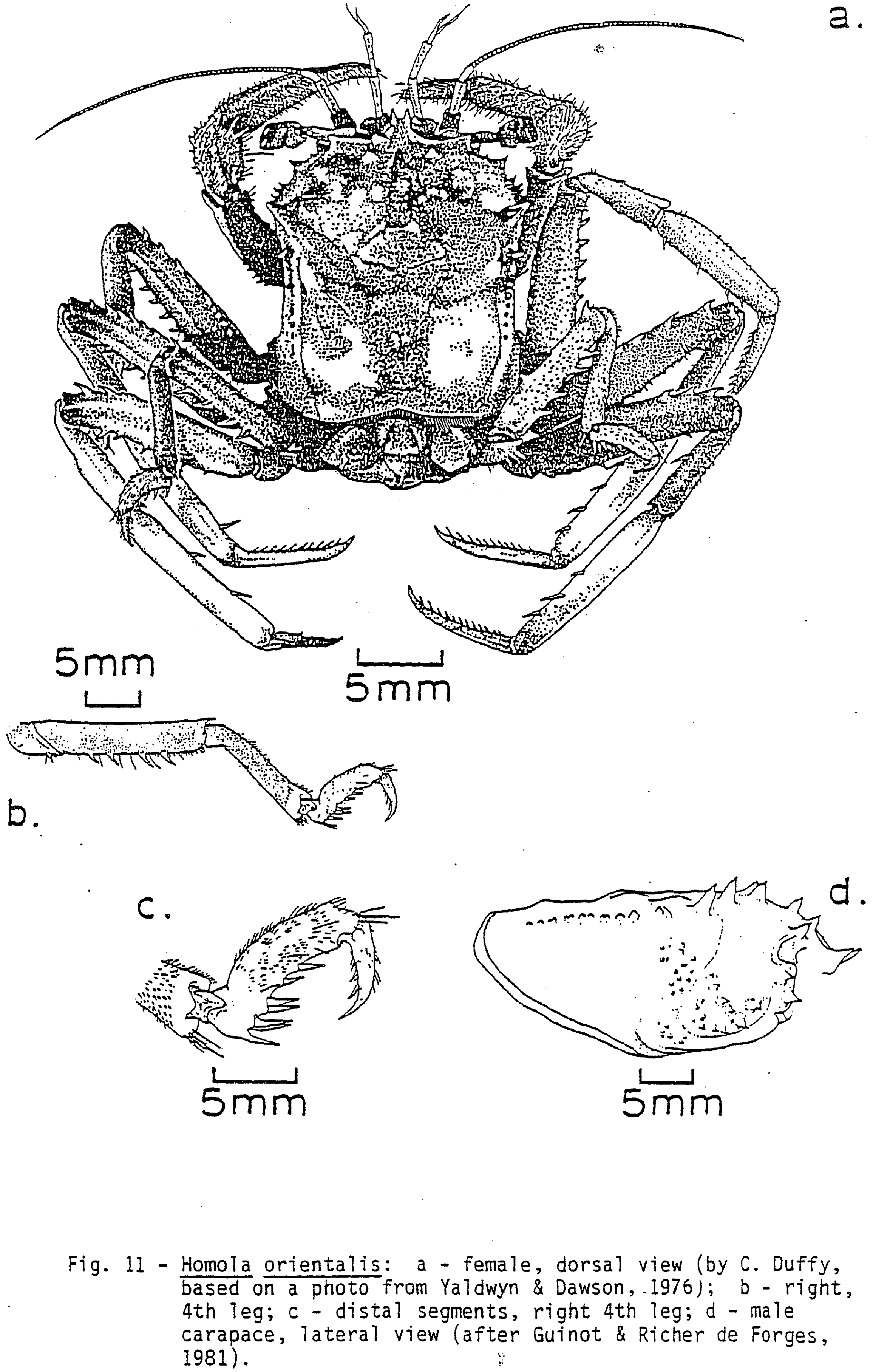


Fig. 11 - *Homola orientalis*: a - female, dorsal view (by C. Duffy, based on a photo from Yaldwyn & Dawson, 1976); b - right, 4th leg; c - distal segments, right 4th leg; d - male carapace, lateral view (after Guinot & Richer de Forges, 1981).

Breeding

Ovigerous female collected in September. Egg size and numbers not recorded.

Development and Growth

Probably 5 or more zoeal stages, only fourth zoea known from plankton (Wear & Fielder 1985).

Behaviour, Ecology

Unknown.

References

Guinot & Richer de Forges (1981), Serene & Lohavanijaya (1973), Wear & Fielder (1985), Yaldwyn & Dawson (1976).

Latreillia australiensis Henderson, 1888

Synonymy

Latreillia australiensis Henderson, 1888; Whitelegge, 1900; Rathbun, 1923; Dell, 1963a; Williamson, 1965; 1967; Dell, 1968a; Campbell, 1971; Serene & Lohavanijaya, 1973; Wear & Fielder, 1985.

Type Locality

Southeastern Australia.

Distribution

Bass Strait to southeast Queensland and northern New Zealand (SE of Poor Knights Islands, off Doubtless Bay, NE of Arid Island, Bay of Plenty).

Diagnosis (Fig. 12a-c)

Carapace much longer than wide, margins converging and strongly produced anteriorly beyond cheliped bases. Rostrum consists of a short, simple spine with very long supraorbital spines on either side. These spines are almost as long as the eyestalks which carry very bulbous eyes. Chelipeds long (2.5 - 3.5 times CL), propodus expanded, fingers long, narrow, distal half occluding. Male movable finger has a small proximal tooth. First three pairs of legs very long, last pair of legs sub-dorsal. Seven abdominal segments in both sexes. Spines on abdominal terga, three or four abdominal segments visible dorsally.

Colour

White or purplish with red markings.

Size

Male 15.3mm CL. Female 19mm CL.

Habitat

Soft mud and sand.

Depth

Outer continental shelf and continental slope, 54-330m.

Breeding

Off New Zealand ovigerous females have been collected in November but off Australia they have been collected in all months. Newly laid eggs are white, 0.3mm diam. and when nearly ready to hatch eggs are transperant, 0.4mm diam. (Wear & Fielder 1985).

Development and Growth

Wear & Fielder (1985) have described the first zoea from laboratory hatched eggs while Williamson (1967) has described a megalopa from Australia which he attributed to L.australiensis.

Behaviour, Ecology

Unknown.

References

Dell (1963a), Rathbun (1923), Serene & Lohavanijaya (1973), Wear & Fielder (1985).

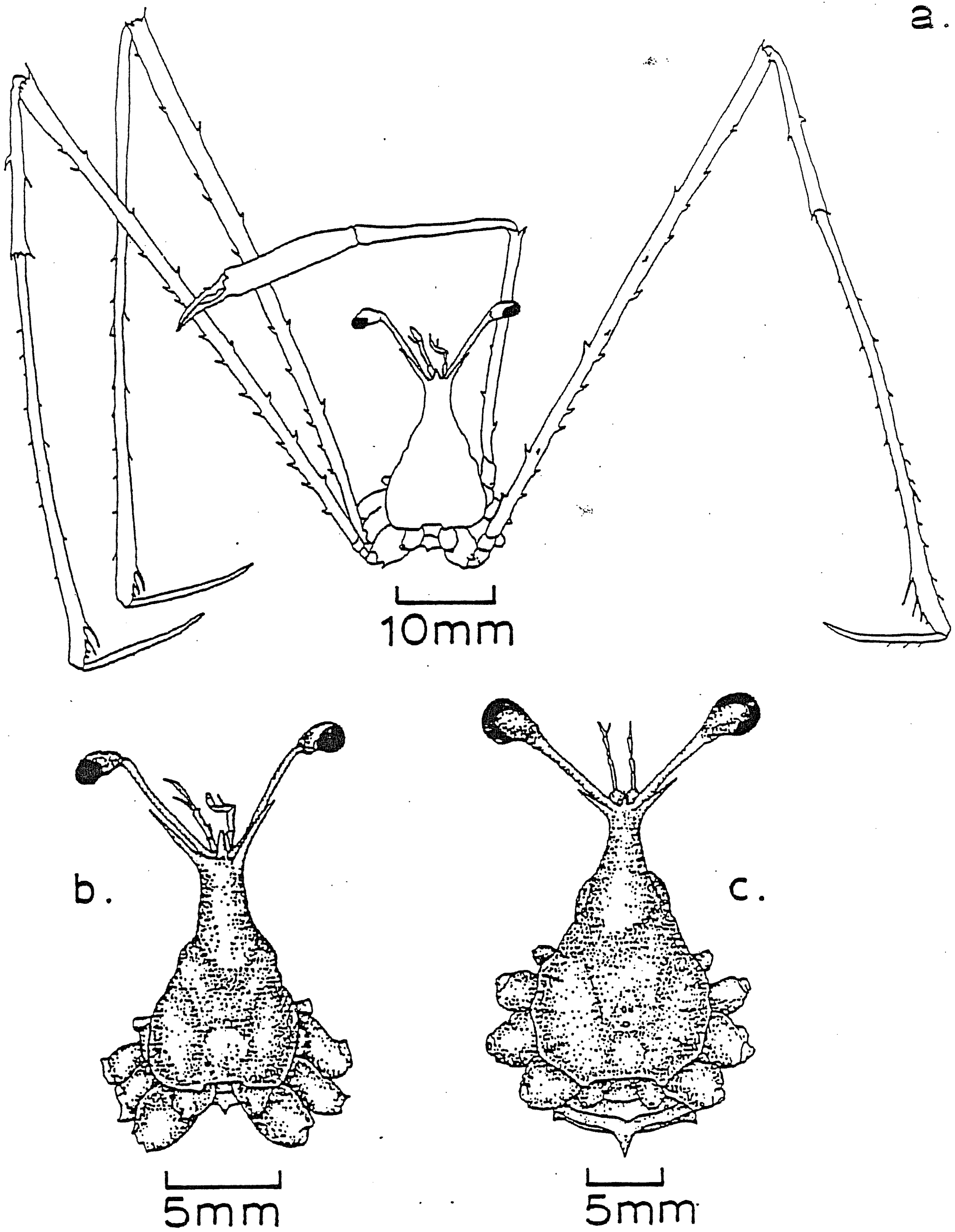


Fig. 12 - *Latrellia australiensis*: a - male, dorsal view; b - carapace of male; c - carapace of female (after Dell, 1963a).

Paromola petterdi (Grant, 1905)
Antlered Crab

Synonymy

Latreillopsis petterdi Grant, 1905; McCullough, 1907; Rathbun, 1923; Hale, 1927; Dell, 1955; 1963a; 1963b; Griffin, 1965; *Paromola petterdi* Williamson, 1965; *Latreillopsis petterdi* Webb, 1972; *Paromola petterdi* Serene & Lohavanijaya, 1973; *Latreillopsis petterdi* Griffin & Brown, 1975;, *Paromola petterdi* Wear & Fielder, 1985.

Type Locality

About 45km east of Sydney Harbour Heads.

Distribution

Southern and southeastern Australia, New Zealand (Cavalli Islands to Banks Peninsula, Fiordland and also the Snares Islands).

Diagnosis (Fig. 13a)

Carapace longer than wide (length 1.2 times width), armed with tubercles and spines, produced in front to form a simple rostrum. There is a prominent antler-like supraorbital spine above each eye, this peculiar structure being branched. They are probably easily broken off in life and may be different in different specimens. Young specimens have numerous sharp spines on the carapace but in other specimens there may be only rounded tubercles. Eyestalks are short and eyes are bulbous and prominent. Behind the eyes is a series of 4-5 short acute spines on the carapace margin. Chelipeds long, merus spinous, propodus generally enlarged in older males, fingers long, pointed and curved inwardly. First three pairs of legs much longer than chelipeds (4 times CW), meri spinous. Last pair of legs sub-dorsal in position and dactyls are sub-chelate. Several segments of the abdomen visible in dorsal view. Median spine or tubercle on segments 1-4 and 6; segments 3, 4 and 6 also bear a spine on each side. Uropods absent from base of telson.

Colour

Greyish white with black eyes, cheliped fingers also black, and deep orange around joints on limbs and on dactyls.

Size

Male 69mm CW, 85mm CL. Female 73mm CW 90mm CL.

Habitat

Soft grey mud. Sometimes caught in deepwater crayfish pots.

Depth

Continental slope, 188-517m.

Breeding

Unknown.

Development and Growth

Williamson (1965) described a megalopa, dredged off Port Hacking NSW, which he attributed to *P.petterdi*. Zoea unknown (Wear & Fielder 1985).

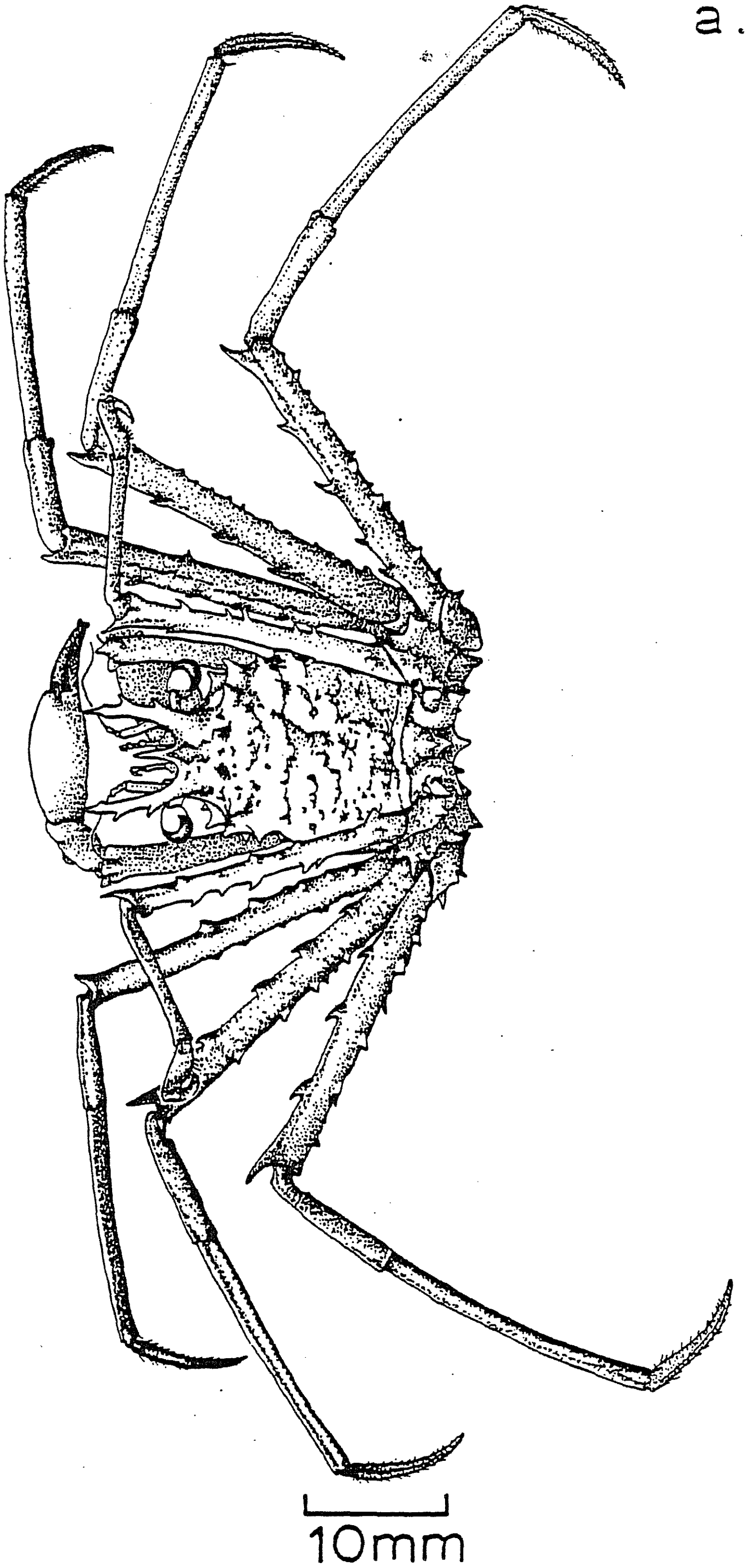


Fig. 13 - Paramola petterdi: a - male, dorsal view (by C. Duffy).

Behaviour

Using its long legs P. petterdi probably holds itself above the soft mud on which it lives.

Using film footage from a submersible Wicksten (1985) has reported that P.japonica off the Hawaiian Is. use the sub-chelate last pair of legs to carry pieces of sponges, antipatharians or gorgonians over the carapace but value of this behaviour remains obscure. It could be anti-predatory or perhaps food-carrying. (See also Wicksten 1986 for discussion of brachyuran carrying behaviour.)

Ecology

Habib (1975) found that red cod (Pseudophycis bacchus) from Banks Peninsula ate small quantities of P.petterdi, March (0.5% of gut volume), May (1.1%) and October (0.8%).

References

Bennett (1964), Dell (1955,1963a,1963b), Griffin & Brown (1975), Hale (1927), Serene & Lohavanijaya (1973), Wear & Fielder (1985), Webb (1972), Wicksten (1986).

Paromola spinimana Griffin 1965

Synonymy

Paromola spinimana Griffin, 1965; Dell, 1968a; Serene & Lohavanijaya, 1973; Wear & Fielder, 1985(list).

Type Locality

Off North East Island, Three Kings, 92m.

Distribution

Known only from the type locality.

Diagnosis (Fig. 14a-c)

Carapace urn-shaped, convex, longer than wide, anterior and lateral surfaces armed with coarse, conical, sharply pointed spines, largest anteriorly. Medial rostral spine sharp, simple, dorsally weakly concave with a longitudinal groove basally. Supraorbital, infraorbital and anterolateral spines as long as medial spine. Eye-stalks relatively short, not obvious in dorsal view. Chelipeds very long (almost four times carapace length), moderately stout, coarsely spinose, fingers carinate on inner edges, inwardly curved and ending in a sharp 'hook'. Legs also very long, compressed, dactyls of first three pairs long and weakly tapering with spinules along ventral edge. Fourth pair of legs shorter, dactyl sub-chelate. Abdomen of seven segments.

Colour

Carapace and legs uniform bright orange, fingers black.

Size

Male 41mm CW (excluding spines), 53mm CL.

Habitat

Continental shelf.

Depth

Continental shelf, 92m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Griffin (1965), Serene & Lohavanijaya (1973).

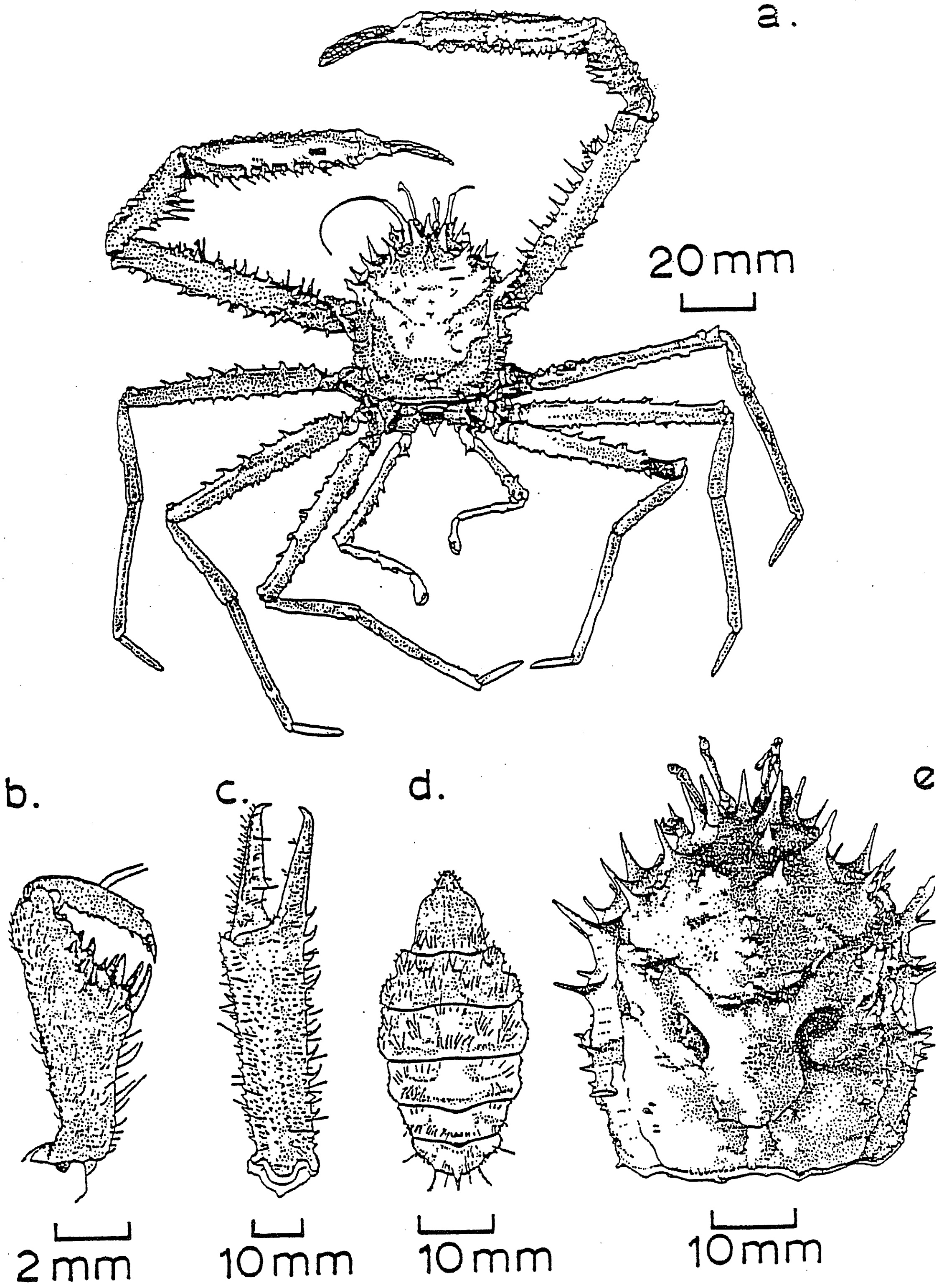


Fig. 14 - Paramola spinimana: a - male, dorsal view (by C. Duffy, based on a photo from Griffin, 1965); b - distal segments of right 4th leg; c - right chela, male, outer face; d - male abdomen, ventral view (after Griffin, 1965); e - detail of male carapace, dorsal view (by C. Duffy, based on a photo from Griffin, 1965).

Lyreidus tridentatus De Haan, 1841
Harp Crab

Synonymy

Lyreidus tridentatus De Haan, 1841; Lyreidus elongatus Miers, 1879b; Lyreidus tridentatus Haswell, 1882a; Wood-Mason, 1887; Henderson, 1888; Ortmann, 1892; Whitelegge, 1900; Doflein, 1902; Chilton, 1906a; Parisi, 1914; Balss, 1922; Yokoya, 1933; Lyreidus australiensis Ward, 1933; Lyreidus tridentatus Sakai, 1934; 1936b; Miyake, 1936; Sakai, 1937; Lyreidus australiensis Richardson & Krefft, 1949; Lyreidus tridentatus Powell, 1949; McNeill, 1953; Dell, 1955; Utinomi, 1958; Dell, 1963a; 1963b; Lyreidus fossor Bennett, 1964; Lyreidus tridentatus Tinker, 1965; Williamson, 1965; Dell, 1968a; Griffin, 1970; Hartnoll, 1979; Wear & Fielder, 1985; Feldmann, 1986.

Type Locality

Japan.

Distribution

Western Pacific : southeastern and western Japan, South China Sea near Hong Kong, central and southeastern coast of Australia, Fiji, New Caledonia, northern New Zealand. Central Pacific Ocean : Hawaii. Eastern Indian Ocean : southwestern coast of Australia. New Zealand distribution is whole of North Island and Cape Campbell at the northern tip of the South Island. Habib (1975) recorded L.tridentatus from stomachs of red cod (Pseudophycis bacchus) captured off Banks Peninsula.

Griffin (1970) has provided a key to the five recent species of Lyreidus.

Diagnosis (Fig. 15a-e)

Carapace much longer than wide, anterolateral margins gradually convergent, frontal width one-third of CW or more. Strongly convex from side to side and weakly convex from front to back, surface smooth and polished, regions undefined. Rostrum is a subacute spine, external orbital spine strong, divergent, no longer than rostrum. Single lateral carapace spine short to moderately long, straight or weakly curved. Chelipeds short, spinous, fingers almost at right angles to palm, minutely dentate, gaping and tips crossed. First two pairs of legs shorter than chelipeds, dactyls long and narrowly triangular. Third legs shorter, dactyls expanded close to base. Fourth pair of legs also short, sub-dorsal, dactyls expanded and triangular. Abdomen of six segments plus telson in both sexes. First four abdominal segments visible dorsally, third and fourth segments bearing spines. Penultimate segment winged and locking with processes on the bases of the first legs. Last segment rounded and very small.

Colour

Not recorded.

Size

Male 29.8mm CW, 49.5mm CL. Female 28.7mm CW, 47.9mm CL.

Habitat

Mud, muddy sand, mud and shell.

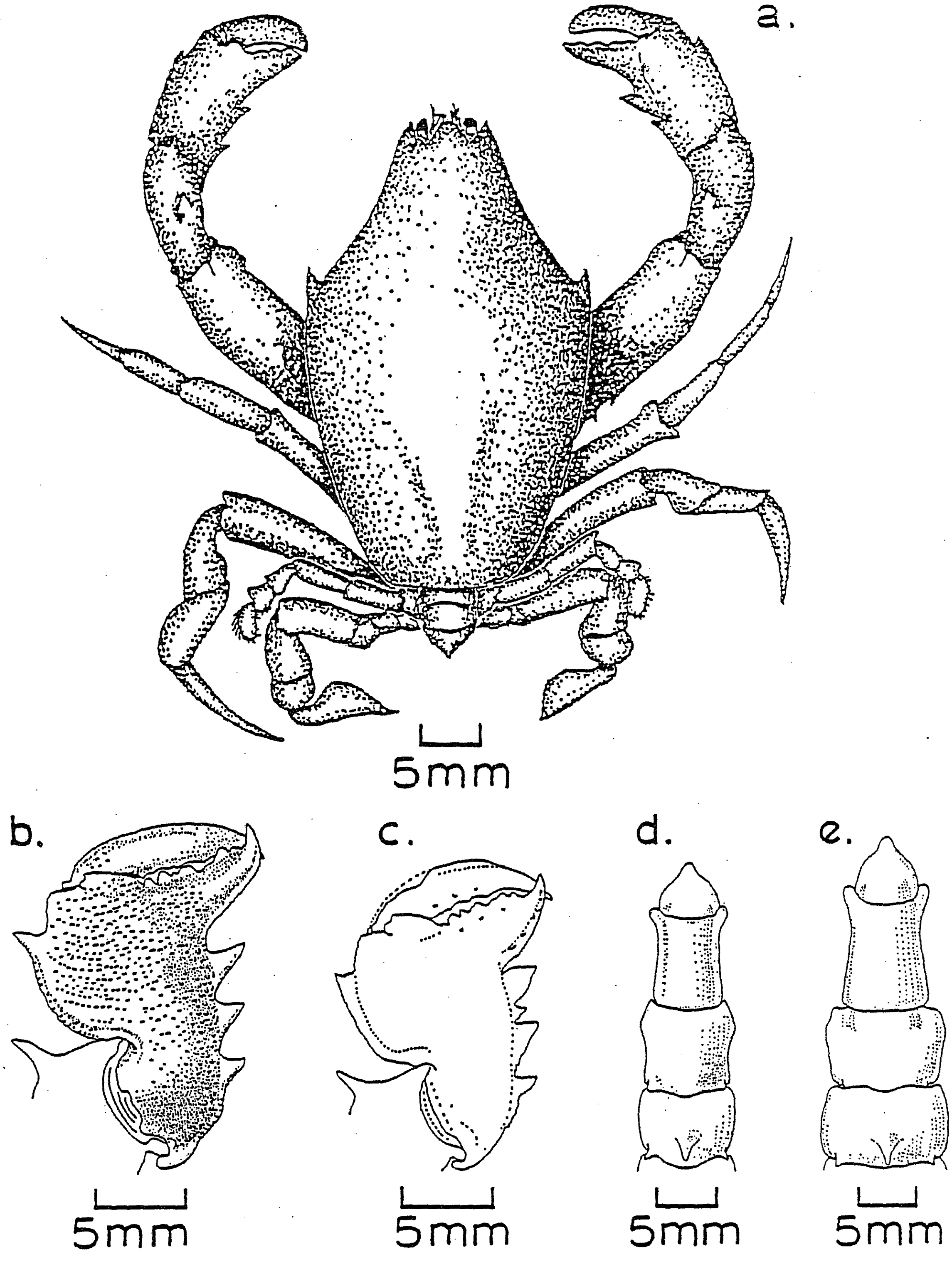


Fig. 15 - Lyreidus tridentatus: a - male, dorsal view (after Dell, 1963); b - right chela, male, outer face; c - right chela, female, outer face; d - distal segments of abdomen, male; e - distal segments of abdomen, female (after Griffin, 1970).

Depth

Continental shelf and slope, 27-382m.

Breeding

An ovigerous female of unspecified CW, collected in December with approx. 1000 eggs (diameter 0.5mm) was recorded by Bennett (1964). Newly laid eggs are bright orange to red 0.47-0.5mm diam., ready to hatch, red, 0.6-0.65mm.

The Brachyura consist of both primitive and advanced forms and the morphology of the female reproductive system is an important criterion in separating these forms. In the primitive Brachyura the oviducts open on the coxa of the second walking leg and the spermathecae are separate integumental pouches which have no internal connection with the oviducts. In the advanced Brachyura oviducts open on the sternum and spermathecae are enlargements of these oviducts. Hartnoll (1979) showed that L.tridentatus females have paired rather than single spermathecae close to the coxal oviduct openings confirming the Raninidae as the most advanced of the primitive Brachyura. In these crabs there is no possibility of trans-moult sperm retention and re-mating must follow female moulting to ensure egg fertilization.

Development and Growth

Probably 6 zoeal stages, zoea 1 (Wear & Fielder 1985), zoeae 2-6 (Williamson 1965) and megalopa (Wear & Fielder 1985). Chace & Barnish (1976) and Kidd & Rice (1986) have recorded swarms of Atlantic raninid megalopae in the eastern Caribbean but similar swarms have not yet been recorded off New Zealand.

Some aspects of relative growth have been investigated by Griffin (1970) but nothing in his investigation is useful for detecting changes in relative growth during adult maturation.

Behaviour

L.tridentatus lives on soft bottoms and escapes predators by burrowing, with only the rostral area showing. The legs and carapace are well adapted for burrowing and it is probable that this species has a reversed respiratory current.

Ecology

This crab is preyed upon by sharks (Mustelus sp.). Snapper (Chrysophyrs auratus) from the Hauraki Gulf eat small numbers of L.tridentatus (Godfriaux 1969), but in the Western Bay of Plenty this crab makes up 2.1% of snapper gut volume (Godfriaux 1974b). Also tarakihi (Cheilodactylus macropterus) from this area eat (0.5%) this crab. Habib (1975) found L.tridentatus in stomachs of Banks Peninsula red cod (Pseudophycis bacchus) in March (0.4%).

Two fossil species have been described from the South Island: L.waitakiensis from middle to late Eocene rocks and another undescribed species from the late Eocene (Glaessner 1980), and L.elegans (Glaessner 1960). L.elegans may have been the ancestor of L.tridentatus.

References

Bennett (1964), Bourne (1922), Dell (1963a), Griffin (1970), Powell (1949), Wear & Fielder (1985).

Cymonomus bathamae Dell, 1971

Synonymy

Cymonomus bathamae Dell, 1971; Wear & Batham, 1975; Chapman, 1977; Probert et al., 1979; Wear & Fielder, 1985.

Type Locality

Off Otago Peninsula, Papanui Canyon, 45°51'S, 170°02'E, 732m.

Distribution

Off Otago coast, Chatham Rise.

Diagnosis (Fig. 16a-d)

Carapace quadrate, as wide as long, slightly swollen posteriorly (more so in female). Surface finely granular, regions not distinct except for deep furrows marking lateral borders of cardiac area. Rostrum well developed, shorter than eyestalks, narrowly triangular, sides ornamented by granules or scales. Front straight and produced into prominent post-orbital teeth. Eyestalks narrowly tapering, armed with strong, blunt spines, no visible cornea although cornea area is smooth and polished. Eyestalks solidly fixed in position, from two to three times the length of the rostrum. Antennae and antennules long and prominent. Basal joint of antenna stout, shorter than eyestalks. Second segment of antennules extending well beyond the eyes. Antero-lateral border of carapace begins behind post-orbital tooth and forms almost a right-angle, margin granular. No antero-lateral teeth, borders slightly divergent, posterior carapace border distinctly concave. Chelipeds well developed, granulate, propodus deep in male, much narrower in female, fingers relatively short in male, more elongate in female. First two pairs of legs longer than chelipeds, granulate, dactyls especially long and slightly curved. Last two pairs of legs reduced, sub-dorsal, similar in length, directed forwards. Abdomen consists of only five segments, ovate in both sexes, narrower in male. Female abdomen projects posteriorly, telson triangular. No uropods and only three pairs of pleopods in female.

Colour

Unknown.

Size

Male 3.8mm CW, 4mm CL. Female 5.0mm, 4.9mm.

Habitat

Fine, grey mud, over edge of continental shelf, in association with sponges, molluscs and echinoderms.

Depth

200-800m.

Breeding

Ovigerous females have been collected in November, January and May. Dell (1971) recorded females of CW 4.0-5.0mm with 12, 14, 17, 19, 21 & 23 eggs up to 1.4mm diameter. In May Wear &

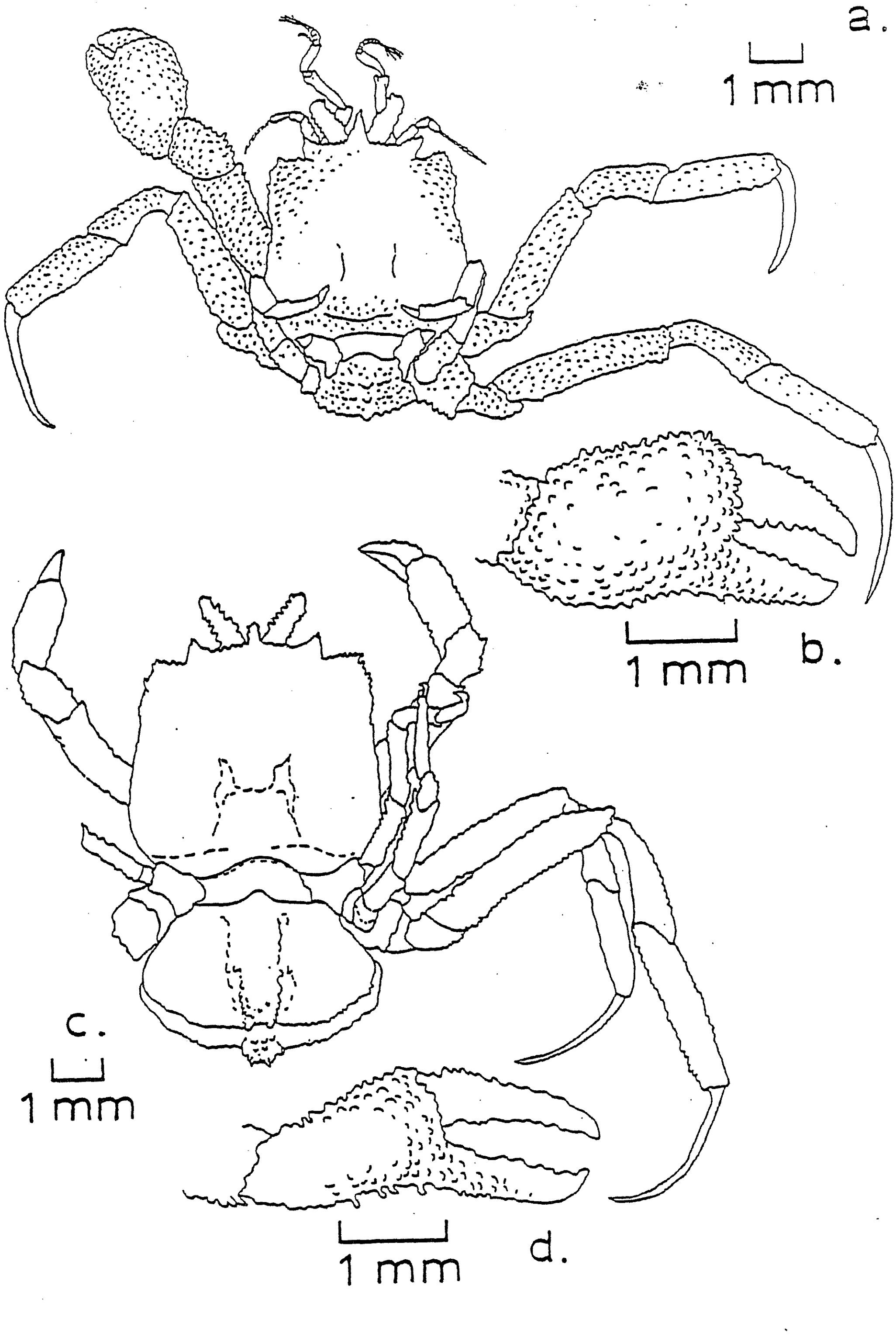


Fig. 16 - Cymonomus bathamae: a - male, dorsal view; b - right chela, male, outer face; c - female, dorsal view; d - right chela, female, outer face (modified after Dell, 1971).

Batham (1975) recorded one female, CL 5.0mm, carrying 17 eggs close to hatching. The maximum number of eggs carried was 26 by a female 5.1mm CL. Eggs, freshly laid, measure 1.2 x 1.0mm, with orange yolk and when ready to hatch they measure 1.4mm diameter.

Development and Growth

At least one and possibly two zoeal stages, which are weak swimmers, followed by the megalopa. Development abbreviated, larvae possess primitive characters (especially the telson) which suggest close relationship to the Raninidae and Homolidae (Rice, 1980).

Behaviour

Chapman (1977) has examined the structure of the sessile eyes of C.bathamae. Although the eyes lack corneal facets the corneal region is only relatively slightly smaller than corneas of shore-dwelling crabs. There are no crystalline cones and the rhabdomes vary in size and are irregular in shape and number of constituent rhabdomeres. Rhabdomes are arranged parallel to the eyestalk axis so that illumination from above passes through the sides of the rhabdomes instead of passing lengthwise as is usual with compound eyes. The eyes lack any lens system or tapetum and only have photoreceptors. Thus image formation is impossible. The exact role of the eyes in C.bathamae has not been established because experiments have not been performed on live crabs.

It is not clear whether the reduced and modified last two pairs of legs are used for carrying camouflage material.

Ecology

Unknown.

References

Dell (1971), Gordon (1963), Rice (1980), Wear & Batham (1975).

Cymonomus aequilonius Dell, 1971

Synonymy

Cynonomus aequilonius Dell, 1971; Wear & Fielder, 1985 (list).

Type Locality

N.E. of Mayor Island, Bay of Plenty, 37°10′S, 176°23.5′E, 731m.

Distribution

Known only from the type locality.

Diagnosis (Fig. 17a-d)

Carapace quadrate, as wide as long, wider posteriorly, surface with fine rounded granules, some fine hairs especially near the margins. Regions not distinctly marked except for cardiac. Rostrum well developed, longer than eyestalks, narrowly triangular, sides ornamented with granules. Front straight and becoming small, post-orbital teeth. Eyestalks tapering, armed with spines and scales especially along inner margins, no marked cornea. Eyestalks solidly fixed, a little more than two-thirds the length of the rostrum. Antennae and antennules well developed, basal joint of antennae almost as long as eyestalks, second segment of antennule extending beyond the eyestalks. Antero-lateral margins of carapace begins behind post-orbital tooth and forms almost a right-angle, margin granular. No antero-lateral teeth, margins slightly convex, posterior carapace border concave. Chelipeds well developed, granulate, fingers of female especially elongate. First two pairs of legs longer than chelipeds, granulate, dactyls especially long and slightly curved. Last two pairs of legs, reduced, sub-dorsal, similar in length, directed forwards. Abdomen consists of only five segments, no uropods and only three pairs of pleopods in female. Female abdomen projects posteriorly, telson triangular.

Colour

Unknown.

Size

Female 7.0mm CW, 7.0mm CL (including rostrum).

Habitat

Muddy bottoms over edge of continental shelf.

Depth

731m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Dell (1971).

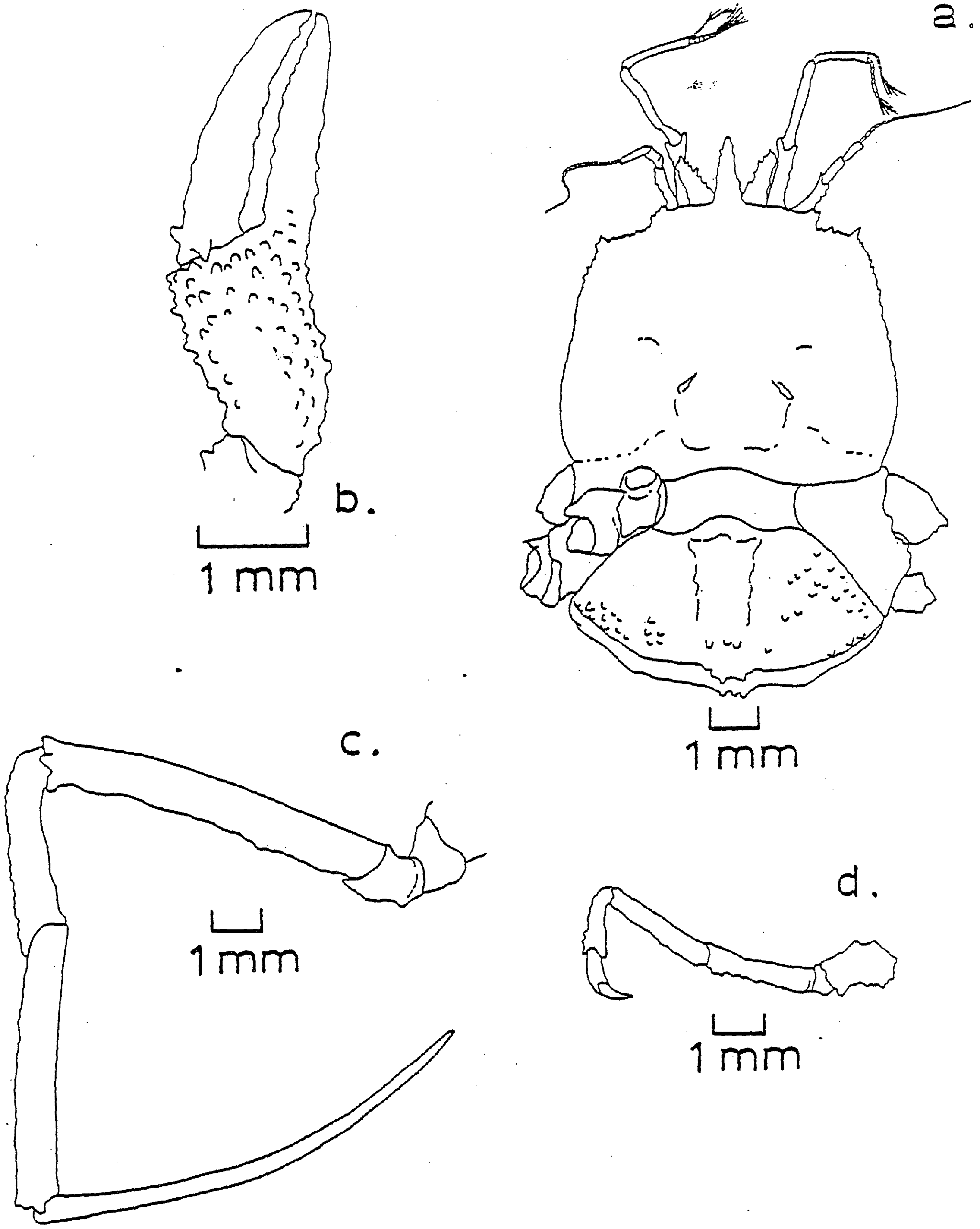


Fig. 17 - *Cymonomus aequilonius*: a - body, female, dorsal view; b - right chela, female, outer face; c - left, 2nd walking leg; d - left, 3rd walking leg (modified after Dell, 1971).

Ebalia laevis (Bell, 1855)
Nut Crab

Synonymy

Phlyxia laevis Bell, 1855; Miers, 1876b; Phlyxia tumefacta Kirk, 1878; Phlyxia laevis Filhol, 1886; Phlyxia cheesemani Filhol, 1886; Ebalia laevis Miers, 1886; Chilton, 1906a; 1911a; Young, 1929; Richardson, 1949b; Ebalia tumefacta Richardson, 1949b; Ebalia cheesemani Richardson, 1949b; Dell, 1960; Ebalia laevis Dell, 1963a; Bennett, 1964; Dell, 1968a; Takeda & Miyake, 1969; Wear & Fielder, 1985.

Type Locality

New Zealand.

Distribution

Endemic to New Zealand. Little Barrier Is. to Stewart Is., Wanganui to Dusky Sound and also Chatham Islands.

Diagnosis (Fig. 18a-c)

Carapace as wide as long, granulated regions well marked, less prominently swollen in female than in male. Branchial region much swollen, separated from cardiac and posterior gastric regions by a broad depression. Front concave in dorsal view with a median linear groove, orbit minute, circular, with two sutures above. Anterolateral margin with two concavities, a single lateral, conical tooth. Posterolateral margins sharply convergent and posterior margin with three projections : these are highly variable and more prominent in males but usually consist of a median cardiac projection which is longest and a marginal pair. Chelipeds very long, granular all over, fingers long, fixed finger inclined, small sharp denticles on both fingers, gape narrow, nearly half length of fingers. Chelipeds of female shorter, fingers without gape. Legs also granular, decreasing in length from first to last pair, dactylus straight and smooth. Tip of male abdomen acutely rounded, female abdomen broader and with three fused distal sutures.

Colour

Uniformly whitish-grey with pink or orange tinges. Cheliped fingers, carpi and distal ends of meri of legs pale orange.

Size

Male and female 20mm CW.

Habitat

Sand, shell, Bryozoa and sand.

Depth

Continental shelf and slope, 18-373m.

Breeding

Ovigerous females have been collected December-January also May and August. Newly laid eggs are light orange, 0.38mm diam. Schembri (1982) found that in Ebalia tuberosa, off Scotland, females attain sexual maturity at 11-12mm CL and mate in November, both sexes being hard-shelled and eggs are laid soon

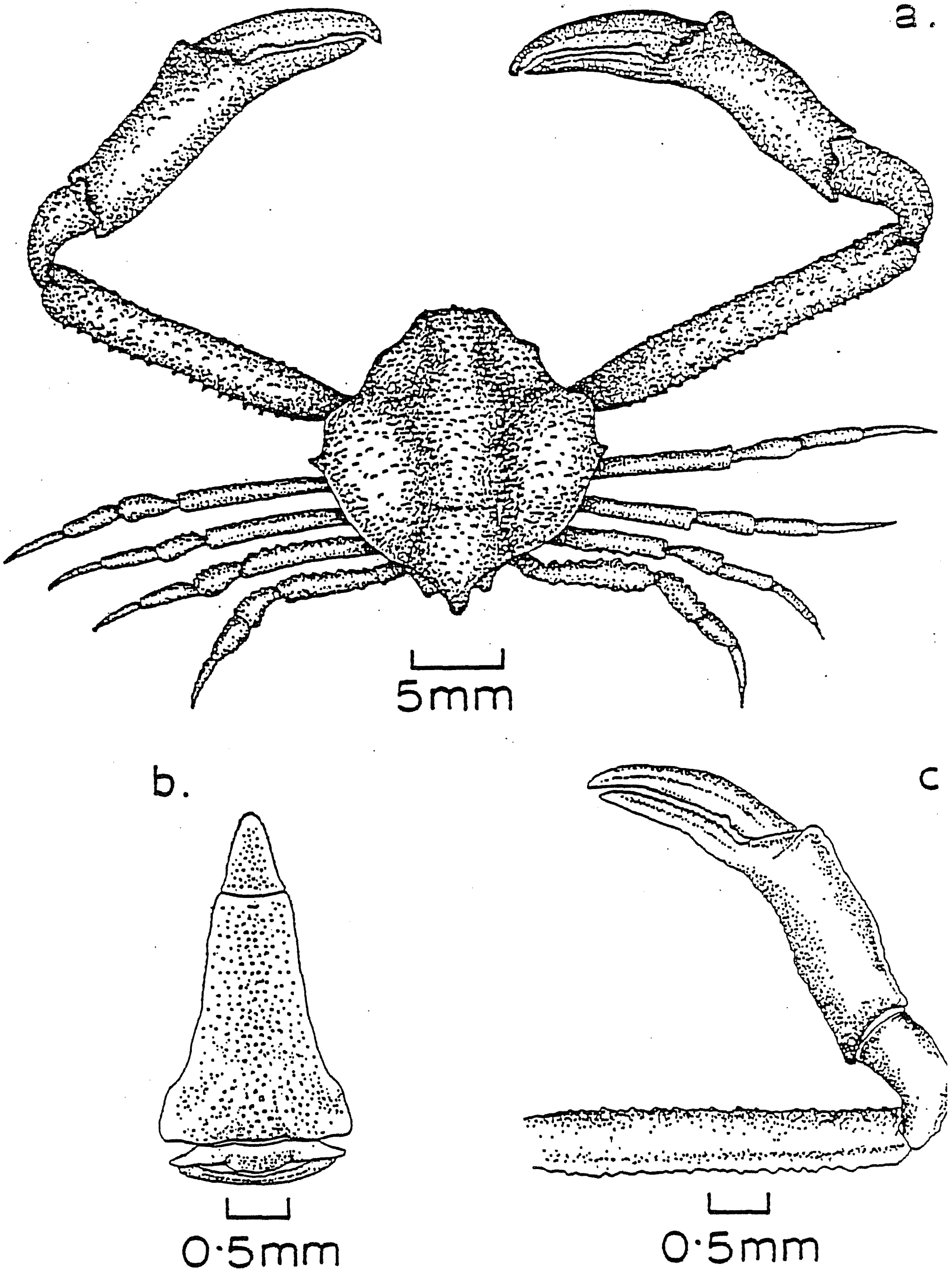


Fig. 18 - *Ebalia laevis*: a - male, dorsal view (after Dell, 1963); b - male abdomen, ventral view (after Takeda & Miyake, 1969); c - left chela, male, outer face (by J. Black).

afterwards and incubated for 7-8 months over winter. In June hatching begins and larvae appear in the plankton. A 12mm CL female carries about 1000 eggs and a 16mm female about 3000 eggs. This pattern may also be true for E.laevis. Egg size is approx. the same as E.laevis and females only produce a single brood each year.

Development and Growth

Four zoeal stages (Wear & Fielder 1985), megalopa unknown. Zoeae often found in inshore plankton samples at or near the bottom. Quintana (1986) has described megalopae of some Japanese leucosiids.

Schembri (1982) observed that moulting in E.tuberosa was restricted to late July-early September i.e. warmer months. Males above 9.5mm CL and females above 11.0mm did not moult and probably have terminal anecdysis. These crabs survive for at least two years. Females grow to a larger size than males and while small crabs (7mm CL) have moult increments of around 30%, large females grow about 20% but males only grow about 10%. The population structure did not show any seasonal progression of modes and appeared static. However, the combined size-frequency data suggest a population dominated by large, old individuals and the presence of three or possibly four classes. The sex ratio, 1.14 females:1 male was significantly different from 1:1.

Behaviour

E.laevis burrows in sandy substrates. Crabs back into the sand using the legs till about half buried and then alternately use each long cheliped to pull scoops of sand over the rest of the carapace till only the cheliped tips are visible. A 15mm CW crab buried in about 60sec. This burying behaviour is similar to that of E.tuberosa reported by Schembri (1981a) which remains in one spot for long periods (Schembri, 1981b). E.laevis is extremely sluggish in its movements and easily handled.

With E.tuberosa the male is the active partner in courtship and mating which occurs when both sexes are hard-shelled. The copulating pair may partly bury themselves in sediment or remain on the surface. They may remain in copula for up to 9 hours (Schembri, 1983).

Ecology

Sometimes recorded in large numbers in dredge samples and frequently preyed upon by fish. Young (1929) found E.laevis in blue cod (Parapercis colias) stomachs from the Chatham Islands. Snapper (Chrysophrys auratus) from the Hauraki Gulf and Bay Of Plenty eat E.laevis, 1.5-6.2% of gut volume (Godfriaux 1969), trevally (Caranx lutescens), 0.3%, red gurnard (Chelidonichthys kumu), 2.2%, eagle ray (Holorhinus tenuicaudatus), 0.9% (Godfriaux 1970a) and tarakihi (C.macropterus), 2.1% (Godfriaux 1974a). Red cod (Pseudophycis bacchus) from Banks Peninsula in October also ate (0.5%) this crab (Habib 1975).

References

Bennett (1964), Dell (1963a), Schembri (1979a, 1979b, 1981a, 1981b, 1982, 1983), Wear & Fielder (1985).

Merocryptus lambriformis A. Milne Edwards, 1873
Rough Nut Crab

Synonymy

Merocryptus lambriformis A.Milne Edwards, 1873; Miers, 1886; Whitelegge, 1900; Balss, 1922; Rathbun, 1923; Hale, 1927; Ebalia rugulosa Yokoya, 1933; Merocryptus lambriformis Sakai, 1935; 1937; Serene, 1955; Bennett, 1964; Sakai, 1965; Dell, 1968a; Campbell, 1971; Wear & Fielder, 1985 (list).

Type Locality

Upolu Is., Samoa.

Distribution

Japan to Samoa, Australia and New Zealand. Within Australia from the Great Australian Bight, Bass Strait, Port Hacking, Crowdy Head and Queensland. Within New Zealand Little Barrier Is., off Patea, South Taranaki.

Diagnosis (Fig. 19a-c)

Carapace somewhat rhomboidal, wider than long (ratio 1.25), covered in bead-like granules, very convex and uneven behind the bilobed rostrum. Two conical, forwardly directed gastric tubercles, and a large cardiac tubercle. Two small spines on margins behind hepatic region. Branchial region has a stout, laterally directed process. Posterior margins bearing two projections which are most prominent in young males. Chelipeds well developed, densely tuberculated, propodus short and inflated, finger s long slender and curved inward. Legs shorter than chelipeds, covered in bead-like granules, some granules are sagittate in shape.

Colour

Not recorded.

Size

Male 14.3mm CW,10.8mm CL. Female 19.3mm CW,14.8mm CL.

Habitat

Rough bottom with sand and shell.

Depth

40-219m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Bennett (1964), Campbell (1971), Dell (1968a), Hale (1927), Rathbun (1923).

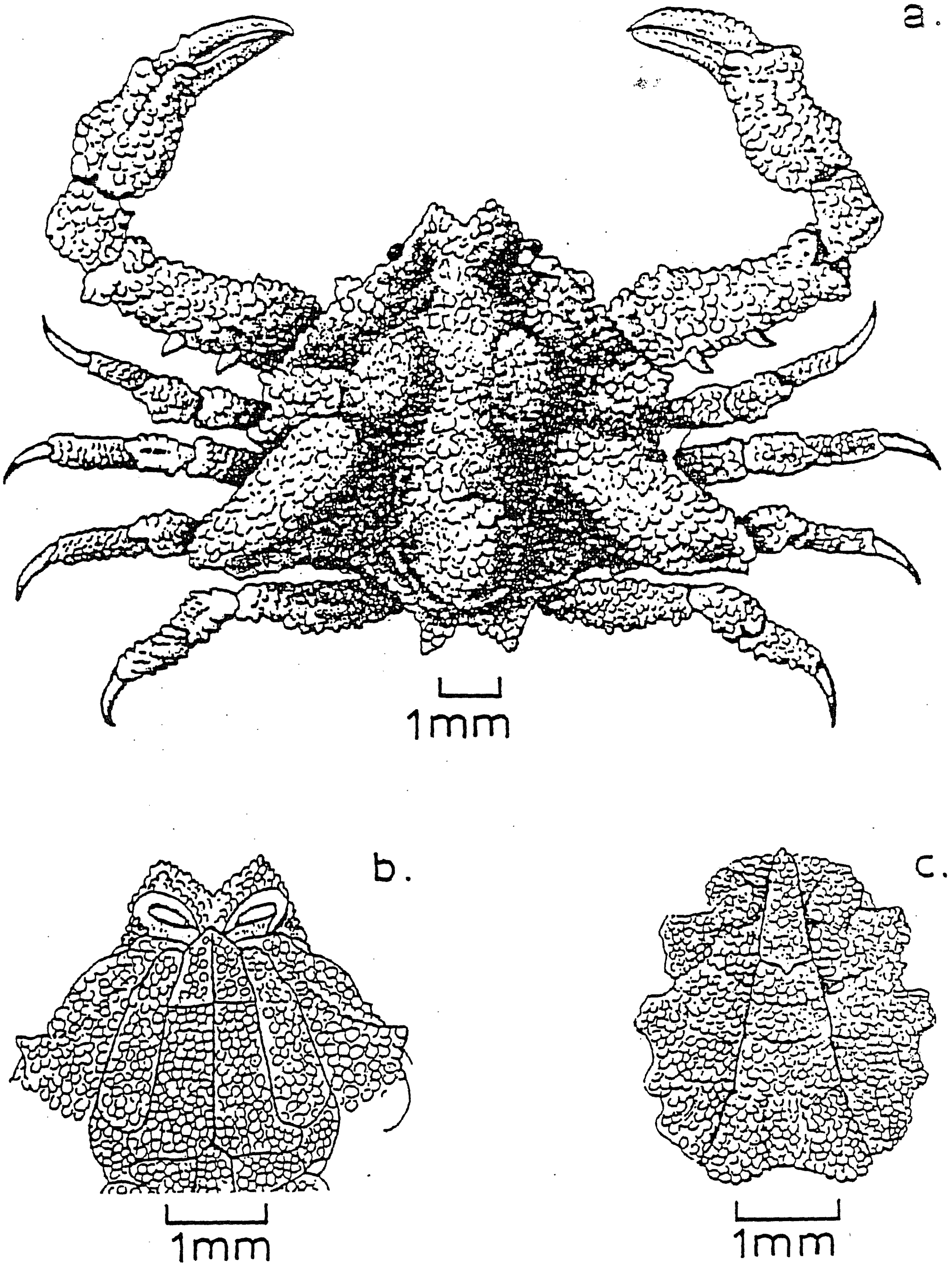


Fig. 19 - *Merocryptus lambriformis*: a - male, dorsal view; b - anterior end, ventral view; c - male abdomen, ventral view (after Milne Edwards, 1873).

Randallia pustulosa Wood-Mason, 1891
Purse Crab

Synonymy

Randallia pustulosa Wood-Mason, 1891; 1892; Alcock, 1896; 1899; Doflein, 1904; Ihle, 1918; Yaldwyn & Dawson, 1976; Wear & Fielder, 1985 (list).

Type Locality

Indian waters.

Distribution

Indo-west Pacific, off East Africa, Arabian Sea (Laccadive Sea), Bay of Bengal (Andaman Sea), Indonesia (Strait of Macassar) and northern New Zealand.

Diagnosis (Fig. 20a)

Carapace globular, strongly convex, circular in outline, granulate, regions defined by grooves. Mouth-frame anteriorly prolonged and orbits dorsally emarginate with two clefts. Lateral margins of carapace with three or four pronounced tubercles and the posterior margin has a pair of lobes on either side of a conspicuous intestinal spine. Chelipeds very long (about twice CL) and slender, evenly and finely tuberculate. Propodus not inflated, fingers long and curved and not gaping. Legs short and slender, finely tuberculate, dactyls pubescent with a dense brush of setae laterally.

Colour

White when preserved.

Size

Male 42mm CL, female 43mm CL.

Habitat

Deep water mud and sand.

Depth

Deep water on the continental slope 402-977m.

Breeding

One ovigerous female has been collected in December.

Development and Growth

Unknown.

Behaviour

Unknown for this species but other species in this family commonly bury themselves with only the eyes exposed above the substrate. Some species feign death when disturbed.

Ecology

Unknown, but related species with long, finely toothed fingers capture small fish and crustaceans.

References

Yaldwyn & Dawson (1976).

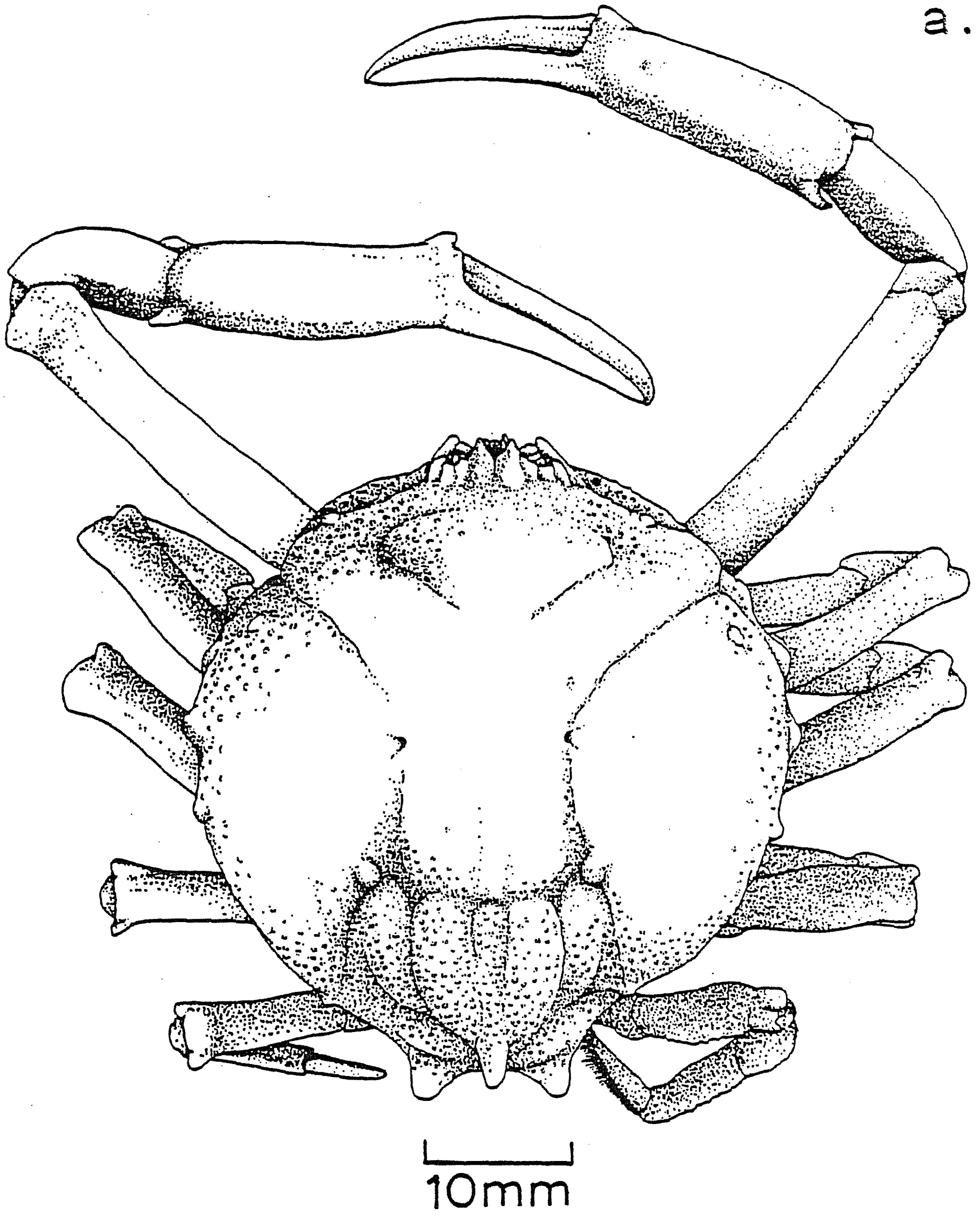


Fig. 20 - Randallia pustulosa: a - female, dorsal view (by C. Duffy, based on a photo from Yaldwyn & Dawson, 1976).

Eurynome bituberculata Griffin, 1964

Synonymy

Griffin, 1964; 1966a; Griffin & Tranter, 1986a (key).

Type Locality

Off Glen Burn (East Wairarapa Coast, North Island), in 200m.

Distribution

North Cape, lower half of North Island, Cape Egmont to Cape Palliser.

Diagnosis (Fig. 21a-e)

Carapace pyriform, surface setose, bearing flat-topped tubercles, flattened lobes and short conical spines. Almost uniformly convex in profile. Tubercles irregularly crenulate and arranged in groups separated by wide smooth areas. Rostrum of two, short, flattened truncate lobes. Orbit consisting of supraorbital eave, intercalated spine and postorbital lobe, the three closely approximated. Orbit completed below by basal antennal article and infraorbital plate. Lateral margins of carapace with three prominent, triangular, flattened lobes, one postorbital, one hepatic and one branchial at the widest part of the carapace. A fourth, branchial lobe, situated subdorsally behind marginal lobe and surrounded by flat-topped tubercles. Chelipeds very long, slender, subcylindrical, covered by numerous blunt tubercles. Merus very long, fingers acute, weekly toothed, down-turned. Legs short, cylindrical, covered by short, blunt tubercles. Abdomen of six segments in both sexes.

Colour

Pale pink with white tubercles when preserved.

Size

Male 8mm CW, CL 11.5mm. Female 8.5mm CW, 11.5mm CL.

Habitat

On bottoms with sponges and on muddy sand with broken shell.

Depth

Lower continental shelf, 80 to 280m.

Breeding

Ovigerous females have been collected in September and March (Wear & Fielder, 1985).

Development and Growth

Unknown, but probably two zoeal stages (Wear & Fielder, 1985).

Behaviour & Ecology

Unknown.

References

Griffin (1964, 1966a), Wear & Fielder (1985).

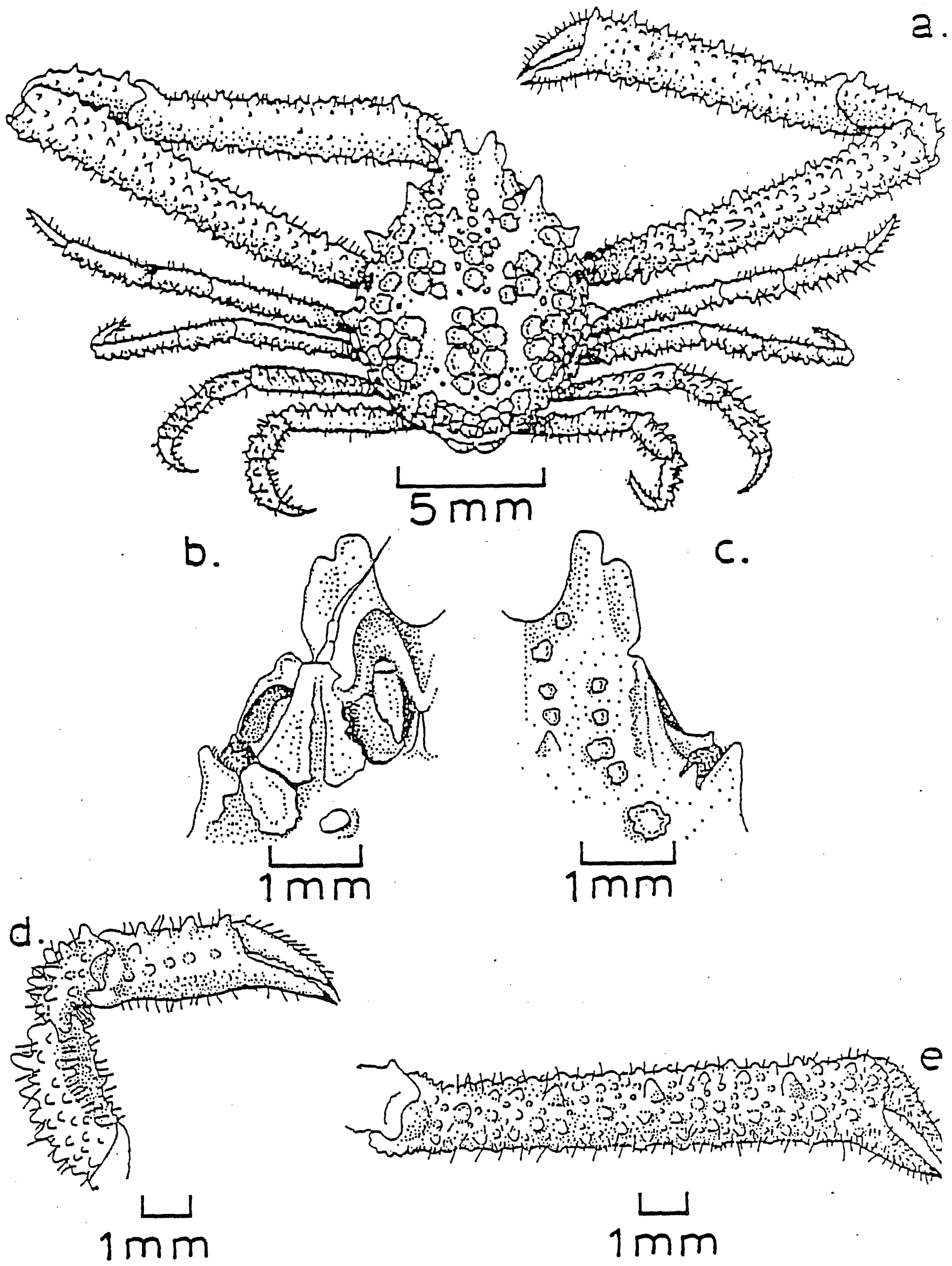


Fig. 21 - Eurynome bituberculata: a - male, dorsal view; b - ventral view of orbit; c - dorsal view of orbit; d - right cheliped, female, outer face; e - right chela, male, outer face (after Griffin, 1966).

Cyrtomaia lamellata Rathbun, 1906

Synonymy

Cyrtomaia lamellata Rathbun, 1906; _Echinomaia hispida_ Borradaile, 1916; Chilton & Bennett, 1929; _Cyrtomaia hispida_ Balss, 1929; Ihle & Ihle-Landenberg, 1931; _Cyrtomaia platypes_ Yokoya, 1933; Sakai, 1938; _Echinomaia hispida_ Richardson, 1949b; _Cyrtomaia hispida_ Bennett, 1964; Griffin, 1966a; Dell, 1968a; _Cyrtomaia platypes_ Takeda & Miyake, 1969; _Cyrtomaia hispida_ Serene & Lohavanijaya, 1973; Griffin & Brown, 1976; Sakai, 1976; _Cyrtomaia platypes_ Takeda & Kurata, 1976; _Cyrtomaia lamellata_ Guinot & Richer de Forges, 1982; _Cyrtomaia hispida_ Guinot & Richer de Forges, 1982; Wear & Fielder, 1985; _Cyrtomaia lamellata_ Griffin & Tranter, 1986a.

Type Locality

Hawaiian Islands.

Distribution

Japan, Ryukyu Is., Ogasawara Is., Timor, New Caledonia, Hawaii, New Zealand (Three Kings Islands, off North Cape and east of Papanui Inlet, Otago).

The 17 species of _Cyrtomaia_ have been reviewed and keyed by Griffin & Tranter (1986a).

Diagnosis (Fig. 22a-d)

Carapace subcircular, slightly broader than long, swollen in profile, margins armed with a few spines and numerous spinules. Rostrum of three short, slender, sharply pointed, hooked spines. Dorsal surface of carapace with a single medial urogastric spine and a pair of prominent submedial cardiac spines. Carapace surface otherwise bearing numerous small tubercles. Eyestalks exposed, ornamented, post-orbital spine strong. Hepatic margin with a single spine. Branchial region also with a single long spine and a row of about 15 spinules along anterolateral part of branchial margin. Chelipeds moderately long (slightly more than twice CL), bearing sharp spines. Fingers moderately gaping for their entire length, irregularly toothed along inner edges. Legs long and armed with spines. Propodus and dactyl of first leg with long spines which intersect when dactyl is folded back. This prehensile arrangement may be involved in prey capture (Guinot & Richer de Forges 1982). Abdomen of six segments plus telson. The first segment with a sharp medial spine and the second with a pair of lateral spines on each side and a single medial spine. Margin of telson broadly rounded .

Colour

Unknown.

Size

Male 16.9mm CW, 15.5mm CL. Female (ovigerous) 15mm CW, 13.7mm CL. Smallest ovigerous female 11.5mm CL.

Habitat

Associated with bryozoa and shell together with sponges, hydroids, gorgonian and soft corals.

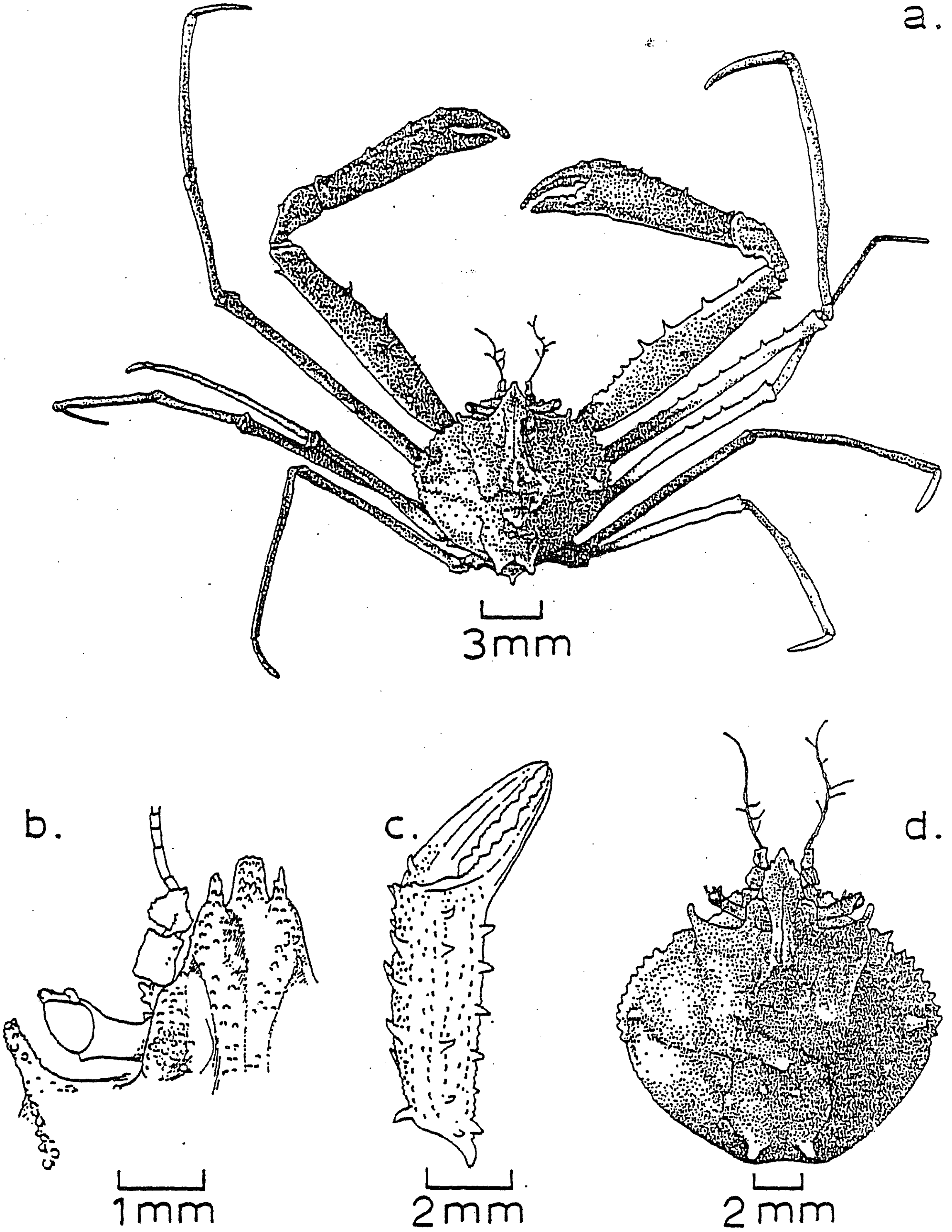


Fig. 22 - Cyrtomaia lamellata: a - male, dorsal view (by C. Duffy, based on a photo from Guinot & Richer de Forges, 1982); b - orbit, dorsal view (after Guinot & Richer de Forges, 1982); c - right chela, male, outer face (after Bennett, 1964); d - detail of carapace, male, dorsal view (by C. Duffy, based on a photo from Guinot & Richer de Forges, 1982).

Depth

Off-shore on continental shelf 70-216m.

Breeding

Ovigerous females have been collected in January and February from SE of Three Kings Island. Newly laid eggs are red, 0.63mm diam and eggs ready to hatch are 0.72mm.

Development and Growth

Two zoeal stages (Wear & Fielder 1985). Megalopa unknown.

Behaviour, Ecology

Unknown.

References

Bennett (1964), Griffin (1966a), Griffin & Tranter (1986a), Guinot & Richer de Forges (1982), Sakai (1976), Wear & Fielder (1985).

Platymaia maoria Dell, 1963

Synonymy

Platymaia maoria Dell, 1963b; Griffin, 1966a; Dell, 1968a; Serene & Lohavanijaya, 1973; Guinot & Richer de Forges, 1985; Wear & Fielder, 1985 (list); Griffin & Tranter, 1986a.

Type Locality

ENE of Poor Knights Is., 555-618m.

Distribution

Eastern Australia and New Zealand (East-North-East of Poor Knights Islands, North of Cape Brett, North-East of Cavalli Islands, Challenger Plateau 168°23′E, 38°41.1′S).

Six species of Platymaia have been reviewed and keyed by Griffin & Tranter (1986a) who note that another species (intensely spinous) from Australia and New Zealand remains to be described. Guinot & Richer de Forges (1985) provide a key to 9 species of Platymaia with some differences from Griffin & Tranter.

Diagnosis (Fig. 23a-d)

Carapace subcircular, irregularly granular with sparse spines. Rostrum consisting of a single spine (about twice as long as lateral spines) which curves upward. Lateral rostral spines extending obliquely upwards. All three spines long, narrow and tapering. Carapace with three mesogastric spines, a single central metagastric spine, two cardiac spines, a single epibranchial spine and several smaller mesobranchial spines. Margins of carapace with two prominent hepatic spines, five medium branchial spines and a single prominent spine on the posterolateral margin. Chelipeds long (less than twice CL), spinous (especially propodi), fingers acute, dactyl with three short spines above, and cutting edges with strong, rounded teeth. Legs very long (first pair 4.4 times CL) and spinous (especially on first pair). Abdomen of six segments plus telson in both sexes.

Colour

Dull white-greyish when preserved. Tips of dactyli brown, tips of all spines pinkish.

Size

Male 60mm CW, 60mm CL. Smallest ovigerous female 51mm CL, 48mm CW.

Habitat

Unknown.

Depth

Deep water 275m-937m.

Breeding

An ovigerous female has been collected in November.

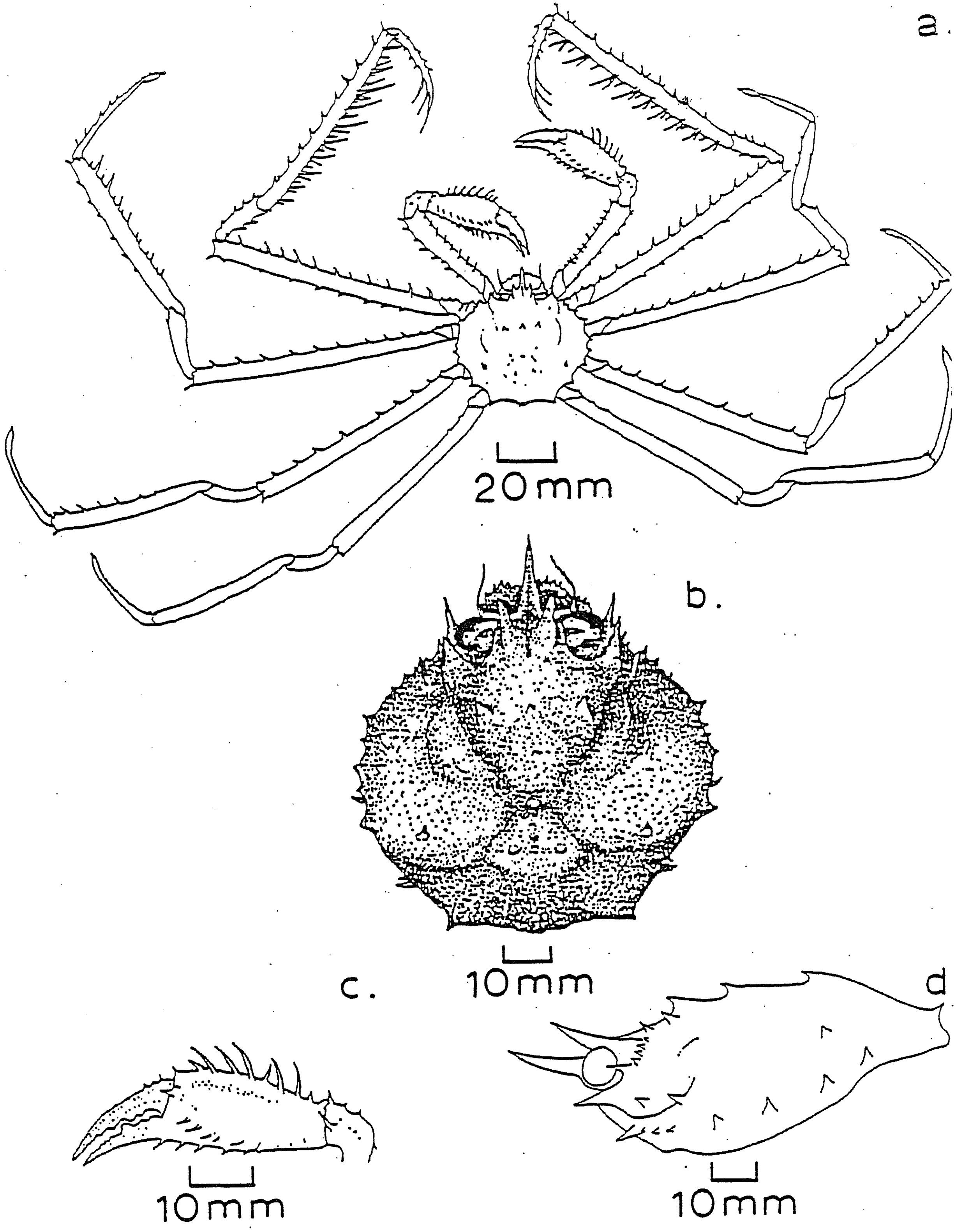


Fig. 23 - Platymaia maoria: a - male, dorsal view; b - detail of carapace; c - right chela, male, inner face; d - carapace, female, lateral view (after Dell, 1963b).

Development and Growth, Behaviour, Ecology

Unknown.

References

Dell (1963b), Griffin & Tranter (1986a).

Pyromaia tuberculata (Lockington, 1877)

Synonymy

Inachus tuberculatus Lockington, 1877; Miers, 1886; Inachoides magdalensis Rathbun, 1893a; Neorhynchus mexicanus Rathbun, 1893a; Dasygyius tuberculatus Rathbun, 1898; Holmes, 1900; Weymouth, 1910; Hilton, 1916; Inachoides tuberculatus Schmitt, 1921; Pyromaia tuberculata Rathbun, 1925; 1926; Collodes granosus Boone, 1930; Pyromaia tuberculata Crane, 1937; Ricketts & Calvin, 1939; Garth, 1948; 1958; Ricketts & Calvin, 1968; Sakai, 1971b; Smith & Carlton, 1975; Sakai, 1976; Morris et al, 1980; Webber & Wear, 1981; Wear & Fielder, 1985.

Type Locality

Mouth of San Diego Bay (type not extant, Rathbun 1925).

Distribution

New Zealand, Orere Point, Firth of Thames, Tamaki Estuary, Auckland. West Coast of North America, San Francisco to Bay of Panama, Sagami Bay, Japan. Probably introduced to Japan and New Zealand as megalopa larvae attached to bottom of ships.

Diagnosis (Fig. 24a)

Carapace pyriform (pear-shaped), convex, finely pubescent, rough with tubercles and spines. A large tubercle, often spiniform, on the mesogastric, cardiac and intestinal regions and sometimes on summit of branchial regions. Rostrum simple, of variable length. Supra-orbital spine usually present, post-orbital tooth large, curving about the extremity of the eye, tip directed nearly forward. Sternum conspicuously granulate or tuberculate, pubescent, deeply grooved between segments, a large tubercle opposite base of each cheliped. A short spiniform tubercle pointing upward and backward on first segment of the abdomen. Chelipeds stout, shorter than first two or three pairs of walking legs. Propodus inflated, sub-globular, sparsely granulate, a longitudinal row of four or five tubercles through middle of proximal end of outer surface. Fingers nearly as long as propodus, triangularly gaping when closed, a large tooth at proximal third of fixed finger. Fingers not gaping in female. Walking legs long, slender, similar, diminishing in length from first to fourth pair, dactyli moderately curved, almost smooth.

Colour

Unknown.

Size

Males 17.7mm CW. Females 15.1mm CW.

Habitat

Under rocks in bays, sub-littoral on protected wharf pilings, often encrusted with sponges and algae. Also on sand and mud.

Depth

Intertidal to 650m.

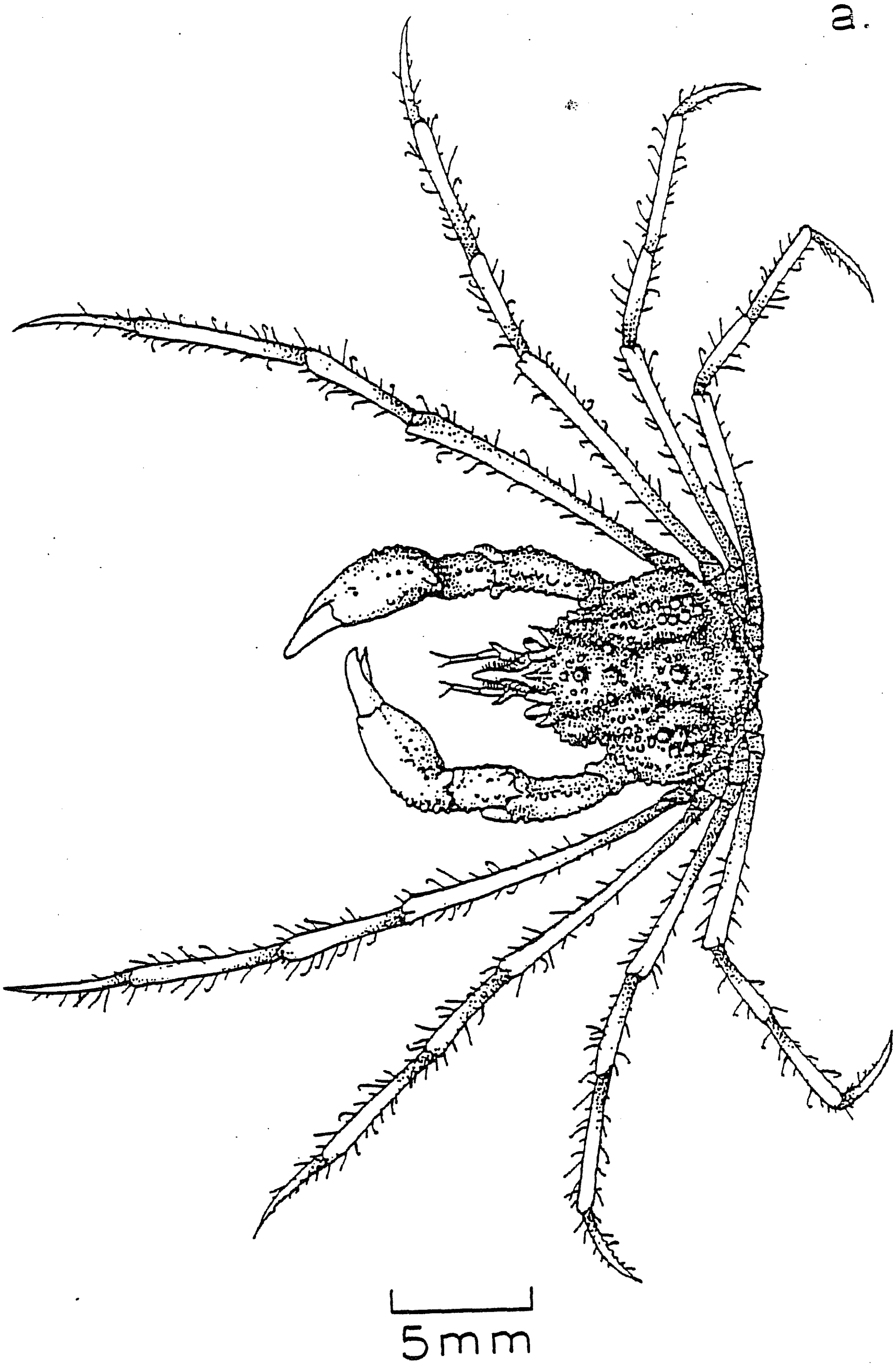


Fig. 24 - Pyromaia tuberculata: a - male, dorsal view (after Sakai, 1971b).

Breeding

In Southern California ovigerous females occur over most of the year with maximum numbers in summer months. In New Zealand ovigerous females have been collected April to August which suggests that this species has not yet modified its breeding pattern since its introduction to the Southern Hemisphere. Eggs are red or orange-red when new and measure 0.6 x 0.5mm when ready to hatch Webber & Wear (1981).

Development and Growth

The first stage zoea larva has been described by Webber and Wear (1981) and the second zoea by Wear & Fielder (1985). Megalopa unknown.

Behaviour

Nothing is known about the behaviour of this species but since it is usually covered by sponges and algae it probably exhibits similar masking behaviour to other spider crabs.

Ecology

Unknown.

References

Garth (1958), Morris, Abbott & Haderlie (1980), Ricketts & Calvin (1968), Sakai (1971b,1976), Schmitt (1921), Smith & Carlton (1975), Wear & Fielder (1985), Webber and Wear (1981).

Achaeopsis ramusculus (Baker, 1906)

Synonymy

Stenorhynchus ramusculus Baker, 1906; Achaeopsis thomsoni Rathbun, 1918c; Achaeopsis ramusculus Hale, 1927b; Griffin, 1966a; Dell, 1968a; Wear & Fielder, 1985(list); Griffin & Tranter, 1986a.

Type Locality

Off Neptune Islands, South Australia coast, 200m.

Distribution

South Australia, New Zealand, N.E. of Mayor Is.

The 4 species of Achaeopsis are reviewed by Griffin & Tranter (1986a).

Diagnosis (Fig. 25a-d)

Carapace broadly pyriform, inflated and weakly convex, margins with several long spines and numerous spinules. Rostrum of two long spines (almost one third of CL) and a few curled hairs above orbit and on dorsal surface. Margins of carapace with 10 prominent spines : 1 supraorbital, 1 postorbital, 4 hepatic and 4 branchial (the last subdorsal), and several spinules. Dorsal surface of carapace with two subequal, slender spines posteriorly. Carapace otherwise smooth and minutely granular. Chelipeds long (slightly longer than carapace in female), spinous, hairy. Fingers acute, curved inwardly at tips, finely denticulate along adjacent inner edges for entire length. Legs long, slender, first pair longest (almost three times CL), following legs decreasing slightly in length. Curled and long hairs scattered along dorsal surfaces of legs. Female abdomen of six segments.

Colour

White after preservation.

Size

Male 9mm CL. Female 6mm CW, 10mm CL.

Habitat

Unknown.

Depth

Deep water 200-800m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Griffin (1966a), Griffin & Tranter (1986a).

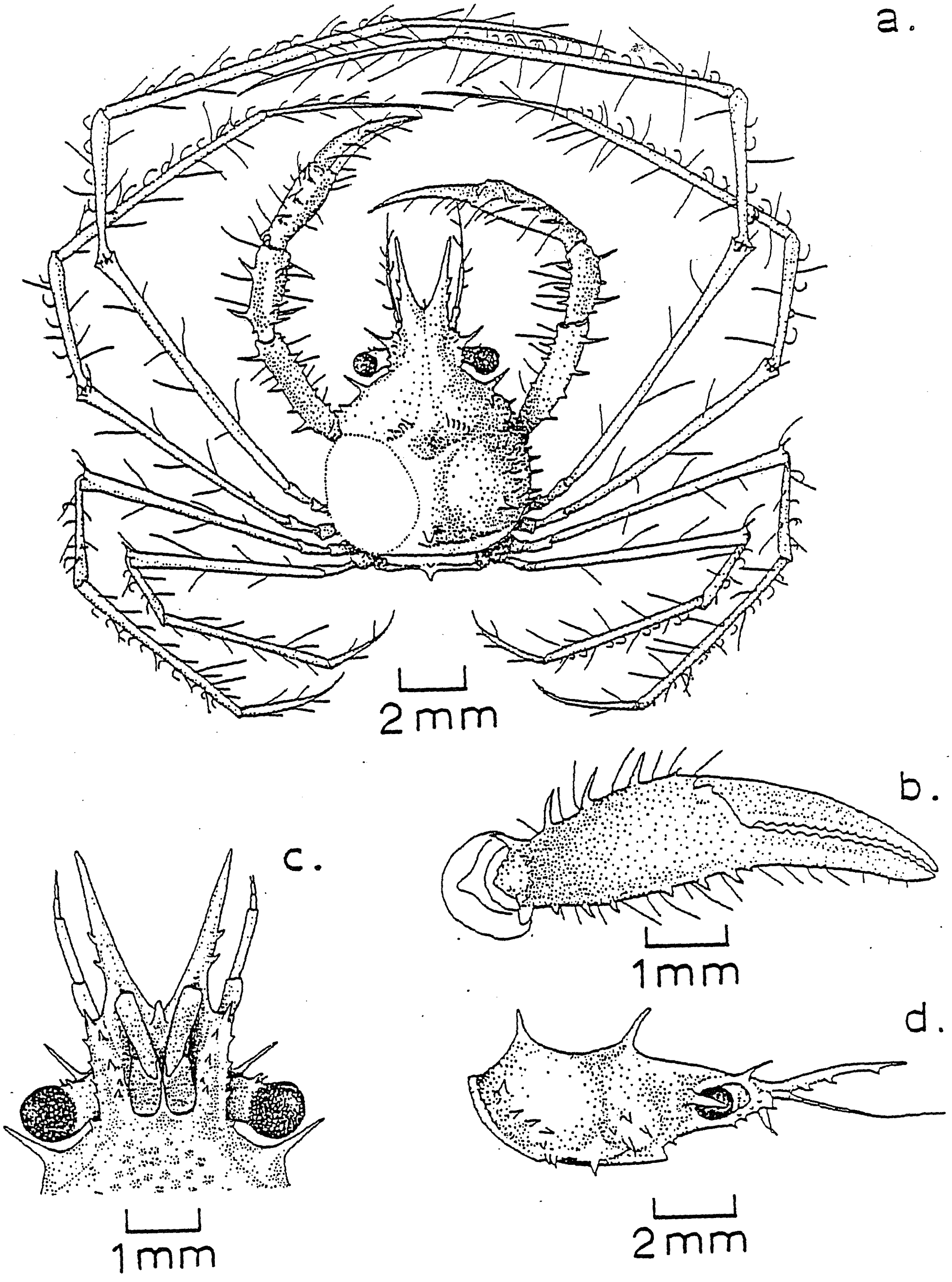


Fig. 25 - Achaeopsis ramusculus: a - female, dorsal view; b - left chela, female; c - anterior end, ventral view; d - carapace, lateral view (after Griffin, 1966).

Achaeus curvirostris (A. Milne Edwards, 1873)

Synonymy

Stenorhynchus curvirostris A. Milne Edwards, 1873; Stenorhynchus fissifrons Haswell, 1879; 1880a; 1880b; 1882a; Achaeopsis fissifrons Miers, 1886; Achaeus tenuicollis Miers, 1886; Whitelegge, 1900; Rathbun, 1918c; Stenorhynchus fissifrons Chilton & Bennett, 1929; Bennett, 1930; Achaeus elongatus Sakai, 1938; Stenorhynchus fissifrons Richardson, 1949b; Achaeus fissifrons Griffin & Yaldwyn, 1965; Griffin, 1966a; Dell, 1968a; Campbell & Stephenson, 1970; Griffin, 1970; Achaeus curvirostris Griffin, 1974; Achaeus fissifrons Wear & Fielder, 1985; Achaeus curvirostris Griffin & Tranter, 1986a.

Type Locality

Bass Strait.

Distribution

Widespread Indo-West Pacific: eastern Africa, Philippine Is., Japan, western and eastern Australia and New Zealand (predominantly northern half of the North Island).

The 27 Indo-West Pacific species of Achaeus are reviewed by Griffin & Tranter (1986a).

Diagnosis (Fig. 26a-c)

Carapace elongate, subtriangular (length 1.3 times width), almost truncate anteriorly, branchial regions inflated. Margins of carapace with few prominent spines and several spinules. Dorsal surface weakly tuberculate and sparsely pubescent. Rostrum consists of two very short, slender, acute spines. Chelipeds very long (almost twice CL in adult male), stout, surfaces granular, spines and long hairs scattered along dorsal and ventral surfaces. Fingers acute, curved inward distally, adjacent inner edges toothed irregularly for entire length. Legs extremely long and slender. First leg longest (5 times CL), following legs decreasing. Abdomen of five segments plus telson in both sexes.

Colour

Preserved specimens are dull creamy white.

Size

Male 6mm CW, 8mm CL. Female 7.2mm CL. Smallest ovigerous female 5.5mm CL.

Habitat

On sandy bottom associated with extensive sponges, pink and white coralline algae, Petrolisthes novaezelandiae, Petalomera wilsoni, Liocarcinus corrugatus.

Depth

Continental shelf 36-170m.

Breeding

Ovigerous females have been collected in January - March, July and September. Females carry only 20-30 eggs, newly laid

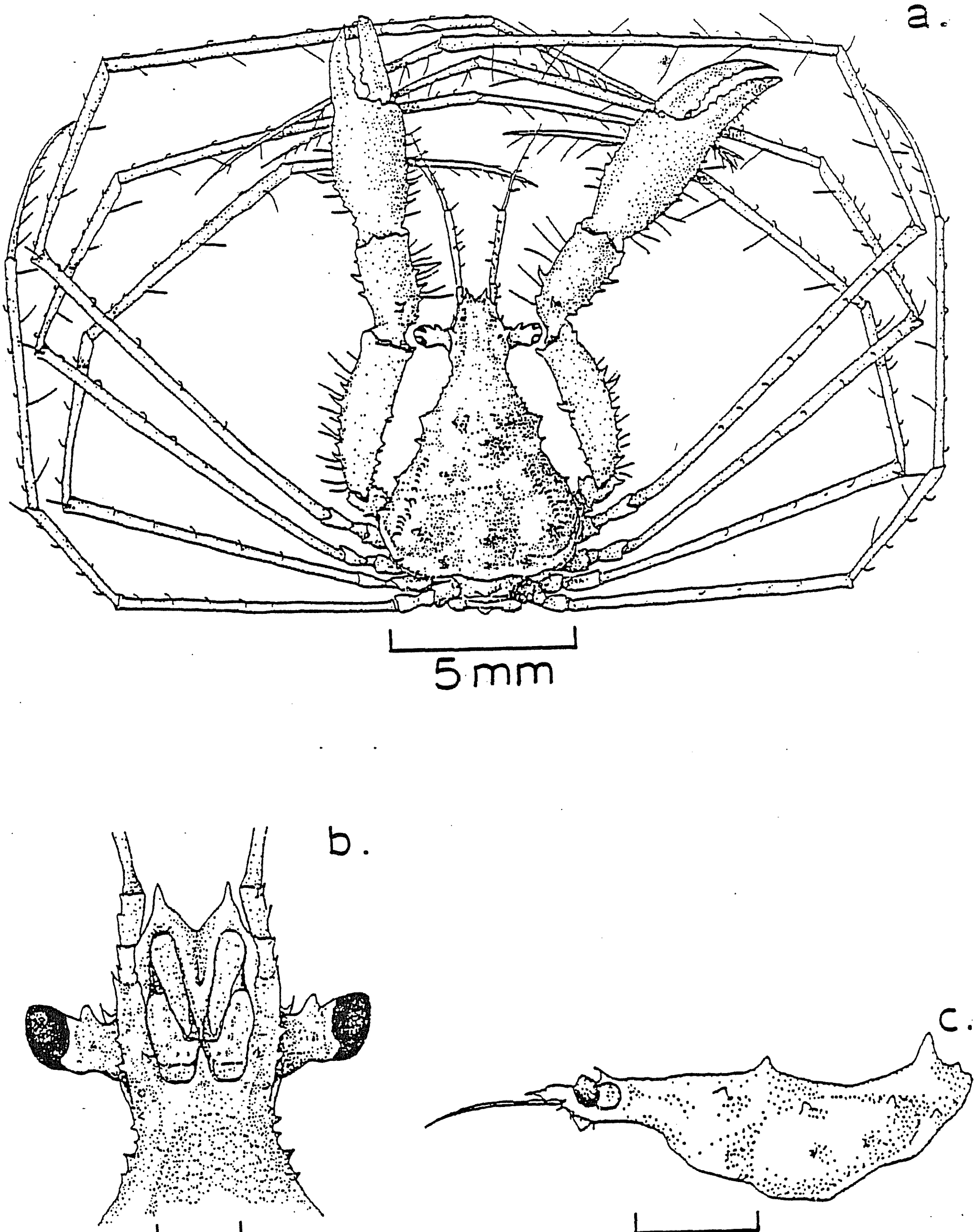


Fig. 26 - *Achaeus curvirostris*: a - male, dorsal view; b - anterior end, ventral view; c - carapace, lateral view (after Griffin, 1966).

0.62 x 0.58mm, yellow and when ready to hatch, 0.61 x 0.67mm, pale yellow.

Development and Growth

A.curvirostris is the only majid crab with a single planktonic zoeal stage (usual number is 2 zoeae). The zoea and megalopa have been described by Wear & Fielder (1985).

Behaviour, Ecology

Unknown.

References

Bennett (1964), Campbell & Stephenson (1970), Griffin (1966a), Griffin & Tranter (1986a), Griffin & Yaldwyn (1965), Wear & Fielder (1985).

Rochinia riversandersoni (Alcock, 1895)

Synonymy

Scyramathia rivers-andersoni Alcock, 1895; Alcock & Anderson, 1896; Alcock, 1899; Doflein, 1904; Rochinia rivers-andersoni Serene, 1968; Rochinia rivers-andersoni Serene & Lohavanijaya, 1973; Rochinia riversandersoni Yaldwyn & Dawson, 1976; Griffin, 1976; Wear & Fielder, 1985; Griffin & Tranter, 1986a.

Type Locality

India.

Distribution

Indo-West Pacific off East Africa, Arabian Sea (Malabar Coast), Bay of Bengal (Nicobar Islands), South China Sea, Philippine Is., and off northern New Zealand and the Kermadec Islands.

The 29 Indo-West Pacific species of Rochinia from the Pacific coast of America are reviewed by Griffin & Tranter (1986a).

Diagnosis (Fig. 27a-c)

Carapace pyriform (pear-shaped), rostrum of two very long, divergent, sharp spines. Surface spinous and bearing scattered, hooked hairs in among a short, close pubescence. Three medial spines, the last at the posterior margin of the carapace and two spines on either side of these. Margins with two spines : 1 hepatic and 1 long branchial spine. Chelipeds not enlarged, fingers acute, curved, gaping basally and hooked distally. Legs relatively long, first pair longest. Abdomen of six segments and telson in both sexes.

Colour

White when preserved.

Size

Male 26.5mm CL. Female 25mm CL. Smallest ovigerous female 11mm CL (not including rostrum).

Habitat

Pumice pebbles, coral, small angular boulders on sand and mud.

Depth

Deep water 375-1362m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Griffin & Tranter (1986a), Serene & Lohavanijaya(1973), Wear & Fielder(1985), Yaldwyn & Dawson (1976).

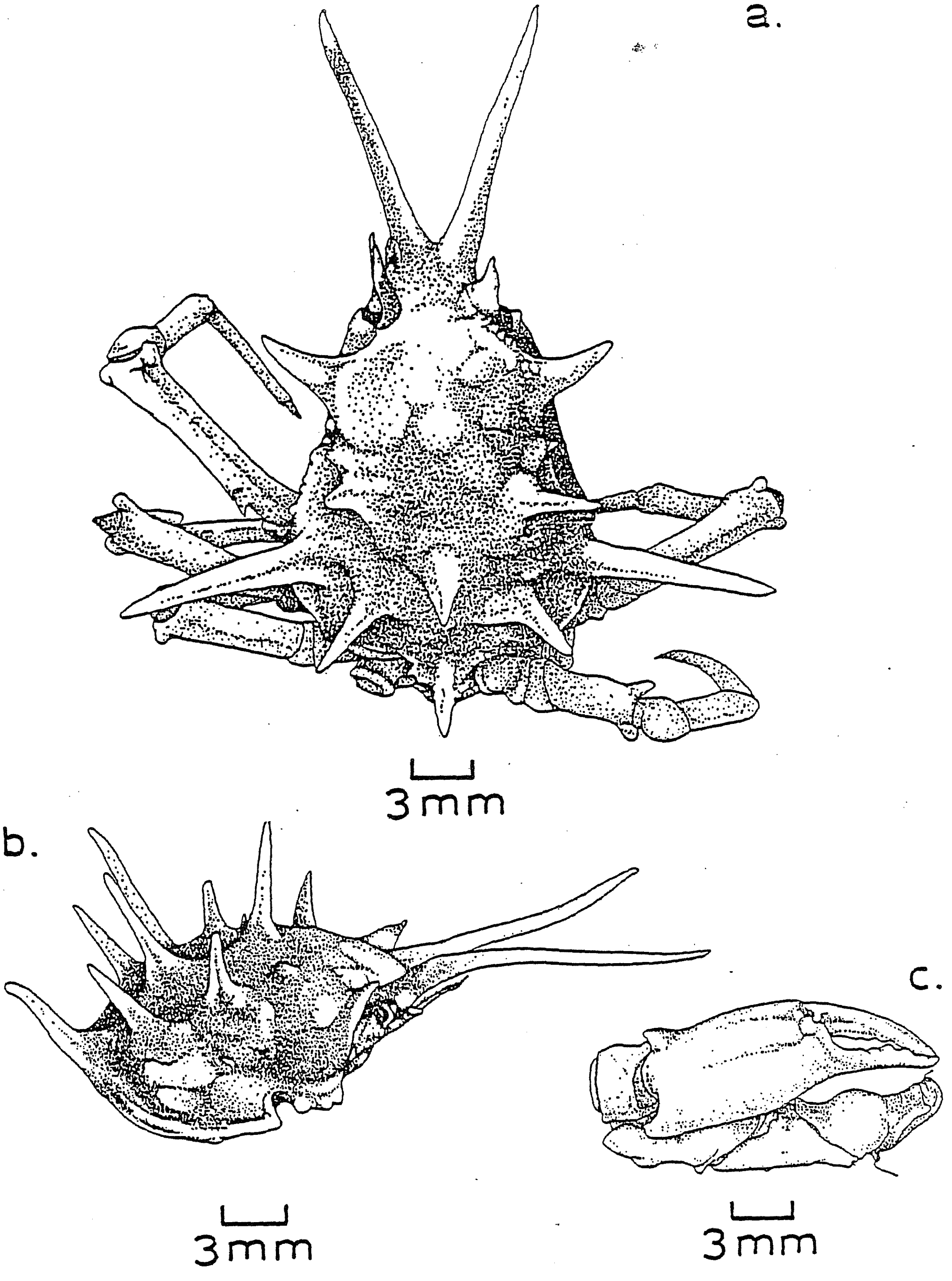


Fig. 27 - *Rochinia riversandersoni*: a - female, dorsal view; b - carapace, oblique lateral view; c - right chela, male, outer face (by C. Duffy, based on photos from Yaldwyn & Dawson, 1976).

Eurynolambrus australis H. Milne Edwards & Lucas, 1841

Triangle crab

Synonymy

Eurynolambrus australis H.Milne Edwards & Lucas, 1841; Dana, 1852; Miers, 1876b; Filhol, 1885d; 1886; Lenz, 1901; Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Richardson, 1949b; Krefft, 1952; Dell, 1960; 1963a; Bennett, 1964; Griffin, 1966a; Dell, 1968a; Probert et al., 1979; Marsden, 1981; Webber & Wear, 1981; Wear & Fielder, 1985; Griffin & Tranter, 1986a.

Type Locality

New Zealand.

Distribution

Endemic to New Zealand. Cape Maria van Diemen to Stewart Island, also Chatham Islands.

Diagnosis (Fig. 28a-c)

Carapace broadly sub-triangular, depressed, branchial region greatly expanded laterally on each side to overhang the legs. Rostrum of two short lobes (bearing opposing rows of hooked hairs) separated by a narrow groove. Dorsal surface of carapace naked, margin coarsely scalloped, forming four short teeth. Chelipeds stout long (1.8 times CL in male) surface irregularly tuberculated and ridged. Fingers acute, weakly curved inward at tips, closely approximated, inner edges finely toothed for their entire length. Legs short, weakly compressed, lateral and medial surfaces expanded as irregular crests.

Colour

Claws purple, inner margins white. Carapace dark red irregularly mottled with white. Cavities under carapace margins are contrasting white. Antennules pale yellow, eyestalks deep red above, pale beneath, cornea darkly translucent. Legs mottled, white, orange and dark red. Leg bases honeycombed, orange and spotted white.

Size

Male 65mm CW, 41.5mm CL. Female 49mm CW, 32mm CL.

Habitat

A littoral species frequenting rocky, muddy shores on moderately exposed coasts, found under boulders covered with coralline algae. Also found offshore frequently associated with bryozoans.

Depth

Intertidal to 80m.

Breeding

Ovigerous females found from October to February. New eggs are bright orange, 0.65mm diam., eggs ready to hatch are brown, 0.84mm x 0.79mm.

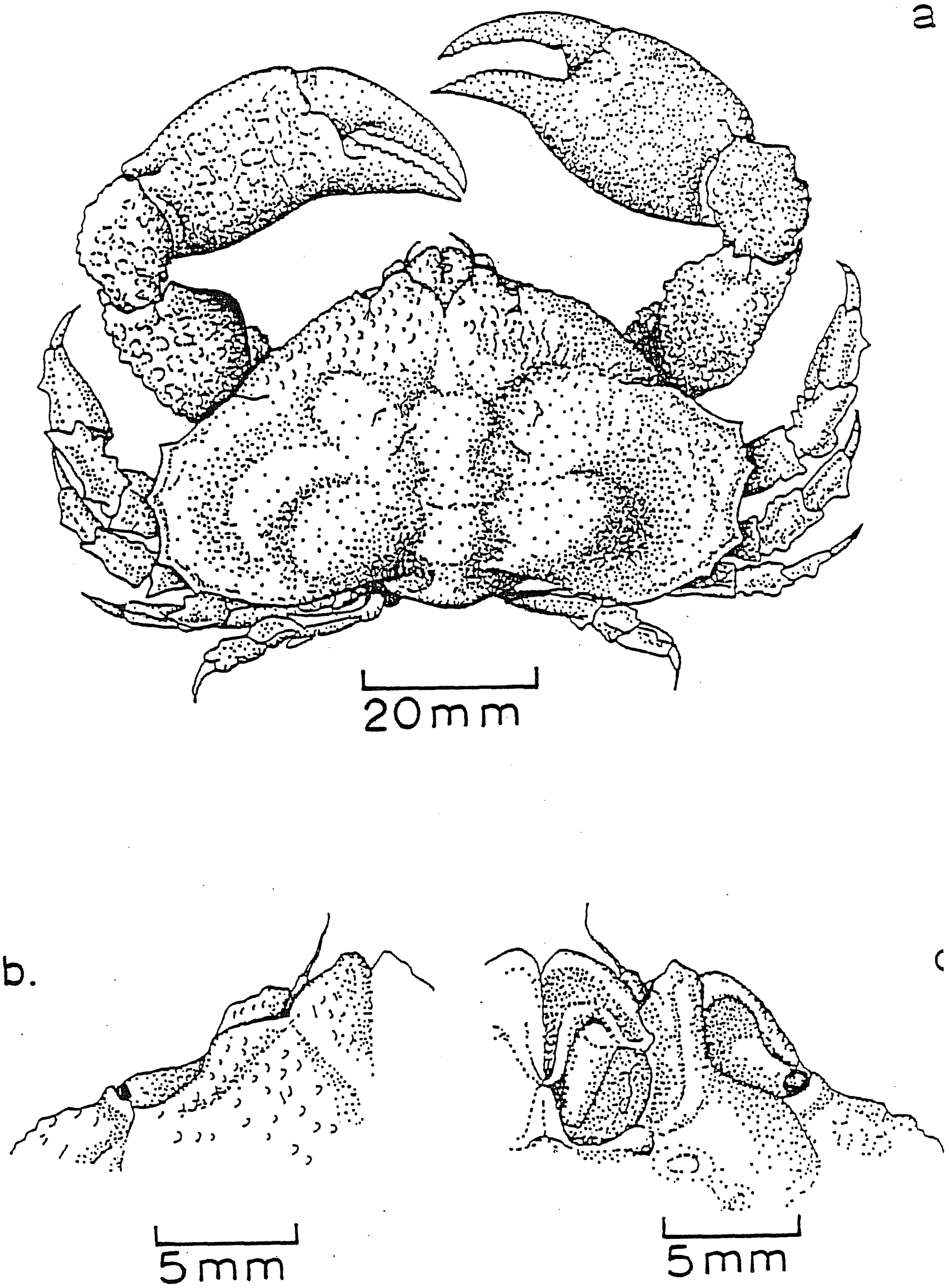


Fig. 28 - Eurynolambrus australis: a - male, dorsal view; b - orbit, dorsal view; c - orbit, ventral view (after Griffin, 1966).

Development and Growth

Pre-zoea, 2 zoeal stages and megalopa larva have been described by Webber & Wear (1981) and Wear & Fielder(1985). The zoeal stages last 6-8 days each and the longest surviving megalopa lasted a further 15 days. Post-larval, juvenile stages have been described by Krefft (1952). Juveniles have well developed rows of hooked hairs and lack the laterally expanded carapace of adults, giving a more pyriform shape.

Behaviour

Unlike the other spider crabs this species does not actively camouflage itself. The shape of the adult carapace excludes the chelipeds access to the dorsal surface although they can reach up on to the frontal area. When uncovered beneath a boulder this crab usually remains immobile, the mottled colour patterns making it difficult to see. The legs and bright purple chelipeds are folded and hidden underneath.

Ecology

Carapace surface often has small tubiculous polychaetes and occasionally small anemones (*Anthopleura aureoradiata*).

King & Clark(1984) found that rig (*Mustelus lenticulatus*) from Golden Bay ate small numbers of *E.australis*.

References

Bennett (1964), Dell (1963a), Griffin (1966a), King & Clark (1984), Krefft (1952), Probert & Batham (1979), Webber & Wear (1981), Wear & Fielder (1985).

Leptomaia tuberculata Griffin & Tranter, 1986

Synonymy

Leptomaia tuberculata Griffin & Tranter 1986a.

Type Locality

Middleton Reef, Tasman Sea, 54-72m.

Distribution

Middleton Reef, Lord Howe Is, Kermadec Is, North New Zealand.

Diagnosis (Fig. 29a-d)

Carapace much longer than wide, narrow pyriform, with many low tubercles. Rostral spines slender, divergent, widely separated from base. Orbital eave expanded, preorbital angle produced into a broad spine, antorbital lobe short and blunt, postorbital lobe separated from eave by only a narrow slit, narrowing distally, apex subacute. Eyestalks short, stout, a row of club setae distally above cornea. Hepatic region weakly elevated, a short spine and two tubercles on margin. Branchial margin with a tubercle on anterior border and a second tubercle behind it. Beginning more ventrally an irregular row of about twelve small tubercles extend to posterolateral margin. Posterior margin produced backward as a broad triangular lobe, a short blunt spine at its apex. Cheliped of male slightly shorter than postrostral CL, merus smooth with a short, blunt terminal spine, carpus with a small proximal tubercle and a terminal tubercle, palm smooth, fingers with a few low teeth and a narrow gape. Female cheliped similar but shorter. First leg slightly longer than postrostral CL, merus with a low terminal tubercle. Fourth leg shorter, dactyl with about five very small teeth ventrally on distal half. Abdomen of six segments and telson in both sexes.

Colour

Unknown.

Size

Male and female 15mm CL.

Habitat

Rocky bottom, gravel and stones.

Depth

Shallow water, 21.5-72m.

Breeding

Ovigerous female collected in November.

Development and Growth, Behaviour, Ecology

Unknown.

Reference

Griffin & Tranter 1986a.

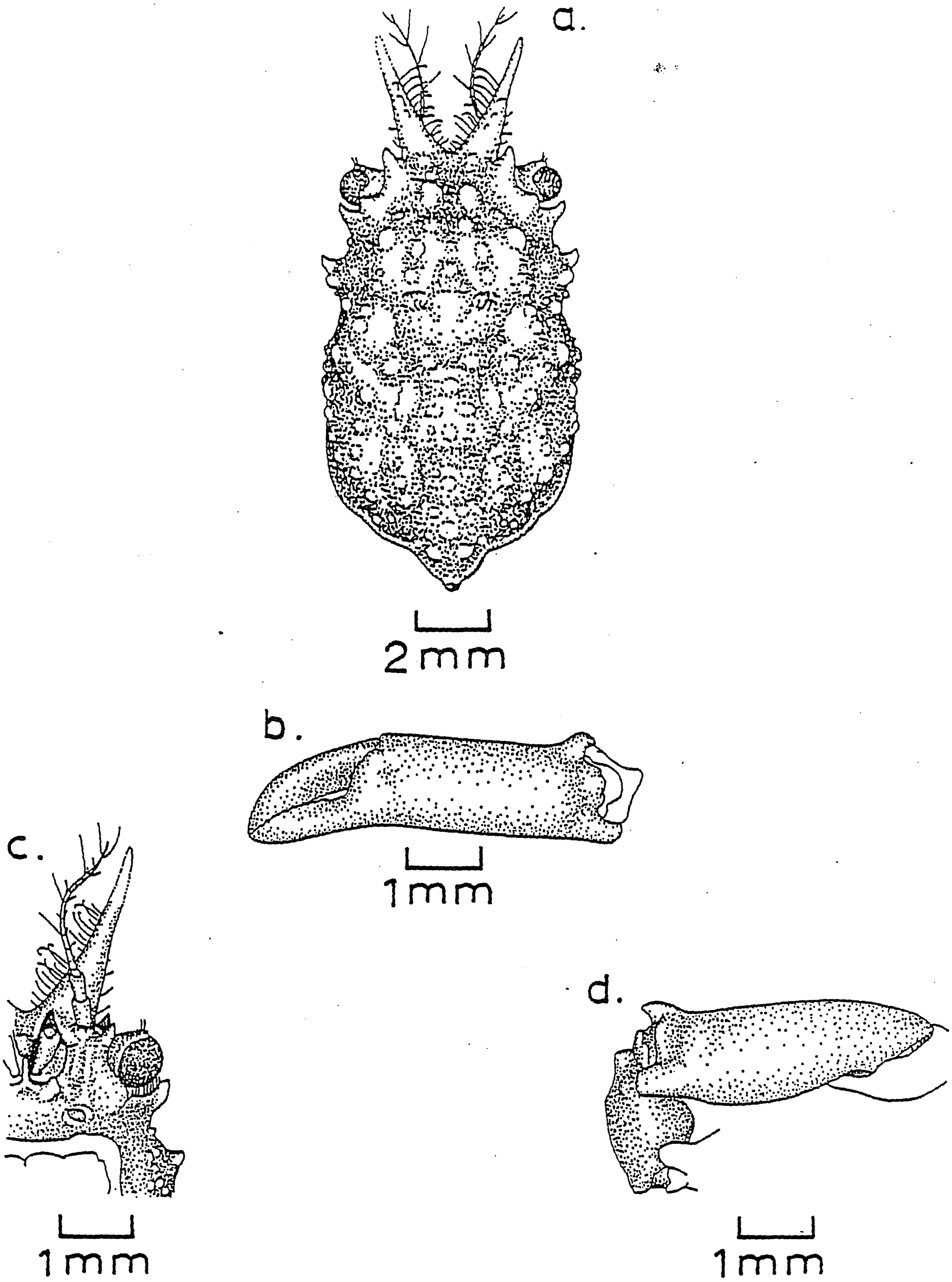


Fig. 29 - *Leptomaia tuberculata*: a - female, carapace, dorsal view; b - left chela, female, outer face; c - left orbit, ventral view; d - left cheliped, female, merus and carpus (after Griffin & Tranter, 1986).

Trichoplatus huttoni A. Milne Edwards, 1876
Hutton's Masking Crab

Synonymy

Trichoplatus huttoni A. Milne Edwards, 1876; Halimus hectori Miers, 1876a; 1876b; Trichoplatus huttoni Hector, 1877; Halimus rubiginosus Kirk, 1881; Trichoplatus huttoni Filhol, 1885d; 1886; Halimus rubiginosus Filhol, 1886; Trichoplatus huttoni Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Naxia huttoni Richardson, 1949b; Dell, 1963a; Trichoplatus huttoni Bennett, 1964; Naxia huttoni Griffin, 1966a; Trichoplatus huttoni Griffin & Tranter, 1986a.

Type Locality

Coast of New Zealand.

Distribution

Endemic to New Zealand, mainly southern, including Stewart and Chatham Islands. Northern limits Napier and Cavalli Islands.

Diagnosis (Fig. 30a-c)

Carapace narrowly pyriform, in profile almost uniformly convex. Several prominent spinous tubercles, longer anteriorly, scattered over the carapace. Regions moderately well defined by shallow grooves. Tubercles arranged in a medial series of two anteriorly, and submedial of two pairs posteriorly, with five pairs more distant from midline. Two prominent medial mesogastric tubercles, cardiac region with a pair of small submedial tubercles and a smaller pair on posterior intestinal margin. Four prominent protogastric tubercles arranged in pairs, six small branchial tubercles. Very straight, stiff, long hairs on the supraorbital eave and arising in tufts from tubercles. Surface of carapace otherwise covered by a thick mat of short fine hairs. Rostrum of two long slender cylindrical, weakly divergent spines. Short, curled hairs fringing rostral spines. Margins of carapace have three prominent outwardly directed spines. Orbit consisting of supraorbital eave, intercalated spine and postorbital spine remote from orbit. Close behind an hepatic spine, slightly longer than postorbital, sharply pointed. Chelipeds very long, stout; merus long with a row of strong spines along dorsal edge; propodus compressed, enlarged in male, fingers acute, weakly curved gaping basally in male, closely approximated in female, finely toothed. Legs of moderate length, stout, smooth except for a few small ventral spinules, covered by a mat of short hairs, groups of curled hairs in a dorsal row and long stout hairs. Propodi strongly compressed and greatly expanded with dactyli strongly curved to make all legs subchelate. Abdomen of five segments in male and female, with sixth segment and telson almost completely fused.

Colour

Carapace and chelipeds pink to deep red or pale purple.

Size

Male 49mm CW, 82mm CL. Female (ovigerous) 43mm CW, 62mm CL.

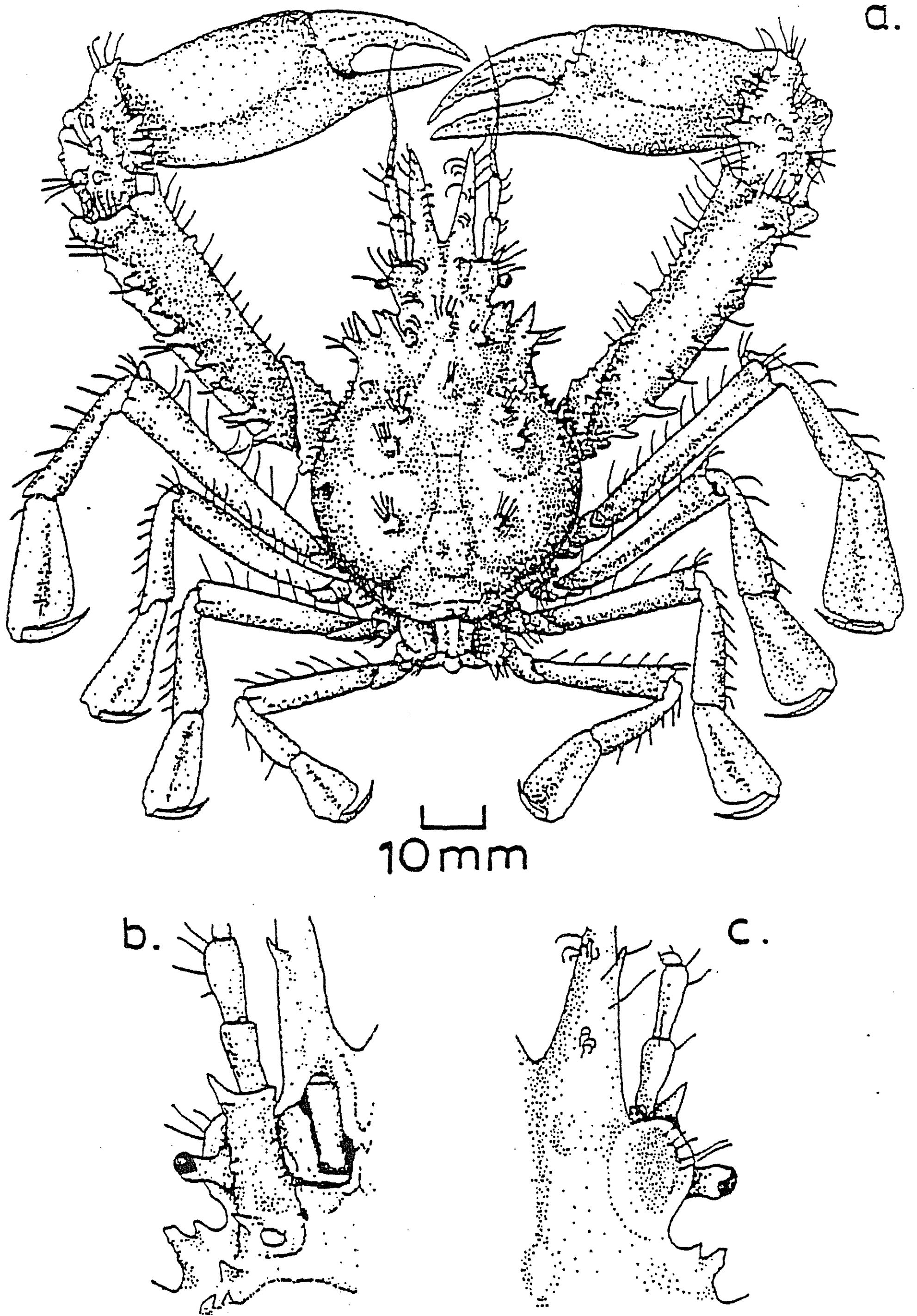


Fig. 30 - Trichoplatus huttoni: a - male, dorsal view; b - orbit, ventral view; c - orbit, dorsal view (after Griffin, 1966).

Habitat

Exposed rocky coasts, among seaweed.

Depth

Low tide to 60m.

Breeding, Development and Growth

Unknown.

Behaviour

T.huttoni sparsely decorates its carapace and legs with pieces of red seaweed. The behaviour may be similar to that used by Notomithrax ursus but it has not been studied.

Ecology

Only ever collected in small numbers, sometimes in crayfish pots. The subchelate legs are used to cling to seaweed. T. huttoni has rarely been recorded from fish guts. Habib (1975) found it in red cod (Pseudophycis bacchus) from the Canterbury area: 5.1% of gut volume in December and 1.0% in June.

References

Bennett (1964), Dell (1963a), Griffin (1966a).

Notomithrax minor (Filhol, 1885)

Synonymy

Paramithrax (Paramithrax) peronii Haswell, 1880a; 1880b; Paramithrax minor Filhol, 1885d; 1886; Paramithrax peronii, Fulton & Grant, 1906; Grant & McCulloch, 1906; Chilton, 1911a; Paramithrax parvus Borradaile, 1916; Paramithrax minor Rathbun, 1918c; Chilton & Bennett, 1929; Paramithrax parvus Chilton & Bennett, 1929; Paramithrax minor Powell, 1937; Paramithrax parvus Richardson, 1949b; Paramithrax minor Richardson, 1949b; Dell, 1963a; Notomithrax minor Griffin, 1963; Paramithrax minor Bennett, 1964; Notomithrax minor Griffin, 1966a; Dell, 1968a; Batham, 1969; Hayward, 1974; Knox & Bolton, 1978; Webber & Wear, 1981; Wear & Fielder, 1985; Griffin & Tranter, 1986a (key).

Type locality

Massacre Bay, Cook Strait, 15m.

Distribution

New Zealand from Cape Maria van Diemen to Stewart Island. Southeast Australia including Tasmania.

Diagnosis (Fig. 31a-d)

Carapace broadly pyriform, rostrum of two short, sharp spines. Short hooked hairs scattered over the dorsal surface of the carapace. Margins with 12 short, outwardly directed spines : 3 supraorbital, 2 hepatic and 7 branchial (the last 3 sub-dorsal). Dorsal carapace surface covered by small spines and tubercles. Chelipeds long (1.5 times CL in adult male), dactyl almost as long as palm, fingers acute, finely toothed along inner edges, fixed finger for distal half and dactyl for entire length. Legs long and slender, first pair longest, following legs decreasing in length. Dorsal surface of legs bearing a double row of hooked hairs arranged in opposing groups. Abdomen of six segments plus telson in both sexes.

Colour

Pale yellowish, 'muddy', dorsal surface of chelae dark red or purple. Tips of fingers are white. Thickly covered by brownish hairs.

Size

Male 31.5mm CW, 40mm CL. Female (ovigerous) 24mm CW, 30.5mm CL.

Habitat

Sand, mud or coarse shell bottoms and rocky shores. Usually covered by small pieces of seaweed or more commonly by sponges which are permanently fixed.

Depth

Intertidal to 35m, rarely 90m.

Breeding

Ovigerous females have been previously collected from September to April. At Leigh females with advanced eggs have been found in June and with new eggs in June, July and November. In

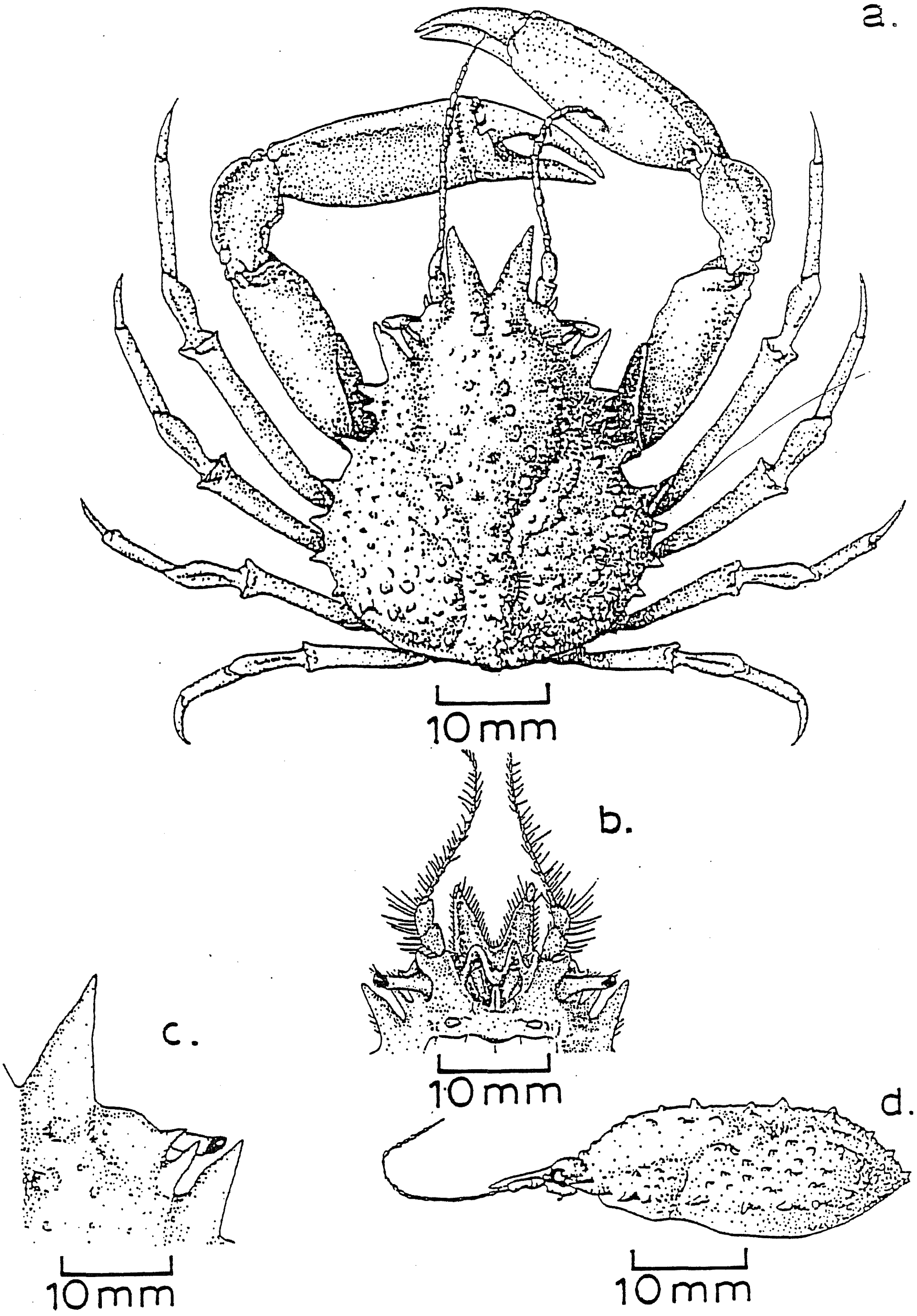


Fig. 31 - *Notomithrax minor*: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Wellington Harbour larvae occur in plankton throughout the year (Webber & Wear 1981) but in the Avon Heathcote Estuary very few were found from March to August, 1982 (Roper, Simons & Jones 1983). Probably breeds throughout the year near Wellington. New eggs are bright orange (0.6 x 0.56mm) and eggs ready to hatch are bright orange (0.63 x 0.61mm).

Development and Growth

Pre-zoea, 2 zoeal stages and megalopa larva have been described by Webber and Wear (1981). The zoeal stages last for approximately 9 days each. Zoeae are most abundant during spring and summer.

Behaviour

Carapace commonly adorned with sponge. As sponges become permanently fixed to the carapace it is likely that this species makes only very limited use of its masking behaviour, perhaps only once after each moult. Like other spider crabs movement is rather sluggish.

Ecology

N.minor is eaten (0.1-2.4% of gut volume) by Hauraki Gulf and Bay of Plenty snapper (Chrysophrys auratus) (Godfriaux 1969,1974b, Colman 1972) and rarely by tarakihi (Cheilodactylus macropterus) from western Bay of Plenty (Godfriaux 1974a). Rig (Mustelus lenticulatus) from West Coast also eat this crab (King & Clark 1984). Habib (1975) found that Banks Peninsula red cod (Pseudophycis bacchus) ate N.minor in May(0.6%) and July(0.3%).

Glaessner (1960) has recorded upper pleistocene fossil specimens of N.minor.

References

Bennett (1964), Colman (1972), Dell (1963a), Godfriaux (1969, 1974a,1974b), Griffin (1963,1966a), Habib (1975), King & Clark (1984), Roper, Simons & Jones (1983), Webber & Wear (1981), Wear & Fielder (1985).

Notomithrax peronii (H. Milne Edwards, 1834)

Synonymy

Paramithrax peronii H.Milne Edwards, 1834; Jacquinot & Lucas, 1853; Paramithrax (Paramithrax) peronii Miers, 1876a; 1876b; Paramithrax peroni Filhol, 1885d; Paramithrax (Paramithrax) peronii Rathbun, 1893b; Paramithrax peronii Lenz, 1901; Chilton, 1906a; 1911a; Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Young, 1929; Richardson, 1949b; Notomithrax peronii Griffin, 1963b; Paramithrax peroni Dell, 1963a; Bennett, 1964; Notomithrax peronii Griffin, 1966a; Dell, 1968a; Webber & Wear, 1981; Wear & Fielder, 1985; Griffin & Tranter, 1986a (key).

Type Locality

New Zealand.

Distribution

Endemic to New Zealand. Cape Maria van Diemen to Stewart Island and also Chatham Islands.

Diagnosis (Fig. 32a-d)

Carapace broadly pyriform, rostrum of two moderately long sharp spines, weakly divergent. Long, stout hooked hairs along the dorsal surface of the rostral spines and also present on the dorsal surface of the carapace. Margins of carapace with 10 outwardly directed spines : 3 supraorbital, 2 hepatic and 5 branchial (the last 2 being sub-dorsal). A characteristic feature of this species are a pair of small spines on posterior carapace margin. Dorsal surface of carapace densely covered by spines and tubercles. Chelipeds long (nearly twice the CL in adult male). Fingers acute, toothed along inner edges for entire length, male dactyl has a large basal tooth. Legs long and slender, lacking spines, dorsal surface with groups of hooked hairs. First pair of legs longest and following legs decreasing in length. Abdomen of six segments plus telson in both sexes.

Colour

Dorsal surface of carapace, chelipeds and legs are deep brownish orange to dark red. Tips of fingers are white. Hairs are brownish.

Size

Male 54mm CW, 77mm CL. Female (ovigerous) 41.5mm CW, 57mm CL. Smallest ovigerous female 18mm CL (Chilton 1911a).

Habitat

Rocky shores, among seaweed, rock pools also on sand or mud. Usually thickly covered by small pieces of seaweed.

Depth

Intertidal to 50m but most common just off-shore.

Breeding

Ovigerous females found from late July to end of March. New eggs are bright orange and dark brown when ready to hatch (0.79 x 0.78mm). At Kaikoura Pack (1982) recorded peak breeding in late

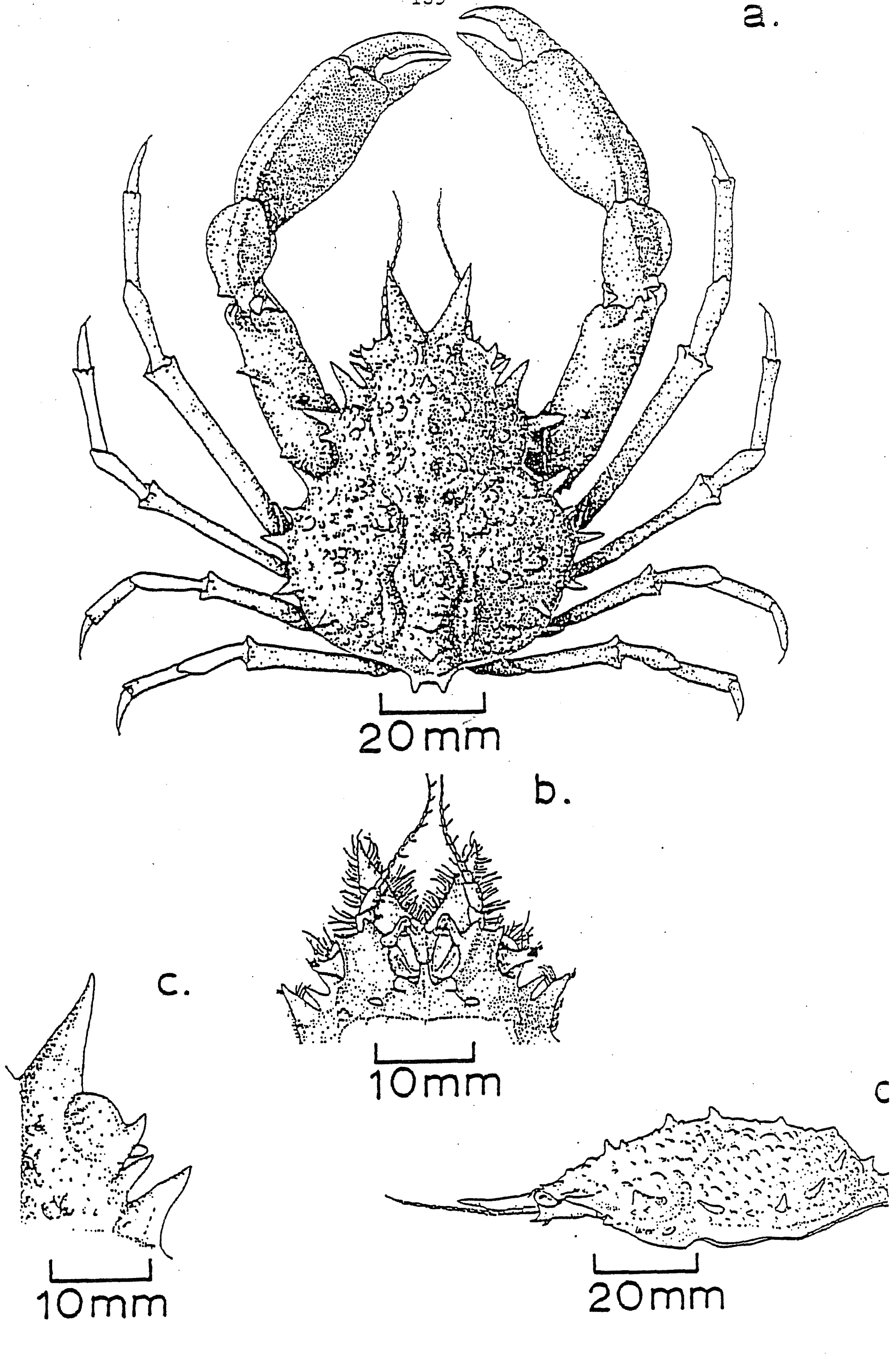


Fig. 32 - Notomithrax peronii: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

July, August and October, about 2 months later than N.ursus in the same study area.

Development and Growth

Larval life is 34 days at 17°C. The pre-zoea, 2 zoeal stages and megalopa larva have been described by Webber & Wear (1981). The first zoea lasts about 7-9 days and the second zoea 5-9 days. Larvae occur mainly in shallow water plankton samples taken near the bottom (Wear & Fielder 1985).

Behaviour

The seaweed camouflage on carapace and legs is attached to the hooked hairs using chelipeds. This masking behaviour is used continually by the crabs to change its covering and thereby match its surroundings. At Kaikoura seasonal migrations are made from shallow to deeper water and back again. Like other spider crabs movement is sluggish. N.peronii is active at night and concealed during the day (Pack 1982).

Ecology

At Kaikoura N.peronii was found in an intertidal study area throughout the year in small numbers with a large influx in late July when females greatly outnumbered (3:1) males (Pack 1982). At other times the sex ratio was approx. equal. In this area N.ursus was encountered much more frequently than N.peronii (6:1).

King & Clark (1984) found that rig (Mustelus lenticulatus) from Golden Bay ate small numbers of N.peronii. Banks Peninsula red cod (Pseudophycis bacchus) also eat this crab (Habib 1975). Crabs that have died from other causes are consumed by Coscinasterias calamaria in Otago Harbour (Crump 1969).

References

Bennett (1964), Dell (1963a), Griffin (1963b,1966a), Habib (1975), King & Clark (1984), Pack (1982), Webber & Wear (1981), Wear & Fielder (1985).

Notomithrax ursus (Herbst, 1788)
Hairy Seaweed Crab

Synonymy

Cancer (Mithrax) ursus Herbst, 1788; Paramithrax ursus Gerstaecker, 1856; Paramithrax (Paramithrax) barbicornis Miers, 1876a; 1876b; Paramithrax (Paramithrax) latreillei Miers, 1876a; 1876b; Paramithrax (Paramithrax) barbicornis Haswell, 1880a; 1882a; Paramithrax cristatus Filhol, 1885d; Paramithrax (Paramithrax) latreillei Rathbun, 1893b; Paramithrax latreillei Chilton, 1906b; 1911a; Thomson, 1912; Paramithrax (Paramithrax) latreillei Borradaile, 1916; Paramithrax latreilli Thomson & Anderton, 1921; Paramithrax ursus Balss, 1929; Paramithrax latreillei Young, 1929; Chilton & Bennett, 1929; Richardson, 1949b; McNeill, 1953; Dell, 1960; Paramithrax ursus Dell, 1963a; Notomithrax ursus Griffin, 1963b; Paramithrax ursus Bennett, 1964; Notomithrax ursus Griffin, 1966a; Dell, 1968a; Hayward, 1974; Marsden & Fenwick, 1978; Webber & Wear, 1981; Marsden, 1981; Wear & Fielder, 1985; Griffin & Tranter, 1986a (key).

Type Locality

Pacific Ocean.

Distribution

South-east Australia, New Zealand mainland, Stewart Island and Chatham Islands.

Diagnosis (Fig. 33a-d)

Carapace broadly pyriform, rostrum of two short, sharp spines. Short, stout, hooked hairs on dorsal surface of rostral spines and carapace. Very long, dense hairs along lateral margins of rostrum and also covering carapace, almost concealing hooked hairs. Margins of carapace with nine outwardly directed, sharp spines : 3 supraorbital, 3 hepatic and 3 branchial. Dorsal carapace surface entirely lacking spines, densely covered by numerous large and small tubercles. Chelipeds of moderate length, propodus compressed, fingers acute. Fingers in male are widely gaping, toothed along inner edges for distal third only, in female adjacent and toothed for entire length. Dactyl in male has a large tooth, absent in female. Legs long and slender, dorsal surface with a longitudinal row of short, hooked hairs, obscured by very long straight hairs. First leg longest, following legs decreasing in length. Abdomen of six segments plus telson in both sexes.

Colour

Dorsal surface of carapace, chelipeds and legs are orange to deep red. Hairs of carapace and legs are brownish.

Size

Male 42mm CW, 60mm CL. Female 36mm CW, 43mm CL.

Habitat

Along rocky shores, in rock pools among seaweed. Whole crab usually thickly covered by red, green or brown seaweed.

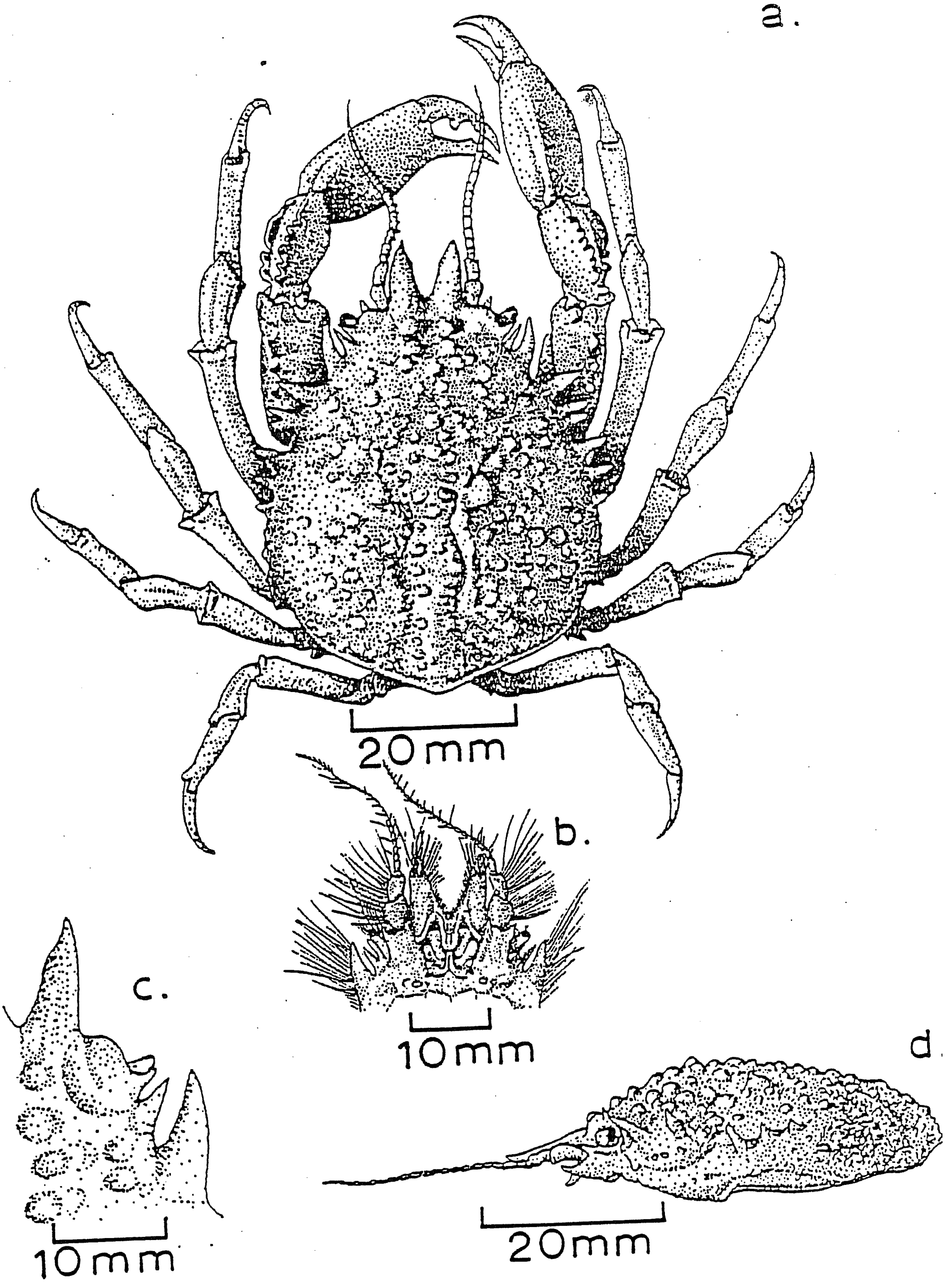


Fig. 33 - *Notomithrax ursus*: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Depth

Intertidal to 75m.

Breeding

Ovigerous females found from June to February at Kaikoura with a peak from June to August (Pack 1982). New eggs are bright orange and just before hatching they are brown (0.75 x 0.7mm). At Kaikoura, stage 1 eggs first appeared in June and stage 4 eggs in late July. Since ovigerous females were found until March, it is likely that they can produce more than one brood per breeding season. A few of these may breed a second time in the following year, however males are probably longer lived and may survive for 2 or more years.

At Leigh ovigerous females have been found in May and June. Females collected in May had advanced eggs so that breeding clearly begins in March or April.

Development and Growth

The pre-zoea, 2 zoeal stages and megalopa larva have been described by Webber & Wear (1981). Larval life is 40 days at 16°C. First stage zoeae live from 8-16 days and second stage zoeae live 12-15 days. Zoeae occur chiefly in shallow water plankton samples taken near the bottom. They are very similar to zoea of N.peronii.

At Kaikoura late stage eggs first appear near the end of July and very small juveniles were first found in October, suggesting that larval development is probably about 60 days.

Pack (1982) has investigated relative growth of N.ursus at Kaikoura. Majid crabs have 3 identifiable growth stages: immature, pre-pubescent and mature (Hartnoll 1963). These stages are separated by 2 important moults in the growth of the crab: the moult of pre-puberty (coincident with gonad development) and the puberty moult (which is terminal). Maturity is associated with changes in relative growth of the abdomen and chelipeds, which are important in reproduction. Fitting the power function, $\log y = a + b \log x$ gives values of 'b' which allow assessment of relative rate of growth, $b < 1$ (negative allometric growth), $b = 1$ (isometric growth), $b > 1$ (positive allometric growth). Growth of male abdomen width and female chela width of N.ursus are both isometric ($b = 0.9$ and $b = 1.09$ respectively), while growth of female abdomen width and male cheliped width are both positively allometric ($b = 1.29$ and $b = 1.34$ respectively). For all sizes (>10mm CL) females have broader abdomens than males of the same CL and the pubertal moult can occur in females as small as 23-24mm CL.

Only after this moult do the female genital openings become large enough to accommodate the male pleopod. Small males (<20mm CL) have similar chela widths to females but the divergent trend becomes more pronounced in larger males. The male pubertal moult can occur in males as small as 31-32mm CL after which they have substantially larger chelae. A pre-pubescent stage is not evident in female N.ursus but male gonad development suggests that males may have a pre-pubescent stage.

O'Brien (1984) found that the Californian kelp crab Pugettia producta parasitized by the rhizocephalan barnacle, Heterosaccus californicus, show precocious maturity by moulting to puberty after fewer juvenile instars.

Behaviour

Almost all kinds of seaweed are applied to the body and legs using the chelipeds. Small pieces of seaweed are snipped off by chelipeds and poked into the hooked hairs so that the uncut end is upper-most. Camouflage is continually changed with 10 -20% of the cover being replaced each day. The number of seaweed pieces applied is independent of crab-size but larger crabs achieve the same cover by using larger pieces. Like other spider crabs movement is sluggish.

In the field nearly all hard shelled N.ursus are camouflaged and usually closely match their immediate surroundings (89.2% of 813 crabs). Only 11.4% were covered in different algal species and were most commonly found in June and July. But even these crabs may still be cryptic because they are concealed beneath the algae. Even newly moulted soft crabs carry a few pieces of algae, usually over the rostral area. The only unmasked crabs were those which had lost both chelipeds (Pack 1982).

Wicksten (1980) has proposed an hypothesis about the origin and evolution of masking behaviour by spider crabs. She suggests that masking evolved as an extension of normal feeding behaviour with the attachment of food items to the body serving as camouflage against predators and perhaps as a food store. The next stage may have involved the attachment of non-edible, offensive materials. Wicksten suggests that some crabs may have lost the masking habit but her arguments for this are unconvincing. There is an opportunity here for someone to make a valuable contribution by making a comparative study which encompasses not only masking behaviour but also distribution of hooked hairs on the bodies of both decorator and non-decorator crabs. Wilson (1987) suggests that the spider crab Acanthonyx petiveri can acquire pigment from the algae on which it feeds. This adds a new dimension to the problem of spider crab camouflage.

Copulation with hard-shelled N.ursus females has been observed in the laboratory. The male approached the female, rostrum to rostrum, gripped her carapace with the first 2 pairs of walking legs, manipulated her into the sternum to sternum position using his chelipeds and then rocked backward into a female over male position. The female was held closely with the male chelipeds folded over her carapace and the male's legs interlocked with hers and grasping her carapace. The male was usually larger than his mate. One female spawned within 24 hrs of copulation. The algal mask does not seem to be important in copulation. Mating probably occurs soon after the pubertal moult but several weeks may elapse until eggs are laid.

During the day N.ursus remains under cover of seaweed and/or rocks, sometimes partially buried in the sand. By contrast, at night, crabs are more active and some venture away from their place of concealment. Activity is clearly nocturnal and shows no superimposed tidal rhythm. Pack (1982) found a rapid loss of marked crabs from her study area in February (less than 10% remaining after 4 days) and corresponding immigration of unmarked crabs to keep the population density roughly the same. Marked crabs moved out and back into the area several times during the study. This suggests a high turnover rate of the population composition.

N.ursus is negatively phototactic and can bury itself in sandy substrates by excavating a depression using its chelipeds. These are pushed away from the body, shovelling sand forward and to the sides. In coarse substrates individual stones are picked up and released at the point of fullest extension of the cheliped. As the depression deepens the legs on one side and then the other move into it, causing the crab to rock from side to side. Excavation continued until the crab is buried with only the eyestalks and part of the carapace visible (Pack 1982).

During the day N.ursus has a clumped distribution often occurring with conspecifics in groups as large as 15 and containing both males and females. They also occur in groups as large as 28 with the congeneric masking crab N.peronii. Clumping was more apparent during the breeding season, January to August Pack 1982).

Ecology

At Kaikoura Pack (1982) found that abundance of N.ursus fluctuated seasonally with lowest numbers in October and highest numbers in April. Sex ratio also fluctuated seasonally: Dec.-Feb. 1.36 males/female, Mar.-May 0.73, June-July 1.08 and Aug .-Nov. 2.29. Over a year the population composition was unimodal (mean CL = 28mm) with no difference between average size of males (28.3mm) and females (27.6mm), but males attained a larger maximum size. Smallest average size was recorded in October, increasing through the summer and autumn to reach the largest average size in June and then declining again. Males and females had essentially the same pattern except in February when males were larger and in September when they were significantly smaller than females. Recently moulted crabs were only recorded from September to May, mostly during March and April.

Recruitment occurs during October-December producing the smallest average size and by March these crabs are undergoing their pubertal moult. During February-April there is an influx of large males from deeper water. Growth of the new cohort plus immigration from deeper water produces the largest average size in June. The small average size in the spring and early summer is partly due to recruitment and partly due to off-shore migration of larger crabs. Similar migrations of the kelp crab, Pugettia producta, off California have been recorded by Wicksten & Bostick (1983).

Leader & Bedford (1978) examined the composition of muscles and haemolymph of N.ursus and found that ion concentrations were similar to other crabs from the same habitat.

N.ursus is eaten by blue cod (Parapercis colias) at the Chatham Islands (Young 1929) and by red cod (Pseudophycis bacchus) from Banks Peninsula in January (1.0% of gut volume), May (0.6%) and September (0.8%) (Habib 1975). Town (1979) found that the large starfish *Astrostole scabra* ate small numbers of this crab. In the laboratory *Octopus maorum* and *Robsonella australis* will eat both masked and unmasked *N.ursus* (Pack 1982). The crab is also eaten by another crab, *Ovalipes catharus* (Wear & Haddon, 1987).

References

Bennett (1964), Dell (1963a), Griffin (1963b,1966a), Leader & Bedford (1978b), Pack (1982), Webber & Wear (1981), Wear & Fielder (1985).

Leptomithrax australis (Jacquinot, 1853)
Giant Masking Crab or Painted Spider Crab

Synonymy

Maia australis Jacquinot & Lucas, 1853; Paramithrax (Leptomithrax) australis Miers, 1876a; 1876b; Leptomithrax brevirostris Miers, 1879a; Leptomithrax australis Filhol, 1885d; 1886; Paramithrax (Leptomithrax) australis Rathbun, 1893b; Leptomithrax australis Chilton, 1909; Thomson, 1913; Thomson & Anderton, 1921; Stephensen, 1927; Chilton & Bennett, 1929; Balss 1930; Richardson, 1949b; Dell, 1960; 1963a; 1963b; Leptomithrax (Leptomithrax) australis Bennett, 1964; Leptomithrax australis Griffin, 1966a; Dell, 1968a; Calcott, 1970; Ritchie, 1970; Roberts, 1972b; Webb, 1972; Ritchie, 1973; Fenwick, 1975; Yaldwyn, 1975; Ryff & Voller, 1976; Fenwick, 1978; Griffin & Tranter, 1986a.

Type Locality

Auckland Islands.

Distribution

Cook Strait to Stewart Island, Chatham Islands, Snares Island, Auckland Island, Bounty Islands, Pukaki Rise and Campbell Island.

The 13 recent species of Leptomithrax are keyed out by Griffin & Tranter (1986a).

Diagnosis (Fig. 34a-d)

Carapace broadly pyriform, moderately swollen, surface covered by short hairs and small spinous tubercles surrounded by hooked hairs. Rostrum of two short spines, weakly convergent. Orbit consisting of supraorbital eave, intercalated spine and postorbital lobe, closely approximated. Postorbital lobe with a small accessory spinule midway along anterior, upper edge. Margins of carapace with six prominent, conical equidistant spines, one postorbital, one hepatic, and four branchials, curving on to dorsal surface posteriorly. Chelipeds very long, upper surface of merus and carpus covered by small, closely set conical spines. Propodus compressed, smooth, fingers acute, finely toothed and gaping basally. Dactyl with large basal tooth in male, absent in female. Legs long, slender, dorsal surfaces bearing a double row of opposing hooked hairs. Abdomen of six segments and telson in both sexes.

Colour

Orange-red to very deep red, propodus of cheliped finely marked with white and fingers white. Limb joints marked by patches of dark orange-red.

Size

Male 88mm CW, 102mm CL. Female 48mm CW, 62mm CL.

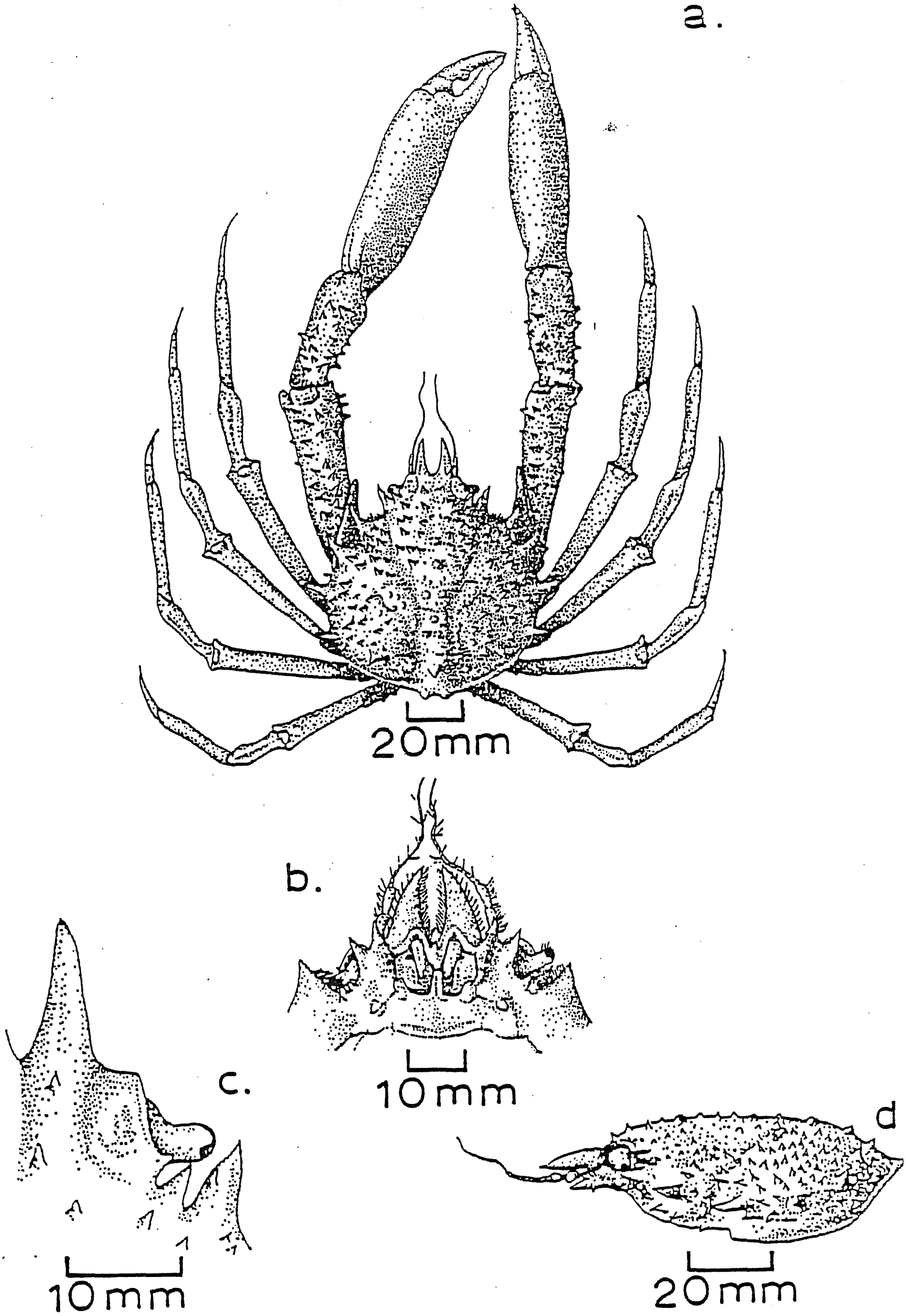


Fig. 34 - *Leptomithrax australis*: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Habitat

On southern off-shore islands this crab occurs intertidally and has been observed among seaweeds in areas of strong tidal currents and surge (Ritchie 1970, 1973, Fenwick 1978).* On the mainland it only occurs in deeper water.

Depth

Intertidal to 100m.

Breeding

No ovigerous females have been collected.

Development and Growth

Larval stages are unknown (Wear & Fielder 1985).

Behaviour

L. australis masks itself with pieces of seaweed when it lives in shallow water. These are placed on the carapace and legs by the long chelipeds, each piece of seaweed being selected and cut to an appropriate size before being placed on the body where it is held by the rows of hooked hairs. At Campbell Island the crabs use the algae *Shizoseris davisii*, *Streblocladia glomerulata*, *Chondria macrocarpa*, *Rhodophyllis acanthocarpa*, *Delessaria* sp., *Callophyllis* sp. and *Ceramium* sp. Crabs from deeper water are uncamouflaged except for pieces of sponge and polychaete tubes which probably colonize the crab as larvae. Hence the size of these epizoites will be related to the length of time since the crab last moulted.

Ritchie (1970) found that *L. australis* was common at the Auckland Islands but it did not enter crayfish pots. However, Ryff & Voller (1976) potted large numbers on the Pukaki Rise.

While diving at the Bounty Islands Westerkov (1987) recorded a gathering of *L.australis* and he published a photo showing two large males fighting while surrounded by many, smaller females. Each male grasped his opponent by the cheliped merus or carpus and stood 'face-to-face' for over 30 min. The males may have been contesting the ownership of females.

Ecology

Ritchie (1973) observed a large male *L. australis* feeding on ribbed mussels (*Aulacomya maoriana*) at the Auckland Islands and also saw many small weed-covered females which appeared to be feeding on red algae. He also observed females 3m up a *Macrocystis* stipe (see also Calcott 1970). Around the Auckland Islands this crab was relatively common.

L. australis is eaten by rig (*Mustelus lenticulatus*) caught off Kaikoura (King & Clark, 1984) and by red cod (*Pseudophycis bacchus*) in February from the Canterbury area, 2.3% of gut volume (Habib, 1975). Ritchie (1970) found one crab in the stomach of a notothenid fish captured at Campbell Island.

Glaessner (1960) has recorded three fossil species of *Leptomithrax*: *L.irirangi* from the lower pliocene and *L.atavus*, *L.uruti* from the upper miocene. These species appear to be more closely related to recent Australian species rather than recent New Zealand species of *Leptomithrax* (Griffin, 1966a).

References

Bennett (1964), Dell (1963a, 1963b), Griffin (1966a), Ritchie (1973).

Leptomithrax garricki Griffin, 1966
Garrick's Masking Crab

Synonymy

Leptomithrax garricki Griffin, 1966a; Dell, 1968a; Takeda & Miyake, 1969; Webb, 1972; Wear & Fielder, 1985 (list); Griffin & Tranter, 1986a (key).

Type Locality

Off Kaikoura, South Island, 785m.

Distribution

Cape Palliser to Kaikoura and eastward on Chatham Rise.

The 13 recent species of Leptomithrax are keyed out by Griffin & Tranter (1986a).

Diagnosis (Fig. 35a-g)

Carapace broadly subpyriform, inflated and weakly convex in profile, margins strongly spinous. Surface sparsely covered by short spines and tubercles, finely pubescent, slender hooked hairs fringing margins of rostral and marginal spines and in groups on protogastric and branchial regions. Rostrum of two short subconical spines, weakly convergent. Orbit consisting of supraorbital eave, intercalated spine and postorbital lobe, the three closely approximated. A small accessory tubercle on upper anterior edge of postorbital lobe. Margins of carapace with seven strong, outwardly directed spines, one postorbital, two hepatic and four branchials forming a semi-ellipse, the last distant from margin. Chelipeds very long, subcylindrical except for compressed propodus, merus and carpus covered on all surfaces by short spines. Fingers acute, moderately gaping for basal half in male, for entire length in female, inner edges finely toothed in both sexes. Legs of moderate length, cylindrical, smooth faintly pubescent. Abdomen of six segments and telson in both sexes.

Colour

Carapace yellowish-brown to greenish-white mottled with brick red. Tubercles on cheliped coloured with orange, inner surface reticulated with brick red. Irregular regions of pale orange on legs.

Size

Male 77mm CW, 100mm CL. Female 53mm CW, 67mm CL.

Habitat

Mud, rocks and sea anemones.

Depth

Edge of continental shelf and slope, 180-785m. L. garricki is one of our deepest-living spider crabs.

Breeding

Ovigerous females of L. garricki are unknown.

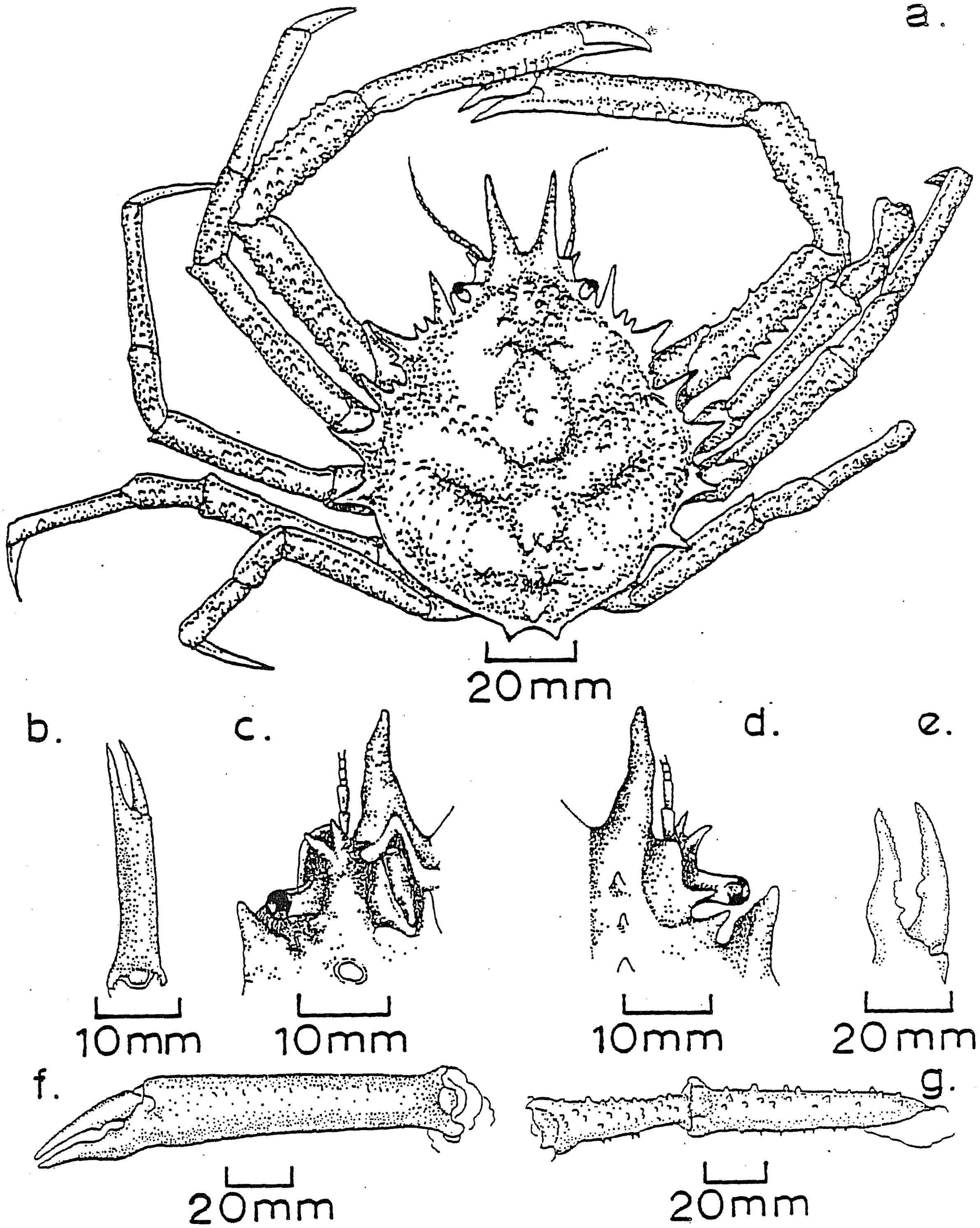


Fig. 35 - Leptomithrax garricki: a - male, dorsal view (by C. Duffy, based on a photo from Takeda & Miyake, 1969); b - left chela, female, outer face; c - orbit, ventral view; d - orbit, dorsal view; e - fingers, male cheliped; f - left chela, male, outer face; g - left cheliped, male, merus and carpus (after Griffin, 1966).

Development and Growth

Unknown.

Behaviour

Griffin (1966a) recorded that the carapace of the holotype male was completely covered by a single large sea anemone which was probably 'planted' by the crab. Hand (1975) has described the behaviour of *Leptomithrax longipes* towards the anemones *Calliactis conchicola* and *Paracalliactis rosea*.

Ecology

Unknown.

References

Griffin (1966a), Hand (1975), Takeda & Miyake (1969).

Leptomithrax longimanus Miers, 1876

Synonymy

Paramithrax (Leptomithrax) longimanus Miers, 1876a; 1876b; Leptomithrax longimanus Filhol, 1885d; 1886; Paramithrax (Leptomithrax) longimanus Rathbun, 1893b; Paramithrax (Leptomithrax) affinis Borradaile, 1916; Leptomithrax affinis Chilton & Bennett, 1929; Balss, 1929; Leptomithrax longimanus Chilton & Bennett, 1929; Richardson, 1949b; Leptomithrax affinis Richardson, 1949b; Leptomithrax longimanus Dell, 1963a; Leptomithrax (Leptomithrax) longimanus Bennett, 1964; Leptomithrax longimanus Griffin, 1966a; Dell, 1968a; Webber & Wear, 1981; Wear & Fielder; 1985; Griffin & Tranter, 1986a (key).

Type Locality

New Zealand.

Distribution

Endemic to New Zealand. Three Kings Islands to Stewart Island.

The 13 recent species of Leptomithrax are keyed out by Griffin & Tranter (1986a).

Diagnosis (Fig. 36a-d)

Carapace broadly pyriform, rostrum of two short spines weakly convergent. Short hooked hairs fringe margins of rostral spines and also occur on carapace borne on small rounded tubercles. Margins of carapace with six very short conical, equidistant spines, 1 postorbital, 1 hepatic and 4 branchial (the last subdorsal). Dorsal surface of carapace densely covered by small rounded tubercles. Chelipeds very long (2.2 times CL of adult male) covered on all surfaces by numerous small tubercles. Fingers acute, widely gaping in male and coarsely toothed along inner edges for distal halves of both fingers. Dactyl with a large tooth about one third from base, absent in female. Legs long and slender with a double row of opposing hooked hairs. First pair of legs longest, others decreasing in length. Abdomen of six segments plus telson in both sexes.

Colour

Dull yellowish brown body and legs. Chelipeds in adult males dark brown with yellowish markings on propodus. Females paler in colour.

Size

Male 49mm CW, 60.5mm CL. Female 34mm CW, 47.5mm CL.

Habitat

Occasionally found in rock pools but much more common offshore on muddy or sandy bottom associated with polychaetes, bivalve molluscs, sponges and bryozoans.

Depth

Intertidal (rarely) to 200m, occasionally to 550m.

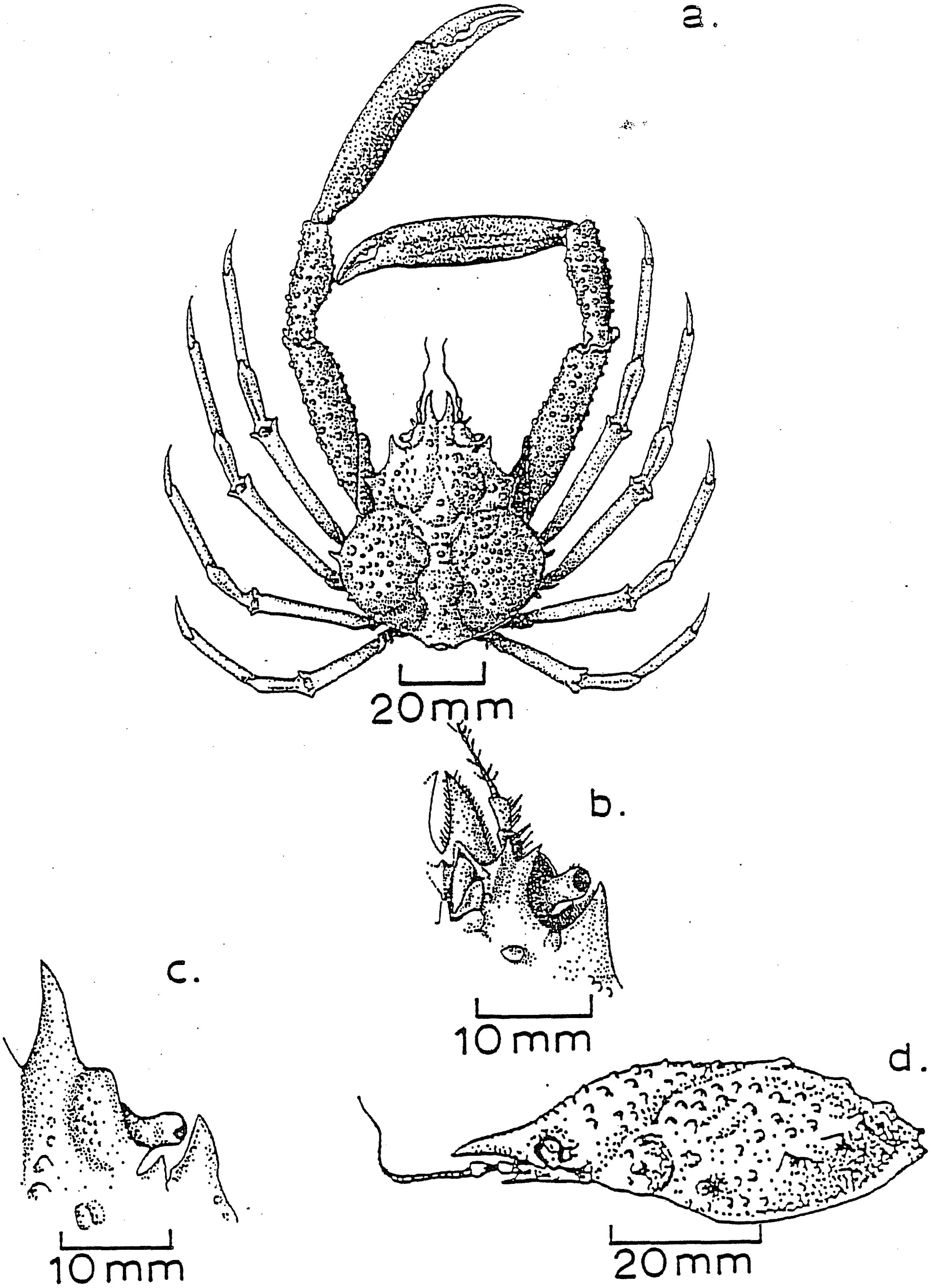


Fig. 36 - *Leptomithrax longimanus*: a - male, dorsal view; b - orbit, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Breeding

Ovigerous females found from October to April. New eggs are bright orange-yellow, 0.6mm diam., becoming dark brown, 0.63-0.65mm, before hatching.

Development and Growth

The pre-zoea and first stage zoea have been described by Webber & Wear (1981). Second zoea and megalopa unknown. Larval stages have not been collected in plankton (Wear & Fielder 1985).

Behaviour

Unknown.

Ecology

Carapace of adults often carries serpulid worm tubes and sponge.

Rig (Mustelus lenticulatus) from Tasman Bay and Kaikoura eat L.longimanus (King & Clark 1984). Red cod (Pseudophycis bacchus) from Banks Peninsula ate L.longimanus in October(1.2% of gut volume) and also red cod from Otago, February (0.11%) (Habib 1975). In Otago Harbour Crump(1969) observed over 200 Pateriella regularis feeding on a large crab although it is unlikely that these starfish killed it.

Glaessner (1960) has recorded three fossil species of Leptomithrax: L.irirangi from the lower pliocene and L.atavus, L.uruti from the upper miocene. These species appear to be more closely related to recent Australian species rather than recent New Zealand species of Leptomithrax (Griffin, 1966a).

References

Bennett (1964), Dell (1963a), Griffin (1966a), Hand (1975), Webber & Wear (1981), Wear & Fielder (1985).

Leptomithrax longipes (Thomson, 1902)
Long-legged Masking Crab

Synonymy

Paramithrax longipes Thomson, 1902b; Chilton, 1911a; Thomson, 1912; Thomas & Anderton, 1921; Chilton & Bennett, 1929; Young, 1929; Leptomithrax longipes Richardson, 1949b; Dell, 1960; 1963a; Leptomithrax (Zemithrax) longipes Bennett, 1964; Leptomithrax (Zemithrax) molloch Bennett, 1964; Leptomithrax longipes Griffin, 1966a; Dell, 1968a; Takeda & Miyake, 1969; Hand, 1975; Fenwick, 1978; Roper, 1979; Probert et al., 1979; Webber & Wear, 1981; Wear & Fielder, 1985; Griffin & Tranter 1986a (key).

Type Locality

Sixteen kilometres off Cape Saunders, 100m.

Distribution

Cook Strait to Foveaux Strait, Chatham Islands, Macquarie Island.

The 13 recent species of Leptomithrax are keyed out by Griffin & Tranter (1986a).

Diagnosis (Fig. 37a-d)

Carapace broadly pyriform, swollen and almost uniformly convex in profile, margins spinous. Dorsal surface covered by groups of large and small tubercles separated by large smooth areas. Elevated in midline as a ridge of numerous small closely spaced tubercles. Single blunt spine on posterior margin of carapace. Regions poorly defined. Short hooked hairs fringing inner margins of rostral spines and also present on carapace borne on small tubercles. Rostrum of two short dorsoventrally flattened spines, distally depressed. Orbit consisting of supraorbital eave intercalated spine and postorbital lobe, the three closely approximated and separated by narrow, deep fissures. Intercalated spine excluded from rim of supraorbital margin. Margins of carapace with a series of six short, conical spines: one postorbital, one hepatic and four branchials, the latter forming a semi-ellipse, the last subdorsal. A distinctive feature is a naked, median boss at junction of ischium and merus of third maxilliped. The remainder of the surface is densely covered by short hairs. Chelipeds of moderate length, subcylindrical except for compressed propodus, surfaces of merus and carpus partially covered by small tubercles. Fingers in male gaping moderately for basal half, toothed along inner edges, in female gaping for entire length meeting only at tips, finely toothed. Legs very long, slender. Abdomen of six segments and telson in both sexes.

Colour

Very pale yellowish white. Chelipeds and legs splotched with irregularly shaped patches of dark red, especially on inner surface of propodus.

Size

Male 71.5mm CW, 84mm CL. Ovigerous female 30mm CW, 42mm CL.

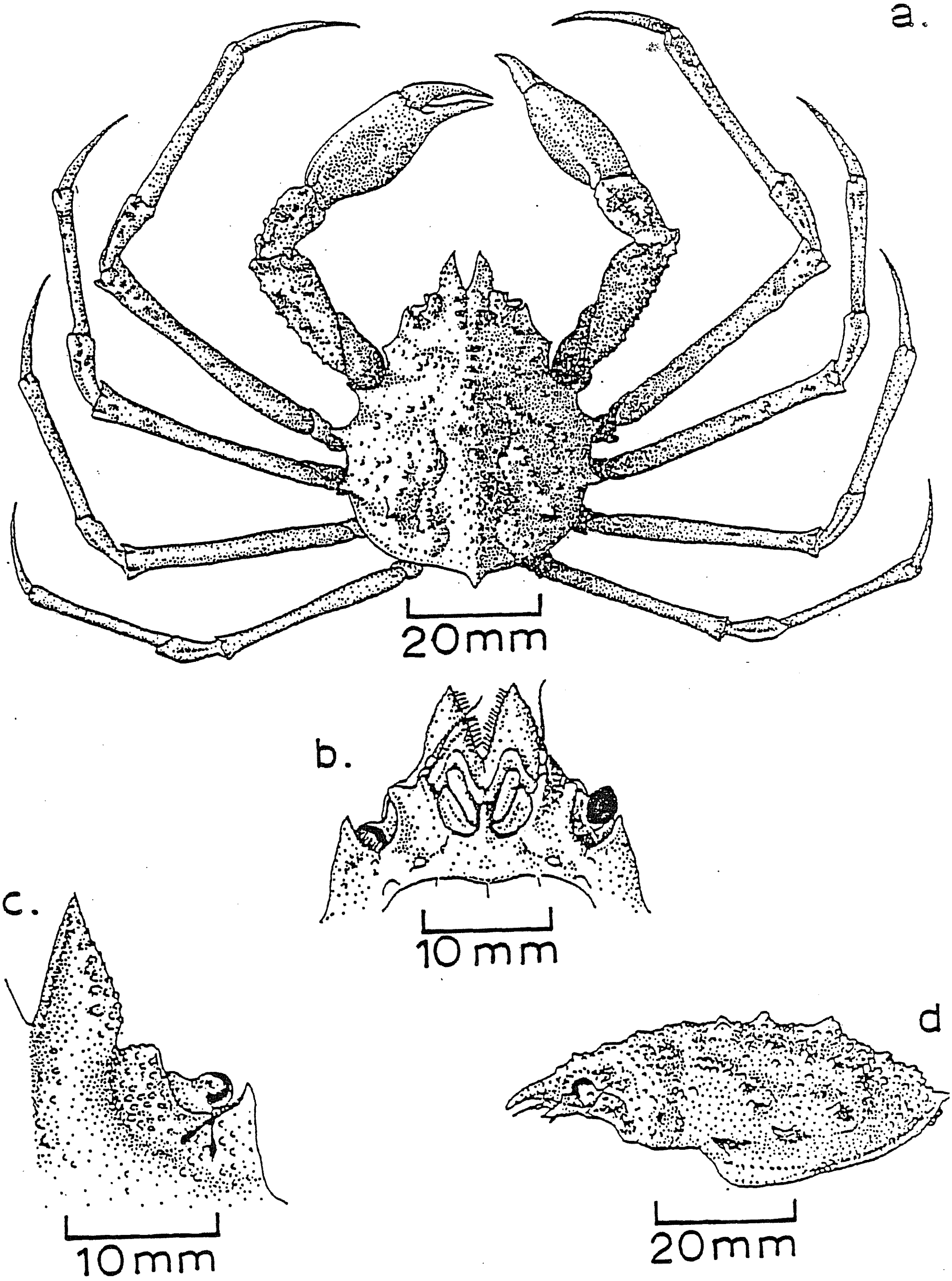


Fig. 37 - Leptomithrax longipes: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Habitat

Usually found on contintental shelf muddy or sandy bottoms in association with sponges, sea anemones, bryozoa and polychaetes.

Depth

On continental shelf, 20-380m.

Breeding

Ovigerous females have been collected September-March. Eggs are orange, size unknown.

Development and Growth

Two zoeal stages (Wear & Fielder 1985), megalopa unknown. The zoea of *L. longipes* differs considerably from those of other members of this genus (Webber & Wear 1981).

Roper (1979) measured growth of male propodus width relative to carapace length for *L. longipes* off Otago Peninsular. He found that propodus width increased gradually up to 45mm CL and then increased much more rapidly. A CL of 45mm was assumed to indicate the smallest size at maturity for males.

Behaviour

Hand (1975) reported that *L. longipes* carries specimens of four kinds of sea anemones: *Calliactis conchicola*, *Paracalliactis rosea*, *Bunodactis chrysobathys* and *Phellia aucklandica*. Of 256 male crabs 38 (14.8%) carried anemones on their carapaces and legs. Larger crabs tended to carry more and larger anemones. In touching a *Calliactis* with a dactyl, the crab moves over it, touching the anemone with its chelae and the walking legs. These actions usually cause the anemone to close. Prising the anemone loose involves placement of the tips of both chelae around the basal margin with the crab raising itself upwards and repeatedly pushing with the chelipeds. The pushing is not rhythmical but it eventually leads to insertion of one or both chelae between the substrate and the base of the anemone. Once the chelipeds are under the base the anemone quickly releases its hold whereupon the crab lifts it to its mouth. The anemone is manipulated by the chelae and slowly turned around against the maxillipeds. This cleaning activity seems to remove adherent debris from the anemone and may last for only a few minutes or more than 20 minutes. Following cleaning the crab holds the anemone in one chela and lifts it over on to the carapace or legs where it is held until it reattaches to the crab. During the cleaning process the anemone commonly expands almost fully. Before finally releasing hold of the anemone the crab will tug once or twice and then release it. If the anemone is unattached, it is returned to the mouth for further cleaning and then replaced on the carapace. Male crabs smaller than about 55mm CL and all females show little interest in planting anemones on their body. Given an abundance of anemones a large male *L. longipes* will cover itself in anemones except for the chelipeds. Once the available sites for attachment are occupied the crab ceases to respond to anemones it encounters. Removal of anemones renews the interest of the crab. When several crabs carrying anemones are placed together an interminable series of "robberies" is initiated. If small crabs with anemones are placed with large crabs, then all the anemones will end up on the large crabs! None of the four species of anemones listed above show any mounting response towards the crab, its isolated carapace or legs. Thus the anemones are a passive partner in the interaction. By contrast Calliactis and Paracalliactis both mount gastropod shells e.g. Austrofusus glans.

Hand (1975) conducted preliminary experiments with Octopus maorum to see whether Calliactis conchicola protected crabs against predation. When offered crabs with and without anemones those without anemones were rapidly consumed but the others were rejected when an arm of the octopus touched an anemone. However Calliactis does not seem to protect L. longipes from predation by rig Mustelus lenticulatus: John Ottway (see Hand 1975) found crabs bearing anemones in stomachs of these fish caught off Kaikoura. It is puzzling that females show little interest in the anemones. Lack of anemones on females in nature could be due to stealing by dominant males but even in the laboratory females do not pick them up. The low incidence of males with anemones (14.8%) may indicate that anemones are a resource in short supply.

Leptomithrax longipes also applies algae, sponges, hydroids and foreign objects such as bits of paper to itself (Hand 1975). These are picked up, sometimes torn or cut into smaller pieces by the chelae, mouthed and placed on the carapace and legs. The bits are trapped among the hooked hairs by skillful use of the chelipeds. This behaviour is similar to that shown by Notomithrax ursus and results in a mask of camouflage rather than detering predators. Other epizoites such as barnacles, oysters, tubiculous polychaetes and ascidians also colonize the crab's surface and provide camouflage.

Ecology

Hand (1975) sampled the L. longipes population off Otago Peninsula and of 833 specimens, 256 (30.7%) were males and 498 (59.8%) were females but 79 (9.5%) were of indeterminate sex. The ranges of CL of the crabs were: males 28-82mm, females 35-59mm and indeterminate 19-60mm. These observations led Roper (1979) to investigate why some crabs possessed a combination of female and male characters. He found that the sex ratio was different in different areas. Higher densities were recorded in deeper water near the edge of the continental shelf where the sex ratio was 1 male:21 females, but inshore the ratio was 10 males:1 female. Also immature females and mature males tend to be found inshore and mature females offshore. This suggests inshore transport of larvae, settlement in coastal waters and offshore migration of females to deeper water as they mature. Roper (1979) found a much lower percentage (only 1%) of crabs of indeterminate sex. They occurred at most depths greater than 33m. These had both male and female pleopods, closed female genital openings, small chelipeds and an oval abdomen resembling a young female. The gonad was similar to a normal female but sometimes spermathecae were absent. Tissue and blood smears contained a rod shaped bacterium not found in normal crabs. Roper suggested that the bacterium may have caused the feminisation of male crabs by upsetting hormone balance. Unfortunately these crabs were not kept alive to see whether they became sexually mature.

L. longipes off Kaikoura is eaten by rig (Mustelus lenticulatus) (Hand 1975) and also recorded from the same fish caught off Banks Peninsula by King & Clark (1984). Red cod (Pseudophycis bacchus) from the east coast of the South Island also eat significant amounts of L. longipes: October (0.5% of gut volume), November (2.8), December (7.2) and February (3.8) from the Canterbury area, February (0.11) from the Otago area and May (0.1) from Cloudy Bay-Cape Campbell area (Habib, 1975). Godfriaux (1974a) reported L. longipes (<.01%) in tarakihi (Cheilodactylus morocropterus) guts from Western Bay of Plenty but since this is well outside the known range for L. longipes it is likely that this is an error and perhaps refers to L. longimanus.

Glaessner (1960) has recorded three fossil species of Leptomithrax: L.irirangi from the lower pliocene and L.atavus, L.uruti from the upper miocene. These species appear to be more closely related to recent Australian species rather than recent New Zealand species of Leptomithrax (Griffin 1966a).

References
Griffin (1966a), Hand (1975), Roper (1979), Webber & Wear (1981), Wear & Fielder (1985).

Leptomithrax tuberculatus mortenseni Bennett, 1964

Synonymy

Leptomithrax (Austromithrax) mortenseni Bennett, 1964; Leptomithrax tuberculatus mortenseni Griffin, 1966a; 1966b; Dell, 1968a; Wear & Fielder, 1985; Griffin & Tranter, 1986a. This is regarded as a sub-species of Leptomithrax tuberculatus (Whitelegge 1900) from eastern Australia.

Type Locality

Off Little Barrier Island, Hauraki Gulf, 60m.

Distribution

This species occurs in south-eastern Australia and is represented in New Zealand by a sub-species. Kermadec Islands, northern part of New Zealand from Cape Maria van Diemen to Hauraki Gulf.

The 13 species of Leptomithrax are keyed out by Griffin & Tranter (1986a).

Diagnosis (Fig. 38a-e)

Carapace narrowly pyriform, rostrum of two moderately short, weakly divergent, sharp spines. Hooked hairs fringing margins of rostral spines and scattered in groups on carapace. Margins of carapace with six spines : 2 hepatic and 4 branchials, all conical and outwardly directed except the last. Hepatic spines very short. Chelipeds naked, moderately long (1.1 times CL in male), fingers acute with an oval gape basally, inner edges finely toothed for distal two-thirds in male, smooth in female. Fixed finger has a small tubercle at base in male (not in female), dactyl with a slightly more distal tubercle. Legs moderately long, slender, smooth, dorsal groups of hooked hairs except on dactyl. First leg longest, others decreasing in length. Abdomen of six segments plus telson in both sexes.

Colour

Uniformly white when preserved.

Size

Male 23mm CW, 33.5mm CL. Female 18.5mm CW, 26.5mm CL.

Habitat

Among sponges and bryozoans on rough bottoms.

Depth

Upper continental shelf, 10-100m.

Breeding

Ovigerous females have been collected in November to February. Eggs newly laid are orange, 0.6mm diam. and when ready to hatch, 0.78 x 0.72mm.

Development and Growth

Two zoeal stages (Wear & Fielder 1985), megalopa unknown.

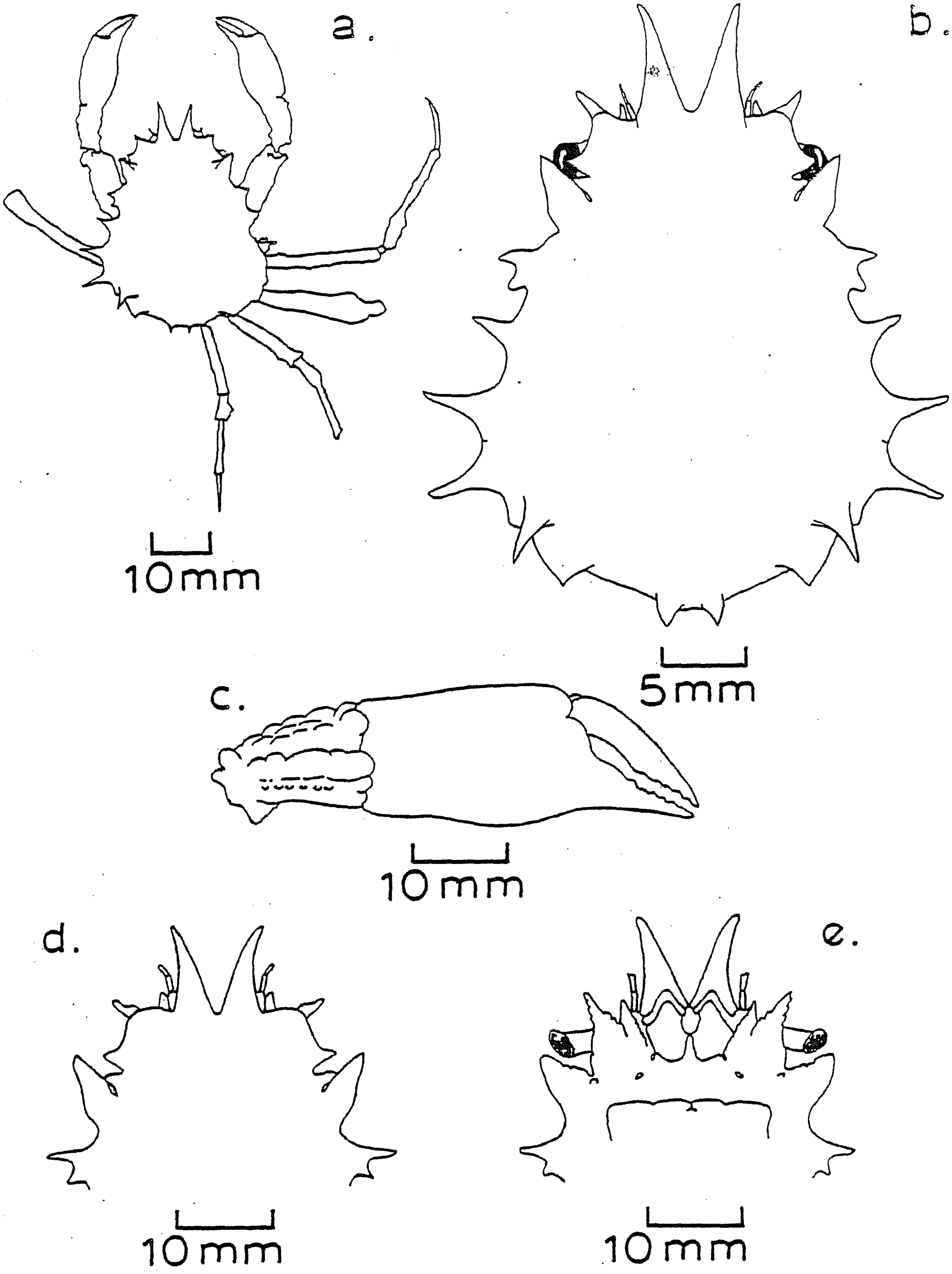


Fig. 38 - Leptomithrax tuberculatus mortenseni: a - male, dorsal view; b - carapace, dorsal view (by J. Black, based on a photo from Bennett, 1964); c - right chela, male, outer face; d - anterior end, dorsal view; e - anterior end, ventral view (modified, after Bennett, 1964).

Behaviour

It is not known whether this species has the normal spider crab masking behaviour. Bennett (1964) states that these crabs are free from attached organisms except for small quantities of sponge, serpulids and bryozoans.

Ecology

Unknown.

References

Bennett (1964), Dell (1963a), Griffin (1966a,1966b), Wear & Fielder (1985), Whitelegge (1900).

Teratomaia richardsoni (Dell, 1960)
Spiny Masking Crab

Synonymy

Leptomithrax richardsoni Dell, 1960; 1963a; Griffin, 1966a; Griffin & Brown, 1976; Wear & Fielder, 1985 (list); *Teratomaia richardsoni* Griffin & Tranter, 1986a; 1986b.

Type Locality

Chatham Rise, between Banks Peninsula and Chatham Islands, 44°04′S, 178°04′W, 500m.

Distribution

Endemic to New Zealand, known from Chatham Rise and off Milford Sound.

Diagnosis (Fig. 39a-f)

Carapace pyriform, margins and dorsal surface set with moderately long, conical spines and sparse raised tubercles. Numerous fine curled hairs. Dorsal surface of carapace with three subequal median spines, and four pairs of submedian spines or tubercles. Regions moderately well defined. Rostrum of two long slender, acuminate divergent spines. Orbit consists of supraorbital eave bearing a preorbital and antorbital spine, intercalated spine and postorbital lobe which has two small tubercles on the posterior edge near base. Margins of carapace with eight prominent, outwardly directed spines: two orbital, two hepatic and four branchial (fourth spine subdorsal). A single large, sharp spine on the posterior margin of the carapace. Chelipeds long (especially in male), slender, merus and carpus strongly tuberculate. Fingers acute, very coarsely toothed along inner edges, moderately gaping basally in male, adjacent in female, a large basal tooth on both fixed finger and dactyl. Legs of moderate length, cylindrical, first legs longest. Abdomen of six segments and telson in both sexes.

Colour

Dull creamy white (preserved material).

Size

Male 48m CW, 65mm CL. Female (ovigerous) 40mm CW, 53mm CL.

Habitat

Fine sandy mud bottoms in deep water.

Depth

310-610m.

Breeding, Development and Growth, Behaviour

Unknown.

Ecology

Mitchell (1984) recorded *L. richardsoni* from the guts of ling (*Genypterus blacodes*) captured on the Chatham rise (125-177m).

References

Dell (1960,1963a), Griffin (1966a), Griffin & Tranter (1986a).

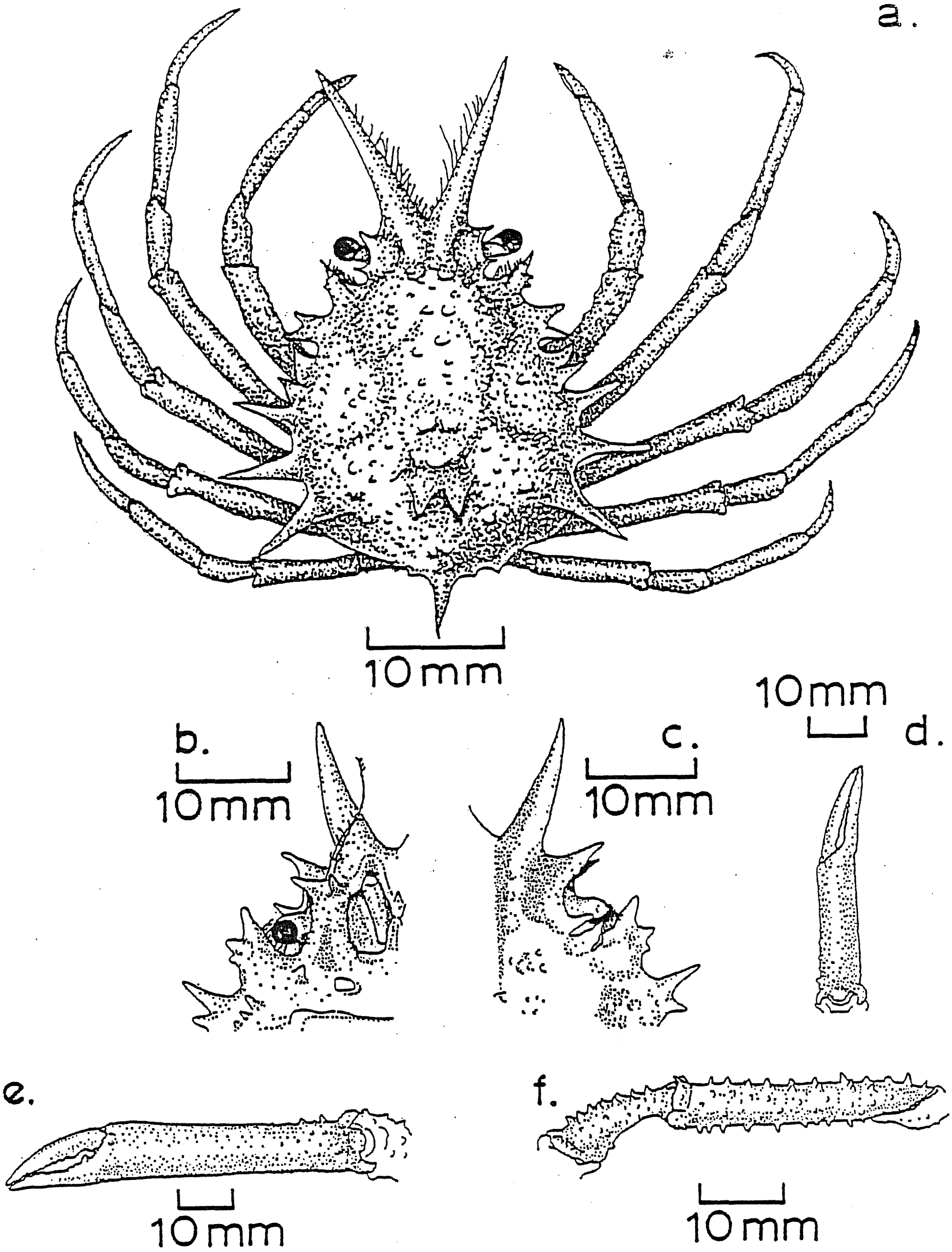


Fig. 39 - Teratomaia richardsoni: a - female, dorsal view (by C. Duffy, based on a photo from Dell, 1960); b - orbit, ventral view; c - orbit, dorsal view; d - right chela, female, outer face; e - left chela, male, outer face; f - left chela male, merus and carpus (after Griffin, 1966).

Thacanophrys filholi (A.Milne Edwards, 1876)
Plate-Backed Crab

Synonymy

Acanthophrys filholi A.Milne Edwards, 1876; *Acantophrys filholi* Filhol, 1885d; *Chlorinoides filholi* Miers, 1886; *Acanthophrys filholi* Chilton, 1911a; Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Richardson, 1949b; Dell, 1960; 1963a; Bennett, 1964; *Chlorinoides filholi* Griffin, 1966a; Dell, 1968a; Takeda & Miyake, 1969; Probert et al., 1979; Wear & Fielder, 1985; *Thacanophrys filholi* Griffin & Tranter, 1986a (key).

Type Locality

Stewart Island, deep rock pool.

Distribution

Endemic to New Zealand. North, South and Stewart Islands. Mainly southern, including Chatham Islands and Auckland Islands, but also recorded 16 km North-West of Cape Maria van Diemen, off West King, Three Kings Islands.

The 12 species of *Thacanophrys* are reviewed by Griffin & Tranter (1986a).

Diagnosis (Fig. 40a-d)

Carapace narrowly pyriform (pear-shaped), rostrum of two long, sharp, widely divergent spines fringed with hooked hairs. Dorsal surface of carapace with spines, tubercles and hooked hairs. There are three median spines and two prominent mesogastric spines at the posterior end. Margins of carapace with eight spinous or lamellate lateral projections: 4 supraorbital, 1 hepatic and 3 branchial. Chelipeds long (about 1.5 times CL of adult male), crested and naked. Fingers acute, gaping basally, coarsely toothed along inner edges for entire length. Legs of moderate length, much shorter than chelipeds and slender. Long, hooked hairs scattered in groups along dorsal and ventral surfaces. Abdomen of six segments plus telson in both sexes.

Colour

Carapace and legs orange. Chelipeds reddish orange, propodus red, dactyl purple.

Size

Male 39mm CW, 58.5mm CL. Female (ovigerous) 30mm CW, 43.5mm CL. Smallest ovigerous female 22.3mm CW, 30.8mm CL.

Habitat

On sand, mud or muddy gravel among seaweed and sponges. Often covered with large sponges, polychaete tubes, encrusting bryozoa and brown algae.

Depth

Continental shelf, 25m to 550m, most common between 75 and 150m.

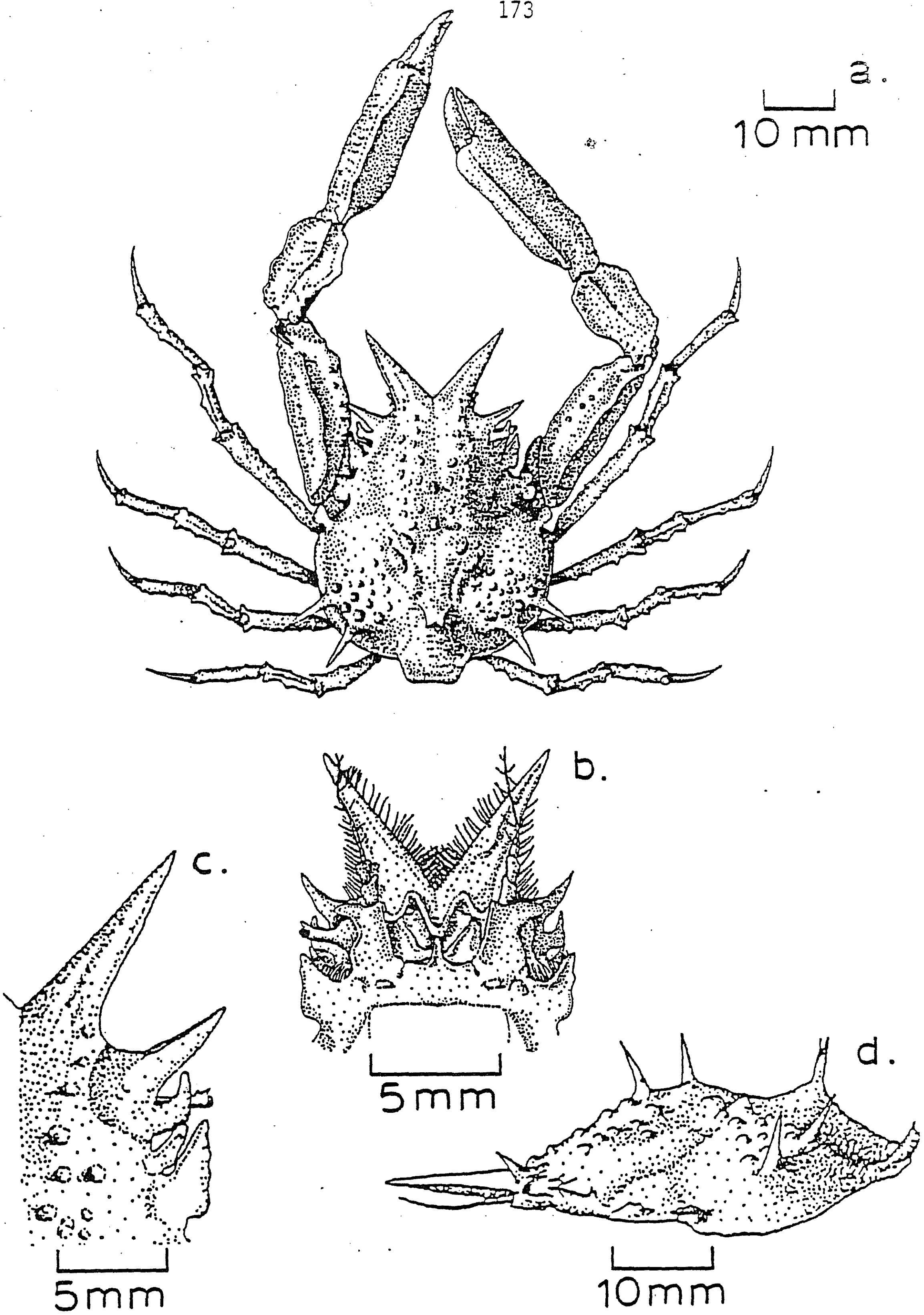


Fig. 40 - *Thacanophrys filholi*: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Breeding

Ovigerous females found from March to July.

Development and Growth

Unknown.

Behaviour

T.filholi shows the masking behaviour typical of spider crabs although the presence of large sponges suggests that turnover of the camouflage may only be intermittent.

Ecology

Often heavily covered with polchaete tubes.

References

Bennett (1964), Dell (1963a), Griffin (1966a), Takeda & Miyake (1969), Griffin & Tranter (1986a).

Jacquinotia edwardsii (Jacquinot, 1853)
Jacquinot's Southern Spider Crab

Synonymy

Prionorhynchus edwardsii Jacquinot, in Jacquinot & Lucas, 1853; Miers, 1876b; Filhol, 1886; Rathbun, 1892; Paramicippa grandis Hector, 1899; Prionorhynchus edwardsii Hodgson, 1902; Chilton, 1909; 1911a; Thomson, 1912; Thomson & Anderton, 1921; Stephensen, 1927; Chilton & Bennett, 1929; Campbellia kohli Balss, 1930; Jacquinotia edwardsii Balss, 1930; Richardson, 1949b; Campbellia kohli Richardson, 1949b; Jacquinotia edwardsii Griffin, 1963a; Campbellia kohli Bennett, 1964; Jacquinotia edwardsi Dell, 1963a; Bennett, 1964; Jacquinotia edwardsii Griffin, 1966a; Inoue, Arai & Abe, 1968; Dell, 1968a; Ritchie, 1970; Roberts, 1972b; Webb, 1972; Ritchie, 1973; Rae, 1974; Fenwick, 1975; Yaldwyn, 1975; Ryff & Voller, 1976; Yaldwyn & Beu, 1977; Fenwick, 1978; Griffin & Tranter, 1986a.

Type Locality

Auckland Islands.

Distribution

Southern New Zealand (northern limit, Kaikoura Peninsula), Stewart Island, Chatham Island, Auckland Islands, Pukaki Rise, Snares Island, Campbell Island, Bounty Is.

In the early pleistocene (1.8m yr. ago) J.edwardsii extended as far north as the latitude of Napier when the cold Southland current flowed further up the coast making sea surface temperatures 4^{0} lower than at present (Beu, Grant-Taylor & Hornibrook 1977). At present J.edwardsii does not extend further north than the sub-tropical convergence off the Kaikoura coast. The best preserved structures are the large fingers on the chelae found in limestone rocks. These fossils have been collected on land and also from eroded material deposited in the sea off the Kaikoura coast.

Diagnosis (Fig. 41a-d)

Carapace very broadly pyriform, swollen and almost uniformly convex in profile, surface granular and weakly tuberculate. A few large tubercles scattered along midline and on branchial regions. Rostrum short, strongly deflexed, flattened, wide basally, consisting of two lobes fused for almost their entire length, separated only by a small V-shaped indentation at the tip. Orbit consisting of supraorbital eave, intercalated spine and postorbital lobe, all three adjacent, not separated by fissures. Eye stalk concealed in both dorsal and ventral view when retracted. This results from the expansion of the basal antennal article to form a floor to the orbit. Margins of carapace ornamented by a series of seven conical, spinous tubercles, two hepatic and five branchial branchiols forming a semi-ellipse, last two subdorsal. Chelipeds very long, subcylindrical except for compressed propodus, surfaces granular. Merus long, carpus smaller, propodus almost half total length of cheliped. Merus and carpus with tubercles scattered all over surface. Palm very high in male, fingers acute, bluntly toothed or smooth, moderately gaping for entire length in both sexes.

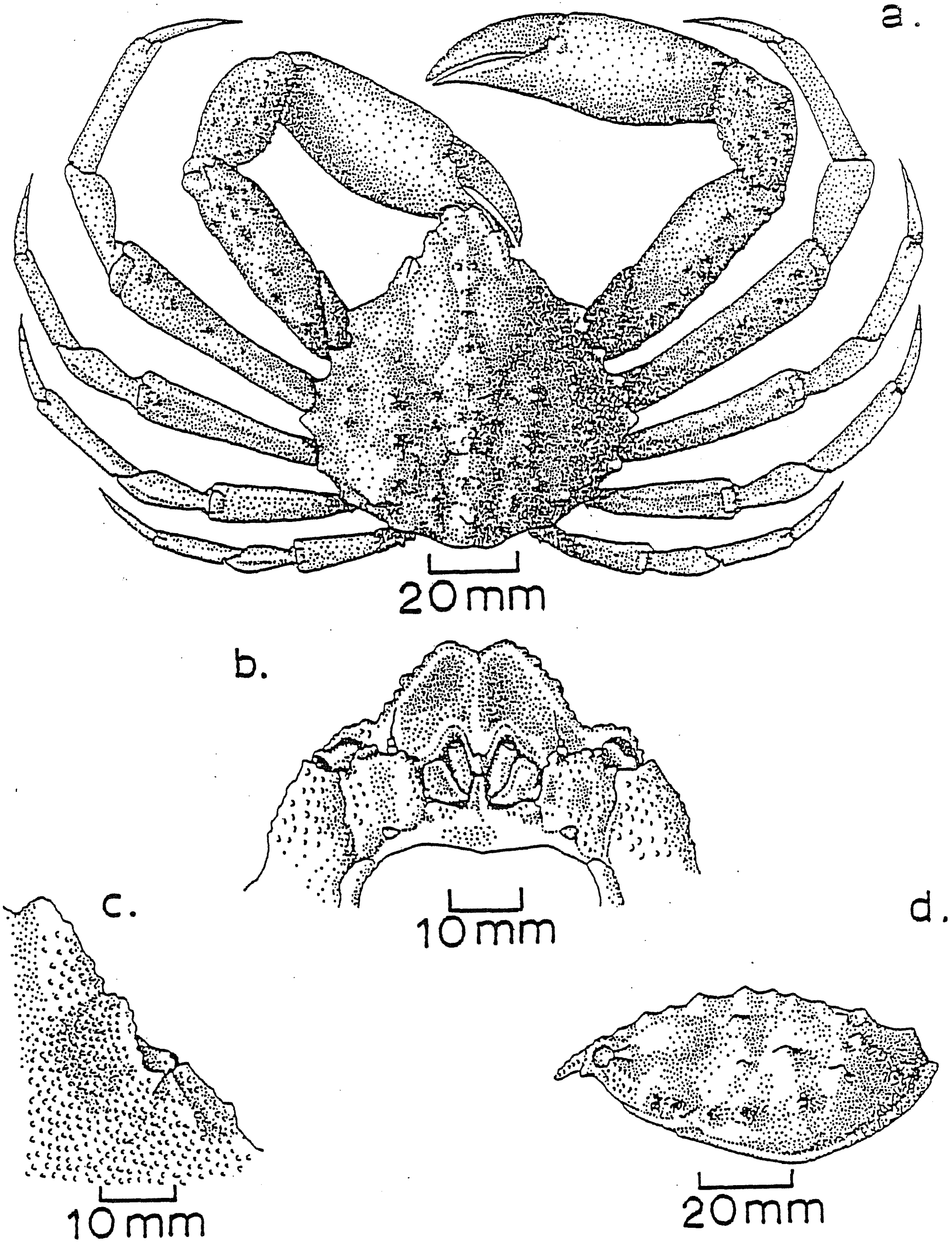


Fig. 41 - *Jacquinotia edwardsi*: a - male, dorsal view; b - anterior end, ventral view; c - orbit, dorsal view; d - carapace, lateral view (after Griffin, 1966).

Legs very long, stout, minutely granular. First leg longest. Abdomen of six segments plus telson in both sexes.

Colour

Carapace brick red, chelae brighter red to yellowish white, often marbled or blotched with red on outer surface.

Size

Male 200mm CW, 220mm CL. Female 128mm CW, 144mm CL.

Habitat

On offshore islands, found in rockpools among seaweed at certain times, even walking over intertidal rocks, also in deeper water on sandy bottoms. J.edwardsii is a southern, stenothermal, cold-water species.

Depth

Intertidal down to 550m.

Breeding

Egg-laying occurs from September to February (probably concentrated in late September - early October) but ovigerous females are found throughout the year because eggs are carried by the female for almost 12 months. Eggs newly laid are orange-yellow, mean diameter 0.94mm, swelling to 1.0 x 1.4mm when ready to hatch the following year. Thus only one batch of eggs is produced each year and the interval between release of one lot of eggs and extrusion of the next batch of eggs is very short. A female of 101mm CL carries about 37,500 eggs and a female of 126mm, about 71,200 eggs (Ritchie 1970). Egg numbers increase at approx. 10,500/cm CL.

In the Tanner Crab Chionoecetes bairdi primiparous females are approximately 70% as fecund as equal-sized multiparous females. A 100mm CW multiparous female carries about 220,000 eggs whereas a primiparous female carries only 150,000 eggs. This is because primiparous females (reproducing for the first time) moult and grow before extruding eggs, whereas multiparous females do not moult (Somerton & Meyers 1983). As in J.edwardsii eggs are incubated for almost 12 months so that only one clutch per year is possible. Wickham (1986) recorded nemertean egg predators from C.bairdi but these worms have not been reported from New Zealand.

Development & Growth

Although eggs may be laid in September there are no signs of development until February (5 months later) when sea temperatures reach their maximum (10.5°C). Sea temperature increase may trigger development (Ritchie 1973). There are two zoeal stages but the megalopa is unknown (Webber and Wear 1981). Zoeae probably occur in the plankton during the period September-November (Roberts 1972b). Larvae of Chionoecetes spp. are pelagic for about 90 days (Jamieson 1986).

Some aspects of relative growth have been studied by Webb (1972) whose log/log regressions suggest that carapace width and length are isometric ($b = 0.923$) while length of the first leg and cheliped are negatively allometric ($b = 0.79, 0.83$) in relation to carapace length for males. Ritchie (1973) also measured some Auckland Island specimens but did not measure relative growth. Males reach maturity at 110mm CL and females 100mm CL (Ritchie 1970). For crabs >140 mm CL weight increase is fairly linear with CL. Males reach 3600 grams wet weight at 220mm CL and females reach 765gm at 140mm CL.

Three colour phases are recognizable: 1) dark phase with prolific epizoic growth (Lithothamnion, Rhodophyceae, Pomatoceros, Balanus and bryozoa), 2) intermediate phase with a small amount of encrusting organisms, and 3) light phase with no encrusting organisms. Dark phase crabs have obviously not moulted recently and are probably post-pubertal. Like other spider crabs the moult in which maturation by female J. edwardsii is achieved is probably terminal (Hartnoll 1963). No newly forming integument was found under the old integument of dark phase crabs. By contrast light phase crabs are recent moults. Data from the Auckland Is. population suggest that in February 25% of females and 37% of males were light phase (Ritchie 1970). Moulting is probably continuous from November to March. Nothing is known about increment at each moult or intermoult intervals so it is impossible to estimate the maximum age achieved.

In male Chionoecetes bairdi growth increments decrease from 35% (20mm CW) to 15% (130mm CW), 50% of females moult to maturity at 83mm (instar 13) and males mature around 110mm CW, instar 14 or 15 (Donaldson, Cooney & Hilsinger 1981). Whereas females reach their maximum size at around 83mm, in about 5 years, males continue to moult through 18 instars to over 200mm CW and may live for about 12 years. Males become sexually mature about 1 year before they can be legally exploited (Jamieson 1986) but there are regional variations in size of male maturity (Somerton 1981b). Male and female snow crabs, C.opilio, both mature at smaller sizes (Watson 1970). Examination of setae on the maxilla can be used for moult staging (Moriyasu & Mallet 1986). Fecundity of C.opilio decreases with increasing latitude and egg size is larger (Jewett 1981).

Behaviour

Ritchie (1970, 1973) has made extensive observations of pot-caught crabs as well as underwater at the Auckland Islands. J.edwardsii show a disjunctive sex distribution with females and pre-puberty males in shallow water, close to shore, and large mature males in deeper water. Males seen to be migratory, moving inshore in spring (September - November) to pair up with females. At this time crabs may come ashore. Some large males have been tagged and recovered in approximately the same place but they were only at liberty for a few days (see also Ryff & Voller 1976). This separation of males and females makes sex-ratio estimation difficult. An extended and complicated interaction in the spring occurs between male and female Chionoecetes opilio. The male assists with moulting, provides protection, obtains food and assists with larvae release making the female very dependent upon the male (Watson 1971,1972, Hooper 1986).

During pair formation in J.edwardsii there is considerable loss of legs by females. The male clasps the female by one of her legs and sometimes she is carried around beneath the male. Males contest each other for females and two males grasping a female in a tug-of-war often results in her losing a leg. Of females missing legs, 38.4% had lost one leg, 24.4% (two), 14% (three), 10.5% (four), 5.8% (five) and 1.2% (eight). Some females had even lost both chelipeds. By contrast only 11% of males had lost one limb, 1% (two limbs) and 9% had lost one cheliped. Female leg loss is cumulative because mature females do not moult and therefore cannot regenerate lost limbs. Clasped females made no attempt to escape from the male. Similar observations have been made on the Snow Crab, Chionoecetes opilio, off Newfoundland (Hooper 1986). Growth per moult and limb regeneration of this species has been investigated by Miller & Watson (1976). Pairs of J.edwardsi caught in pots usually involved spent females (80%) but others were in new berry (8.6%) and old berry (11.4%). These results suggest that there is pre-copulatory male guarding and possibly post-copulatory guarding. Males clasping females with new eggs may be a pot-artifact since they are probably not receptive and these couplings usually involved small males.

Copulation by J. edwardsii has been observed underwater by Ritchie (1973). One pairing occurred while the crabs were fully exposed on a sandy bottom. The male was much larger (CW = 182mm) than the female (CW = 102mm) which was carrying mature eggs. The male raised his body into a vertical position, with his abdomen in a shallow depression in the sand, and clasped the female using his massive chelae and last pair of legs. The female rested upon his abdominal flap and with her own abdomen extended was inseminated by the male. Thus both crabs were vertical rather than one being underneath the other as is common in other species. Furthermore both crabs were in the hard-shell condition so that the female must have been a multiparous crab. Similar copulatory activity has been observed in captivity for the African spider crab Pleistacanthia moselevi (Berry & Hartnoll 1970). In Chionoecetes bairdi Paul & Adams (1984) found that the fertile period for primiparous females ranged from less than 1 to 28 days. Multiparous females either use sperm stored from a previous mating or mate prior to egg extrusion. These crabs are only receptive to breeding from less than 1 to 7 days. Paul (1984) found that ten was the maximum number of multiparous females that could be mated by a single male. Sperm remain viable in the female for up to two years after mating. Males from 65-104mm CW are competent to fertilize the initial and subsequent clutches from a single insemination (Adams & Paul 1983). These facts are important because only male Tanner Crabs are taken by the Fishery and sufficient males must be left to ensure that all females are mated .

Bennett (1964) and Ritchie (1970) have recorded several instances of "mounding" behaviour which seems to be associated with moulting and mating. Large aggregations have been recorded in spring and these seem to be associated with mating. In March immature and moulting crabs of both sexes form large clumps which are surrounded by large males on the outside. This seems to provide protection for the soft crabs. These observations and those reported above suggest that J.edwardsii females mate either when they are soft-shelled (i.e. primiparous) or hard-shelled (i.e. multiparous). Hartnoll (1969) has found that Hyas coarctatus and Maja squinado copulate in both the hard- and soft-shell state. When a H.coarctatus male mates with a hard-shell female the liaison is very short with no post-copulatory guarding, but when he mates with a soft-shell female he may carry her around for several days. The situation in J.edwardsii is unclear because we do not have enough information. However at least some majid crabs would seem to depart from the standard brachyuran pattern of being either hard-shell or soft-shell maters but not both.

With modifications to the proposal of Ritchie (1973) the annual cycle of events in the J.edwardsii population at the Auckland Islands consists of:

1) Pair formation of males and females in Spring, September-November.

2) Copulation during September-November when primiparous females moult to maturity and multiparous females have released their larvae.

3) Egg-laying September-February, with a peak probably in late September-early October.

4) Egg development delayed until after February.

5) Main moulting period (both pre-puberty moults and perhaps pubertal males) in March.

6) Larval release in September-November with a probable peak in late September.

Depths at which recruitment of J.edwardsi juveniles occurs is unknown but it may be similar to Chionoecetes opilio and C.bairdi in which juveniles settle in deeper water (Brethes et al. 1987).

Ecology

Male, female and juvenile J.edwardsii seem to have different feeding behaviours (Ritchie 1973). Large males have been observed feeding on ribbed mussels (Aulacomya maoriana) and probably also feed on other shellfish such as Mytilus, Mactra, Haliotis, Maurea and Struthiolaria. Although both males and females enter baited pots, only males have been observed feeding on the fish bait. The largest males seem to have priority in feeding, forming a 'peck order' over smaller males. A male would often have a female clasped in one claw and be feeding with the other claw. By contrast, females are detritus feeders, on sandy bottoms, moving slowly forwards with legs semi-buried and picking up minute detrital particles using both chelae. Juveniles of both sexes seem to feed on drift algae (red gelatinous and filamentous algae) especially in shallow water around dusk. Juveniles are rarely caught in pots.

Near Kodiak Island, Alaska, Chionoecetes bairdi are highly cannibalistic, eating juvenile C.bairdi, as well as other Crustacea (shrimps, pagurids), fishes, molluscs (mainly the bivalves Macoma spp. and Yoldia spp.) and polychaetes but there were no significant differences between the sexes. Significant differences were apparent in quantity of food consumed between times, areas, depths, size groups and crab exoskeleton classes (Jewett & Feder, 1983).

At the Auckland Islands sea lions (Neophoca forsteri) are the most important predator of J. edwardsii. Large numbers of soft-shelled crabs are eaten during the moulting period in March (Falla 1970). Fish predators have only been rarely recorded: Habib (1975) found J. edwardsii in guts (2.0% of gut volume) of red cod (Pseudophycis bacchus) caught off Banks Peninsula in April.

The existence of a large resource of crabs in southern New Zealand waters was first discovered in 1968 by fishing vessels sailing to the Auckland Islands in search of new crayfishing grounds (Rae 1974). Further investigation was carried out by Ritchie (1970, 1973) and Ryff & Voller (1976) with some incidental data coming from the study of Webb (1972) of crabs off the west coast of Stewart Island. Commercially takeable crabs have been defined as those with CL 140mm (i.e. CW 120mm or 765gm wet weight) or larger. This effectively excludes females which do not reach this size. The best type of pot is one about 1.6 x 1.6 x 0.75m, covered with coarse (10cm x 7.5cm) mesh, with a throat at each end and baited with fish carcasses. Poor catches have been recorded at Campbell Island, where takeable crabs are in deep water and localized, also Bounty Islands, but good catches have been made at Auckland Islands and on the Pukaki Rise where crabs have been taken from 452m depth. Catch rates of up to 235 crabs/10 pots have been achieved in shallow water but catch rates decline with depth although the percentage of takeable crabs increases. On the Pukaki Rise catch/unit efforts have reached 59kg/10 pots and meat recovery is in the range of 15-20% by weight. Most of the meat is in the large chelae. Length of fishing did not affect catches when all sizes and both sexes occurred but where large males predominated long fishing periods (20-28 hrs) produced bigger catches than short periods (1-12 hrs). The sex ratio in catches depends upon pot mesh-size and depth of fishing. Working 40 pots, 2 tons of takeable crabs could be caught per day and 2-3 tons/week on a voyage should be possible (Ritchie 1970).

While some J.edwardsii have been landed and sold in the South Island occasionally, no effort has been made to make regular catches. There has been strong Japanese interest in the crab resource with some catches being marketed there. Ritchie (1973) made some management recommendations which limited the Auckland Island fishery to only 3 licences each covering up to 2 boats. However Ryff & Voller (1976) recommended that the Auckland Island fishery be closed to commercial fishing until the population biology of J.edwardsii is more clearly understood. At present we know very little about growth and age and nothing about recruitment. Hence sustainable yields are unknown. If the fishery concentrated on males only then the research on competence of Chionoecetes males discussed above will be very relevant. Another management problem results from the fact that the Pukaki Rise area is outside our 200ml EEZ in international waters where management regulations could not be enforced.

References

Dell (1963a), Fenwick (1975), Griffin (1966a), Griffin & Tranter (1986a), Ritchie (1970, 1973), Ryff & Voller (1976), Webb (1972), Yaldwyn & Beu (1977).

Pteropeltarion novaezelandiae Dell, 1972

Synonymy

Pteropeltarion novaezelandiae Dell, 1972.

Type Locality

Campbell Plateau, 49°34.5'S, 170°51'E, 499m.

Distribution

In deep water from the latitude of Auckland (37°S) to south of Stewart Island (50°S), both west and east coasts from 169° to 176°E.

Diagnosis (Fig. 42a-e)

Carapace pentagonal with a simple, long lateral spine on each side and a moderately elongate rostrum. The rostrum is flattened, about one-fifth of CL, terminating in three broad spines (laterals longer than the central spine), and bearing a group of long, slender, stiff hairs terminally. Carapace surface finely granular, especially towards margins. Orbit marked by a weak, blunt supra-orbital spine and a more strongly developed post-orbital spine. Chelipeds in adult females and sub-mature males sub-equal in size although even in females the right cheliped is enormously developed. Legs long and slender, set with a row of feathery branched hairs along the upper surface, dactylus with two rows of stiff, short hairs. Male and female abdomens of six segments plus telson.

Colour

White when preserved.

Size

Holotype male 24.5mm CW (including spines), 16.8mm CL (including rostrum). Female 22mm CW, 16.6mm CL.

Habitat

Deep water muddy substrates. The shape of this crab, elongate rostrum, and forwardly-placed mouth-frame suggests that this crab may burrow into soft substrates.

Depth

Deep water on the continental slope 499-903m.

Breeding

Ovigerous females have been collected in October and January. One female (size not given) carried 12 eggs and another female (22mm CW, incl. spines) carried 57 eggs, many pushed out beyond the abdomen. Preserved eggs are light brown and large (up to 1.5mm diameter) which may indicate direct development (Dell 1972). Another specimen in the N.Z.O.I. collection, 21.7mm CW, carried 78 eggs, diameter 1.4-1.6mm.

Development and Growth, Behaviour, Ecology

Unknown.

References

Dell (1972).

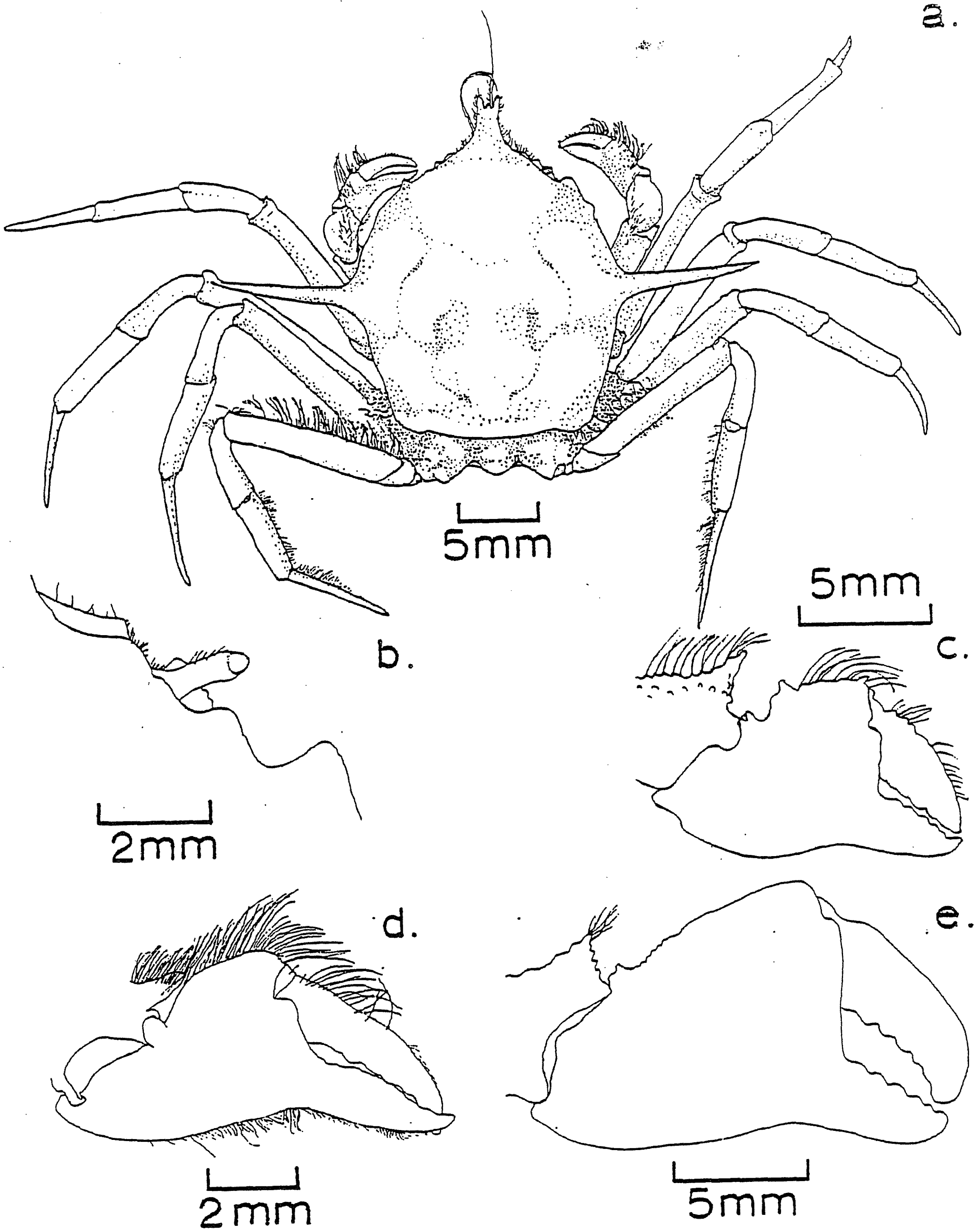


Fig. 42 - Pteropeltarion novaezelandiae: a - female, dorsal view; b - detail of orbital area, dorsal view (by J. Black); c - right chela, sub-adult male, outer face (after Dell, 1972); d - right chela, adult female, outer face (by J. Black); e - right chela, adult male, outer face (after Dell, 1972).

Trichopeltarion fantasticum Richardson & Dell, 1964
Frilled Crab

Synonymy

Trichopeltarion n.sp. Dell, 1960; *Trichopeltarion* sp. Dell, 1963a; *Trichopeltarion fantasticum* Richardson & Dell, 1964; Dell, 1968a; Takeda & Miyake, 1969; King & Clark, 1984; Dawson, 1984; Wear & Fielder, 1985.

Type Locality

Palliser Bay in c.180m, 41°32'30"S, 174°52'E.

Distribution

Endemic to New Zealand, Bay of Plenty to Foveaux Strait on the east coast, Chatham Rise, Kaipara to Fiordland on the west coast.

Diagnosis (Fig. 43a-d)

Carapace much wider than long (including lateral spines), broadly oval-shaped, front broadly rounded, margins irregularly frilled and with strong lateral spines. Surface uneven, set with sparse, short, stiff brown hairs and widely spaced rounded tubercles. Regions well marked. Rostral area has three acute spines, laterals longer than the central spine. Pre-orbital tooth strong with subsidiary lateral spines, supra-orbital tooth similar, and post-orbital tooth acute, bearing strong spines on the posterior margin. Eye stalk slender, eye comparatively small, reddish-orange in colour. Behind the post-orbital tooth are two compound anterolateral teeth bearing three or four spines. Much farther back is a long lateral spine, one-sixth the width of the carapace, set with strong subsidiary spines. Posterolateral margin also set with small spines. Chelipeds in adult females and small males, small and equally developed, set with stiff setae along outer edge, surface with sparse, short, stiff brown hairs. Upper margin of propodus spinulous with a large raised boss at the point of articulation with the carpus. Lower proximal margin of propodus with an elongate curved projection which articulates with the carpus. In mature males the right cheliped is enormously developed, length more than twice CL. Manus largely smooth, roughened along posterior margin, two granular patches distally. Carpus strongly granular along posterior border. Propodus smooth, deep, fixed finger short, obsoletely toothed, dactyl longer, stout, with six strong teeth. Legs long, slender, with stiff hairs along upper and lower margins, surface with short brown hairs, two spines on upper distal margin of merus. Abdomen of seven segments, first three segments bearing a pair of median tubercles with traces visible on the fourth. Edges of abdominal segments with long stiff hairs.

Colour

Greyish white with reddish-orange eyes.

Size

Male 85.3mm CW, 65.5mm CL. Female 86.0mm CW, 67.4mm CL.

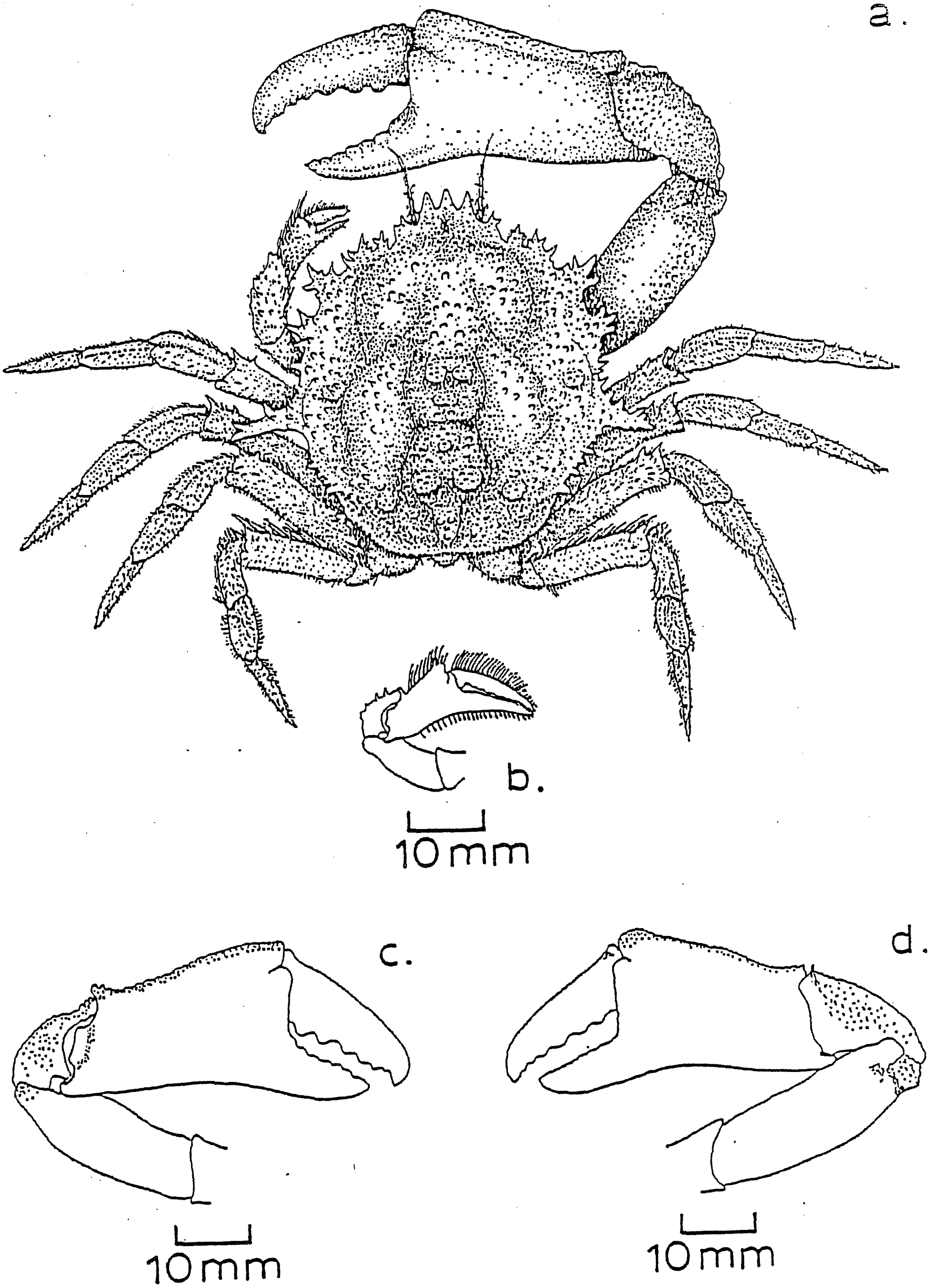


Fig. 43 - *Trichopeltarion fantasticum*: a - male, dorsal view; b - right chela, female, outer face; c - right chela, male, outer face; d - right chela, male, inner face (after Richardson & Dell, 1964).

Habitat

Fine muddy bottoms in deep water.

Depth

Usually 70-720m with an exceptional record from 15-22m in Te Waewae Bay.

Breeding

Ovigerous females have been collected in June and October. Newly laid eggs are dark maroon or dull red-orange (Richardson & Dell 1964). New eggs measure 1.44mm x 1.33mm and when ready to hatch, almost transparent and 1.75mm x 1.65mm.

Development and Growth

Probably only one zoeal stage, large, heavily built and very poor swimmers. Unlikely to be found in plankton samples because it is short-lived and remains at or near the bottom in deep water (Wear & Fielder 1985).

Behaviour

The presence of the enormous right cheliped in males raises the question of its function, whether it is used in feeding and/or agressive interactions. When this crab is landed on the deck of a ship it is very lethargic and it shows no sign of aggression.

Ecology

Richardson & Dell (1964) recorded five females from the stomach of a dogfish (?Mustelus lenticulatus) caught at about 130m between Maunganui Bluff and Kaipara Bar. Also King & Clark (1984) found T. fantasticum in the stomach of rig (Mustelus lenticulatus) caught off Banks Peninsula. Red Cod (Pseudophycis bacchus) from the Canterbury area also eat this crab: October 0.5% of gut volume and February 1.2% (Habib 1975).

A closely related fossil species, Trichopeltarion greggi, has been described from pliocene deposits from North Canterbury by Dell (1969). These fossils are found in concretionary boulders derived from siltstone at Motunau Beach and while males have the greatly enlarged right cheliped they lack the long lateral spines of T. fantasticum. Co-occurring fossils indicate that T. greggi probably lived in shallow water, similar to Cancer novaezelandiae, whereas T. fantasticum is found mostly in deep water. It may be that T. greggi is ancestral to the modern species which is of comparatively recent origin. Dell (1969) discussed some of the difficulties concerning the validity of generic distinctions between Peltarion, Trichopeltarion and Trachycarcinus that follow from this hypothesis.

References

Dawson (1984), Dell (1963a, 1969), Richardson & Dell (1964), Wear & Fielder (1985).

Cancer novaezelandiae (Jacquinot, 1853)
Pie-Crust Crab

Synonymy

Platycarcinus novae-zelandiae Jacquinot, 1853; Cancer novae-zealandiae A.Milne Edwards, 1865; Miers, 1874; 1876b; Filhol, 1886; Lenz, 1901; Chilton, 1909; 1911a; Thomson, 1912; Thomson & Anderton, 1921; Stephensen, 1927; Chilton & Bennett, 1929; Young, 1929; McNeill & Ward, 1930; Richardson, 1949a; Cancer novaezelandiae Dell, 1963a; 1968a; Dell, 1969; Vermeij, 1977; Marsden & Fenwick, 1978; Probert et al., 1979; Marsden, 1981; Knox, 1983b; Wear & Fielder, 1985.

Type Locality

New Zealand.

Distribution

Endemic to New Zealand. North, South and Stewart Island. Also Auckland and Chatham Islands. Possibly self or accidentally introduced to south-eastern Australia and Tasmania. The fossil record of and speciation in the genus Cancer has been reviewed by Nations (1975,1979).

The European Edible Crab Cancer pagurus was introduced to New Zealand at Portobello in 1907, 1908 and again in 1913. In all 59 crabs were imported. Both larvae and adults were liberated around Otago harbour and off the coast but they failed to become established (Thomson & Anderton 1921).

Diagnosis (Fig. 44a-b)

Carapace much wider than long (approx. 1.6 times), flattened front, broadly rounded, covered with tiny granulations, regions scarcely distinct. Anterolateral margins produced and bearing numerous small lobes. Supra-orbital margins without teeth but preceded by a small pre-orbital tooth. Frontal margin with three teeth of which the median is much smaller and more depressed. Chelipeds large and granulous externally. Granules on propodus arranged in four longitudinal rows. Movable finger granulous above, both fingers strongly dentate, four teeth on each finger. Legs robust and moderate length, segments fringed with long hairs. Dactyls long, flattened, without teeth. Abdomen of six segments plus telson in both sexes.

Colour

Dark brown, dull red with darker rim around carapace margin and with black finger tips. Young crabs can be mottled dark green on the carapace with dark brown spots. Legs orange banded and with orange dactyls.

Size

Male 150mm CW, 94mm CL. Female 112mm CW, 73mm CL.

Habitat

Under stones and among large seaweeds in the lower intertidal. Adults usually only in deeper water on sandy bottoms. Sometimes caught in crayfish pots.

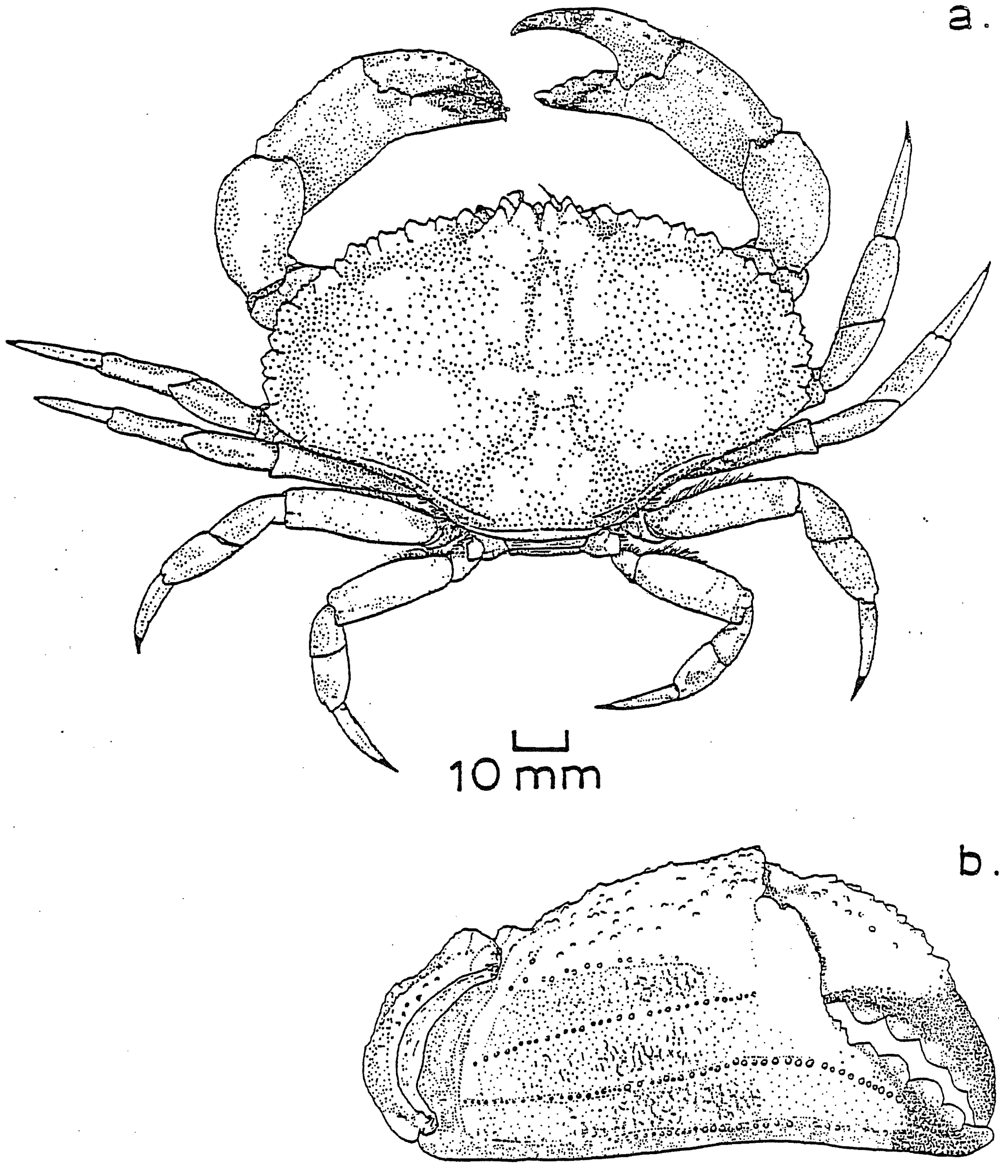


Fig. 44 - Cancer novaezelandiae: a - male, dorsal view; b - right chela, male, outer face (by J. Black).

Depth

Intertidal - ?40m.

Breeding

Thomson & Anderton (1921) stated that ovigerous C.novaezelandiae were rarely caught off Otago believing that spawning occurred in very deep water as in C.pagurus (see Nichols, Thompson & Cryer, 1982). However Bennett (1964) recorded ovigerous females (size not given) in January and May, carrying approximately 12,000 eggs. However, a series of females in the Otago Museum have much larger broods: 75mm CW, 671,000 eggs (Port Chalmers), 38mm, 47,200 (Golden Bay, SS "Doto"), 24.4mm, 35,200, 38mm, 105,300 (Bay of Plenty, SS "Doto", 1901). These data indicate that C.novaezelandiae produces very large broods of eggs and matures at a surprisingly small size. Eggs newly laid, orange, 0.38mm diameter, ready to hatch 0.4mm.

C.pagurus kept at Portobello 1907-08 mated in Jan.-Feb. and became ovigerous in June. Females had eyed eggs in October and larvae began hatching in November thus maintaining their northern hemisphere breeding pattern (Thomson & Anderton 1921).

The species of Cancer in different parts of the world exhibit a considerable diversity of breeding patterns. Cancer pagurus females mature at around 110-120mm CW (3-5 yr age) and carry eggs over winter (Bennett 1974), C.magister females mature at 100-115mm CW (11th-12th instar, approx. 2 yr old) and carry eggs over winter (Butler 1960, 1961, Wild & Tasto 1983), C.borealis females mature at about 80mm CW and carry eggs during summer (Haefner 1977), C.antennarius females mature at 60-80mm CW (10-12th instar, approx. 2 yr old) but carry eggs all year round (Carroll 1982), C.irroratus females can mature as small as 20mm CW (6th instar, 1+ yrs) but most mature by 70-80mm (10-12th instar, 5+ yrs) and carry eggs from late summer and over winter (Scarratt & Lowe 1972, Krouse 1972, Reilly & Saila 1978, Briggs & Mushacke 1982) and C.oregonensis mature as small as 10mm CW in instar 4 and carry eggs over winter (Orensanz & Gallucci 1988). The breeding pattern of C.novaezelandiae seems to resemble that of the Atlantic C.irroratus based on the little information that we have. Both of these species seem to be capable of 'precocious' sexual maturity and have similar fecundity/size relationships (C.novaezelandiae females may have slightly larger egg masses).

Recent work has shown that nemertean egg predators can be major sources of egg mortality in Cancer magister (Wickham 1979, 1980, Kuris and Wickham 1987). Nemerteans have not been reported from C.novaezelandiae.

Development and Growth

Five zoeal stages and megalopa described by Wear & Fielder (1985). First 2 or 3 zoeal stages can be abundant in near-surface layers during September and October at Wellington. Shanks (1986) found that larval stages of Cancer spp. off the coast of southern California make diurnal vertical migrations between neuston and waters near the bottom and may experience net onshore transport due to surface currents generated by onshore winds. This would enhance recruitment into shallow water coastal areas. Anderson & Ford (1976) have investigated larvae rearing of C.anthonyi and have produced second generation crabs in the laboratory. Nicholls, Thompson & Cryer (1982) have analysed C.pagurus larval distribution and drift off north-east coast of England to estimate seasonal production and mature stock size.

There is wide intraspecific variation in megalopae size among Cancer spp. Megalopae of C.novaezelandiae have a CL (tip to tip of rostral and dorsal spines) of 4.5mm (Wear & Fielder 1985) and thus are similar to C.productus, C.oregonensis and C.pagurus which produce medium sized megalopae (Orensanz & Gallucci 1988).

Juvenile C.novaezelandiae crabs have been reared from megalopae collected at Kaikoura in early September. First stage crabs are about 3mm CW and second stage 5mm CW. On a separate occasion a male moulted from 41.6mm to 52.5mm CW (26% increase) in June. Juvenile crabs (<10mm) have been collected on the shore at Kaikoura in December with small crabs (<20mm) through to May which suggests that recruitment may well be protracted. Small C.novaezelandiae seem to be extraordinarily rare considering the high female fecundity. Adult moulting, mating and spawning probably occur during the latter half of the year and eggs are probably carried for 5-6 months.

My own relative growth analysis of C.novaezelandiae from the Canterbury area shows that they are homeochelous (left and right chelae of similar size) and at least up to about 70mm CW male and female chelae have the same relative growth (allometric constants for propodous depth 1.1 for both sexes, propodus length 1.1, males and 1.07 females). Above 70mm CW males tend to have larger chelae, especially propodous length suggesting a pubertal moult. This may indicate that male C.novaezelandiae do not reach sexual maturity until about 70mm but a study of male gonad development is needed to confirm this. However, divergence in abdomen width begins at 23mm CW (allometric constants 0.96 for males and 1.41 for females). Below 23mm CW male and female abdomens show similar allometry. The smallest ovigerous female known is 24.4mm CW. Clearly some females mature at a very small size and they may mature well in advance of males. However, Chatterton (1986) suggests that most Otago crabs mature around 50-60mm CW when they are about 1 year old. Two year old crabs are around 80mm CW and with annual moults may reach maximum size in 4-5 years.

Relative growth of C.antennarius chelae by Carroll (1982) suggests that both males and females have pubertal moults at around 70mm CW (allometric constants 0.99, juveniles, 1.17, adult females and 1.22 adult males). The study by Orensanz & Gallucci (1988) of allometry in a guild of four Cancer species from Puget Sound shows a previously unsuspected diversity of relative growth among these species. C.magister shows no indication of sexual dimorphism or allometric phases in chelae while C.oregonensis shows a clear dimorphism from a very small size. But in C.gracilis and C.productus males there are two distinct phases which overlap in the size range CW = 70-87mm. Allometric constants range from 1.08-1.11 for the first phase and 1.07-1.13 for the second phase with the two phases separated by a distinct but overlapping discontinuity suggesting a pubertal moult. The female abdomen in C.magister, C.gracilis and C.productus shows two allometric phases and the same is probably true for

C.oregonensis. These phases are separated by the achievement of sexual maturity.

Growth/age studies of Cancer spp. are amongst the most numerous and detailed of any brachyuran genus. These may be briefly summarized as follows: C.pagurus have moult increments ranging from 30% (at 90mm CW) to 15% for larger crabs (females lower than males), maximum sizes are 267mm CW for males, 242mm CW for females, maximum age >20 years (Bennett, 1974); C.magister moult increments range from 29 to 16% for males, 27 to 11% for females, maximum size for males is 210mm CW, 182mm CW for females, maximum age 5-6 years with 13-16 instars (Butler 1961) but there is some regional variation (Orensanz & Gallucci 1988); C.antennarius moult increments range from 26 to 13%, maximum sizes 160mm CW for males, 150mm CW for females, maximum age 7 years with 16 instars (Carroll 1982); and C.irroratus moult increments 42% (instar I) to 26% (instar XII) (Krouse 1976) although Haefner & van Engel (1975) suggest a smaller range of 27 to 19%, maximum sizes 127mm CW for males, 100mm for females, maximum age 7-8 years with 14 instars (Reilly & Saila 1978). Additional data for C.gracilis, C.productus and C.oregonensis are given by Orensanz & Gallucci (1988). Maximum sizes for C.novaezelandiae are similar to C.irroratus and if the growth curve is similar then it may live for a maximum of about 8 years.

Hartnoll (1985) considered that growth of Cancer spp. is indeterminate so that moulting continues indefinitely after puberty until death, with no clear terminal anecdysis. However the data presented by Orensanz & Gallucci (1988) suggest that growth of these species may in fact be determinate: C.magister, C.gracilis, C.productus and C.oregonensis moult through 11-13 instars with the number of post-pubertal instars ranging from 2-3 for males and 3-7 for females and their evidence suggests that growth is terminated by physiological senescence.

Crab limb loss can affect growth rates by decreasing moult increments or inhibiting/stimulating ecdysis depending upon stage of the moult cycle. In C.pagurus severe limb loss (2 chelae or 6 legs) caused a reduction in CW increment of up to 25%. The incidence of chelae loss in Norfolk, Yorkshire and Devon populations was around 10% but this is unlikely to have an important effect on growth rate (Bennett 1973).

Behaviour

C.novaezelandiae will burrow in soft sandy-mud, leaving only the carapace exposed. Burrowing occurs in 2 stages: using legs to reach down into the sand and pull downwards, with carapace horizontal, till limbs are covered then pushing back into the sand using the legs to cover the carapace. Burrowing is much slower than for Ovalipes catharus, taking about 120 sec for a small crab (26mm CW). There is no evidence of a reversed respiratory current in C.novaezelandiae. These crabs are usually very sluggish and easily handled. When disturbed they remain motionless with all limbs tightly folded against the body. The easiest way to handle them is to turn them upside down!

Activity patterns of C.novaezelandiae under constant laboratory conditions show an endogenous circadian rhythm with a single peak of activity during what would have been the hours of darkness. Activity began at or near the expected time of dusk (Chatterton 1987). Furthermore, catches in subtidal pots were influenced by the day/night cycle as well as the timing of high tide. Catches in intertidal pots peaked on night-tme high tides between midnight and dawn. Few crabs were caught on high tides during daylight hours. Rebach (1987) found that C.irroratus had a weak endogenous rhythm and that activity is synchronized by exogenous cues (light/dark, tidal) when the crabs migrate to shallow, inshore areas.

C.novaezelandiae is a nocturnal feeder. Bennett(1964) states that it can open cockles and oysters, breaking away the thin edges of the shell until a chela can be inserted. They will also eat the flesh from broken mussel shells. The feeding behaviour of this crab may be similar to Atlantic rock crabs (Cancer irroratus) from eastern Canada which prey on scallops (Placopecten magellanicus) and other shellfish. Elner & Jamieson (1979) found that rock crabs (90-130mm CW) crushed small scallops (up to 10mm) with either chela while larger scallops (10-60mm) were opened by hinge crushing. The scallop was held by one chela while the other chela crushed the shell about the hinge in a lateral direction. With the hinge broken the scallop was left gaping and flesh was torn out using the chela. Scallops larger than 50mm were attacked by chipping pieces of shell from the margin (usually near the hinge) using the chela until a dactylus tip could be inserted between the valves. Each valve was then grasped by a chela and the two valves were torn apart to expose the flesh. Larger crabs preferred larger scallops.

Little is known about movements of C.novaezelandiae but Chatterton (1986) found a marked increase in winter population density in Blueskin Bay, related to a migration of crabs into the area to moult and mate. Chatterton (1987) reported that crabs foraged in the intertidal zone during night-time high tides. In an estuarine population of C.magister crabs were more abundant sub-tidally, leaving the tidal flats during low tide but becoming more abundant by night in the intertidal. Daily movements seem to be in response to availability of food, especially shrimps Crangon spp. (Stevens, Armstrong & Hoeman 1984). C.magister are recruited in summer along the California coast but those entering San Francisco Bay grow faster and all crabs migrate off-shore at about 1.5 years old (Collier 1983, see also Stevens & Armstrong 1984). Tagging of adults in northern California suggests that many remain in the same area for long periods (Gotshall 1978). Cancer irroratus from the mid-Atlantic Bight migrate annually from deep water (700m) to shallower inshore areas (1-20m) in the colder months (October-November) remaining until March-April. Moulting and mating occur in shallow water, females moulting in December prior to mating after which they return to deeper water. Males moult in January and remain in shallow water until the spring (Haefner 1976, Rebach 1987). The Dungeness crab C.magister is highly mobile with populations along the Pacific coast of North America migrating distances of 50km and tagged crabs have been recovered 440km from their release site (Stevens, Armstrong & Hoeman 1984). C.pagurus off Britain is also a mobile species with a few movements exceeding 90km (Bennett & Brown 1983). A tagging study of C.antennarius resulted in nearly half of the recaptures at the site of release after 2-18 months but movements of up to 7km were found (Carroll 1982).

Seasonal migrations by Cancer spp. may be summarized as follows: 1) both sexes remain in the same area year-round (e.g. C.antennarius, C.gracilis, C.oregonensis), 2) only females migrate offshore following moulting/mating (e.g. C.productus, C.pagurus, C.borealis), 3) both sexes migrate (e.g. inshore C.irroratus, or offshore C.magister). Several hypotheses have been proposed to explain these migrations: a) crabs migrate following their thermal preference, b) female crabs migrate so as to enhance larval survival, c) female crabs migrate inshore because they require suitable sandy bottoms for extrusion of egg masses, d) sexes converge during the mating season to facilitate mating encounters and e) emigration of gravid females away from estuaries may avoid exposure of eggs to osmotic stress.

The mating behaviour of C.novaezelandiae has not been studied but it is likely to be similar to behaviour of other Cancer species. It is interesting to recall that Thomas Anderton (in Thompson & Anderton 1921) made some of the earliest obervations on the mating behaviour of the European Edible Crab C.pagurus kept at Portobello from 1907. In the northern hemisphere mating of this crab follows post-larval release and seasonal inshore migration by females in the summer. Edwards (1966) kept between 20 and 30 labelled C.pagurus in concrete tanks $1m^2$. Females about to moult were closely attended by males for 3 to 21 days (mean 8 days) prior to moulting and for a futher period of 1 to 12 days (mean 5 days) after the moult. (In a later experiment Hartnoll & Smith 1979 obtained similar values for pre- and post-moult attendance.) During attendance the male assumed a protective position astride the female's back with claws held in front. Females were very cooperative in this behaviour. If another male crab approached the male became very aggressive. Seventy eight percent of females were accompanied by only one male, the other 22% involved a change of partner in the early pre-moult attendance phase, always a larger male. In these laboratory tanks males were polygamous, one male impregnated 3 females in 18 days and another male attended 10 different females during a period of 4 months pairing with 60% of the females which moulted. In 78% of the cases the male was larger than the female prior to moulting but as a result of moulting the female usually became larger than their attendant male. Copulation took place a short time (up to 48hrs) after the female moulted when she was soft-shelled, and was successful in 80% of pairings. Post-moult attendance by the male prevented copulation by other males.

The whole moulting and copulation sequence was observed for one pair of C.pagurus by Edwards(1966). During the moult the male remained in the pre-moult position astride the female, supporting his own weight. The male appeared to actually assist by pushing off the old carapace with his chelae (also observed in other cases). Once moulted the male gently turned the female on to her back and exposed her genital openings by using his chelae to unfold her abdomen. Copulation then occurred and lasted for 3 hours (in other cases copulation occurred mainly at night). After copulation a "plug" was observed to fill each genital opening. According to Williamson(1900) this plug is formed from fluid produced from glands lining the spermathecae of the female. On withdrawal of the male organ this fluid hardened on contact with seawater. These "plugs" remained visible for 3-8 weeks after which they had moved up the oviduct towards the spermathecae. Males normally moult about a month later than females, i.e. in late summer.

Snow & Neilsen (1966) have also recorded mating behaviour of the Dungeness crab (Cancer magister) from the west coast of America. A pair of crabs were observed, the male attending the female for 8 days prior to moulting and for 2 days after moulting and copulation. Whereas in C.pagurus the pre-mating embrace involved female carapace against the male sternum, in C.magister the embrace was sternum to sternum with the male firmly controlling the female's attempts to free herself and pacifying her by stroking her carapace with his chelipeds. Once moulting had begun the female was allowed to reverse her position and continue moulting within the "cage" of his walking legs and chelipeds. Copulation occurred about 1.5 hours after moulting when the female was still soft (as Ricketts & Calvin 1968 so aptly point out, "The exoskeleton of a crab presents a formidable barrier to lovemaking."). The male turned the female on her back and she obliged by extending her abdominal flap, allowing him to insert his gonopods into her genital openings and they settled down to over 2 hours of connubial bliss!

Males have at least the potential for being polygynous but clearly there are some differences in the mating behaviour of Cancer species and it will be interesting to find out whether C.novaezelandiae behaviour resembles either of the 2 above species or perhaps is different from both of them. Christy (1987) classifies male competition for mates by Cancer spp. as involving the defence of receptive females rather than breeding sites or refuges. Thus competition is female-centred. However Orensanz & Gallucci (1988) argue that mate competition is more complex, involving resource defence (C.oregonensis), female defence (C.gracilis) and male dominance involving explosive breeding assemblages (C.magister), and that patterns of sexual dimorphism and chelae allometry are consistent with these differences in competition for mates.

Ecology

C.novaezelandiae feeds on cockles and oysters and in captivity they will eat about one shellfish per day (Bennett 1964). Thompson (1930) recorded pieces of shellfish and worms from stomachs of crabs from the Avon-Heathcote Estuary. Cresswell (1987) found that crabs from Lyttelton Harbour fed mainly on bivalves and gastropods, crustaceans such as amphipods, isopods and crabs, as well as fish, sponges, coelenterates and algae occasionally. There were no effects of season, size or sex on diet. In a study of C.magister in a Washington estuary Stevens, Armstrong & Cusimano (1982) found that they consumed juvenile fish, shrimps (Crangon spp.), and small bivalves (Cryptomya, Macoma, Tellina). First year crabs preyed primarily on very small bivalves or small crustaceans (including conspecifics), second year crabs preferred Crangon spp. and fish, and third year crabs preyed less on Crangon spp. and more on fish. There was wide variability from place to place. Such an ontogenetic change in food habits probably reflects the effect of increasing predator size on ability to handle different foods. Gotshall (1977) found significant differences in diet over the depth range 0-89m. Atlantic Rock crabs, C.irroratus, >25mm CW eat polychaetes, mussels, starfish and sea urchins (Scarratt & Lowe 1972). Also these crabs can eat about 5-6 scallops per day (Elner & Jamieson 1979). It may be that C.novaezelandiae is an important predator of scallops in New Zealand and in view of the present problems with the scallop fishery this should be investigated.

In northern California C.magister passes through 11 moults before attaining maturity at about 2 years after settling, at a size of 100-115mm CW (Butler 1960,1961, Poole 1967). After maturity, growth of females is slow relative to males and females rarely exceed the size of harvestable males. Males attain legal size about 3 years after settling and have a maximum age of about 6 years. Little is known about the age structure of the female population because only males are harvested. Copulation occurs in early summer, eggs are extruded in the autumn and hatch over the winter period. The number of eggs laid range from 700,000 - 2,000,000 per female, depending upon female size. After hatching, the young pass through 5 pelagic zoeal stages and the megalopa before settling approx. one year after copulation of adults. In a unique and elegant analysis of the C.magister fishery, McKelvey et al. (1980) used simulation modelling techniques to investigate possible reasons for the regular cycling pattern that has been exhibited since the early 1940's. This investigation was based on a multistage recruitment model, essentially a non-linear Leslie matrix. In this fishery only males are taken, minimum CW 160-165mm in a restricted season, and this allows them to breed at least once before capture. Landed catches have shown a 9-10 year interval between peaks with increasing amplitude swings as the fishery has expanded, perhaps foreshadowing an eventual crash in the population. A variety of biological feedback mechanisms (predator-prey interaction, density dependent recruitment) or exogenous environmental effects have been proposed to account for variable year-class strength. The modelling work helped to eliminate some of the possible combinations of assumptions that were used. McKelvey et al suggest the hypothesis that recruitment must be determined in very early life stages, egg or larval, prior to settling on the bottom. Neither over-compensated natality nor intense juvenile cannibalism are likely significant factors in the dynamics of this population. Later, Johnson et al. (1986) have shown that cyclic variations in wind-generated off-shore and on-shore currents are correlated with recruitment. Also, Botsford (1986) presented an elegant analysis which suggests that some of the mechanisms previously considered independently may well interact to produce the observed cyclic pattern. This work has some relevance to the problem of large numbers of paddle crabs (Ovalipes catharus) around the New Zealand coast.

There has been some interest in commercial exploitation of C.novaezelandiae but a fishery has not yet been established. The main problem seems to be that the large crabs are not readily captured. An alternative may be pond-rearing and the previous work on culture of Cancer spp. reviewed by Oesterling & Provenzano (1985) is relevant here.

C.novaezelandiae is an important component of the diet of fish. Megalopae larvae are consumed by kahawai (Arripis trutta) in Wellington harbour (Baker 1971). Thompson (1930) found that red cod (Pseudophycis bacchus) from the Avon-Heathcote Estuary ate this crab as well as blue cod (*Parapercis colias*) from the Chatham Islands (Young 1929). King & Clark (1984) found that this crab was eaten especially by female rig (*Mustelus lenticulatus*) feeding in shallow water (<10m) in Golden Bay and was eaten more frequently by both larger male and female fish. Rig from Otago Harbour (Graham 1939), Banks Peninsula, Wellington and Kaikoura also eat *C.novaezelandiae* (King & Clark 1984). This crab is also eaten by the starfish *Patiriella regularis* in Otago Harbour (Crump 1971) although these may have already been dead from other causes. Another starfish, *Coscinasterias calamaria*, also eats dead crabs (Crump 1969).

Leader & Bedford (1978b) examined the composition of muscles and haemolymph of *C.novaezelandiae* and found that ion concentrations were similar to other crabs from the same habitat. Some preliminary experiments suggest that this crab can osmoregulate in dilute seawater (East & Peterson 1967). Two crabs placed in 76% seawater became isotonic after 3-4 hours but 2 crabs in 55% seawater remained 20-45 mM/l above the medium after 4 hours. Experiments with *C.irroratus* gave similar results (Haefner & van Engel 1975). These experiments with *C.novaezelandiae* need to be repeated and a thorough investigation would allow comparison with other species which also enter estuaries.

The European Edible crab (*C.pagurus*) was introduced into New Zealand waters between 1907-1913 and 20 million larvae and 19 adults were liberated at Portobello and off Otago Heads but the species did not become established (Thomson & Anderton 1921, Thomson 1922). In captivity many crabs were attacked and eaten by octopus and those released may have suffered the same fate. Failure of the larval releases may have resulted from dispersal and perhaps unavailability of suitable food.

Glaessner (1960) reported *C.novaezelandiae* fossils from lower pliocene to lower pleistocene deposits, while Dell (1969) records upper pliocene (1.8 million years before present) fossils of *C.novaezelandiae* in concretionary boulders from Motunau, Canterbury. An extinct species of *Trichopeltarion* (*T.greggi*) also occurs in these boulders. It is possible that *C.novaezelandiae* replaced the giant xanthid crab *Tumidocarcinus giganteus* which lived in shallow depths on the continental shelf (Fleming 1962) and died out during the upper miocene. According to Nations (1975,1979) the genus *Cancer* originated during the eocene, in the northeast Pacific and was well diversified in the miocene (about 15 million years ago) radiating throughout the Pacific and into the north Atlantic. It seems likely that earlier *C.novaezelandiae* fossils will be found in New Zealand. Nations (1975) suggests that *C.novaezelandiae* is most likely to have colonized New Zealand from South America along the coast of Antarctica during the warmer period in the miocene or early pliocene. It shows a close similarity to *C.edwardsi* (present distribution Ecuador to Strait of Magellan) although this species is not known in the fossil record of South America.

References

Bennett (1964), Chatterton (1986,1987), Chilton & Bennett (1929), Crump (1969,1971), Dell (1963a), Jones (1983), King & Clark (1984), Leader & Bedford (1978b), Morton & Miller (1968), Thompson (1930), Wear & Fielder (1985).

Ovalipes catharus (White, 1843)
Paddle Crab

Synonymy

Portunus catharus White, 1843; Platyonichus bipustulatus Miers, 1874; 1876b; Hector, 1877; Filhol, 1885d; Chilton, 1906b; Ovalipes bipustulatus Chilton, 1911a; 1911b; Thomson, 1912; Thomson & Anderton, 1921; Platyonischus bipustulatus Oliver, 1923; Ovalipes bipustulatus Chilton & Bennett, 1929; Ovalipes trimaculatus Young, 1929 ; Ovalipes bipustulatus Powell, 1949; Richardson, 1949a; Dell, 1960; Ovalipes c.f. punctatus Glaessner, 1960; (pleistocene fossil), Ovalipes punctatus Dell, 1963a; Bennett, 1964; Ovalipes catharus Stephenson & Rees, 1968; Ovalipes bipustulatus Dell, 1968a, Ovalipes catharus Stephenson, 1969; 1972; Dawson & Yaldwyn, 1974; Ovalipes punctatus Hayward, 1974; Ovalipes catharus Knox & Fenwick, 1978b; Jones, 1983; Wear & Fielder, 1985.

Type Locality

New Zealand.

Distribution

Australia (South Australia, Victoria) and New Zealand. Within New Zealand, Hohoura Harbour to Stewart Island, Muriwai to Westland also Chatham Islands.

Diagnosis (Fig. 45a-d)

Carapace convex, wider than long (ratio 1.37), distinct cervical groove, surface smooth. Front armed with four sharp teeth (including inner orbital teeth), medial pair close together and slightly further forwards. Orbits deeply set, dorsal border concave with a prominent supraorbital tooth laterally. Anterolateral margins with five large, acutely tipped teeth, the first anterolateral tooth directed forward and projecting as far as frontals. Second and third teeth also directed forward and last pair directed more anterolaterally. Below the level of the anterior and lateral carapace margins is a fringe of setae which is evident at the base of the teeth. Posterolateral margins convergent, posterior margin sinuous. Chelipeds relatively short, robust, subequal. No sexual dimorphism of chelae, but right chela is usually larger and a crusher while the left chela is smaller and a cutter. Carpus with a long, robust inner spine, propodus not swollen, upper surface has three ridges (innermost ending in a spine) and outer surface has two ridges. Under-surface of the propodus has 20-26 stout striae. Fingers long, curved inwards and with needle-sharp tips. Fixed finger has two ridges on each side and movable finger has three dorsal ridges, inner margins of both fingers armed with 6-7 blunt teeth. First pair of legs slightly longer than chelipeds, other legs decreasing in length posteriorly. Segments flattened, dactyls with grooved surfaces and carinated edges. Last pair of legs shortest, segments broadest, especially propodus and the paddle-shaped dactyl which is reniform.

Colour

Carapace pale orange background densely covered with dark red-brown dots which are concentrated in 4 spots (2 smaller

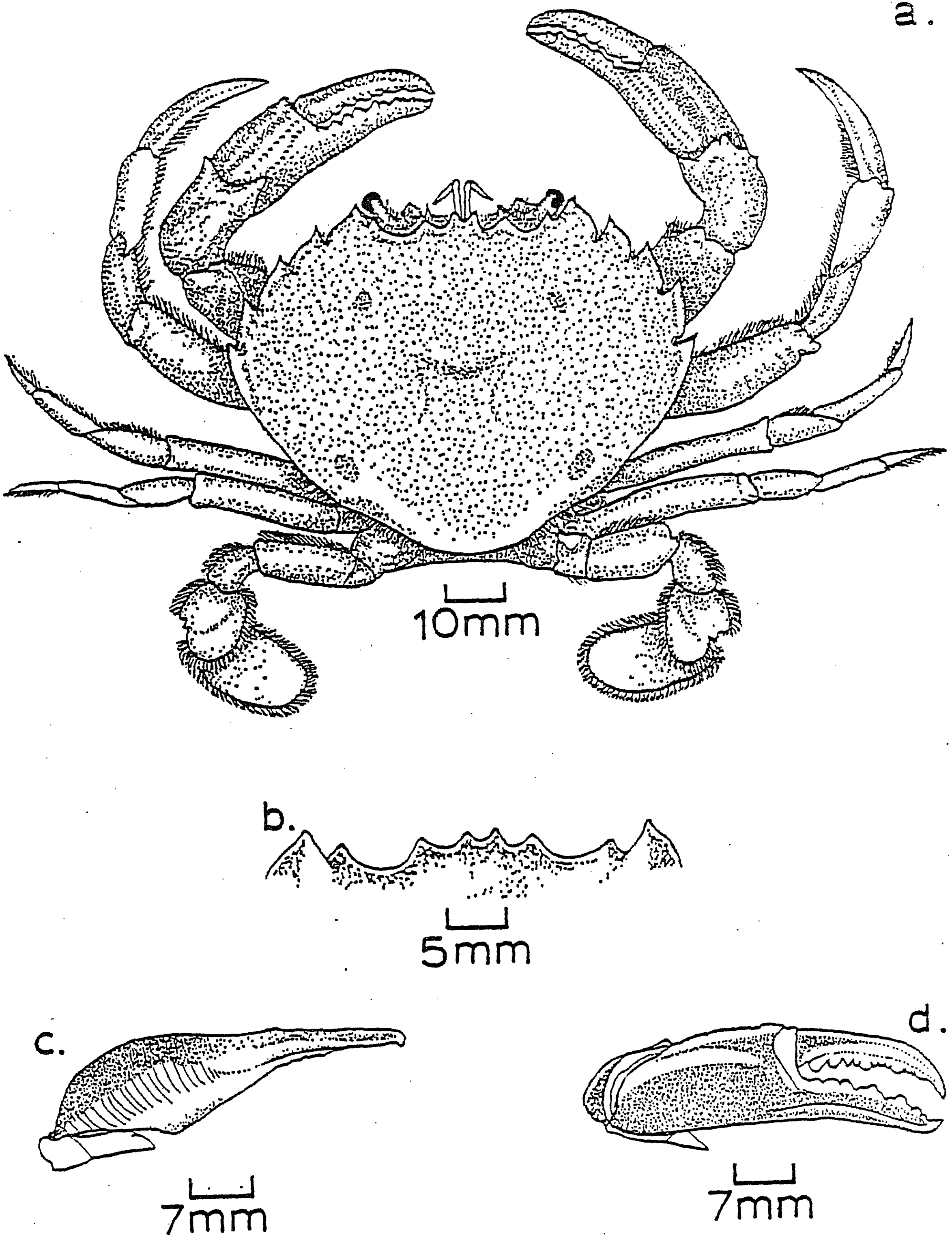


Fig. 45 - Ovalipes catharus: a - male, dorsal view (after Dell, 1963); b - outline of frontal margin, dorsal view; c - ventral surface, d - right male chela, outer face (by J. Black, based on photos from Stephenson & Rees, 1968).

anterior branchial, 2 larger postlateral) and also in the gastro-cardiac area where there is a 'butterfly' shaped pattern. Darker pigment also concentrated along anterior edges of the carapace teeth. Legs pale orange but chelipeds have dark red-brown markings on inner face of merus, propodus and both fingers. Ventral surfaces white.

Size

Male 150mm, female 115mm CW.

Habitat

Along sandy beaches and in sandy estuaries. Some beach-seining fishermen regard O.catharus as a pest because they become entangled in the net and are difficult to remove. But if these fishermen bothered to cook up a few and eat them they would find out what a delicacy they are throwing away.

Depth

Surf zone and continental shelf, 2m-100m.

Breeding

Ovigerous O.catharus females are found from July to May with a peak in January. The main spawning and egg-bearing season in Pegasus Bay is from November to March but in Tasman Bay, further north, egg-bearing occurs from August to March (Osborne, 1987a). Females moult from May - September and mating occurs in shallow coastal waters and estuaries when the female is soft-shelled. The interval between mating and spawning is about 2 months in summer but up to 6 months in autumn. Newly laid eggs, yellow, brown - orange, 0.3mm diameter, ready to hatch, black, 0.37mm (Wear & Fielder 1985). Incubation is 33-56 days depending on water temperature and occurs off open sandy beaches or in deeper water. Samples of crabs from shallow water have few (1-3%) females carrying eggs. The smallest female recorded with eggs is 46mm CW (carrying about 100,000 eggs). In Pegasus Bay the size of 50% female maturity is 71.5mm CW but in Tasman Bay it is only 50.1mm CW (Osborne, 1987a). Sexual maturity can be attained in the first year of benthic life. Females of 110mm CW can carry up to 850,000 eggs and can produce up to 3 batches of eggs each breeding season, without re-mating or moulting (Osborne, 1987a). Most soft-shelled crabs and ovigerous females are found from September to December. The net result of differences in life history traits suggests that the reproductive potential of Tasman Bay females may be up to three times greater than in Pegasus Bay.

In South Africa the main spawning period of O.punctatus occurs from April to August with a minor peak in January (Du Preez & McLachlan 1984c). Ovigerous females may produce a second brood shortly after the first. Fecundity increases with cube of CW and the smallest females (30-35mm CW) produce about 76,000 eggs, while the largest females (60-65mm CW) produce about 490,000 eggs per brood. The mean ratio of reproductive to somatic mass is high, 1:3.5. Diameter of newly laid eggs is 0.35mm and for eggs ready to hatch it is 0.38mm (similar to O.catharus). In the laboratory larval eyes were visible after 13 days and eggs hatched 17-22 days after extrusion. First stage zoeae have a narrow temperature and salinity optima: 15-22^{o}C and 33-35 ppt (Du Preez & McLachlan 1984d).

Nemertean egg predators have been recorded from ovigerous O.occelatus and Callinectes spp. from North America but these worms have not been reported from New Zealand as yet.

Development and Growth

Larval life of O.catharus lasts for about 2 months and involves 8 planktonic zoeal stages followed by the megalopa (Wear & Fielder 1985). Larvae occur mainly offshore and large numbers have been captured down to almost 700m off East Cape. Murdoch (1985) found only 27 paddle crab zoeae during his zooplankton survey off Otago Peninsula, mostly over the mid- to outer shelf in oceanic water with only 7% in in-shore neritic water. Sulkin (1984) has reviewed the environmental stimuli which are important in larval depth regulation. In addition Sulkin & van Heukelem (1986) have demonstrated that temperature and salinity variations produce variability in length of the megalopal stage of Callinectes sapidus and thereby affect dispersal and recruitment. The final O.catharus zoea moults to a planktonic megalopa which migrates inshore and juvenile crabs settle in sheltered waters, estuaries and harbours which are the nursery grounds. In a survey of the Avon-Heathcote Estuary plankton from March to August,1982. Roper, Simons & Jones (1983) found small numbers of zoea.

Osborne (1987a) recognized three phases of growth: juvenile, up to 30mm CW, sub-adult, from 30 to 55mm and an adult phase for larger crabs. A total of 13 instars can be recognized in field data. Variation in individual moult increments result in increasing variation around mean-instar size in successive juvenile instars, but after sexual maturity is attained variation in instar size decreases. O.catharus grows from 6mm to about 60mm in about 12 months. Allometric change in the growth of the abdomen occurs between 50-70mm CW. At Wellington males mature at 67mm CW and females at 58mm. Carapace width increases by approx. 22% at each moult (35% for juveniles and 17% for adults). Juveniles moult frequently but after maturity they moult only once or possibly twice per year. Growth is probably slower in the Otago area, due to colder temperatures (Armstrong, 1985). Males are usually larger than females and reach 120mm CW by their third year. Females rarely grow larger than 110mm CW. The largest males (140 CW) are probably about 4 years old and have been most commonly recorded from the Chatham Islands. Maximum size in Tasman Bay is attained in 3-3.5 years, probably because of warmer temperatures. Compared to other warm temperate and tropical portunids, O.catharus is relatively long-lived and slow-growing, but it is large and fast growing compared to other species of Ovalipes (Osborne 1987a).

The Atlantic portunid Carcinus maenas living on the coast of Maine shows a number of life cycle differences from populations off southern Britain & Holland where it is 4-5ºC warmer. Off Maine megalopae settle later, growth is slower, maturity is delayed, generation time and life span are longer. These differences may account for the inability of C.maenas to colonize waters much colder than those of the central coast of Maine (Berrill 1982).

Relative growth of O.catharus from near Christchurch has been studied by Davidson and Marsden (1987). In males carapace length and chelae propodus width are both negatively allometric, abdomen width is isometric and gonopod length is positively allometric showing that it grows faster relative to CW. In females carapace length is negatively allometric, chelae width is isometric and abdomen width is positively allometric. However, Davidson & Marsden (1987) did not distinguish between adult and sub-adult growth phases and their use of only relative growth characteristics led them to underestimate the size of sexual maturity. Evidence of gonad maturation and physical signs of copulation are needed to clarify interpretations of relative growth data.

By contrast, O.punctatus from South Africa grows to a maximum CW of only 63mm (Du Preez & McLachlan 1984a). There are no differences between male and female wet or dry weights nor in relative growth of the fifth leg which is isometric in both sexes. However cheliped propodus length is significantly larger in males but propodus width is not different. Female abdomen width shows a discontinuity at approx. 24mm CW and grows much wider in larger crabs. The smallest ovigerous female was 32mm CW. O.punctatus seems unusual in that all the body dimensions show isometric growth. In the laboratory the absolute increment per moult remains roughly constant with size but percentage moult increment declines from 19.1% (30-40mm CW) to 14.5% (50-60mm CW) (Du Preez & McLachlan 1984b). Size frequency histograms did not reveal anything about the nature of growth in the field which is not surprising because spawning occurs nearly all year round. Females moulted from April to December but moulting can occur all year round (Du Preez & McLachlan 1984c). Maximum life span appears to be about 3 years.

Behaviour

O.catharus is a large, active, pugnacious crab and definitely not a crab to be handled carelessly, especially by the faint-hearted! Its needle-sharp chelae can deliver some painful bites. It is sometimes encountered during day or night, swimming freely at the surface in large swarms and is attracted to strong lights. Swimming behaviour of paddle crabs has not been studied but it is probably similar to the behaviour of Callinectes sapidus (see Spirito 1972, Hartnoll 1971, Blake 1985). O.catharus is capable of swimming rapidly (approx. 1m/sec.) in short bursts when disturbed by SCUBA divers and then rapidly re-burrowing in the sand. When burrowing the crab first digs its paddle-shaped last pair of legs into the sand then using its other legs and chelae can disappear backwards into the sand in a matter of seconds leaving only the eyes and antennules exposed. Burrowing time increases with crab size (McLay & Osborne 1985). Paddle crabs are active soon after sunset and are most easiy caught in pots at this time. The best catches are made at high tide. Soft-skinned, oily fish provide the best bait (Clark 1978). Observation of crabs around the pot suggest that there is no direct defence of the pot or bait against other crabs.

There are undoubtedly on-shore and off-shore migrations of O.catharus associated with moulting and reproduction but these are complex and not well understood. In some areas males predominate but in other areas males are rare. Migrations of both males and females may be related to the coastal habitat available. In Canterbury coastal waters Osborne (1987b) found that O.catharus were abundant at Little Akaloa (a sheltered, confined bay) in winter and less common in summer, whereas in Pegasus Bay (exposed coastline) crabs were more abundant in summer than in winter. Males and females aggregate and mate at Little Akaloa during winter at the time of the female moult. Males probably moult after mating and move out of the bay at the end of spring whereas females leave earlier and migrate to offshore spawning grounds. A similar pattern is seen in O.punctatus from Japan (Sasaki & Kawasaki 1980). In shallow water Du Preez & McLachlan(1984c) found a female-biased sex ratio but off-shore the sex ratio was 50:50 for O.punctatus, perhaps indicating a different pattern of movements in South African waters.

O.catharus is a nocturnal predator and feeds on shellfish, excavating its prey by balancing on the fourth pair of legs, using the last pair as stabilisers, and rocking forward to bulldoze the shellfish out with the second and third legs (Wear 1984). The most favoured prey - toheroas (Paphies ventricosa) 20-50mm, tuatuas (Paphies subtriangulata), cockles (Austrovenus stutchburyi) and pipis (Paphies australis) up to 30mm, and Tellina (Macomona) liliana up to 60mm - are simply crushed by the chelae. Larger shellfish are dextrously manipulated by the chelae so that the opening edges are pressed at right angles to the lateral crushing action of the mandibles, thereby allowing deep chips to be made in the shell margin. Then the chelae are inserted into the gap between the valves. Larger prey were hammered against the sand to wedge the valves open using the larger crusher chela, so that the more slender, sharper cutting chela can sever the adductor muscle and open the shell. Measurements of the force required to open these shelfish show that 20kg is sufficient to crush-fracture thinner-shelled prey. Thicker-shelled bivalves such as Dosinia subrosea require at least a 50kg force. Thus shell thickness is very important in determining prey preference. Schofield (1987) has suggested that ingestion of shell fragments, requiring regurgitation, is an important factor in determining the optimal diet of paddle crabs.

When opening mussels, Mytilus edulis aoteanus, a total of five distinct opening techniques are used (Davidson 1984, 1986). The opening technique used is direct crushing, anterior crushing, posterior crushing, wedging or edge-chipping depending upon mussel size. Handling times increased exponentially with mussel length from 4-5sec for small mussels to 600sec for 3cm mussels. Prey profitability decreases with increasing prey size, decreasing much more rapidly for smaller crabs. When unlimited numbers of prey (equal numbers of each size class) were available, large crabs (80-92mm CW) ate prey most frequently from the 15-20mm class but all size classes were attacked. Preferred prey size increased with predator size, 10-15mm for small crabs and 15-20mm for large crabs. Lower consumption of large mussels (25-30mm length) results from high rejection rates. When presented with the same range of prey sizes (but without replacement of those consumed) the paddle crabs initially consumed small mussels up to the preferred size and later began to attack larger prey, requiring the use of slower 'edge-chipping' methods of opening. When O.catharus encounters small mussels it does not reject them in favour of larger and perhaps more valuable prey. On the other hand large mussels were sometimes dropped several times before a serious attack was initiated. Improvement of handling times suggests that O.catharus is able to learn or gain information by experience about the prey. It remains to be established whether optimal foraging has any relevance to the field situation where many alternate prey-types are available, some mobile, others immobile and each differing in their value to the predator.

The work of Du Preez (1984) on mollusc predation by the South African three-spot swimming crab, Ovalipes punctatus shows some interesting differences from O.catharus. The chelae of O.punctatus are heteromorphic, one chela is chiefly used for crushing and the other chiefly for holding, shearing and cutting prey. This crab feeds mainly at night and buried prey were detected by chelae and dactyls of the walking legs as crabs walked across the sand surface and dug out by vigorous scooping movements of dactyls and chelae. Bivalves were either crushed and eaten or prised open by inserting the free fingers which caused chipping of the shells. Alternatively, the fingers were inserted into the siphon openings of the bivalve. Whelks were opened by one of 3 methods: 1) grasping the shell with one chela, inserting the free finger of the other chela into the aperture and shredding the foot, 2) by crushing the tip of the outer body whorl, or 3) by crushing the spire. Crabs from different areas showed slightly different prey preferences and size of preferred prey increased with crab size. Lau (1987) has reviewed the predatory tactics used by decapods to open molluscs. This demonstrates that a wide variety of attack techniques are used by brachyurans.

O.catharus mate when the female is soft-shelled and males are able to recognize females about to moult. The female is clasped by the male who carries her beneath him by wrapping his legs around her. (The same behaviour has been recorded for O.punctatus by Du Preez & McLachlan 1984c.) Eales (1974) has demonstrated that in Carcinus maenas a pheromone produced by the female is responsible for male attraction. Male O.catharus defend the female against other males for several days before moulting and also after mating (Osborne pers.comm.). Such 'cradling' has also been observed in the American blue crab Callinectes sapidus (Tagatz 1968, Steel 1979). Copulation by O.catharus occurs in shallow water while spawning and larval development probably occurs off-shore (Kung 1973). Christy (1987) classifies this kind of male competition for mates as involving defence of mobile, receptive females rather than defence of breeding sites or refuges.

Stephenson (1969) investigated sound production in O.catharus involving the use of various plectra rubbing against the striae on the undersurface of the cheliped propodus. These may be important in encounters between crabs but it is unclear how these sound signals are detected. Osborne (pers. comm.) has observed sound production by male paddle crabs in the presence of a female about to moult or when freshly moulted. The sound seems to be involved in some kind of courtship display. The male stands up on its second and third pairs of legs and has its paddles elevated almost vertically. The first pair of walking legs are folded at the merus/carpus joint, exposing a ridge on the carpus, and the chelipeds are pulled backwards so that the ventral surface of the propodus rubs across the carpal ridge. This produces a low frequency 'sawing' or 'grating' sound. A female paddle crab about to moult and a male already clasping a female have also been recorded producing sound.

Ecology

Leader & Bedford (1978b) examined the composition of muscles and haemolymph of O.catharus and found that ion concentrations were similar to other crabs from the same habitat.

Wear & Haddon (1987) investigated the natural diet of paddle crabs around central and northern New Zealand. Over 4000 guts were examined, approx. 25% were empty and just over 50% contained recognizable food items. A total of 72 species were identified including polychaetes, gastropods, bivalves, crustacea, echinoderms and fish. Diet was dominated by molluscs and crustaceans. Most of the molluscs were juvenile bivalves of Paphies spp. and Callianassa filholi, O.catharus, isopods and amphipods were important Crustacea at different localities. Paddle crabs are clearly versatile and opportunistic predators whose diet reflects local relative abundance of prey. They may influence recruitment to commercially important populations of Paphies spp. but adults of these species have a refuge from predation by virtue of their burrowing habits and occurrence in dense patches (Haddon, Wear & Packer, 1987). The impact of paddle crabs may not be as severe as was earlier suspected (Haddon 1988, Wear 1988a). Brachyura eaten by O.catharus include members of the same species and Notomithrax ursus, Halicarcinus cooki, H.whitei, Hymenosoma depressum, Neohymenicus pubescens, Planes sp. and Pinnotheres novaezelandiae (small males only).

In crab foraging studies it has become customary to starve crabs for 24-48 hours in order to standardize their 'hunger level' but Haddon & Wear (1987) found that a starvation period (up to 28 days) had no effect on number of cockles (A.stutchburyi) consumed. In captivity number of cockles eaten per day tends to decline with time. When fed tuatua (P.subtriangulata) and the burrowing shrimp (Callianassa filholi) paddle crabs process the meal in about 11 hours (at 11^{o}C) with shell fragments being regurgitated. No regurgitation occurred with C.filholi as prey. Gut clearance rates increase with crab size as does ingestion efficiency and crabs take longer to empty a full foregut. Gut volume increases exponentially with CW and sets an upper limit to food intake.

Evidence from fish gut samples suggest that O.catharus is eaten by over 30 species of commercially taken fish including snapper (Chrysophrys auratus), grouper (Polyprion oxygeneios), blue cod (Parapercis colias) and rig (Mustelus lenticulatus). Mature female rig captured in shallow water (less than 10m) and some males eat the paddle crabs, other rig being further offshore do not have access to the crabs (King & Clark 1984). This crab is also eaten by rig from Kaikoura, West Coast and Wellington. Habib(1975) found that paddle crabs were an important part of the diet of red cod (Pseudophycis bacchus) from Banks Peninsula. They were eaten in most months and made up from 0.2 to 5% of gut volume. Red cod from Otago, Foveaux Strait and Cook Strait areas also consume this crab (0.25 to 0.66%). In Pegasus Bay sand flounder (Rhombosolea plebeia) eat paddle crabs (Mundy 1968) and also moki (Latridopsis ciliaris) from the Avon Heathcote Estuary

(Webb 1973b). Common sole (Peltorhampus novaezelandiae) and adult paddle crabs from Brighton beach eat juvenile paddle crabs. Stomachs of Hector's Dolphins (Cephalorhynchus hectori) caught around Banks Peninsula sometimes contain paddle crabs.

In recent years there has been an upsurge in the number of paddle crabs around New Zealand. This may be part of a natural cycle of abundance but there are no early records of paddle crabs reaching 'plague' proportions. However Waite(1909) recorded in the results of the New Zealand Government Trawling Expedition, 1907, "enormous bags of swimming crabs and crayfish (Jasus edwardsi) were taken in Petre and Hansons Bays at the Chatham Islands" using a trawl net, but this may have been a local phenomenon because similar results were not recorded along the New Zealand mainland coast. One hypothesis suggests that the increase in crab numbers is related to heavy fishing pressure on predators of the paddle crab, allowing many more to survive and reproduce. If this is true we might expect an increase in other crabs (e.g. Cancer novaezelandiae) also eaten by these fish. However the hypothesis may still be correct because O.catharus is a rapidly growing and highly fecund species able to take advantage of reduced predation pressure. Alternatively, favourable hydrological conditions in recent years may have improved larval survival and juvenile recruitment. Whatever the cause paddle crabs could pose a serious threat to shallow water shellfish populations by inhibiting recruitment. It is possible that paddle crabs are at least partly responsible for the decline in toheroa populations.

The abundance, large size, good meat yield (25-35%) and excellent flavour suggest that a substantial fishery for paddle crabs could be developed, thereby removing some of the pressure on rock lobsters (Jasus edwardsi). But marketing and 'education' of the public palate about this new delicacy will require much more effort. Already catches have grown from 775kg in 1977 to 306,000kg in 1985. Armstrong (1986) suggested that a small spring-summer fishery using pots could be established in the Blueskin Bay area near Dunedin. There are no regulations covering catches and no minimum legal size but there is market resistance to crabs smaller than 100mm CW.

At present we have little idea of the actual population size of paddle crabs and whether there are separate stocks or simply a single, wide mixing stock. Tagging studies suggest that adults are highly mobile, a crab tagged at Plimmerton Beach, Wellington was recaptured 40km away after 1 month. A substantial commercial fishery for paddle crabs is feasible provided markets can be established (Stead 1983b, Wear 1988b). Increased catches are unlikely to damage the population provided that large crabs are taken, because most of them are likely to be males. At present the demand is for large whole hardshell crabs but if a demand develops for crabmeat then smaller crabs will be processed and the population may be harmed. (Howgate (1984) has examined the methods of handling and market demands for processed crab meat.) Development of a soft-shell crab industry could also place different demands on the population when different sized crabs are captured and held until they moult.

In his review of several northern hemisphere crab populations Jamieson (1986) provides some cautionary conclusions: 1) little information on the causes or patterns of annual variability is available, 2) management seems to have had no demonstrated effect on the magnitude or incidence of fluctuations, and 3) present crab management has often been structured in a way that does not require advance prediction of future fluctuations in population abundance. Further, numbers of fishermen have typically increased over time in most fisheries, but the abundance of crabs has not, and crab fishing has often become overcapitalized. Jamieson emphasizes the need for detailed study of a species throughout its range in order to obtain an understanding of factors affecting year-class strength. The life-history differences between Pegasus and Tasman Bays O.catharus found by Osborne (1987a) reinforce this conclusion. Past management of crab resources may have done little to enhance overall yield but they have ensured that crab resources have been harvested in a coordinated, generally efficient, socially acceptable manner.

References

Armstrong (1985,1986), Bennett (1964), Caddy (1986), Chilton & Bennett (1929), Clark (1978), Davidson (1986), Davidson & Marsden (1987), Dell (1963a), Du Preez (1984), Du Preez & McLachlan (1984a,1984b,1984c,1984d), Haddon & Wear (1987), Haddon, Wear & Parker (1987), Haefner (1985), Hartnoll (1971), Hines (1982), Jones (1983), King & Clark (1984), Kung (1973), Leader & Bedford (1978b), McLay & Osborne (1985), Mundy (1968), Osborne (1987a,1987b), Quackenbush (1986), Roper, Simons & Jones (1983), Stead (1983a,1983b,1984), Steel (1979), Stephenson (1969,1972), Stephenson & Rees (1968), Tagatz (1968), Wear (1982,1984,1988a,1988b), Wear & Fielder (1985), Wear & Haddon (1987), Webb (1973b).

Ovalipes molleri (Ward, 1933)

Synonymy

Aeneacancer molleri Ward, 1933; McNeill, 1953; *Ovalipes molleri* Stephenson & Campbell, 1960; *Ovalipes irridescens* [in part] Sakai, 1965; *Ovalipes molleri* Stephenson & Rees, 1968; Stephenson, 1972; Dawson & Yaldwyn, 1974; Griffin & Brown, 1975; Wear & Fielder, 1985(list).

Type Locality

South of Montague Is., Australia.

Distribution

Southeast Australia (New South Wales and Victoria) and Northern New Zealand (north of North Cape, 34°7.5′S, 172°47′E, 315-439m).

Diagnosis (Fig. 46a-d)

Front four toothed (including inner supraorbital lobes), median teeth close together and produced further forwards than laterals. Carapace moderately broad (1.28 times CL), finely granulated and slightly convex. A tubercular elevation on each protogastric region and two large reniform areas of very thin cuticle in posterior half. Five anterolateral teeth (including post-orbital tooth), small, sharp and broadly separated. First tooth largest, blunter than second tooth which is smallest and sharpest. Pterygostomial area with conspicuous stridulating ridge. Chelipeds relatively long, thin, granulated and armed with small, sharp spines. Propodus slightly swollen, carinated, movable finger granular. Both fingers relatively long, slender with sharp tips and moderately blunt teeth. *O.molleri* lacks the striae present on the ventral surface of the cheliped propodi of *O.catharus*. First leg longest others decreasing, dactyli very long and sharp. Last pair of legs short with oval paddle shaped dactyls.

Colour

Preserved specimens are white but in life there is iridescence on the carapace, chelipeds and legs.

Size

Male 87.5mm CW.

Habitat

Sandy and muddy bottoms on the continental shelf.

Depth

73-585m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Dawson & Yaldwyn (1974), Griffin & Brown (1975), McLay and Osborne (1985), Stephenson (1972), Stephenson & Campbell (1960), Stephenson & Rees (1968), Ward (1933).

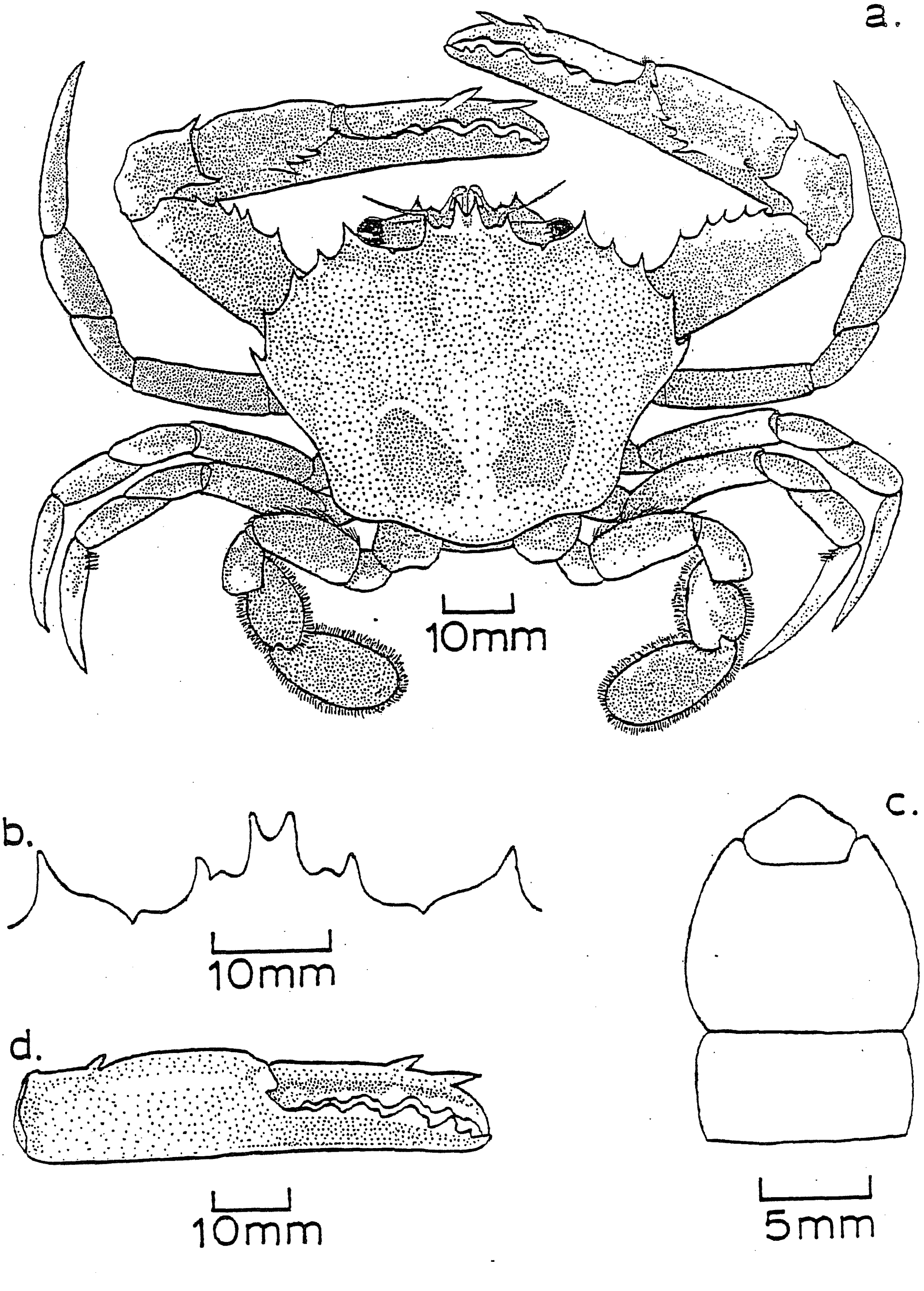


Fig. 46 - Ovalipes molleri: a - male, dorsal view (by J. Black); b - outline of frontal margin, dorsal view (based on a photo from Stephenson & Rees, 1968); c - male abdomen, ventral view (after Stephenson & Rees, 1968); d - right male chela, outer face (by J. Black, based on photo from Stephenson & Rees, 1968).

Portunus pelagicus (Linnaeus, 1766)
Blue Swimming Crab

Synonymy

Cancer pelagicus Linnaeus, 1766; *Portunus pelagicus* Fabricius, 1798; *Neptunus pelagicus* De Haan, 1833; *Lupa pelagica* H.Milne Edwards, 1834; *Neptunus pelagicus* A.Milne Edwards, 1861; Miers, 1876b; Haswell, 1882a; Miers, 1884; Filhol, 1886; Miers, 1886; Ortmann, 1893; 1894; Alcock, 1899; Calman, 1900; Whitelegge, 1900; Rathbun, 1902; *Callinectes alexandri* Rathbun, 1907; *Portunus pelagicus* Rathbun, 1923; Hale, 1927; Chilton & Bennett, 1929; *Neptunus pelagicus* Boone, 1934; Sakai, 1934; Chopra, 1935; Sakai, 1936a; Shen, 1937; Sakai, 1939; *Portunicus mauritanus* Ward, 1942; *Lupa pelagica* Barnard, 1950; *Neptunus pelagicus* Chhapgar, 1957; *Portunus pelagicus* Stephenson & Campbell, 1959; Crosnier, 1962; Dell, 1964c; 1968a; Stephenson, 1968a; 1968b; Stephenson, Williams & Lance, 1968; McNeill, 1968; Campbell & Stephenson, 1970; Healy & Yaldwyn, 1970; Heath, 1971; Stephenson, 1972; Dawson & Yaldwyn, 1974; Shinkarenko, 1979; Wear & Fielder, 1985; Hutton, 1986.

Distribution

From East Africa to Philippine Islands, Japan, Tahiti, Australia, Lord Howe Is. and northern New Zealand. In New Zealand there is a single record from Rangitoto Is., Hauraki Gulf. *P.pelagicus* has migrated through the Suez Canal to colonize the Mediterranean Sea.

Diagnosis (Fig. 47a-c)

Carapace very broad (width 2 - 2.3 times CL), anterolateral borders form a broad arc armed with nine teeth, the first (i.e. outer orbital angle) larger than those immediately after, the ninth very large and projecting straight out laterally. Front not projecting and bearing four (not including inner, orbital angle) acute, tooth-like lobes of which the outer are larger and more prominent, all lower and more rounded in juveniles. Carapace surface granulated, varying from coarse, more widely spaced granules, to finer, closer granules, frequently with a short, dense pubescence between the granules. The following carapace ridges are generally recognizable : mesogastrics set at a slight angle to the antero-posterior line, epibranchials, and indistinct metagastrics. Cardiac and mesobranchial areas bear pairs of low, granular prominences. Chelipeds very long (3 times CL), massive, spinous and ridged. Anterior border of merus armed with four sharp spines. Upper surface of propodus and dactyl with three carinae, typically granular. Fingers very long and strongly flattened, fourth pair of legs shortest, dactyls large and paddle-shaped, posterior surface with fine fringing hairs, no spines or spinules.

Colour

Carapace purplish-brown with pale mottling. Legs blue to lilac with white mottling. There are variations in pigmentation between juveniles and adults and also regional differences.

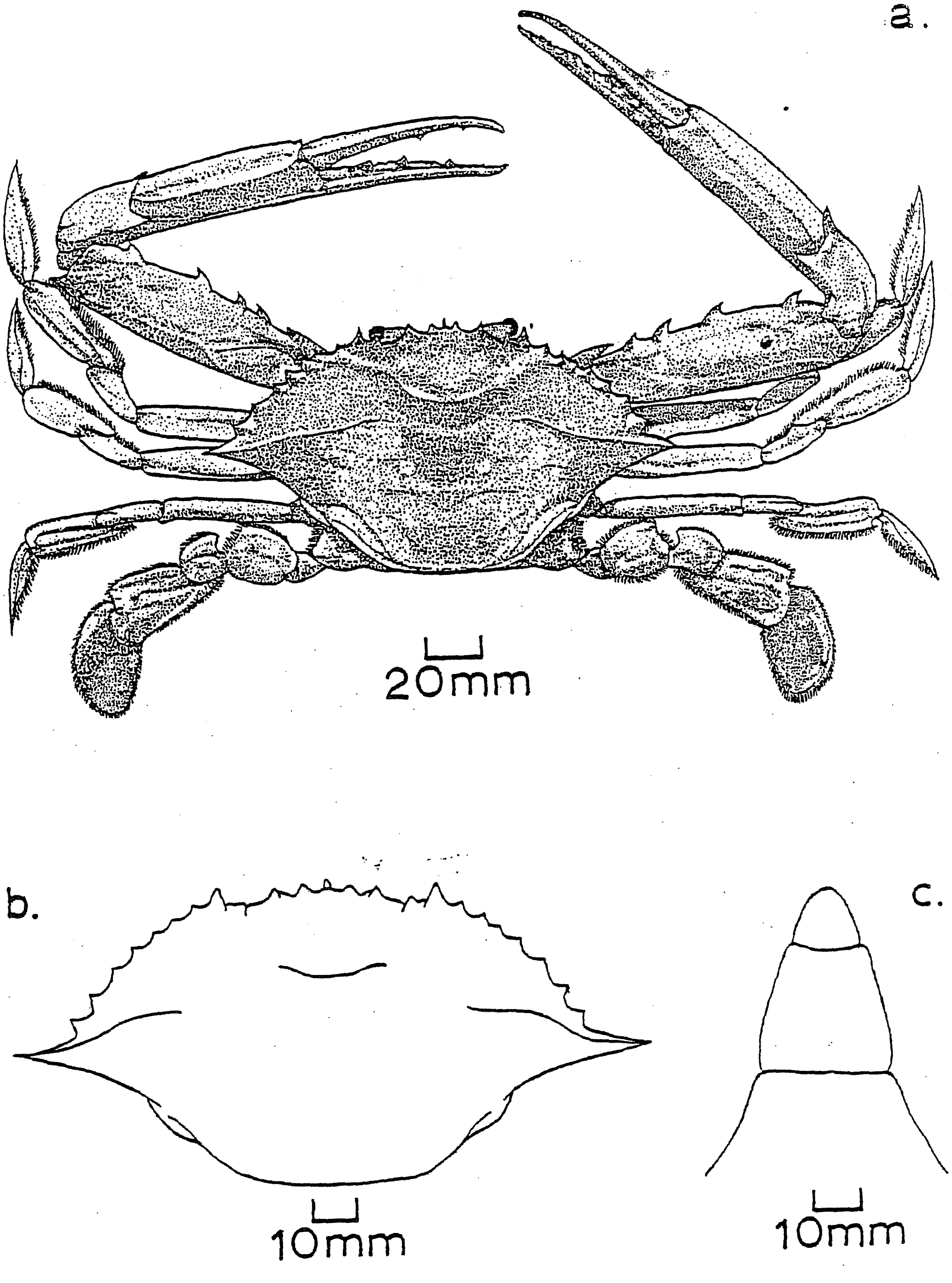


Fig. 47 - Portunus pelagicus: a - male, dorsal view (by J. Black, based on a photo from Hale, 1927); b - outline of carapace (by J. Black, on a figure from Crosnier, 1962); c - distal abdominal segments, male (after Crosnier, 1962).

Size

Male 185mm CW, 83mm CL. Female 170mm CW, 75mm CL, smallest ovigerous female 85mm CW.

Habitat

Intertidal, in sandy mud and Zostera, shallow pools and under stones. At night P.pelagicus may be found swimming near the water surface.

Depth

0-65m.

Breeding

Along the south-west coast of India ovigerous females have been recorded from September to April (Pillay & Nair 1971). Here maximum breeding activity is in December/January. The percentage of body weight made up of gonads is 2% in females but only 0.4% in males. A similar breeding season was recorded for P.pelagicus in Western Australia. The CW of berried females ranged from 85mm to 157mm and fecundity ranged from 270,000 to 848,000 (102mm-136mm CW). Berried females move from estuaries to the sea to release their offspring (Potter et al., 1983). No ovigerous females have been found in New Zealand.

Development and Growth

Shinkarenko (1979) has described the 4 zoeal stages and megalopa (see also Wear & Fielder 1985). The zoea do not possess a gastric mill and prey must be broken down by the mouthparts and serrated setae on the telson. The megalopa stage has a gastric mill and uses its chelipeds for prey handling.

Fielder & Eales (1972) observed that P.pelagicus had a distinct pubertal moult which preceded sexual maturity. The morphological changes which occurred in a female of 111mm CW included:

1) changes in the shape of the abdomen,
2) disappearance of the hooks on the sixth abdominal sternite,
3) increase in size of the genital pore from a comma shape (1.8 x 1.1mm) to a smooth oval (4.0 x 2.5mm), representing a five-fold increase in area, and
4) a great increase in length and density of the pleopod setae. A mature female of 147mm CW which also moulted and then mated, increased to 161mm CW, suggesting that mature females moult several times after maturity.

In Western Australian estuaries growth is very rapid with both sexes reaching 120mm CW after one year, which is almost minimum legal size (127mm CW). At about this size crabs migrate out of estuaries into inshore marine waters (Potter et al. 1983).

Behaviour

P.pelagicus rapidly buries itself in the sand but commonly swims to the surface after nightfall, swimming powerfully, usually with the tidal current.

Brief observations on courtship and mating by P.pelagicus were made by Fielder & Eales (1972). Pre-moult courtship of similar sized males and females lasted for 4 days with one pair of crabs, during which the male clasped the female beneath, with his sternum firmly against her carapace, using his first pair of walking legs. While the female was extremely submissive, the male was exceedingly aggressive towards other crabs. The female moulted at night and copulation occurred soon afterwards. The crabs mated with the female on her back and the sterna opposed. The male abdomen was extended and inserted beneath the female's so that the male's copulatory organs could be inserted in the genital apertures. Copulation lasted for between 4 and 7 hours. After copulation the male assisted the female back into the normal position and assumed the protective pre-copulatory relationship. Post-copulatory attendance did not last more than 24 hours. Ryan (1966) has demonstrated that in P.sanguinolentus a pheromone produced by the female is the basis of their attractiveness to males.

Ecology

Williams (1981,1982) studied the natural food of P.pelagicus in Moreton Bay, Queensland. She found that this crab is a bottom-feeding carnivore, eating a wide variety of sessile and slow-moving invertebrates. Diet was largely dependent upon local availability of prey species: the main foods for intertidal crabs (up to 55mm CW) were small hermit crabs and gastropods and for sub-tidal crabs (up to 150mm CW) bivalves and ophiuroids. Within broad taxonomic groups there was little change in diet with season. The percent similarity between diets of intertidal crabs (mainly juveniles) and subtidal crabs (mainly adults) was 27%. Crabs cease feeding prior to and during moulting. Immediately after moulting, the gastric mill was filled with calcareous fragments (pieces of bleached mollusc shell, coral fragments etc.) picked up from the bottom. Williams (1986) evaluated the use of Floy tags for marking P.pelagicus in Moreton Bay, but found them unsuitable because return rates of crabs by size, sex and area of tagging class were very heterogeneous. The tags were not easily detected on recapture and the fishermen did not pay sufficient attention to categories of unmarketable crabs. Only 4% of 1754 crabs tagged and released were returned. However tags did not affect short-term survival in the laboratory.

P.pelagicus has a wide Indo-West Pacific distribution and is the basis of commercial fisheries in many areas e.g. Australia, India, Japan (Thompson 1951, Prasad & Tampi 1951, Tanoue et al 1967, Guinot 1966). Western Australian commercial landings in 1982-83 amounted to 121,371kg and crabs were caught during summer and autumn.

References

Bawab & El-Sherief (1988), Campbell & Stephenson (1970), Crosnier (1962), Dell (1964c), Fielder & Eales (1972), Hale (1927), Pillay & Nair (1971), Potter et al. (1983), Shinkarenko (1979), Stephenson (1968a, 1968b, 1972), Stephenson & Campbell (1959), Wear & Fielder (1985), Williams (1981,1982,1986).

Liocarcinus corrugatus (Pennant, 1777)
Dwarf Swimming Crab

Synonymy

Cancer corrugatus Pennant, 1777; Portunus corrugatus De Haan, 1833; Bell, 1853; Portunus strigilis Stimpson, 1858; Portunus subcorrugatus A.Milne Edwards, 1861; Portunus pusillus Kirk, 1878; Portunus corrugatus Miers, 1879; 1886; Ortmann, 1893; Liocarcinus strigilis Rathbun, 1902; Portunus corrugatus Fulton & Grant, 1906; Portunus subcorrugatus Nobili, 1906; Liocarcinus strigilis Stimpson, 1907; Parisi, 1916; Portunus corrugatus Borradaile, 1916; Portunus corrugatus strigilis Balss, 1922; Liocarcinus strigilus Urita, 1926; Liocarcinus corrugatus Hale, 1927; Portunus corrugatus Palmer, 1927; Portunus corrugatus Chilton & Bennett, 1929; Portunus borradailei Bennett, 1930; Liocarcinus corrugatus McNeill & Ward, 1930; Portunus corrugatus strigilis Yokoya, 1933; Sakai, 1934; 1936a; Liocarcinus corrugatus Powell, 1937; Portunus corrugatus strigilis Sakai, 1939; Liocarcinus corrugatus Guiler, 1952; Macropipus corrugatus Stephenson & Campbell, 1960; Liocarcinus borradailei Dell, 1963a; Liocarcinus corrugatus Bennett, 1964; Macropipus corrugatus Dell, 1968a; Utinomi, 1969; Stephenson, 1972; Dawson & Yaldwyn, 1974; Liocarcinus corrugatus Ingle, 1980; Crothers & Crothers, 1983; Macropipus corrugatus Wear & Fielder, 1985.

Type Locality

Plymouth, England. Although this species has often been placed in the genus Macropipus I have chosen to follow Ingle (1980) in placing it in the genus Liocarcinus. At some stage we should make a proper comparison of the N.Z. specimens with those from Britain to establish their identity.

Distribution

L.corrugatus has an almost world-wide distribution including British Isles to Azores, Canaries, Sierra Leone, Mediterranean, Adriatic, Red Sea. In the Indo-West Pacific an antitropical distribution with Japan in the North and Australia and New Zealand in the South. Within Australia L.corrugatus occurs from southern Queensland, New South Wales, Tasmania, Victoria, South Australia and southern Western Australia. Within New Zealand from Spirits Bay south to Queen Charlotte Sound, also Wanganui. L.corrugatus has also been found in stomachs from rig (Mustelus lenticulatus) captured at Kaikoura and Banks Peninsula (King & Clark 1984). Also Stewart Island and Chatham Islands.

Diagnosis (Fig. 48a-d)

Carapace wider than long (ratio approx. 1.2), regions well defined and marked by transverse ridges. Front cut into three rounded finely denticulated lobes (not including the orbit) and antero-lateral margins cut into five acute teeth (including the post-orbital tooth). Postero-lateral margins converging sharply, posterior margin slightly convex. Dorsal margins of orbit rounded, deeply set, with a small fissure mid-way. Eyes large, bulbous, protruding. Chelipeds short, inner margin of carpus with a short spine, dorsal margins of propodus armed with a large, distally directed spine, outer propodus surface with three ridges. Movable finger larger than fixed finger, curved downward

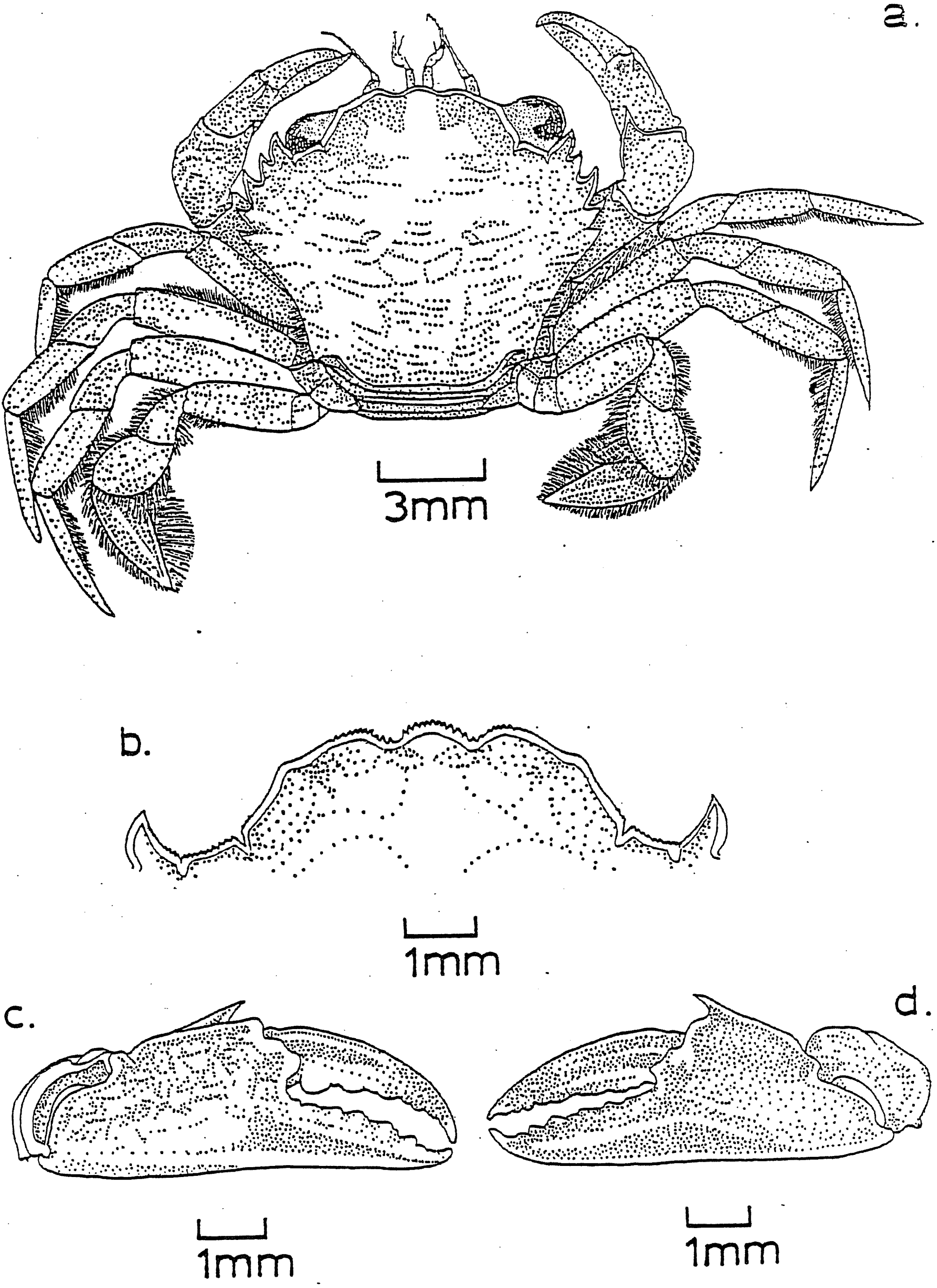


Fig. 48 - Liocarcinus corrugatus: a - male, dorsal view; b - outline of frontal margin, dorsal view; c - right chela, male, outer face; d - left chela, male, outer face (by J. Black).

and crossing on inside of fixed finger, inner margins of both fingers with small teeth, occluding for their entire length. First three pairs of legs as long as chelipeds, segments flattened, dactyls long and narrow, posterior margin fringed with small setae. Last pair of legs shorter, segments flattened and broader, dactyls are lanceolate-shaped paddles, fringed with long setae.

Colour

Variable colour patterns ranging from pure white, mottled grey and white, to grey, often with a white stipe down the middle of the carapace. Base of cheliped and leg dactyls have a red band.

Size

Male 21mm CW. Female 26mm CW.

Habitat

Sandy and sand-shell sub-tidal bottom. Also occurs among weed on the sandy tidal flats and in intertidal rock pools.

Depth

Tidal flats to 137m.

Breeding

No details of breeding in New Zealand. In Europe ovigerous females occur from April to August. Eggs newly laid, red-orange, 0.32mm diam., ready to hatch, speckled brown, 0.4mm.

Development and Growth

Probably 5 zoeal stages. Wear & Fielder (1985) described the first, second and fourth zoea but the megalopa is unknown. Larval stages rarely found in New Zealand plankton, but have been recorded from Leigh.

Behaviour

Kingsford & Choat (1985) found that megalopae, which they attributed to the genus "Macropipus", were very abundant beneath drift algae off the coast of Leigh in December. These megalopae may have belonged to L.corrugatus. Clumps of floating algae were colonized quickly, within 5-8 hours. Thus conventional plankton samples which do not sample close to drifting algae will underestimate the abundance of crab megalopae. Clearly the presence of drift algae will influence recruitment to local populations.

Ecology

L.corrugatus is eaten (0.1 to 1.5% of gut volume) by snapper (Chrysophrys auratus) from Hauraki Gulf and Bay of Plenty (Godfriaux 1969,1974b), trevally (Caranx lutescens), 0.1%, red gurnard (Cheilonichthys kumu),1.8%, eagle ray (Holorhinus tenuicaudatus),0.6%, (Godfriaux 1970a), tarakihi (C.macropterus), <0.1% (Godfriaux 1974a) and by rig (see above).

References

Bennett (1964), Dell (1963a,1968a), Hale (1927), King & Clark (1984), Stephenson (1972), Stephenson & Campbell (1960), Wear & Fielder (1985).

Nectocarcinus antarcticus (Jacquinot, 1853)
Hairy Red Swimming Crab

Synonymy

Portunus antarcticus Jacquinot, 1853; Nectocarcinus antarcticus A.Milne Edwards, 1860; Miers, 1874; 1876b; Hutton, 1879; Filhol, 1886; Hodgson, 1902; Wilson, 1907; Chilton, 1909; 1911a; Thomson, 1913; Rathbun, 1918b; Thomson & Anderton, 1921; Stephensen, 1927; Chilton & Bennett, 1929; Young, 1929; Powell, 1937; Richardson, 1949a; Ralph & Yaldwyn, 1956; Yaldwyn, 1958; Dell, 1960; Stephenson, 1962; Dell, 1963a; 1963b; Bennett, 1964; Dell, 1968a; Inoue, Arai & Abe, 1968; Takeda & Miyake, 1969; Ritchie, 1970; Dell, Griffin & Yaldwyn, 1970; Stephenson, 1972; Dawson & Yaldwyn, 1974; Main, 1974; Fenwick, 1975; Yaldwyn, 1975; Ryff & Voller, 1976; Fenwick, 1978; Probert et al., 1979; Willan, 1981; Wear & Fielder, 1985.

Type Locality

Auckland Islands.

Distribution

New Zealand mainland from Cape Maria van Diemen to Stewart Is., Chatham Islands, Bounty Islands, Auckland Islands and possibly Campbell Island. N.antarcticus has the best known distribution of all New Zealand crabs (see Main 1974). It is found from 166°E-176°E and 34°S-51°S. Although broadly overlapping with N.bennetti it is rarely taken in the same sample.

Diagnosis (Fig. 49a-d)

Carapace wider than long (ratio 1.27 - 1.38), completely clothed in short, fine, dark, tomentum, rounded granules forming distinct ridges projecting through the tomentum, regions distinct. Epibranchial ridge relatively strong with large granules, extending from near fourth anterolateral tooth and converging sharply posteriorly. Front quadrilobate, medial lobes smaller, narrower, blunt and closer together than to submedials which have concave, strongly tuberculate inner margins and smooth, convex outer margins. Orbit shallow, broad, dorsal edge with rounded tubercles, a supraorbital fissure. Anterolateral margin with four small, subequally spaced teeth (including postorbital tooth), first blunt, others acute, third and fourth stronger. Chelipeds subequal in length and size, both right and left chelae with similar teeth on fingers. Carpus broad, with strong, blunt, distolateral spine and a short acute spine medially. Propodus with strong tuberculated ridges and many scattered tubercles. Fixed finger with five very distinct tuberculated, longitudinal ridges merging distally, about fifteen irregular teeth along the inner edge. Dactyl also with five ridges and similar teeth along the cutting edges. Both hands with prominent longitudinal bands of dark-coloured tomentum. Walking legs flattened and unspined, first three pairs slightly longer than chelipeds. Last pair of legs shorter, propodus and dactyl flattened, broad with dactyl oval, lamellate with a central ridge and fringed with hairs. Male abdomen with telson triangular, a little broader than long, apex somewhat truncated and rounded, last abdominal segment with weakly concave lateral margins. First

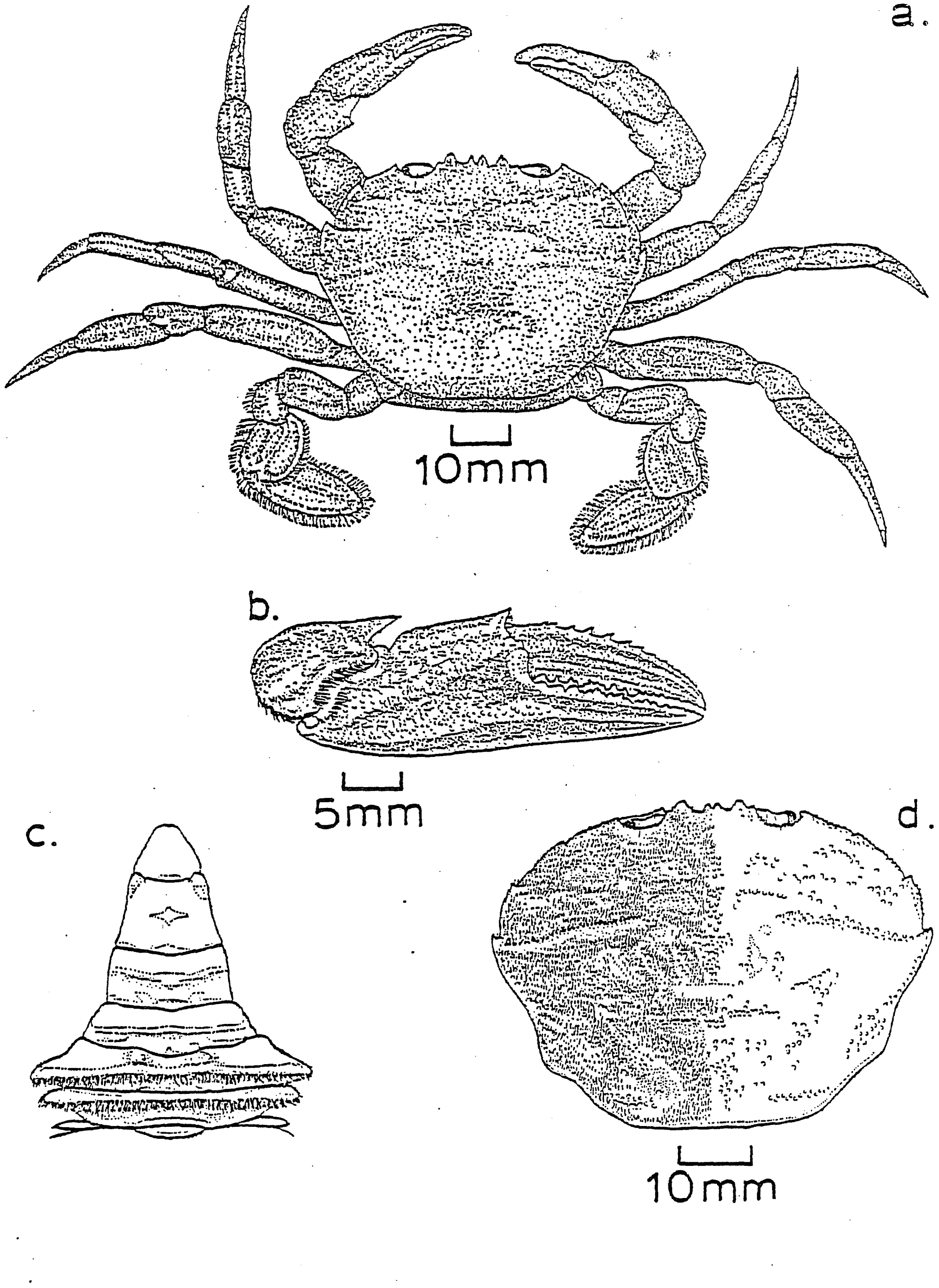


Fig. 49 - Nectocarcinus antarcticus: a - male, dorsal view (after Dell, 1963); b - right chela, male, outer face; c - male abdomen, ventral view; d - detail of carapace, male (after Dell, Griffin & Yaldwyn, 1970).

pleopod of male stout and straight, tip elongate and acute.

Colour

Carapace and dorsal surface of chelipeds and legs mottled with dark and red over a background of pinkish red. No trace of iridescence, but with some small white marks on various ridges and spines. Fingers of chelae dark red.

Size

CW 87.0mm, smallest ovigerous female 8.8mm CW. Larger specimens occur towards the southern limits of distribution.

Habitat

Found on sand, gravel, mud and shell bottoms.

Depth

0-550m.

Breeding

Ovigerous females have been found at depths of 17-263m from April to October, also November & January. Thomson & Anderton (1921) recorded an ovigerous female, about 20mm CW, off Otago Heads and whose eggs hatched in early October. Sex ratio does not differ from 50/50. North of Cook Strait females seem to mature at a much smaller size (around 10mm CW) than crabs from southern areas (Main, 1974). New eggs are pale orange-yellow, 0.42 x 0.35mm, ready to hatch, transparent to light yellow, 0.49 x 0.42mm (Wear & Fielder 1985).

Development and Growth

Five zoeal stages and megalopa described by Wear & Fielder (1985). Frequently the most abundant brachyuran larva in off-shore plankton samples, especially during spring and summer.

Behaviour

Small (15mm CW) N.antarcticus captured at Leigh and placed in a tray of sand showed no evidence of burrowing as seen in Ovalipes catharus. They simply remained immobile on the bottom or hid beneath shell fragments, their mottled colouration providing good camouflage.

Ritchie (1970) caught small numbers of N.antarcticus in baited pots at the Auckland Islands.

Ecology

Leader & Bedford (1978b) examined the composition of muscles and haemolymph of N.antarcticus and found that ion concentrations were similar to other crabs from the same habitat.

N.antarcticus is one of the most important elements in the diet of red cod (Pseudophycis bacchus) from Banks Peninsula (Habib 1975). It was eaten in most months, ranging from 0.7 to 12% of gut volume. Red cod from Otago ate smaller quantities, 0.43 to 0.51% in November and May. Habib (1976) found that barracouda (Thyrsites atun) and southern kingfish (Rexea solandri) will also eat the red swimming crab. It is also an important food item of female rig (Mustelus lenticulatus) captured in shallow water (<15m) in Golden Bay and also rig from Banks Peninsula (King & Clark 1984). N.antarcticus occurred less frequently in rig stomachs from Tasman Bay, Kaikoura, Otago, West Coast and Hauraki Gulf. Graham (1956) recorded these crabs from stomachs of kahawai (Arripis trutta) in Otago harbour. Snapper (Chrysophrys auratus) from Hauraki Gulf and Bay of Plenty ate N.antarcticus, 0.5 to 1.6% of gut volume (Godfriaux 1969,1974b, Colman 1972), also trevally (Caranx lutescens), 0.3%, red gurnard (Cheildonichthys kumu), 3.2%, (Godfriaux 1970a) and tarakihi (C.macropterus), 10.2%, from Western Bay of Plenty (Godfriaux 1974a). Thomson & Anderton (1921) also found this crab in the stomachs of skate (Raja nasuta), elephant fish (Callorhynchus milii), hapuku (Polyprion oxygeneios) and ling (Genypterus blacodes). Young (1929) recorded N.antarcticus from stomachs of blue cod (Parapercis colias) captured at the Chatham Islands. These crabs are also eaten by Hooker's Sea Lion (Phocarctos hookeri) and Southern Elephant Seal (Mirounga leoninus) (Yaldwyn 1958).

The food habits of N.antarcticus are unknown but may be similar to the northern hemisphere portunids, Liocarcinus puber and L.holsatus. These crabs consume brown algae, crustaceans, bivalves and fish, and are opportunistic omnivores (ap Rheinallt & Hughes, 1985, Choy, 1986). L.puber will also eat scallops (Lake et al. 1987).

Glaessner (1980) suggests that Nectocarcinus spp. may be derived from the eocene genus Pororaria.

References

Bennett (1964), Colman (1972), Dell (1963a), Dell, Griffin & Yaldwyn (1970), Godfriaux (1969,1974a,1974b), Habib (1976), King & Clark (1984), Leader & Bedford (1978b), Main (1974), Wear & Fielder (1985).

Nectocarcinus bennetti Takeda & Miyake, 1969
Smooth Red Swimming Crab

Synonymy

?Nectocarcinus antarcticus Inoue, Arai & Abe, 1968; Nectocarcinus bennetti Takeda & Miyake, 1969; Dell, Griffin & Yaldwyn, 1970; Ritchie, 1970; Stephenson, 1972; Ritchie, 1973; Dawson & Yaldwyn, 1974; Main, 1974; Fenwick, 1975; Yaldwyn, 1975; Ryff & Voller, 1976; Fenwick, 1978; Wear & Fielder, 1985.

Type Locality

44°7.2'S, 175°55.5'E, 140m, Chatham Rise, east of Banks Peninsula.

Distribution

Southern South Island, Stewart Island, Snares Island, Auckland Islands, Pukaki Rise and Campbell Island. It is found from 165°-180°E and 44°-53°S. A very detailed distribution map is to be found in Main (1974). Although broadly overlapping with N.antarcticus it is rarely taken in the same sample.

Diagnosis (Fig. 50a-d)

Carapace wider than long (ratio 1.21-1.33), naked, with rounded granules forming distinct ridges on anterior half but more generally scattered on posterior half. Epibranchial ridge relatively strong and densely granulated, extending from near fourth anterolateral tooth. Front quadrilobate, slightly upturned, medial lobes smaller, narrower, more acute, closer to each other than to submedials which have concave, minutely tuberculate inner and convex, smooth, outer margins. Orbit shallow, broad, dorsal edge with rounded tubercles, two supraorbital fissures. Anterolateral margin with four subequally spaced teeth (including postorbital tooth), first subacute, others acute, third and fourth stronger. Margin between teeth edged with granules. Chelipeds with some fringes of long hairs and scattered short hairs, subequal in length and size, right chela armed with strong, rounded lobe-like teeth on fingers, left chela with more numerous, smaller, more acute teeth. Merus relatively short and distally expanded, with a short acute spine on dorsal surface. Carpus broad with a small blunt distolateral spine and a long, stout, acute medial spine. Propodus with tuberculated ridges and scattered tubercles but no carriae, dorsal surface flattened and marked off from inner and outer surfaces by a prominent tuberculated angular ridge. Outer surface of propodus with two irregular longitudinal bands of tubercles, ventral surface with numerous tubercles arranged in irregular, transverse aggregations. Fixed finger with five tuberculated longitudinal ridges merging distally and 10-14 irregular teeth along the cutting edge. Dactyl with five similar ridges and 10-16 irregular teeth on cutting edge. Walking legs flattened and unspined, first three pairs slightly longer than chelipeds. Last pair of legs shorter, propodus and dactyl flattened, broad with dactyl oval, lamellate with a central ridge and fringed with hairs. Male abdomen with telson triangular, a little broader than long, with bluntly rounded apex and last abdominal segment with strongly convex lateral margins. First

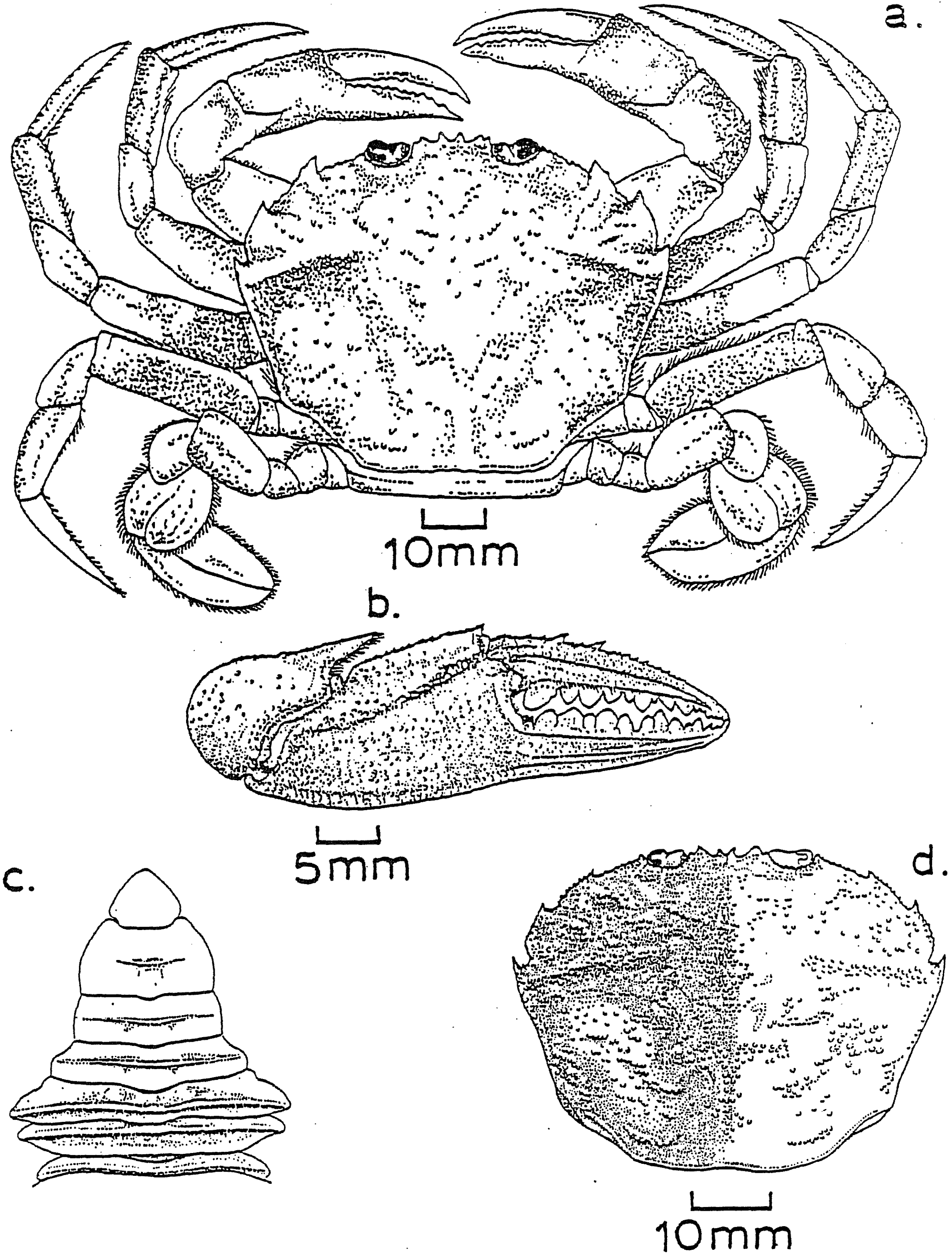


Fig. 50 - Nectocarcinus bennetti: a - male, dorsal view (by C. Duffy based on a photo from Main, 1974); b - right chela, male outer face; c - male, abdomen, ventral view; d - detail of carapace, male (after Dell, Griffin & Yaldwyn, 1970).

pleopod of male stout proximally, bent outwards almost at a right angle.

Colour

Carapace and dorsal surface of chelipeds mainly purplish-red with areas of pink iridescence. Main areas of iridescence are across the front of the carapace, along each anterolateral margin, along the anterior side of each epibranchial ridge in a narrow band and over the carpus, propodus and dactyl of each cheliped. Small specimens show less iridescence. Fingers of chelae not distinctly pigmented.

Size

Male 85mm CL, 65mm CW. Female 68mm, 51mm. Females mature in the size range 12-20mm CL (Main, 1974). Larger specimens occur towards the southern limits of distribution.

Habitat

Found on gravel, shell, sand and mud bottoms.

Depth

20-480m, greatest numbers found between 60-180m.

Breeding

Ovigerous females (32-54mm CL) have been found at depths of 150-183m in May only. Sex ratio does not differ from 50:50.

Development & Growth

Unknown, but probably has five zoeal stages and megalopa as described for N.antarcticus by Wear & Fielder (1985). Recruitment of post-megalopa stages has been recorded in December-January at Auckland Islands (Fenwick, 1975).

Behaviour

Ritchie (1970, 1973) caught many N.bennetti in baited pots at the Auckland Islands. These crabs were observed picking at young red algae on the carapace of Jacquinotia edwardsi. At the sight of a diver they fled rapidly either by walking or swimming.

Ecology

Mitchell (1984) recorded N.bennetti from the guts of ling (Genypterus blacodes) captured on Campbell Plateau - Pukaki rise (341-610m). It is likely that southern elephant seals (Mirounga leoninus) at Auckland Island consume this crab (see Yaldwyn 1958).

Glaessner (1980) suggests that Nectocarcinus spp. may be derived from the eocene genus Pororaria.

References

Dell, Griffin & Yaldwyn (1970), Fenwick (1978), Main (1974), Ritchie (1970, 1973).

Scylla serrata (Forskal, 1775)
Mud Crab or Mangrove Crab

Synonymy

Cancer serratus Forskal, 1775; Cancer olivaceus Herbst, 1796; Portunus tranquebaricus Fabricius, 1798; Scylla serrata De Haan, 1833; Lupa tranquebaricus H.Milne Edwards, 1834; Lupa lobifrons H.Milne Edwards, 1834; Scylla tranquebarica var. oceanica Dana, 1852; Scylla serrata A.Milne Edwards, 1861; Miers, 1876b; Haswell, 1882a; Alcock, 1899; Scylla tranquebarica var. oceanica Stimpson, 1907; Scylla serrata Shen, 1932; Boone, 1934; Leene, 1938; Sakai, 1939; Estampador, 1949; Scylla tranquebarica Estampador, 1949; Scylla serrata var. paramamosain Estampador, 1949; Scylla serrata Barnard, 1950; Serene, 1952; Scylla oceanica Serene, 1952; Scylla tranquebarica Serene, 1952; Scylla serrata var. paramamosain Serene, 1952; Scylla serrata Edmondson, 1954; Chhapgar, 1957; Stephenson & Campbell, 1960; Forest & Guinot, 1961; Dell, 1964b; Tinker, 1965; Dell, 1968a; Utinomi, 1969; Healy & Yaldwyn, 1970, Heath 1971, Stephenson 1972, Dawson & Yaldwyn, 1974, Wear & Fielder, 1985.

Distribution

Throughout the Indo-West Pacific, Tanzania and East Africa, Red Sea to Japan, New Caledonia, Fiji, Tahiti, including Australia and northern New Zealand. S.serrata was introduced to Hawaii from Samoa in the 1920's. Within Australia, from Broome , Western Australia, north and east to Northern Territory, Queensland, and in New South Wales to Port Hacking. Within New Zealand it has recently become established in the far north, Parengarenga to Bay of Islands (see Dell 1964b).

Diagnosis (Fig. 51a-c)

Carapace much wider than long (ratio approx. 1.6), convex, regions well defined. Anterolateral margins rounded, posterolateral margins strongly convergent, posterior margin straight. Front armed with four acute teeth, strong, blunt, pre-orbital tooth, orbital margin concave and divided by two fissures, followed by a strong, acute post-orbital tooth and eight acute, forwardly directed (except the last which is laterally directed), anterolateral teeth. Chelipeds massive, merus with two spines on the posterior border and three spines on the anterior border. Carpus with a strong spine on the inner margin, propodus with two small distal spines on the upper border. Fingers long, curved, inner borders armed with large, rounded teeth. First three pairs of legs shorter than chelipeds, segments flattened, last pair of legs much shorter, propodus and dactyl very flattened, dactyl paddle-shaped.

Colour

Variable, deep ferrugineous brown, light purplish brown with irregular small, whitish spots, green to greyish green, and deep purplish, drab green.

Size

Male 190mm CW. Female 165mm CW.

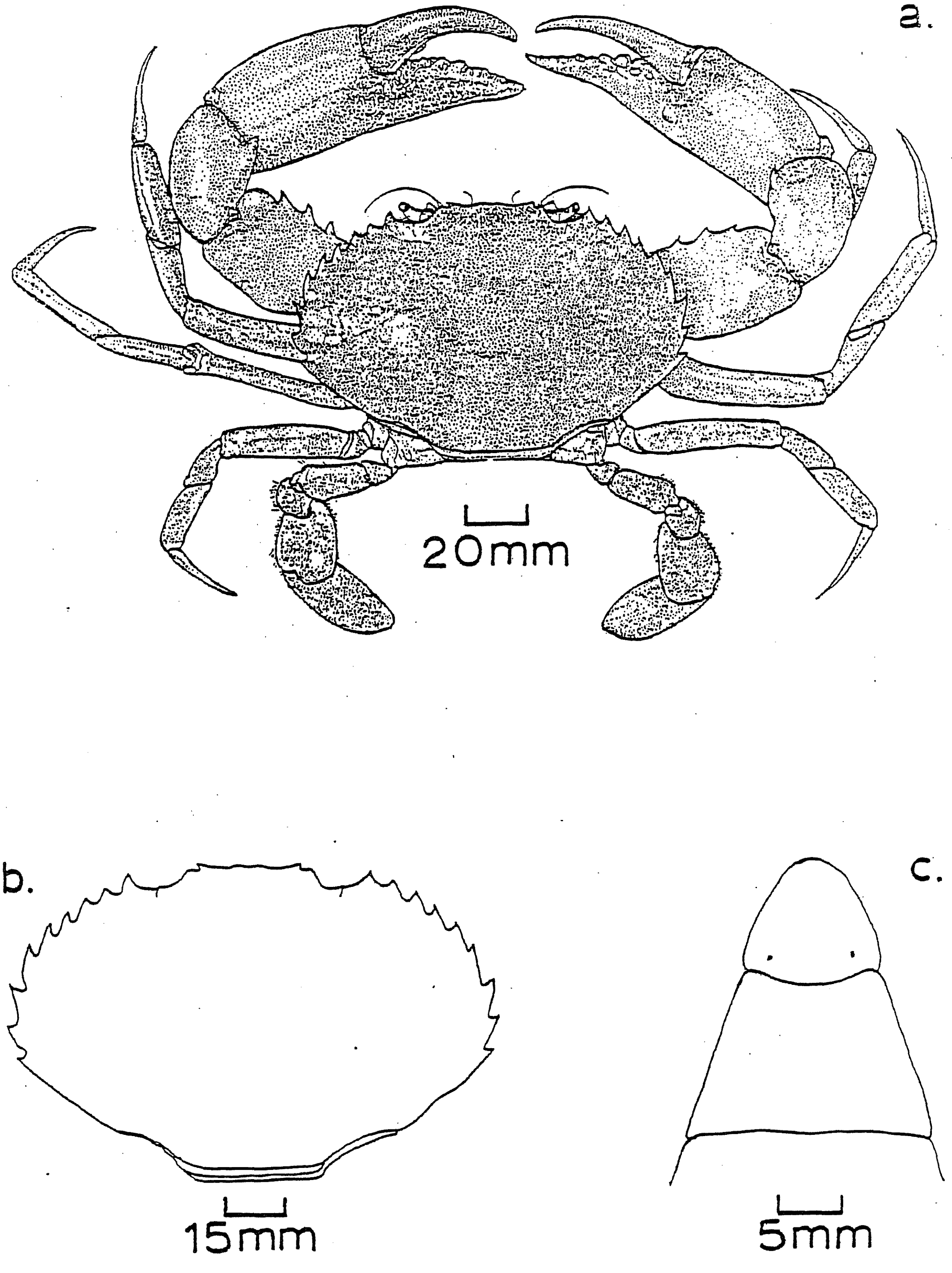


Fig. 51 - Scylla serrata: a - male, dorsal view; b - outline of carapace; distal segments of male abdomen (by J. Black).

Habitat

Mangrove mud flats, burrows on bank at mid-tide level. Frequently found in muddy estuarine conditions, and can penetrate well upstream into waters of low salinity. S. serrata is the largest estuarine crab in the Indo-Pacific area.

Depth

Estuarine areas, intertidal to 5m.

Breeding

In tropical areas ovigerous S.serrata can be found in most months of the year, but with a peak from June to September (Arriola 1940, Quinn & Kojis 1987), while in temperate areas breeding seems to occur from November to March. At least among juveniles (<100mm CW) the sex ratio is usually 50/50. Females as small as 85mm CW can breed although most are usually 100-110mm CW. Females from tropical regions may mature at a much smaller size than females from temperate regions. Mating occurs when females are soft-shelled and are carried by males prior to the moult. Hill (1975) found that males (141-166mm CW) carrying females (103-148mm CW) were usually larger but crabs of the same size will mate. In South Africa paired crabs were caught from October-May with a peak in December. About 1 month after mating there was an exodus of females from the estuary to the sea with crabs climbing over a sand bar. Females (117 to 131mm CW) can carry up to 2 million eggs and repeated spawnings without further mating are possible. Eggs are 0.28-0.38mm diameter and are incubated for about 17 days before hatching. Newly laid eggs are orange becoming almost black as hatching approaches. The structure and histochemical characteristics of spermatophores of S.serrata have been studied by Uma & Subramoniam (1979).

Only two female S.serrata have been recorded in Northland and neither of these had eggs (Manikiam, 1967).

Development and Growth

There are 5 zoeal stages which require 18 days to develop while the megalopa moults to the first crab after 7-8 days (Ong 1966). First stage zoea are unsuited to estuarine conditions, when exposed to temperatures above 25°C and salinities below 17.5 ppt suffer heavy mortality. Zoeae are tolerant of temperatures down to 5°C but are inactive below 10°C. Zoeal development has been described by Arriola (1940), Raja Bai Naidu (1955), Ong (1966) and Wear & Fielder (1985). Brick (1974) has investigated environmental influences on development.

By contrast the benthic crab stage can grow under a wide range of temperatures (13-32°C) and salinities (2-38 ppt). Growth during the first 12-15 months is very rapid with South African crabs reaching 80-160mm CW, subsequently growth is slower and after 3 years they reach 140-180mm CW. Arriola (1940) found that two Philippine crabs grew about 9mm CW per moult which occured on average every 13 days (both increment and interval tended to increase with size) and after 12 to 15 moults reached sexual maturity (103 to 112mm CW) in about 150 days. In crabs larger than 120mm CW there is differential growth of chelae between males and females. At 170mm CW chelae are 45% of total male weight but only 22% in females, while body weight is about the same (females may be slightly heavier). These chelae are well suited to crushing hard-shelled prey.

Behaviour

S.serrata is an active, aggressive, nocturnal crab which is sometimes seen swimming at the surface at night. Using infra-red photography in small tanks Hill (1980) found that adult S.serrata emerge from the sand during the hour after sunset and bury again within 30 min of sunrise. Time spent emerged, number of moves and percentage of crabs feeding were all reduced at lower temperatures (12 and 16^{o}C), with no differences between males and females. When no food was available time on the surface was halved. Lower catches of crabs of all sizes in winter results from lower activity and feeding.

Handling and opening of mussels (Trichomya hirsuta) by S.serrata has been described by Williams(1978). This crab has large, powerful dimorphic chelae: the larger is modified for crushing and has a number of molariform teeth on the fixed finger, while the smaller is a 'biter' with only conical teeth. Crabs normally attempted to remove mussels from rocks by tearing at the byssal threads with their chelae or by breaking them with the large chela, leaving the hinge region still attached to the rocks. Mussels were opened by two methods. In the first method (used especially by large males) the mussel was held at the umbo end by the smaller claw and supported from beneath by the first walking legs, with the plane of the hinge line oriented vertically. The second and third walking legs then dug into the sand and the body was lowered and braced against the substrate. The crusher claw then applied pressure to the thinner anterior shell regions until they fractured.

In the second method (used by a juvenile female) the mussel was held by the smaller claw as in the first method but with the plane of the hinge line inclined at approx. 20^{o} to the substrate. The teeth of the dactyl subjected the upper valve to an outwardly directed force while the fixed finger held the lower valve steady and the upper valve eventually (after 2-3min.) pivoted at the hinge line to make a small gape between the valves. The shell was then repositioned so that the gape was directed away from the mouthparts and the tips of both chelae inserted to enlarge the gape. Once the mussels were opened (by either method) tissue was removed by tearing, with shell fragments held by the third maxillipeds and pulled apart by the chelae. Sometimes the second maxillipeds held the tissue while the third maxillipeds pulled the shell away from the mouth. Adductor muscles were removed by several methods using maxillipeds and/or chelae. Throughout feeding, the distal sections of the exopodites of maxillipeds 1-3 beat continually to create a water current carrying small food particles away from the mouth. Feeding time was approx. 15min. per mussel (20-70mm long). The effect of prey size on feeding time was not investigated. A single clawed crab was able to feed using its smaller cheliped but took more than twice as long to consume a mussel. The structure of the mouthparts of S.serrata has been studied by Barker & Gibson (1978).

Ultrasonic transmitters attached to adult crabs were used to track crab movements (Hill, 1978). Mud crabs in Queensland estuaries moved an average of 461m (219-910m) per day with a modal speed of 10-19 m/h. Crabs did not occupy a distinct territory but remained within the same general area. Restricted movements centered around a more or less permanent home site are combined with free-ranging movements during which crabs may forage extensively.

Only brief details of mating behaviour are known. Prior to mating the female is carried by the male. He clasps her tightly against his ventral surface using his first three pairs of walking legs. These females have either just moulted or are about to moult (Arriola 1940) and remain with male for several days. When mating occurs the female is soft-shelled.

Ecology

In India Veerannan (1972) investigated respiratory metabolism of S.serrata acclimated to 27 and 35°C. The normal positive respiration-temperature response was demonstrated in water but in air respiration was less than one tenth of the aquatic rate for all sizes and the rate was independent of temperature. This subtidal crab has a large gill area (16 gills), which increases linearly with body weight and is better adapted to removing oxygen from water than from air (Veerannan 1974).

S.serrata lives in estuarine, intertidal and subtidal areas. Juvenile crabs are found under stones, sheltering among mangrove roots or buried in soft mud in intertidal regions. Hill, Williams and Dutton (1982) found that only juveniles (up to 80mm CW) were resident in the intertidal, sub-adults and adult crabs only used this area at high tide, retreating to sub-tidal areas at low tide. Some adults are found in burrows among mangroves but the extent of their movements is uncertain. Using mark-recapture methods Hill (1975) found that the density of S.serrata in a South African estuary was 1 crab/124m^2. Mortality in the second year was 41% and in the third year it was 60%. Herons prey on juvenile mud crabs.

S.serrata is a predator of sessile or slow moving benthic macroinvertebrates, chiefly molluscs, but it will eat larger animals (e.g. fish and prawns) which have been incapacitated or are dead. Like Ovalipes catharus it is capable of eating large numbers of bivalves. Hill (1976) found that 120mm CW crabs ate 40-50 bivalves (Plebidonax deltoides, 18-22mm long) in 14 hours of darkness. These shellfish were crushed with the chelae. In a comparative study of the food-habits of S.serrata in South Africa and Australia (Queensland) Hill (1976) found that mollusc remains made up 50% in crabs from both areas. But whereas in South African crabs gastropods were most common (47% with gastropods, 15% with bivalves), Australian crabs ate more bivalves, chiefly mytilids (30% bivalves and 20% gastropods). Crustacean remains (chiefly small grapsid crabs and hermit crabs) were present in 22.5% of South African crabs and 20% of Australian crabs. Small numbers of crabs had plant material present and this may be important in the diet of juveniles. Very few of the crabs studied had full or nearly full guts with only 65% having identifiable remains. Foregut volume increases exponentially with CW, an 80mm crab has a foregut volume of 1ml, 120mm 3.6ml and 160mm has 13.7ml. Food is processed rapidly from the foregut with 50% passing through in 1-2 hours and most of it moving on within 12 hours. Fish bones were retained for up to 2-3 days but mollusc shell fragments were retained for up to 5-6 days. Whereas the weight of bones decreases to zero after 3-4 days, shell weight did not decrease after 8-9 days and it is probably ejected from the gut by regurgitation.

The digestive physiology of S.serrata has been examined by Barker & Gibson (1978) who found that food is initially lubricated by mucoid secretions discharged from oesophageal tegumental glands and then passed on to the gastric mill where trituration occurs and digestive enzymes produced by hepatopancreatic B-cells are added. These cells have three phases of activity in the 12-hour digestive cycle. Digestion is principally extracellular.

S.serrata is the basis of a substantial fishery in Western Australia (commercial landings 1981 - 9977 kg, 1982 - 3919kg, 1983 - 2930 kg), New South Wales, Queensland, Philippines and Vietnam. Crabs are caught by pots and drop nets and their powerful claws must be restrained by tying with strong cord to prevent damage. The meat obtained from the large chelae is considered a great delicacy. Little is known about the population of mud crabs in northern New Zealand but if exploitation by amateur and commercial interests is considered in the future it should be preceded by a thorough study of the stock size, population structure and breeding since at this latitude the species is at the southern limit of its range. Although first reported from 'Auckland' by Heller (1865) and dismissed by subsequent workers it was not until almost 100 years later that it was reported again (Dell, 1964b). An investigation by Manikiam (1967) proved fruitless and all the records of S.serrata are of large crabs (125-200mm CW) taken in 1964-65 by amateur fishermen from nets. It may be that these crabs are an adult invasion which subsequently failed to establish itself.

References

Arriola (1940), Barker & Gibson (1978), Brick (1974), Crosnier (1962), Dell (1964b), Hill (1974,1975, 1976,1978,1980), Hill, Williams & Dutton (1982), Manikiam (1967), Ong (1966), Stephenson (1972), Stephenson & Campbell (1960), Tinker (1965), Veerannan (1972), Wear & Fielder (1985), Williams (1978).

Ozius truncatus H.Milne Edwards, 1834
Black finger Crab

Synonymy

Ozius truncatus H.Milne Edwards, 1834; *Xantho deplanatus* White, 1847; *Ozius truncatus* Dana, 1852; *Ozius lobatus* Heller, 1868; *Ozius truncatus* Miers, 1876b; Haswell, 1882a; Filhol, 1886; Lenz, 1901; De Man, 1902; Stimpson, 1907; Hale, 1927; Chilton & Bennett, 1929; Richardson, 1949a; Trevarthen & Kulka, 1950; Trevarthen, 1951; Dell, 1963a; Wear, 1968a; Hayward, 1974; Vermeij, 1977; Wear & Fielder, 1985.

Type Locality

Australia

Distribution

Australia, Kermadec Islands and New Zealand. Within New Zealand from Spirits Bay to Cook Strait.

Diagnosis (Fig. 52a-c)

Carapace flattened, wider than long (ratio 1.5-1.6), frontal third granulated and furrowed, remainder smooth. Frontal region very wide, bearing four small teeth, the inner two broadly rounded and the outer two narrower and subacute. Pre-orbital tooth distinct, dorsal margin of orbit distinctly concave although not deep, post-orbital tooth also small, but distinct. Antero-lateral margin broadly rounded and divided into four obtuse lobes by three notches. The anterior edge of the second lobe rounded, anterior edges of third and fourth lobes sharply angular. Postero-lateral margins strongly convergent to the posterior margin which is sinuous. Strong frontal groove running back from the median pair of frontal teeth separating two truncated protuberances, groove running back obliquely from behind the orbit and joining another groove which runs obliquely forward from the base of the last antero-lateral tooth and continuing obliquely back to the gastro-cardiac groove. Chelae well-developed, outer face of carpus rough, inner distal corner marked by a large tooth, propodus inflated, inferior surface smooth, superior surface rough, fixed finger straight, bearing four teeth (second largest), dactyl curved with a strong, rounded distal tooth on the crusher claw (usually the right claw but can be on the left). Tips of fingers crossed, fixed finger on the outside. First three pairs of legs much shorter than chelipeds, last pair shortest. Leg segments laterally compressed, covered in long hairs especially on carpus, propodus and dactyl. Abdomen of six segments and telson in both sexes, female abdomen fringed with long hairs.

Colour

Dark chocolate-brown above, paler below, fingers black. Hairs on legs golden. Antennules dark-red brown, antennae light brown. Newly moulted crabs much paler in colour.

Size

Male CW 57mm, female 54.5mm. *O.truncatus* is the largest New Zealand xanthid crab.

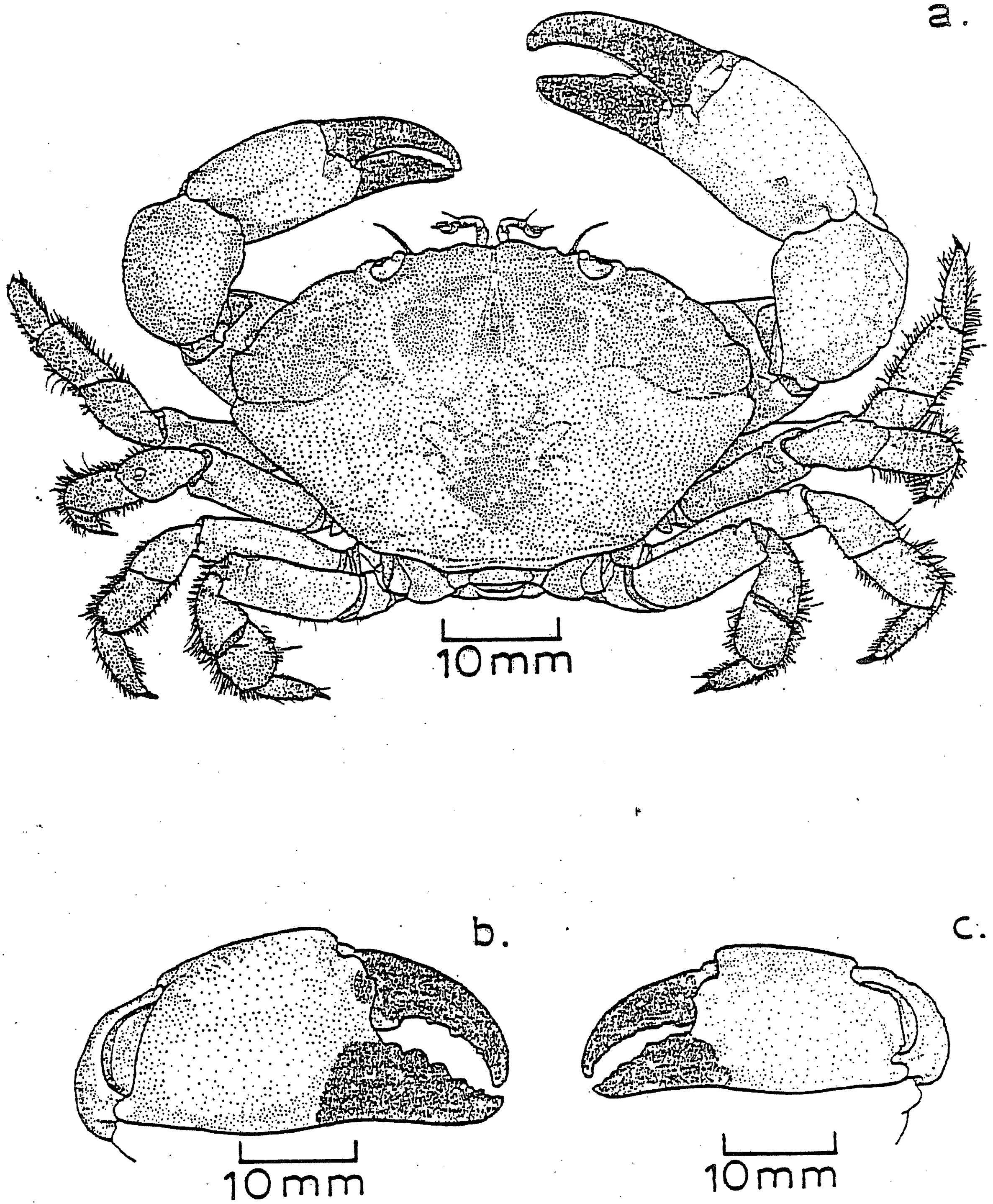


Fig. 52 - *Ozius truncatus*: a - male, dorsal view; b - right chela, male, outer face; c - left chela, male, outer face (by J. Black).

Habitat

Beneath boulders on sheltered shores from upper mid-littoral to low tide. During low tide this crab is exposed to the air for several hours.

Depth

Intertidal

Breeding

Ovigerous females are found from October to January. Newly laid eggs measure 0.5 x 0.45mm and are dark maroon, eggs ready to hatch are 0.7 x 0.65mm. Only a single batch of eggs are produced each year. Mating probably occurs when the female is soft shelled and sperm are stored over the autumn and winter until breeding begins in late Spring.

Stone crabs (Menippe mercenaria) spawn from May through July in North Carolina, but copulation can occur year round in south Florida with sperm being retained by the female through more than one moult (Cheng 1969). Females copulate only when soft. In the estuarine xanthid Rithropanopeus harrisii females copulate when hard-shelled and can produce multiple egg masses from a single mating (Morgan et al. 1983).

Development and Growth

The pre-zoea, 4 zoeal stages and megalopa have been described by Wear (1968a), Wear & Fielder (1985). The pre-zoeal stage is short-lived (1-1.5 hours), each zoeal stage lasts about 6 days in the laboratory and the megalopa moults to the first stage crab after 12-14 days. Zoeal stages are rare in Wellington plankton.

Cronin & Forward (1986) have shown that Rithropanopeus harrisii larvae undergo regular vertical migrations which keep them in dimly lit regions of the water column where risk of predation is reduced and larvae are retained close to the coast.

Behaviour

Usually when O.truncatus is uncovered by removing the boulder it will spread its chelae as wide as possible aiming them in the direction of its 'attacker'. Despite this apparently aggressive behaviour it is easily handled and will usually lie perfectly still with chelae folded if it is turned over on its back. The Atlantic burrowing xanthid stone crab, Menippe mercenaria has similar cheliped displays but displays involving extensive bilateral aggression are infrequent. Dominance is correlated with larger size, the male sex and prior possession of space. Fights are most frequent between crabs of similar size or of the same sex (Sinclair 1977). This interesting crab also stridulates by moving an irregular patch of oblique ridges found on the inner side of the larger, crusher chelae across the second and third teeth of the carapace. This stridulation was observed while stone crabs defended their burrows from conspecifics (see Sinclair 1977). All juvenile stone crabs are right-handed but loss of this cheliped results in reversal of handedness so that only 80% of larger crabs are right-handed. No adult crabs regain the normal stridulatory pattern on a regenerated claw, even after 5 post-regenerative moults (Simonson 1985).

The large crusher claw of O.truncatus (studied at Leigh) is used to open gastropods and hermit crabs in gastropod shells. Prey are detected by the legs when the crab moves sideways but some prey are detected visually. The prey is initially enclosed by the limbs with the first 3 pairs of legs folded underneath to form a 'basket'. The last pair of legs are held sub-dorsally and grasp a stone. The prey is then transferred to the mouth using the minor chela and with the help of the legs and the major cheliped the shell is rotated against the outer maxillipeds. Shell opening usually begins with the major cheliped breaking chips off the outer edge of the aperture working around to the columella. Frequent checks of progress are made by turning the shell over and rotating it against the maxillipeds. With smaller shells a quicker route may be taken by crushing the whole whorl behind the aperture. As soon as the meat is exposed the shell is held hard against the mouthparts so that the mandibles can grasp the meat. The chelipeds are then used to pull the shell away from the mouth tearing out a piece of the snail. Therefore the meat may be either pulled out through the aperture or through the hole made in the outer whorl. Removal of the prey usually continues until all meat has been removed and the shell has been reduced to small fragments. Faced with such a violent onslaught on their home, hermit crabs often make the mistake of emerging from the shell and attempt to escape but they are rarely successful because they find themselves enclosed in a 'basket' of limbs. Handling time increases with shell size and hermit crabs require only about half the time of an equivalent sized snail. Feeding behaviour of O.truncatus has also been studied near Sydney by Skilleter & Anderson (1986). Similar shell-breaking behaviour is shown by O.verreauxii from the Bay of Panama (Bertness & Cunningham 1981).

Chilton & Bull (1986), studying O.truncatus from South Australia, found that the time taken to break open and consume Bembicium nanum and Nerita atrementosa increased exponentially with shell height and when offered a range of prey sizes, the crabs selected prey well below the maximum size that they could handle. The mean prey size selected did not coincide with the size predicted to yield the maximum rate of energy gain. However laboratory experiments do not adequately simulate prey availability found in the natural environment where foraging time and costs and increased predation risk need to be taken into account in determining relative value of prey.

Ecology

O.truncatus is a voracious predator of gastropods eating Turbo smaragda, Melagraphia aethiops and probably many other snails. It also eats hermit crabs Pagurus novizealandiae, P.traversi, Pagurixus hectori and half crabs, Petrolisthes elongatus. But its effect on the intertidal fauna is probably slight because at least in New Zealand it occurs at only a low density (approx. 1 crab per 5 squ m) and it has a patchy distribution. O.truncatus is usually found only under large boulders where it seems to live alone in a small chamber or in crevices and tunnels in solid rock. Near Sydney Skilleter & Anderson (1986) found that O.truncatus consumed limpets (Patelloida latistrigata, Cellana tramoserica, Siphonaria denticulata) and gastropods (Austrocochlea constricta, Nerita atrementosa, Bembicium nanum). They also examined the structure and function of the chelipeds, mouthparts and gastric mill.

Chilton & Bull (1984) examined the impact of O.truncatus on 3 species of gastropods (Nerita atrementosa, Bembicium nanum and Austrocochlea concamerata) living on rocky intertidal platforms in South Australia. These gastropods exhibited shore-level size gradients, with smaller snails occupying the higher intertidal levels. O.truncatus occupied most of the intertidal zone, overlapping with the snails, but it did not occur at upper intertidal levels. The gastropods also occurred throughout the intertidal zone but with greatest densities and smaller individuals in the upper- and mid-tidal levels. In the laboratory the crab consumed all 3 gastropods and there were significant increases in both numbers of snails consumed and mean size of shells selected by larger crabs. An average sized crab (33.6mm CW) consumed about 13 snails per day. The population of about 200 crabs at one study site could have consumed about 2600 snails per day or about 2% of all snails in the area if all were vulnerable to attack. When offered a choice, all sizes of crabs selected small snails. Snails over 10mm in shell height were rarely eaten and had a size refuge from crab predation. Chilton & Bull(1984) put forward the hypothesis that the shore-level size gradient of gastropods is a response to crab predation rather than the result of selective recruitment and down-shore migration of larger snails.

Carapace surface and limbs of O.truncatus at Leigh often carry small white tube-dwelling polychaetes.

References

Bennett (1964), Chilton & Bennett (1929), Chilton & Bull (1984,1986), Dell (1963a), Hale (1927), Miers (1876b), Skilleter & Anderson (1986), Wear (1968a), Wear & Fielder (1985).

Pilumnopeus serratifrons (Kinahan, 1856)
Smooth-handed crab

Synonymy

Ozius serratifrons Kinahan, 1856; Pilumopeus crassimanus A.Milne Edwards, 1867; Pilumnopeus serratifrons Miers, 1876b; Haswell, 1882a; Miers, 1884; Filhol, 1886; Sphaerozius serratifrons Miers, 1886; Heteropanope serratifrons De Man, 1890; Pilumnopeus serratifrons Fulton & Grant, 1906; Heteropanope serratifrons Hale, 1927; Pilumnopeus serratifrons Hale, 1927; Chilton & Bennett, 1929; Pilumnus contrarius Montgomery, 1931(not of Rathbun 1923); Pilumnopeus serratifrons Balss, 1933; Richardson, 1949c; Dell, 1968a; Wear, 1968a; Takeda & Miyake, 1969; Greenwood & Fielder, 1984; Wear & Fielder, 1985.

Type Locality

Port Phillip, Victoria, Australia.

Distribution

Southern Australia and New Zealand. Within New Zealand Whangarei to Auckland.

Diagnosis (Fig. 53a-b)

Carapace moderately convex, regions well-defined, wider than long (ratio 1.4-1.5) anterior region with tuberculated, curved, hairy ridges. A prominent depression in the anterior branchial region. Frontal region produced, lamellar, directed downwards, two broad finely serrated central lobes and a small triangular tooth at the base of each lobe near anterior corner of orbit. Orbits oval, superior border finely tuberculated, orbital hiatus broad, inferior border with an acute tooth at its anterior corner. Posterior corner of orbit produced as a thin elongate ridge extending on to the antero-lateral border which is rounded with three flattened, acute teeth. Postero-lateral borders strongly convergent, posterior border convex. Chelipeds well developed, unequal (right propodus usually larger than left), carpus finely granulated with a strong, acute distal spine on the inner border, propodus compressed, deep, superior border produced as an elongate ridge, fixed finger bent downwards (especially on the minor cheliped) and bearing three or four small teeth. Dactyl on major cheliped thick, shorter than fixed finger and with two broad, flattened teeth. Dactyl on minor cheliped narrow, longer than fixed finger, gaping, with two very small proximal teeth or no teeth at all. Walking legs shorter than chelipeds, decreasing in length posteriorly, segments narrow and laterally flattened and carrying long hairs. Abdomen of six segments and telson in both sexes.

Colour

Carapace chestnut brown, limbs tan-red, fingers dark brown. Colour often obscured by a layer of muddy sediment.

Size

36mm CW, 25mm CL.

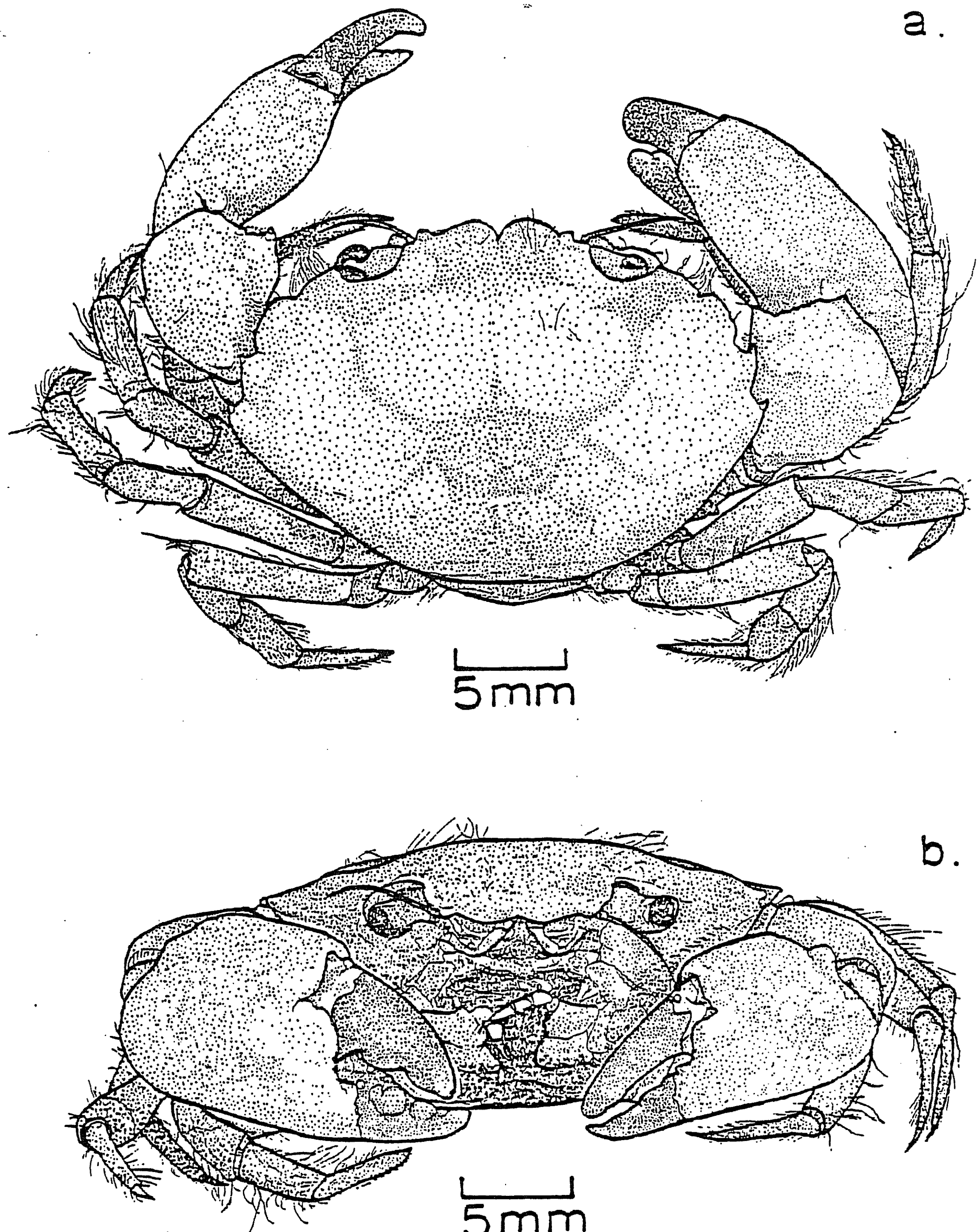


Fig. 53 - *Pilumnopeus serratifrons*: a - male, dorsal view;
b - frontal view, male (by J. Black).

Habitat

Under stones on sandy beaches. P.serratifrons has also been found in burrows similar to those of Helice crassa and Macrophthalmus hirtipes.

Depth

Intertidal

Breeding

Ovigerous females have been collected in November to January and in New Zealand this species probably has a similar breeding season to Ozius truncatus, i.e. October to January. Ovigerous females (7-10mm CW) have been collected in March near Brisbane, Australia (Greenwood & Fielder 1984). Females carry around 2000 small dark brown-green eggs measuring 0.4 x 0.38mm when freshly laid and 0.45 x 0.4mm when ready to hatch.

Development and Growth

The pre-zoea (lasting only about 1 hour) and first stage zoea have been described by Wear (1968a), Wear & Fielder (1985). There are 3 zoeal stages rather than 4 which is typical of xanthid crabs. Greenwood and Fielder (1984) have described the second and third zoea and noted some differences from zoea reared by Wear (1968a). Development is therefore somewhat abbreviated. First stage zoea reared by Greenwood and Fielder in Australia were much larger than those reared by Wear from Whangarei. Strangely, Australian specimens are typically small (6-10mm CW) whereas in New Zealand a much larger size is reached (20-30mm CW). The megalopa stage is not adequately known.

Behaviour

Unknown

Ecology

P.serratifrons probably has predatory habits similar to Ozius truncatus with which it can be confused.

References

Chilton & Bennett (1929), Dell (1968a), Greenwood & Fielder (1984), Hale (1927), Miers (1876b), Wear (1968a), Wear & Fielder (1985).

Pilumnus lumpinus Bennett, 1964
Hairy Crab

Synonymy

Pilumnus vespertilio Young, 1929 (part not of H.Milne Edwards); *Pilumnus* sp. Dell, 1963a; *Pilumnus lumpinus* Bennett, 1964; Wear, 1967; Dell, 1968a; Marsden & Fenwick, 1978; Marsden, 1981; Wear & Fielder, 1985; Marsden & Fenwick, 1986.

Type Locality

Godley Heads, Banks Peninsula.

Distribution

Endemic, Leigh to Banks Peninsula, Chatham Islands.

Diagnosis (Fig. 54a-e)

Carapace flattened, wider than long (ratio 1.3-1.4), densely covered with short hairs, anterior region sloping strongly downwards. Regions defined, surface uneven, deep frontal groove, transverse row of six broad flat swellings and four depressions at the corners of cardiac region. Frontal region advanced, two rounded lobes with denticulate margins, strongly deflexed (not visible dorsally), and a small acute tooth near the orbit. Upper orbital margin almost straight, finely denticulate, a sharp, horizontal post-orbital spine, lower orbital margin strongly denticulate, bearing a large rounded lobe. Antero-lateral border rounded with two conical, sharp teeth. Postero-lateral margins convergent, posterior margin slightly concave. Chelipeds well developed, unequal, densely covered in short hairs except for fingers, lower margins and inner surfaces of both palms, major palm bare over one-third of outer surface. Merus with acute subterminal spine separated by a deep groove from a larger conical tooth behind on the upper margin. Carpus bearing a small, sharp spine on upper distal margin. Outer surface of propodus with stout rounded granules which continue as far as hairs on upper margin and beyond hairs towards the bare lower distal corner. Fixed finger directed slightly downward, bearing five small, rounded teeth, finger on minor cheliped has two longitudinal grooves. Dactyls strongly curved, bearing 5-6 small teeth, dactyl on major cheliped as long as fixed finger, tips crossed, dactyl on minor cheliped shorter than fixed finger. Walking legs densely covered in short hairs and last three segments with longer clavate hairs, segments laterally compressed. First three pairs of legs increasing in length posteriorly, last pair shortest and sub-dorsal in position. Abdomen of six segments and telson in both sexes.

Colour

Muddy-brown, pale underneath, fingers dark brown or black.

Size

Male 22.5mm CW, 17.0mm CL. Female 22.5mm CW, 17mm CL.

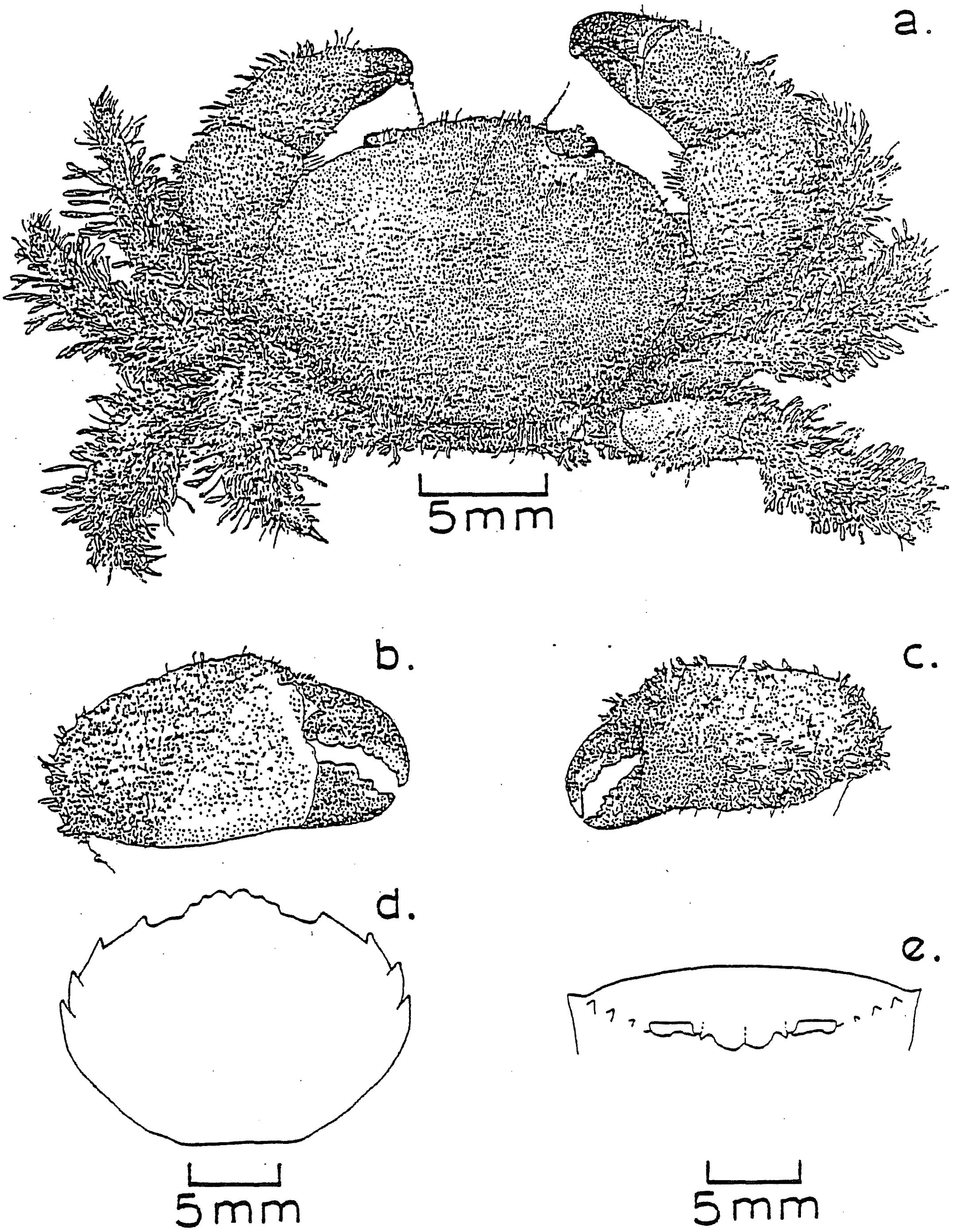


Fig. 54 - Pilumnus lumpinus: a - male, dorsal view; b - right chela, male, outer face; c - left chela, male, outer face (by J. Black - scale for b & c same as a); d - outline of carapace, dorsal view; e - frontal view of carapace (after Bennett, 1964).

Habitat

Probably quite common on rocky shores, sheltering under large boulders, among clusters of serpulid worm tubes, sponges and inhabiting deep inaccessible crevices among broken rock, but easily overlooked.

Depth

Low intertidal

Breeding

Ovigerous females have been collected in October, December and February. Eggs are light pinkish brown when freshly laid and measure 1.1 x 1.25mm, considerably smaller than the eggs of Pilumnus novaezealandiae. Females mature at 12mm CW and carry around 50 eggs, and brood size increases linearly with CW with a 22.5mm CW female carrying around 260 eggs (Wear 1967).

Development and Growth

Egg size increases to 1.5 x 1.4mm before hatching and advanced zoea larvae hatch after about 120 days. In the laboratory eggs hatch over a period of up to five days, a pre-zoeal cuticle is not shed during hatching but is discarded when the single zoea stage hatches to the megalopa (Wear, 1967, Wear & Fielder 1985). The zoeal stage is very short lived lasting only 15-30 minutes at 17°C. Larvae are not held under the female abdomen but lie on the bottom rapidly flexing and extending the abdomen. Megalopa shelter in crevices among stones and coralline algae and use their natatory pleopods to swim to new hiding places. They are more active at night. P.lumpinus appears to be the least evolved in terms of development of the 3 species of Pilumnus in the Australasian region. (The other species is P.vestitus from Australia.) Abbreviated development of P.lumpinus is associated with small brood size and must result in reduced dispersal but it is unclear why this strategy should be advantageous unless this species has very strict habitat requirements. Precisely what these requirements might be is unknown. If this is true then planktonic development would waste many offspring because they would be unable to find a suitable place to settle. Furthermore given its abbreviated development the presence of P.lumpinus on the Chatham Islands is remarkable.

Behaviour

When disturbed from under a boulder P.lumpinus often freezes initially and this coupled with their muddy-coloured appearance and secretive habits combine to make it difficult to see at first sight. However after a short period of exposure to the light they will quickly scramble for the nearest piece of cover, backing in under a stone by pushing sand away. If there is no stone to hide under they will bury in sand.

Ecology

Unknown

References

Bennett (1964), Dell (1963a), Hale (1931), Wear (1967), Wear & Fielder (1985).

Pilumnus novaezelandiae Filhol, 1886

Synonymy

Pilumnus vespertilio Miers, 1876b (not of H.Milne Edwards); *Pilumnus novaezelandiae* Filhol, 1886; *Pilumnus spinosus* Filhol, 1886; *Pilumnus maori* Borradaile, 1916; *Pilumnus novaezelandiae* Chilton & Bennett, 1929; *Pilumnus vespertilio* Young, 1929 (part not of H.Milne Edwards); *Pilumnus novaezelandiae* Bennett, 1930; Powell, 1937; Richardson, 1949a; *Pilumnus maori* Richardson, 1949a; *Pilumnus spinosus* Richardson, 1949a; Dell, 1960; *Pilumnus novaezelandiae* var. *spinosa* Bennett, 1964; *Pilumnus novaezelandiae* Bennett, 1964; Wear, 1967; Dell, 1968a; Marsden & Fenwick, 1978; Wear & Fielder, 1985.

Type Locality

New Zealand (either Stewart Island or Massacre Bay, not specified by Filhol).

Distribution

Endemic, North Cape to Stewart Island also Chatham Islands.

Diagnosis (Fig. 55a-d)

Carapace flattened, wider than long (ratio 1.3-1.4), sparsely covered with long and short hairs which posteriorly do not conceal the surface. Regions obscurely marked, four broad depressions at corners of cardiac region and distinct frontal groove . Frontal region deeply incised, margins of broad lobes denticulated, a small acute tooth near the orbit. Upper orbital margin distinctly concave, faintly notched, post-orbital spine acute, lower orbital margin conspicuously denticulate with a broad inner lobe bearing small spinules. Antero-lateral border rounded with three sharp forwardly-curved spines and there is another smaller spine close behind the post-orbital spine. Sub-branchial regions with small sharp granules close to the marginal spines. Postero-lateral margins strongly convergent, posterior margin almost straight. Chelipeds well developed, unequal (right usually larger), merus with a thin line of hairs on the upper crest, subterminal spine large separated from the slender terminal spine by a deep notch, carpus sparsely hairy, with low scattered granules, an erect, acute spine at the upper inner corner. Propodus of major cheliped has a small patch of hairs near the articulation, half the outer surface granulated. Fingers short and armed with 4-5 small rounded teeth, fingers of minor cheliped grooved. Legs shorter than chelipeds, merus has a small, sharp terminal spine and upper margin of carpus has three long, erect, slender spines.

Colour

Muddy-brown, pale underneath, fingers black, extreme tips white. A mixture of long and short hairs gives this crab a ragged bristly appearance.

Size

CW 20mm, CL 14.5mm.

Habitat

Under boulders and in rock crevices, often gregarious.

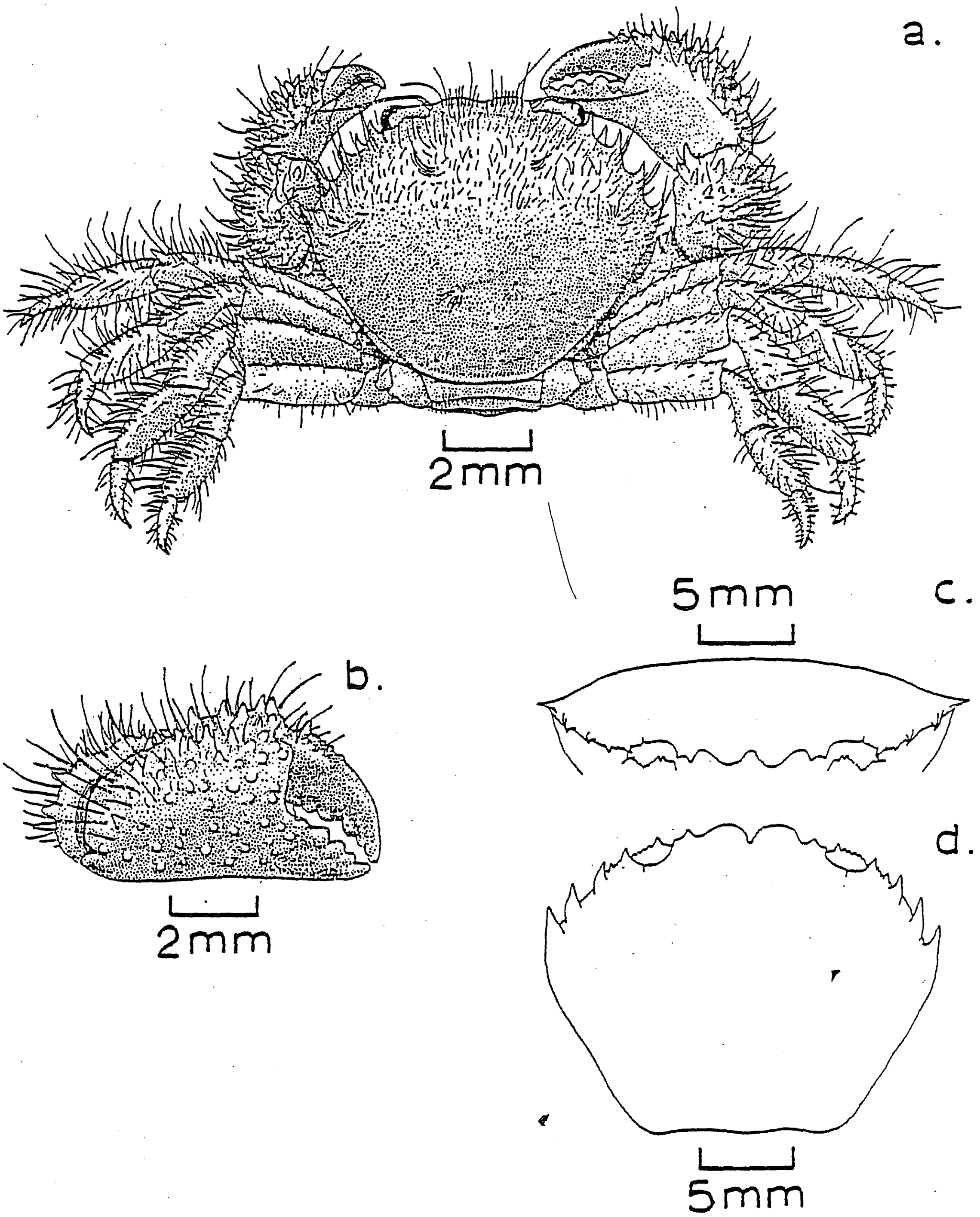


Fig. 55 - Pilumnus novaezelandiae: a - male, dorsal view; b - right chela, male, outer face (after Borradaile, 1916); c - frontal view of carapace; d - outline of carapace, dorsal view (after Bennett, 1964).

Depth

Low intertidal to 130m. Probably more common at shallow depths, Borradaile (1916) reported a single small specimen from 130m.

Breeding

Ovigerous females have been collected in August, October and November. The 2 females 19mm CW carried 67 and 74 eggs and the 22.5mm CW female carried 96 eggs. The female collected in November had eggs at an advanced stage of development. The eggs are large (1.5 x 1.45mm) and light mauve to purple in colour. By the time of hatching size increases to 1.75 x 1.65mm (Wear 1967).

Development and Growth

P.novaezelandiae has the most abbreviated development of all New Zealand crabs. Eggs are probably incubated for about 2 months, during which there are four embryonic zoeal stages, young hatch as megalopa and are carried by the female until they moult into the first juvenile crab stage as in the Australian P.vestitus. Free swimming zoeal stages are absent and the carapace spines normally considered to assist with flotation and orientation, and natatory setae which aid locomotion are reduced or absent (Wear 1967, Wear & Fielder 1985). Hatching requires about 30 minutes and all the eggs hatch over a period of about 8 hours. After about 12 hours the young make short excursions away from the female, using their natatory pleopods to swim in the normal way for brachyuran megalopa larvae. The female makes no attempt to feed the young megalopa larva which remain under the abdominal flap for about 35 days. After 13 months under lab. conditions young reached the sixth juvenile crab stage. The first juvenile crab stage lasts for 41-44 days (at 16-18°C), second stage 72-86 days (at 12-15°C), third stage 92 days (at 10.5-13°C), fourth stage 89 days (at 11-17°C), and fifth stage 76 days. During these stages the ratio of carapace width to carapace length increases from less than 1.2 towards the adult ratio of 1.3-1.4.

Rabalais & Gore (1985) point out that abbreviated development occupies one extreme of a continuum of decapod developmental patterns and include examples in which young hatch in the form of the adult, often with retention of some larval characteristics, to those which hatch as non-functional zoeae retained on the female pleopods. Abbreviated development is associated with large eggs and is widespread across phylogenetic lines.

Behaviour

The usual reaction of P.novaezelandiae is to 'freeze' when disturbed from under its boulder. This coupled with the cryptically coloured body makes them difficult to spot.

Ecology

Found living in small groups (up to 14) usually consisting of many juveniles, in contrast to P.lumpinus which is more solitary. This gregariousness may be a consequence of the abbreviated development and lack of a free-swimming larval phase in the life history and suggests that dispersal of young may be quite restricted until they become mature.

References
Bennett (1964), Dell (1963a), Hale (1931), Wear (1967), Wear & Fielder (1985).

Heterozius rotundifrons A.Milne Edwards, 1867
Big-Handed or Pebble Crab

Synonymy

Heterozius rotundifrons A.Milne Edwards, 1867; Miers, 1876b; Filhol, 1886; Lenz, 1901; Chilton, 1906b; Oliver, 1923; Chilton & Bennett, 1929; Young, 1929; Balss, 1930; Richardson, 1949a; 1949b; Trevarthen & Kulka, 1950; Trevarthen, 1951; Dell, 1963a; Bennett, 1964; Batham, 1965; Dell, 1968a; Wear, 1968a; Hayward, 1974; Puch, 1976; Jones, 1978; Marsden & Fenwick, 1978; Knox & Bolton, 1978; Marsden, 1981; Wear & Fielder, 1985.

Type Locality

New Zealand

Distribution

Endemic to New Zealand. Three Kings Islands to Stewart Island, Jackson Bay, Milford Sound, Thomson Sound, Preservation Inlet. Chilton (1906b) recorded H.rotundifrons from the Chatham Islands but it has not been collected subsequently.

Diagnosis (Fig. 56a-b)

Carapace wider than long (ratio 1.3-1.4), flattened, smooth, regions not well-defined. Cardiac region marked laterally by a curved shallow groove, concave outwards. Front of carapace narrow, rounded and marked by a faint median notch. Antero-lateral margins very long, forming a regular curve with the front, interrupted only by the orbits and three small lateral notches. Postero-lateral margins strongly convergent, posterior margin sinuous. Undersurface of body and legs covered with very short hairs. Chelipeds well-developed, propodus rounded above, smooth except for a faint longitudinal groove along upper outer surface in line with dactyl. On the upper inner propodus surface is a small proximal tubercle, variable in size. Fingers slender, nearly straight, each finger with 6-8 teeth separated by much finer denticulations, fingers cross slightly at tip. The right male chela is greatly enlarged in adults, propodus is much swollen, tubercle more distinct, fingers thick, gaping basally, with larger teeth prominent. Fingers on female chelae close together. Walking legs smaller than chelipeds, decreasing in length posteriorly. Dactyls short and stout. Abdomen of six segments and telson.

Colour

Dull yellowish grey or green with carapace sides and fingers a brighter yellow. Dactyls on legs dark brown. Antennules and eyestalks yellowish-white. Antennule setae delicate light blue. Surface may be encrusted with fine mud in among short hairs.

Size

Male and female, CW 23mm.

Habitat

H.rotundifrons typically buries itself in sand and gravel under stones and boulders on rocky shores and is often found in pairs and small groups. Often found with Petrolisthes elongatus.

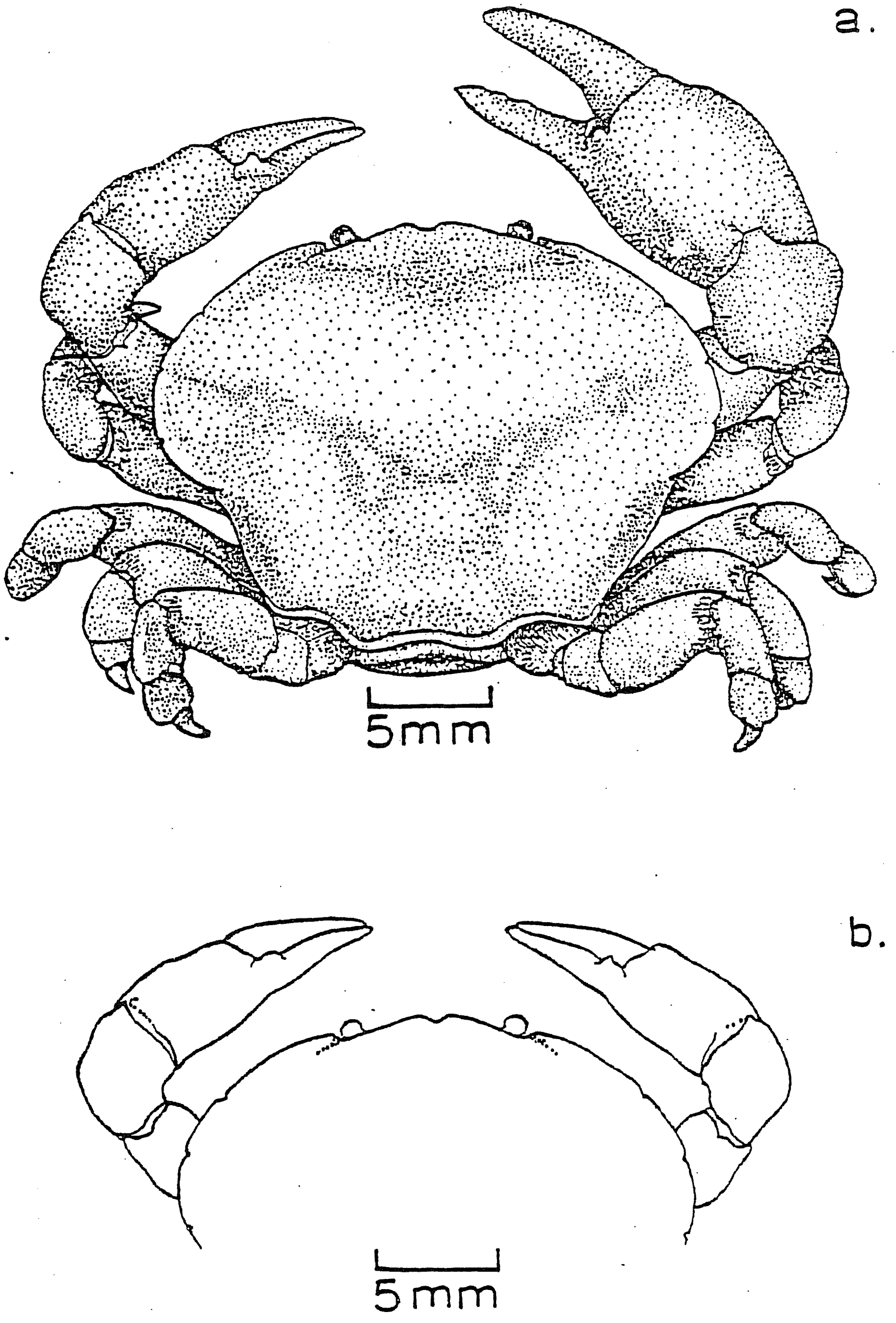


Fig. 56 - Heterozius rotundifrons: a - male, dorsal view; b - outline of female, dorsal view (after Jones, 1978).

Depth

Upper littoral down to low tide level.

Breeding

At Kaikoura and Wellington both males and females mature at approx. 11mm CW (Jones, 1978). Females outnumber males by about 2:1 with many more females than males among larger size classes. For size classes 6-12mm CW the sex ratio is 1:1. The biased sex ratio remains the same for all months of the year. Ovigerous females are found at Kaikoura in all months except February with at least 30% of females carrying eggs during May-December. This percentage does not usually exceed 50% in any month. Small females (<12mm CW) breed May-November whereas large females (>22 mm CW) breed only in June and July. Intermediate sized females breed throughout the period and constitute the bulk of the breeding population. But the average size of ovigerous females shows little fluctuation during the year. At Kaikoura females carrying newly deposited eggs are found from March to October suggesting an 8 month period of egg production. Females carrying final stage eggs are found from August to January. Therefore the incubation period may be approx. 5 months in winter and 3-4 months in summer. H.rotundifrons has comparatively large eggs and so the extended incubation period is not unusual since incubation period of crustacean eggs increases with egg size. There seem to be two main periods of egg production, one in March-April and another in September-October. A female may be able to produce two broods per year and probably has a maximum reproductive life of 2-3 years. However these features need to be confirmed by keeping crabs under natural conditions in the laboratory for an extended time. The relationship between numbers of stage 1 eggs and female CW is linear: $y = -1123.6 + 102.97X$. A female of 13mm CW has about 200 eggs while a 20mm CW female has about 900 eggs per brood. Mean egg mortality during incubation is 9.8%. When freshly laid eggs are orange-yellow, 0.75 x 0.81mm diam. becoming bright orange-red and light yellow near hatching, 0.93 x 1.03mm.

Development and Growth

Pre-zoea, the two zoeal stages and megalopa have been described by Wear (1968a), and Wear & Fielder(1985). The pre-zoea stage is short-lived or non-existent, first stage zoea last 7-8 days and second stage zoea 11-12 days, and the megalopa 15-17 days at a temperature of 15-17^{o}C. At Wellington zoea larvae occur in the plankton from November to April (Wear 1965d).

At Kaikoura juvenile and small crabs (<8mm CW) are rare but are found in most months and there does not seem to be any discrete period of recruitment. This is also reflected in the population structure where there is no clear progression of crabs through modal size groups. For females the 16-18mm CW size class is usually dominant and for males the 12-14mm CW class is usually most common. Unfortunately nothing is known about moulting in H.rotundifrons and so nothing can be deduced about longevity. It may be that sporadic recruitment throughout the year coupled with non-synchronous moulting results in a relatively stable, but dynamic, population structure.

Relative growth of chelae has been investigated by Jones (1978). Growth of pre-pubertal females (<11mm CW) is almost isometric (growth constant 0.97) but is negatively allometric in post-pubertal females (0.88). Growth of the left chela of males increases from negatively allometric (0.83) to isometric (0.99) at puberty. But growth of the male right chela is positively allometric throughout ontogeny, increasing from pre-pubertal (1.21) to the post-pubertal (1.63) phase. Sexual dimorphism in chela size is a common brachyuran feature (Hartnoll, 1965).

Behaviour

At Kaikoura mating has been observed in February between hard-shelled crabs. In the first case, the male and female were of similar size (15mm CW). Mating did not seem to be preceded by any courtship behaviour; a male over female position was adopted with the male clasping the female clumsily with his legs, with his chelae extended and hers folded against the carapace. This lasted for about 4min. but despite the female opening her abdomen, copulation was probably not successful. In the second case, the male was larger (20mm CW) than the female (15mm CW). The two met head-on, the male lifted the female up till they were sternum to sternum then pushed her on to her back and sommersaulted over till he was underneath. The male lay on his back with chelae extended straight out, first legs hooked over the front of her carapace, enclosing her folded chelipeds, other legs grasped her body. Copulation lasted for about 2min. and appeared to be successful.

H.rotundifrons is often found in pairs (or small groups) beneath rocks and these may represent pairs which have mated. When disturbed these crabs usually remain motionless and can be picked up without showing any sign of movement. When large numbers of H.rotundifrons are placed in a tank there is very little sign of aggression or interaction. Occasionally chelipeds are spread with fingers gaping but no physical attacks are observed. When artificially buried in sand they quickly reappear at the surface within 10-20sec., remaining partially buried and not reacting when other crabs walk over them. Sometimes a crab will partially bury itself in sand, using the legs to 'loosen' the substrate and then 'screw' around and down into the sand with the body at an angle of 50-60° and chelipeds spread. Burial is slow, taking 5-10min.

The function of the greatly enlarged male right cheliped is unknown. Sexual dimorphism of brachyuran chelae is related to their widespread use by the male in combat, display and courtship (Hartnoll, 1974) but H.rotundifrons is remarkably unaggressive. A behavioural study of the role played by the large cheliped of male would be very useful.

The feeding behaviour of this crab is not well known although it will eat pieces of mussel even when still attached to the shell. At Kaikoura it feeds chiefly on seaweeds e.g. Hormosira.

Ecology

Pellegrino (1984) estimated water content of H.rotundifrons to be 46.3% with a lethal water loss percentage of 62-66%. This crab has a relatively low surface/volume relationship (compared to Petrolisthes elongatus with which it is often found) and an integument of low permeability to water loss. Small crabs may be restricted to lower shore levels by desiccation stress. H.rotundifrons is subjected to aerial exposure on each tide although its habit of hiding under boulders minimizes exposure to air. Nothing is known about its mobility and the frequency of movements between rocks. At Kaikoura the diet of this crab consists of intertidal seaweeds.

References

Bennett (1964), Chilton & Bennett (1929), Dell (1963a), Hartnoll (1965, 1974), Jones (1978), Miers (1876b), Pellegrino (1984), Wear (1965d,1968a), Wear & Fielder (1985).

Carcinoplax victoriensis Rathbun, 1923
Two-spined Crab

Synonymy

Carcinoplax victoriensis Rathbun, 1923; Dell, 1960; 1963a; 1968a; Takeda & Miyake, 1969; Serene & Lohavanijaya, 1973; Griffin & Brown, 1975; Dawson, 1984; Wear & Fielder, 1985.

Type Locality

South of Gabo Island, Victoria, Australia.

Distribution

South-eastern Australia (Victoria and New South Wales) and New Zealand (from Bay of Plenty to Kaikoura, Chatham Rise, Chalky Sound).

Diagnosis (Fig. 57a-d)

Carapace flattened, surface smooth, polished, very convex fore and aft, much wider than long (ratio 1.4-1.5), antero-lateral margins very short. Frontal region not produced, almost straight, double-edged orbits deeply concave, orbital fissure present, no pre- or post-orbital spines. Two large antero-lateral spines, the first directed more strongly forwards, the second very prominent and directed obliquely forwards and upwards. Postero-lateral margins strongly convergent, posterior margin slightly concave. Chelipeds very well developed, unequal (right usually largest), carpus inflated with a single sharp outer spine and a larger inner spine, propodus smooth with a small proximal tubercle, fingers long, curved with tips crossed. Fingers are gaping, irregularly toothed, teeth larger on major cheliped. Walking legs longer than chelipeds, segments elongate, slender, laterally flattened, carpus and dactyl densely covered with short hairs. Last pair of legs almost sub-dorsal in position. Abdomen of six segments plus telson, fringed with long hairs.

Colour

Carapace pale vermillion, darker anteriorly. Distal end of merus, entire outer surface of carpus and upper border of propodus are also pale vermillion. Fingers pale blackish brown near tips. Walking legs white except for distal parts of meri which are the same as the carapace.

Size

Male 37.4mm CW, 27.3mm CL. Female 27.5mm CW, 20.2mm CL.

Habitat

Mud and sandy bottoms with shell debris.

Depth

Continental shelf and slope, 125-765m.

Breeding, Development and Growth, Behaviour

Unknown

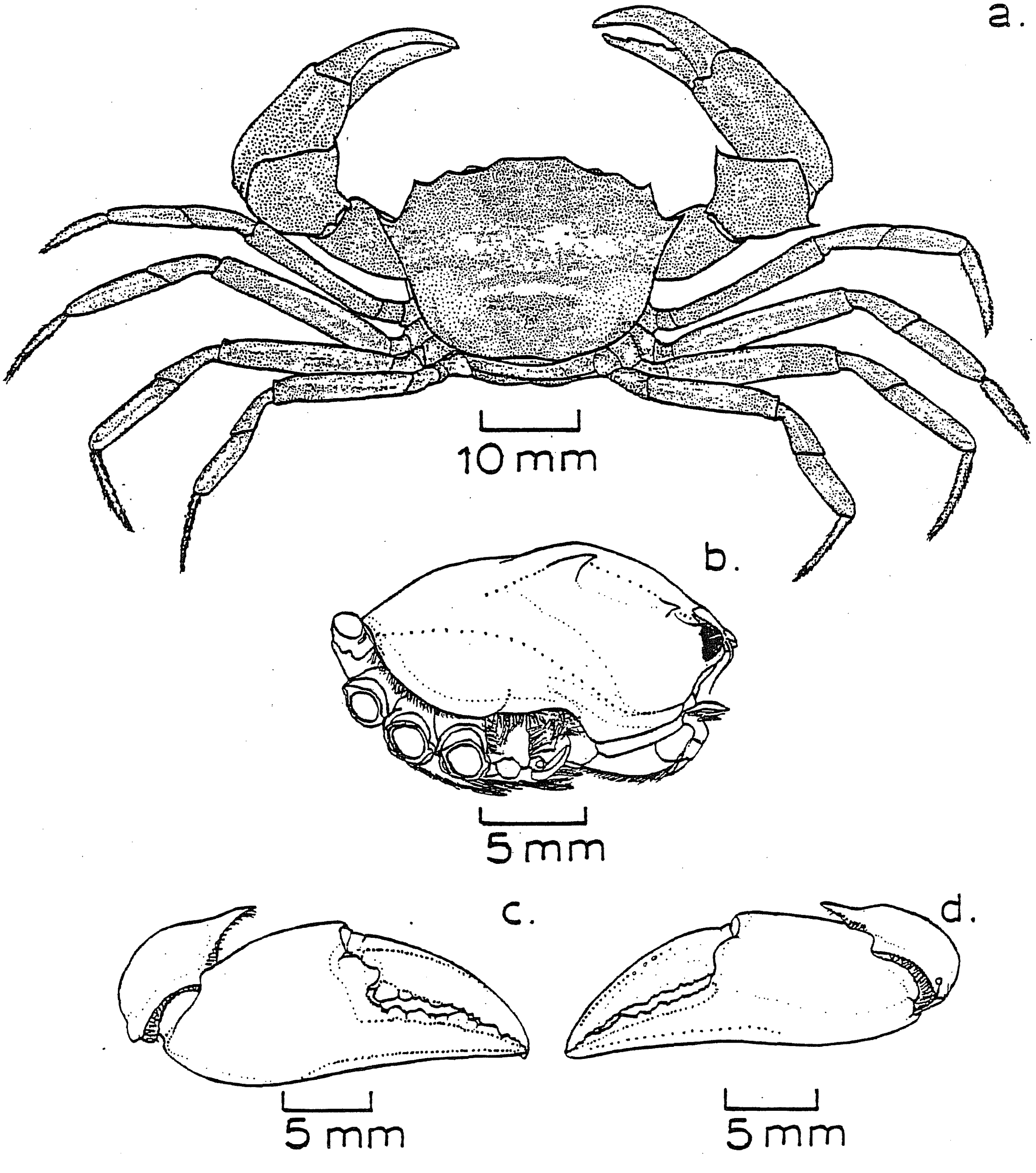


Fig. 57 - *Carcinoplax victoriensis*: a - male, dorsal view (based on a photo from Dell, 1960); b - carapace, lateral view; c - right chela, male, outer face; d - left chela, male, outer face (by J. Black).

Ecology

Godfriaux (1974a) recorded small numbers of C.victoriensis from stomachs of tarakihi (Cheilodactylus macropterus) captured in the western Bay of Plenty, while rig (Mustelus lenticulatus) from Banks Peninsula also eat this crab (King & Clark 1984). Ling (Genypterus blacodes) from Chatham Rise (125-177m), West Coast South Island (450-510m) and North Island (126-490m) also consume C.victoriensis.

References

Dawson (1984), Dell (1963a), Godfriaux (1974a), King & Clark (1984), Mitchell (1984), Rathbun (1923), Takeda & Miyake (1969), Wear & Fielder (1985).

Neommatocarcinus huttoni (Filhol, 1886)
Policeman Crab

Synonymy

Ommatocarcinus huttoni Filhol, 1886; Ommatocarcinus macgillivrayi Miers, 1886; Chilton, 1911a; Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Richardson, 1949a; Ommatocarcinus huttoni Dell, 1951; Ommatocarcinus macgillivrayi Dell, 1960; 1963a; Bennett, 1964; Dell, 1968a; Neommatocarcinus huttoni Takeda & Miyake, 1969; Ommatocarcinus huttoni Probert et al., 1979; Wear & Fielder, 1985.

Type Locality

Queen Charlotte Sound

Distribution

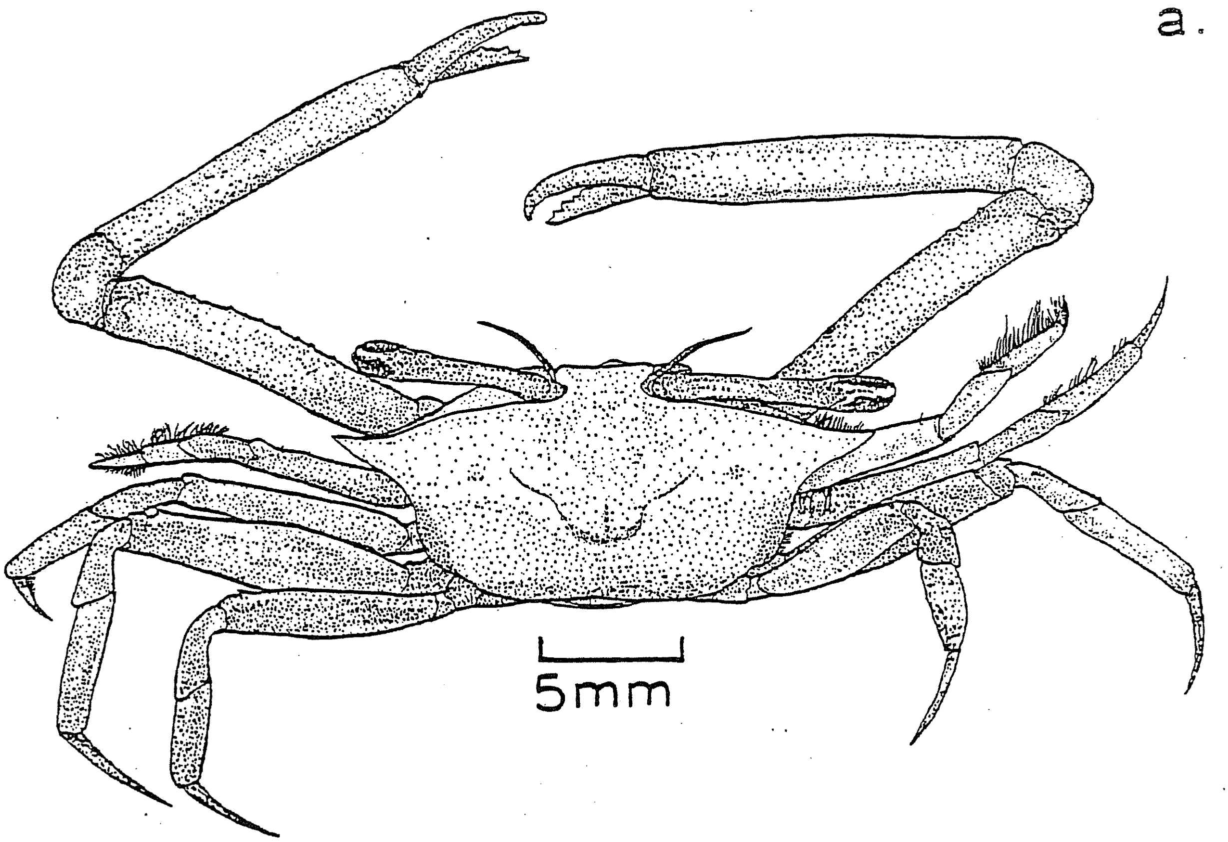
Endemic to New Zealand, from off Little Barrier Island to Stewart Island, Wanganui to Milford Sound, also Chatham Islands.

Diagnosis (Fig. 58a-b)

Carapace much wider than long (ratio 2.3-2.4), strongly curved antero-posteriorly, surface uniformly and microscopically granulated, shallow, short, oblique depression just inside antero-lateral border and gastro-cardiac depression evident. Frontal region strongly deflexed, the true border not visible dorsally, a small median lobe with the lateral angle extended obliquely forwards and forming the anterior corner of the orbit. Supra-orbital border excavated, external orbital spine present with a spiniform region behind. Eyestalk very long, stouter distally, cornea chiefly ventral. No stridulatory infra-orbital ridge and ridge on base of cheliped merus as seen in Ommatocarcinus macgillivrayi White 1852. Antero-lateral margin oblique, posterior margin prominently concave in the middle. Chelipeds equal, very slender and elongate (especially carpus and propodus), male chelipeds much longer than females. Fingers are thin, cutting edges sharply but irregularly toothed. Walking legs slender, merus with one or two sub-terminal spinules, dactylus somewhat twisted and excavated on its inner surface. Carpus, propodus and dactylus borders fringed with a row of long, dense hairs. Segments 3-5 of male abdomen fused together, female abdomen six segments and telson. Male genital opening coxal, female genital opening sternal.

Colour

N.huttoni is one of New Zealand's most beautiful crabs. Most of the carapace is yellowish vermillion, gastric region somewhat darker, white behind the orbit and postero-lateral surfaces, each side of the gastro-cardiac boundary is purple. Eyestalk is blackish brown near the cornea, infra-orbital lobe and anterior margin of buccal cavern are brick red. Chelipeds and legs are mostly creamy white, cheliped merus is brick red along upper border, inner surface yellow for proximal two-thirds, remainder purple, cheliped carpus has a purple outer surface, upper border of palm is pale orange. On the legs upper border of each merus is purplish red, both borders of carpus and upper border of propodus are pale purple.



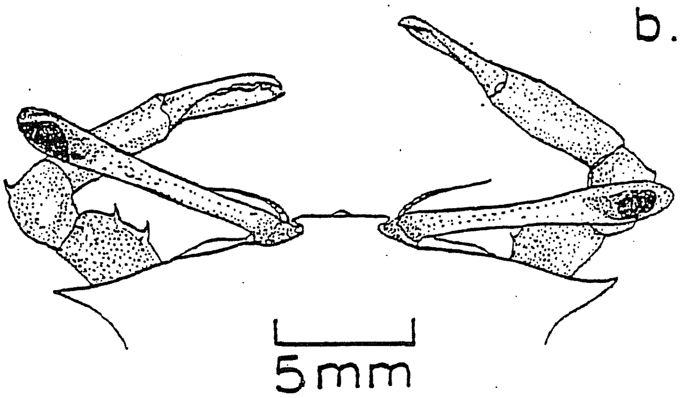


Fig. 58 - Neommatocarcinus huttoni: a - male, dorsal view; b - female, dorsal view (by J. Black).

Size

Male 42mm CW, 18mm CL. Female (ovigerous) 26.8mm CW, 12mm CL. Largest female 35mm CW, 17mm CL.

Habitat

Soft sediments with shells and rocks.

Depth

Continental shelf and slope, 18-594m.

Breeding

Ovigerous females have been collected in March and June.

Development and Growth

Four zoeal stages and megalopa described by Wear & Fielder (1985). Common in the Wellington plankton between August and January. There are marked changes in the proportions of benthic crabs with growth especially with relative length of the eyestalks and chelae. In young specimens the eyestalks are larger in relation to the long spine on each side of the carapace. Chelipeds in young specimens are shorter than the width of the carapace but in adults they become very much longer (2.5 times CW).

Behaviour

N.huttoni moves about in an agile manner over sand, hiding under small flat stones and burrowing in the sand. It may make a furrow in the sand (approx. 10cm long) by gathering up three or four 'armfuls' of sediment using both chelipeds and pushing it to one end of the furrow. Then at the middle of the furrow it backs into the sand folding the chelipeds against the body and allowing sand to spill forwards over the carapace and leave only the long eyestalks protruding. These burrows take 2-3min. to make and are only temporary (1-2 hours). Barnes (1968d) has reviewed the evolution of elongate ocular peduncles in brachyurans and suggests that it is related to burrowing habits and the avoidance of predation whilst feeding on the surface.

When Chione stutchburyi flesh was provided the crab held it in both chelipeds against the mouth where it was grasped and then the flesh was torn by pulling with the chelipeds.

Ecology

N.huttoni is frequently eaten by fish. Snapper (Chrysophrys auratus) from Hauraki Gulf and Bay of Plenty ate this crab, 1-1.3% of gut volume, (Godfriaux 1969,1974b), also red gurnard (Cheilodactylus kumu), 1.9%, (Godfriaux 1970a) and western Bay of Plenty tarakihi (C.macropterus), <.01% (Godfriaux 1974a). Habib(1975) found that red cod (Pseudophycis bacchus) from Banks Peninsula, Otago, Foveaux and Cook Strait areas often ate large quantities (0.2 to 7.2%) at different times of the year. Sand flounder (Rhombosolea plebeia) in Pegasus Bay also eat N.huttoni (Mundy 1968). King & Clark (1984) found that rig (Mustelus lenticulatus) from Wellington and Golden Bay ate small quantities of this crab while fish from Kaikoura and the West Coast ate significant quantities.

References

Bennett (1964), Chilton & Bennett (1929), Dell (1963a), King & Clark (1984), Mundy (1968), Takeda & Miyake (1969), Wear & Fielder (1985).

Leptograpsus variegatus (Fabricius, 1793)
Large Shore Crab or Purple Rock Crab

Synonymy

Cancer variegatus Fabricius, 1793; *Grapsus variegatus* Latreille, 1803; *Grapsus personatus* Lamarck, 1818; *Grapsus variegatus* H.Milne Edwards, 1837; *Grapsus strigilatus* White, 1842; *Grapsus planifrons* Dana, 1852; *Leptograpsus ansoni* H.Milne Edwards, 1853; *Leptograpsus gayi* H.Milne Edwards, 1853; *Leptograpsus verreauxi* H.Milne Edwards, 1853; *Leptograpsus variegatus* H.Milne Edwards, 1853; *Sesarma pentagona* Hutton, 1875; Miers, 1876b; Filhol, 1886; *Leptograpsus planifrons* Cano, 1889; *Sesarma pentagona* Thomson, 1913; *Leptograpsus variegatus* Chilton, 1910; Rathbun, 1918b; Hale, 1927; Chilton & Bennett, 1929; Balss 1935; Cranwell & Moore, 1938; Trevarthen, 1951; Garth, 1957; Shield, 1959; McNeill, 1962; Dell, 1963a; Bennett, 1964; Antezana, Fagetti & Lopez, 1965; Dell, 1968a; Griffin, 1969a; Healy & Yaldwyn, 1970; Wear, 1970a; Griffin & Yaldwyn, 1971; Griffin, 1971; 1972; 1973; Mahon, 1973; Campbell & Mahon, 1974; Hayward, 1974; Wear & Fielder, 1985; Hutton, 1986. (See Chilton & Bennett, 1929; Griffin, 1973 for additional older references.)

Type Locality

"Americae Meridionalis Insulis". Type specimen not exstant.

Distribution

Southern warm temperate Indian and Pacific Oceans from Western Australia to western South America. Western Australia, Tasmania, South Australia, New South Wales and Queensland in Australia, Middleton Reef, Norfolk Is., Kermadec Islands, Easter Is. in the Pacific and western coasts of South America. Within New Zealand from Cape Maria van Diemen to Kaikoura and Hokianga to Westport.

Diagnosis (Fig. 59a-c)

Carapace slightly broader than long, strongly depressed, margins strongly convex, two teeth behind external orbital angle, first tooth larger. Regions of carapace well defined, cervical and branchiocardiac grooves evident. Branchial regions with 7-9 prominent, equidistant weakly curved transverse ridges, hepatic regions with 4 or 5 short unequal ridges parallel to those of branchial regions. Front broad projecting almost horizontally, edged by numerous small tubercles. Orbits with posterior edge notched, sloping to stout, sharp exorbital tooth. Chelipeds massive in mature male, merus subtrigonal, ventromedial edge with a strong, flattened, spinous crest. Cheliped carpus with strong distal spine on inner margin, palm compressed, dorsal surface with numerous strong tubercles, fingers stout, toothed along inner edge, widely gaping proximally in adults. Legs long, strongly compressed, third leg longest (about 1.5 times CL), second leg slightly shorter. Meri very flattened, posterior surfaces bearing interrupted transverse ridges, dorsal border crested and terminating in a small, sharp spine. Other segments also flattened but not as broad as meri, propodi bearing small spines, dactyls terminating in a sharp spine and armed with a double row of long, stout, spine-like hairs. Abdomen of six segments plus telson. Male and female gonopores are sternal.

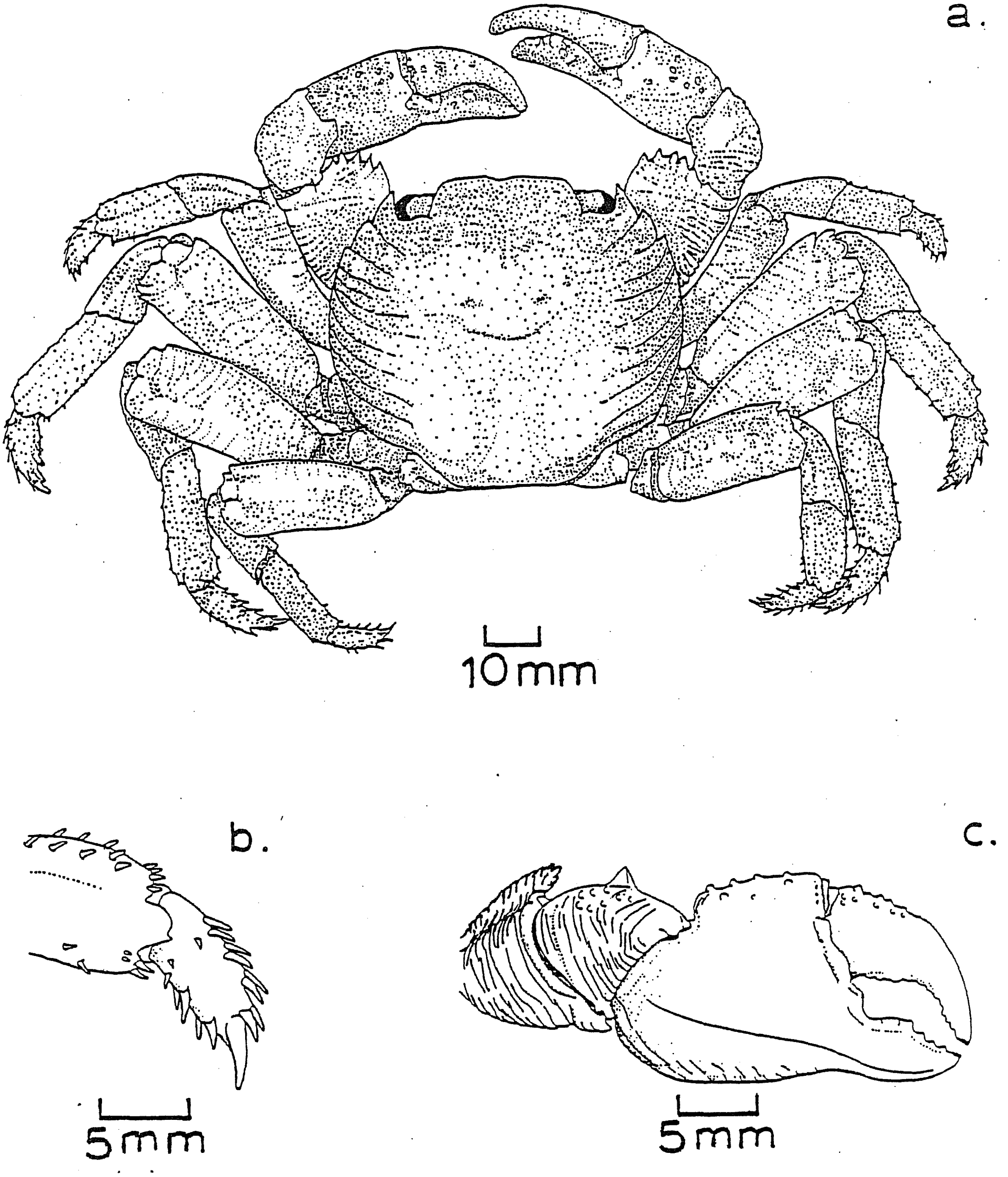


Fig. 59 - *Leptograpsus variegatus*: a - male, dorsal view (by J. Black); b - right first walking leg, propodus and dactyl, posterior view; c - right cheliped, male, outer face (after Griffin, 1973).

Colour

Variable, red and yellow mixed or dotted with violet red, or sometimes whitish. Bluish grey, everywhere transversely lineated and blotched with black, but often reddish. Two distinct morphs ('blue' and 'orange') have been identified in Australia , based on colour, body shape, proteins and ecology (Shield 1959, Mahon 1973, Campbell and Mahon 1974). Only the 'blue' morph has been found in New Zealand (Trenery 1984).

Size

Male 78mm CW. Female 68mm CW.

Habitat

A large, active crab, common on exposed rocky shores in the upper intertidal area where rocks are fissured by deep, narrow cracks. Also in tide pools in this area, hiding under boulders or seaweed. Its counterpart on the lower shore and subtidally is Plagusia chabrus, the red rock crab. Also found in muddy harbours where clay clods provide shelter.

Depth

Intertidal.

Breeding

L. variegatus mates in October-November when the female is hard-shelled. Ovigerous females are found from November until February at Leigh, while at Wellington they occur from November to January with all mature females carrying eggs in December. In Chile ovigerous females are found from October to February (Antezana, Fagetti & Lopez 1965). Incubation period is about 6 weeks and after liberation of larvae ovaries do not regenerate for a second spawning. Newly laid eggs measure 0.37 x 0.35mm and are dark brown or almost black while eggs ready to hatch measure 0.44 x 0.42mm and remaining yolk is light brown and larval chromatophores give the eggs a green iridescence (Wear 1970a).

L.variegatus from Chile show a linear increase in brood size with CL. A female of 32.5mm CL has around 55,000 eggs while a 49mm female has around 140,000 eggs. Garth (1957) found the smallest ovigerous female was 20.3mm CL.

Development and Growth

A short-lived pre-zoea larva hatches into the first of probably five zoeal stages. The first stage zoea has been described by Wear (1970a), Wear & Fielder (1985). The megalopa has not been described but one was collected at Leigh in July. Grapsoid zoea show close affinities with those of Ocypodidae and Gecarcinidae genera (Wear,1970a). Some aspects of relative growth of males and females have been studied by Griffin (1973). Male chelae tend to be longer than those of females for CL greater than 30mm. Relative growth of L.variegatus from New Zealand and Western Australia does not differ (Trenery 1984).

Distinct moulting periods occur at Leigh, with females moulting in November or December before becoming gravid and during February after egg hatching. Males moult in October and January. L.variegatus moults are often found on top of exposed rocks, far from seawater. It is likely that the rock crab has a similar moulting behaviour to that of the Sally Lightfoot crab (Grapsus grapsus) from America which lives in a similar habitat and is a terrestrial moulter (Knudsen 1968).

Behaviour

When mating, chance contact between male and female may initiate a period of leg contact during which legs are rapidly vibrated. This results in either one crab wandering off or the male crab mounting the underside of the female.

L.variegatus is fast-running and elusive and when cornered can be very aggressive with its chelae. These characteristics make it difficult to capture and handle. It feeds by scraping the rocks with the spoon-shaped tips of its chelae and by crushing larger prey with the chelae. Each crab seems to have its own specific shelter site to which it returns after foraging and many crabs restrict their foraging to a few specific areas. Foraging occurs during night low tides, rarely feeding at other times. Large and small crabs have distinct spatial foraging patterns : large crabs migrate down the shore as far as the sublittoral fringe where food is more abundant and different prey types are available, returning to shelter with the incoming tide. Small crabs forage in more restricted areas.

Strong lunar foraging rhythms are exhibited during winter with few crabs being active during the full moon phase. Peak activity occurs in the period starting 10 days before the new moon and ending 2 days after new moon. This rhythm is more pronounced in smaller crabs. Lunar rhythmicity is also dependent upon the season, disappearing during summer, possibly related to the number of night low tides (Trenery 1984).

Ecology

L.variegatus is primarily a predator of sessile organisms or slow moving macro-invertebrates. However, if Enteromorpha is present, it can be highly selective, the larger males (and to a lesser extent the larger females) feeding almost entirely on this alga. Diet varies between localities, seasons and with size and sex of crabs. Small crabs feed mainly on littorines and barnacles (Chamaesipho columna), large crabs on barnacles, the small black mussel Xenostrobus pulex, chitons and large gastropods. Large amounts of coralline turf are ingested after ecdysis. Crab predation is most intense in the upper eulittoral where they are most abundant and can feed for longer periods. L.variegatus has a substantial effect on both Xenostrobus and barnacles, preventing formations of mussel mats or reducing the mean mussel or barnacle size and is often a major creator of bare space for new settlement. Griffin (1971) reported that in Tasmania L.variegatus moves out of crevices and down the shore as the tide recedes, feeding on encrusting algae, mainly green and coralline algae. In contrast Plagusia chabrus moves up the shore with the incoming tide (Trenery 1984). Near Sydney Skilleter & Anderson (1986) found that L.variegatus had a similar diet to crabs at Leigh. They also studied the structure and function of chelipeds, mouthparts and gastric mill.

L.variegatus population is often multimodal, with 2-5 modes and individuals can live for over 5 years. Other members of L.variegatus, rats (Rattus spp.) and tuataras (Sphenodon punctatus) prey upon this crab. In seawater L.variegatus has a haemolymph concentration lower that the external environment while in 50% seawater its haemolymph is hypertonic and it can survive for at least 6 days. In 10% seawater survival is only 2-3 days (Edmonds 1935).

References

Bacon (1971a), Bennett (1964), Campbell & Mahon (1974), Edmonds (1935), Griffin (1969a, 1971, 1972, 1973), Mahon (1973), Skilleter & Anderson (1986), Trenery (1984), Wear (1970a), Wear & Fielder (1985).

Plagusia chabrus (Linnaeus, 1758)
Red Rock Crab

Synonymy

Cancer chabrus Linnaeus, 1758; 1764; Grapsus (Plagusia) capensis De Haan, 1835; Plagusia tomentosa H.Milne Edwards, 1837; Plagusia spinosa Macleay, 1838; Plagusia chabrus White, 1846; Plagusia tomentosa Dana, 1852; Plagusia gaimardii H.Milne Edwards, 1853; Plagusia chabrus Miers, 1876b; 1878; Haswell, 1882a; Filhol, 1886; Miers, 1886; Lenz, 1901; Plagusia capensis Stebbing, 1905; 1914; Plagusia chabrus Rathbun, 1918a; Hale, 1927; Chilton & Bennett, 1929; Plagusia capensis Balss, 1935; Plagusia chabrus Cranwell & Moore, 1938; Richardson, 1949a; Barnard, 1950; Capart, 1951; Garth, 1957; Plagusia capensis McNeill, 1962; Plagusia capense Dell, 1963a; Plagusia chabrus Bennett, 1964; Plagusia capensis (Morton & Miller) 1968; Plagusia chabrus Dell, 1968a; Griffin, 1968a; 1969a; Healy & Yaldwyn, 1970; Wear, 1970a; Griffin, 1971; 1972; 1973; Plagusia capensis Hayward, 1974; Marsden & Fenwick, 1978; Plagusia chabrus Wear & Fielder, 1985; Dawson, 1987. (See Chilton & Bennett, 1929 for additional older references.)

Type Locality

Cape of Good Hope, South Africa.

Distribution

Partly circumpolar southern hemisphere species confined to the Indo-Pacific from South Africa to Chile. East coast of South Africa, Western Australia, South Australia, Tasmania, New South Wales, Lord Howe Is., Norfolk Is., Kermadec Islands, Tonga, New Zealand and West Coast of South America. Within New Zealand P.chabrus has been recorded from Parengarenga Harbour in the north to Lyttelton Harbour in the south, a record from Otago Harbour by Filhol is doubtful. However, Habib (1975) recorded P.chabrus from red cod (Pseudophycis bacchus) stomachs from Otago Harbour.

Diagnosis (Fig. 60a-e)

Carapace as wide as long, lateral margins convex, with three equidistant strong, forwardly directed, sharp subtriangular anterolateral spines. Surface mostly smooth, covered by a mat of short curled hairs, with a shallow semicircular groove centrally. Branchial regions have three short, oblique, weakly tuberculate ridges close to edge. There is a naked, blunt tubercle just behind each orbit, and a row of sharp spines situated transversely immediately behind front which bears 10-14 broad spines or blunt tubercles around edge. Orbits deep, U- or V-shaped, margins smooth, inwardly bearing a ridge of 6-15 flattened spines variously grouped into lobes. Chelipeds moderately long and enlarged in mature males, chelae strongly compressed. Palm with three lobate ridges extending longitudinally along outer surface. Dorsal surface with three rows of laterally compressed tubercles.

Fingers short, widely gaping throughout their length, inner edges bearing a few large blunt teeth, fixed finger excavated and spooned distally. Dactyl with a simple lobate ridge on outer surface and a mid-dorsal and mid-ventral ridge. Chela in juvenile

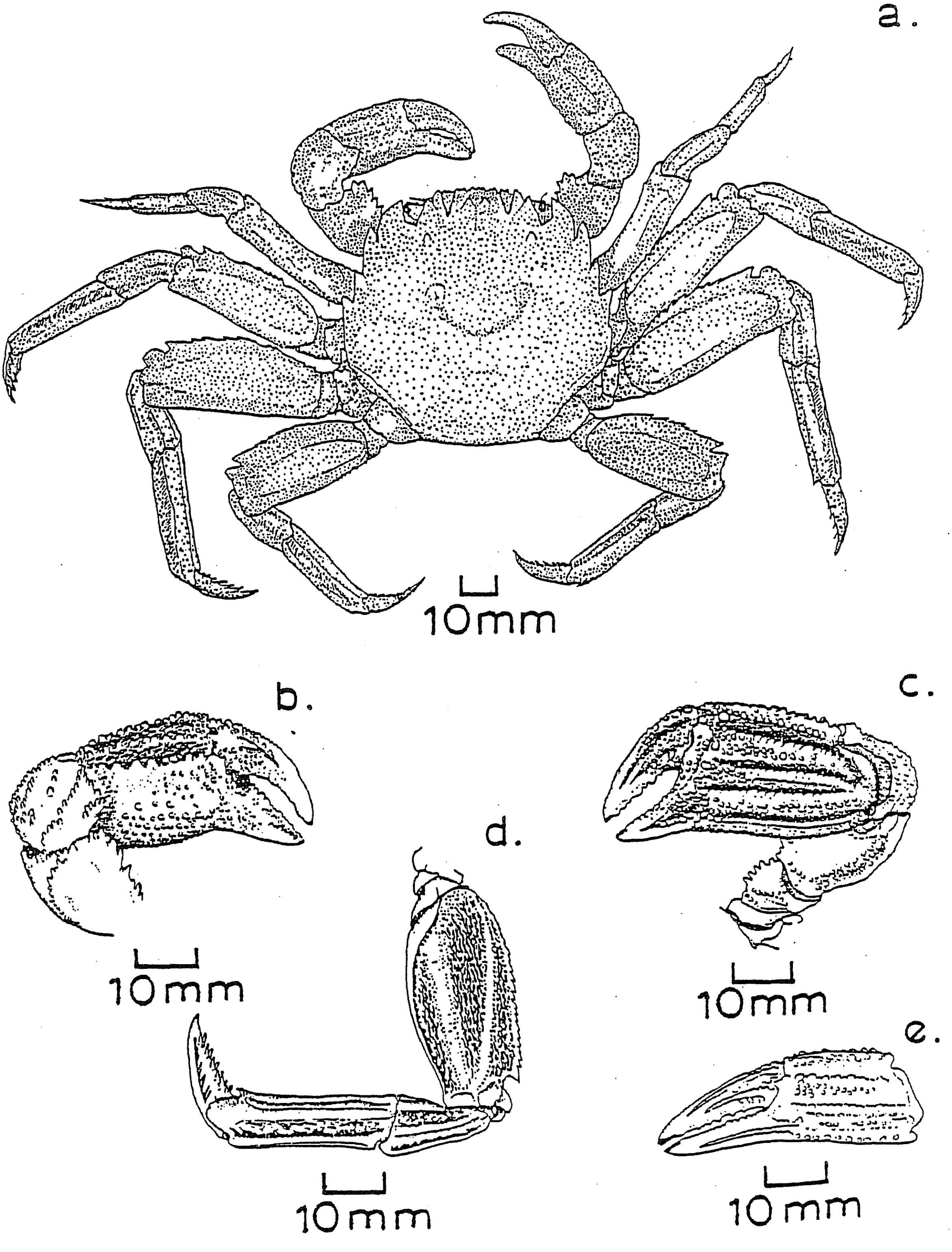


Fig. 60 - Plagusia chabrus: a - male, dorsal view (by J. Black); b - left chela, male, inner face; c - left chela, male, outer face; d - right 3rd walking leg, male, posterior view; e - left chela, female, outer face (after Griffin, 1973).

and, mature females small, palm tapering distally, fingers as long as palm, inner edges adjacent. Legs long, third pair longest (about twice CL), second pair slightly shorter, strongly compressed, long hairs in a dense fringe on posterior surfaces. Meri rather deep, dorsal edge convex, bearing numerous short, compressed, distally curved, sharp spines. Dactyls with two rows of stout, spine-like hairs ventrally. Abdomen of six segments plus telson. Male and female gonopores are sternal.

Colour

Carapace, chelipeds and legs various shades of red, naked ridges on dorsal surfaces darker, hairs yellowish. Ventral surface pale or creamy.

Size

CL 75mm.

Habitat

P. chabrus lives sub-tidally along exposed rocky coasts and spends most of its time sheltering in crevices and under ledges where crayfish (Jasus edwardsii) are also likely to be found. On a low tide at night it can be seen in shallow rock pools, but rarely ventures out of the water. Often seen by SCUBA divers and caught in crayfish pots.

Depth

Low tide level to 25m.

Breeding

Almarzah (1985) found that gonads of females <31mm CW from Leigh were small and showed no seasonal fluctuations in size but gonads of females 31-40mm CW peaked in August-October. Females 41-50mm CW peaked in September-November and again in January-February while females >50mm CW peaked in October-December. Changes in male gonads show a similar pattern. Females 32-55mm CW carry eggs from September to February while larger females 56-75mm CW carry eggs from late October. Eggs freshly laid, 0.39mm diameter, dull orange or brick red, ready to hatch, 0.47mm x 0.45mm and a light green colour (Wear 1970a). Incubation period unknown.

Development and Growth

About 12 zoeal stages, 3 stages described by Wear & Fielder(1985). The pre-zoeal stage moults almost immediately after hatching into the first stage zoea larva, which has been described by Wear (1970a). There may be 2 megalopa stages as in P.dentipes.

Almarzah (1985) found that juveniles (<20mm CW) and small crabs (20-31mm CW) moult throughout the year while larger males and females moult mainly from May to September, prior to the breeding season. Relative growth analysis suggests that in crabs with >45mm CW male chelae grow much larger than those of females.

Behaviour

P.chabrus is active from dusk onwards, very pugnacious and difficult to capture. During the day it hides in sub-tidal crevices. It can run very rapidly over rocks and can cling to rock surfaces with its strong claws, wedging itself in so as to make it difficult to remove. Underwater it can swim rapidly by flicking its flattened legs. P.chabrus does not seem to be territorial but often engages conspecifics in violent fights while foraging or courting, with males tending to engage in more fights than females. It is also very aggressive towards other crabs but does not seem to attack the crayfish with which it shelters. The aggressive and active nature of this crab makes it difficult to keep in tanks. Observations on tagged active crabs suggest that both males and females spend about 50% of their time foraging, 25% feeding, 20% in agonistic encounters and 5% in reproductive behaviour (Almarzah, 1985).

Crabs in shallow (<6m) water perform a daily nocturnal migration into the intertidal zone regardless of whether the tide is in or out, while crabs in deeper water leave their shelters and forage nearby regardless of tidal or light cycles. The predominant influence on activity appears to be circadian but there may be some tidal modification of patterns (Almarzah, 1985). In constant darkness crabs become arrhythmic.

Mating between hardshelled crabs was observed during low tide and night in rock pools. The mating position is female over male with copulation lasting about 7 minutes. During larval release the female assists departure by flexing her body up and down, vibrating her abdomen and pulling the hatching eggs from the pleopods with the chelipeds.

Ecology

P.chabrus is an opportunistic feeder foraging over rock platforms mainly on limpets, chitons, gastropods, mussels, barnacles, brown algae and coralline turf. It also feeds on brittlestars, is highly cannibalistic and eats dead animals e.g. penguins, sea gulls. Consumption of coralline turf increases prior to moulting. Dietary composition is often size dependant, with small crabs mainly herbivorous and large crabs more carnivorous. In Tasmania Griffin (1971) found that P.chabrus moves up the shore with the incoming tide and scrapes encrusting algae from the surface of rocks. Stomach contents consisted mainly of red algae and fragments of coralline algae. Of all the New Zealand Grapsid shore crabs P. chabrus is least tolerant of osmotic or desiccation stress. In general crabs living low on the shore possess higher gill volumes relative to total volume than crabs living high on the shore, but P.chabrus with only 1.72% appears to be an exception (Griffin, 1971). Leptograpsus variegatus, which lives higher up the shore, has a gill volume of 2.93%. However both crabs make extensive movements in the intertidal zone when foraging. P.chabrus tends to take over the ecological niche occupied by L.variegatus higher on the shore.

Hauraki Gulf snapper (Chrysophrys auratus) eat small numbers of P.chabrus (Godfriaux 1969), while snapper and tarakihi (Cheilodactylus macropterus) from western Bay Of Plenty eat small numbers of megalopa (Godfriaux 1974a,1974b). Habib (1975) found that red cod (Pseudophycis bacchus) stomachs from Banks Peninsula (0.3% of gut volume) in October and Otago Peninsula (0.35%) in November contained this crab.

References

Almarzah (1985), Bacon (1971a), Bennett (1964), Chilton & Bennett (1929), Dell (1963a), Griffin (1968a, 1971, 1972, 1973), Wear (1970a), Wear & Fielder (1985).

Plagusia depressa tuberculata Lamarck, 1818

Synonymy

Plagusia tuberculata Lamarck, 1818; Plagusia squamosa Lamarck, 1818 (in part); Plagusia orientalis Stimpson, 1858; 1860; Plagusia tuberculata Miers, 1886; Plagusia depressa squamosa Alcock, 1900; Plagusia depressa tuberculata Lenz, 1901; Laurie, 1906; Rathbun, 1903 (1906); Plagusia depressa squamosa Grant & McCulloch, 1906; Plagusia tuberculata Rathbun, 1910; Chilton, 1910; Plagusia depressa squamosa Stebbing, 1910; Plagusia depressa tuberculata Rathbun, 1918a; Tesch, 1918; Parisi, 1918; Urita, 1926; Plagusia squamosa Barnard, 1926; Plagusia depressa tuberculata Montgomery, 1931; Sakai, 1934; 1939; Edmondson, 1946; Barnard, 1950; Plagusia depressa depressa Chhapgar, 1957; Edmondson, 1959; Miyake, 1960; Crosnier, 1965; Sakai, 1965; Tinker, 1965; Garth, 1965; Day, 1974; Chen, 1975; Sakai, 1976; Branch & Branch, 1981; Morton & Morton, 1983; Dawson, 1987.

Type Locality

Ile de France (i.e. Mauritius).

Distribution

Tropical Indo-West and East Pacific, East Coast of Africa, Indian Ocean, Red Sea, Arabian Sea, Indonesia, China Sea, Hong Kong. Japan, Ryukyu Is., Hawaii, Lower California, Clipperton Is., ? Chile, Australia, Norfolk Is., Kermadec Islands, Whangarei, New Zealand.

Diagnosis (Fig. 61a-b)

Carapace subcircular, slightly wider than long, dorsal surface moderately convex with flattened tubercles with short hairs on anterior edges giving an overall scale-like appearance. Epistome divided into seven lobes although this is not a constant character. Front deeply furrowed, divided into three lobes with antennules exposed. Interantennular septum broad, minutely tuberculate on margins, orbits deeply set, supraorbital margins smooth with a strong tooth at the external orbital angle. A single rounded spine on inner side of suborbital ridge, inner lobe of basal antennal article with a single short spine. Lateral margins convex, armed with three teeth. Chelipeds subequal, carpus with triangular tooth on anterior edge, propodus and dactylus ornamented by rows of tubercles, both fingers blunt and flattened. Walking legs robust, flattened, merus with a row of hairs on both anterior and posterior edges with a prominent distal spine on anterior edge. Dactyls with strong spines along the inner margins. Second and third pairs of legs longest. Male abdomen triangular, segments four to six fused, telson broadly triangular with a rounded tip.

Colour

Reddish, with darker blood-red spots and speckles.

Size

Male 55.2mm CW, 51.8mm CL. Sex unknown, 56mm CW, 54mm CL.

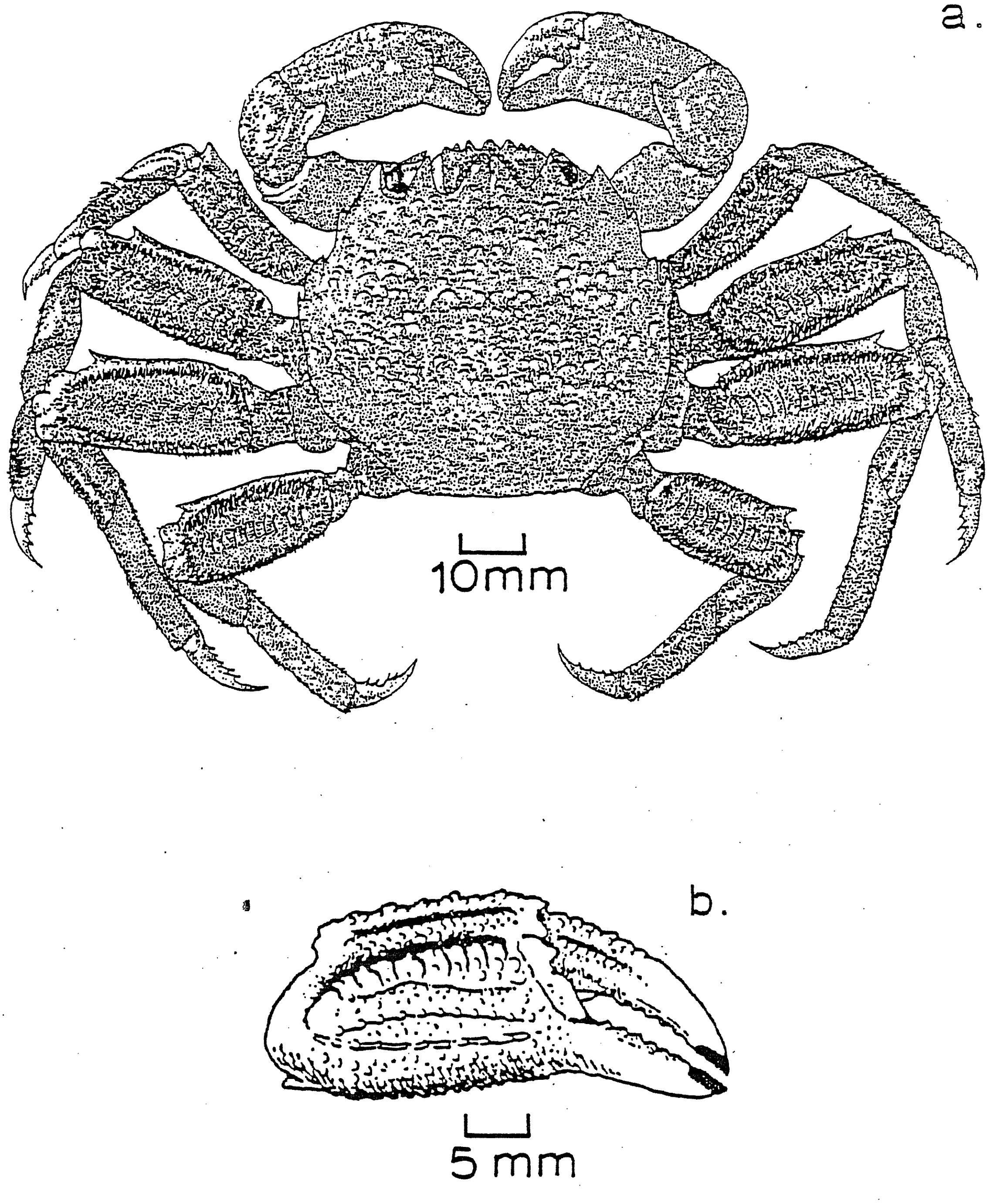


Fig. 61 - *Plagusia depressa tuberculata*: a - male, dorsal view (based on a photograph from Rathbun, 1918, by J. Black); b - right chela, male, outer face (after Barnard, 1950).

Habitat

Rocky coasts clinging to sub-tidal rocks and on floating objects such as driftwood, fishing floats, ships, on the high sea. Dawson (1987) recorded a male specimen from a Taiwanese long-line float off Whangarei. Benech (1978) found specimens of the Japanese shore crab, *Plagusia dentipes*, which had been transported on an oil-drilling platform close to Los Angeles harbour.

Depth

Low tide level to approx. 10m.

Breeding, Development and Growth, Behaviour, Ecology

Unknown.

References

Barnard (1950), Branch & Branch (1981), Crosnier (1965), Dawson (1987), Morton & Morton (1983), Rathbun (1918a), Sakai (1965).

Hemigrapsus edwardsi (Hilgendorf, 1882)
Purple Rock Crab

Synonymy

Cyclograpsus sexdentatus H. Milne Edwards, 1837; White, 1843; Hemigrapsus sexdentatus Dana, 1852; H. Milne Edwards, 1853; Miers, 1876b; Kingsley, 1880; Heterograpsus sexdentatus Haswell, 1882a; Brachynotus edwardsii Hilgendorf, 1882; Miers, 1886; Heterograpsus sexdentatus Lenz, 1901; Thomson, 1905; 1912; Thomson & Anderton, 1921; Oliver, 1923; Hemigrapsus sexdentatus Chilton & Bennett, 1929; Richardson, 1949a; Hemigrapsus edwardsii Richardson, 1949a; Hemigrapsus sexdentatus Trevarthen & Kulka, 1950; Hemigrapsus edwardsi Batham, 1956; 1958; Dell, 1963a; Hemigrapsus sexdentatus Wood, 1963; Bennett, 1964; Hemigrapsus edwardsi Dell, 1968a; Wood, 1968; Wear, 1970a; Knox & Bolton, 1978; Marsden & Fenwick, 1978; Marsden, 1981; Knox, 1983a; Wear & Fielder, 1985.

The use of H.edwardsi rather than H.sexdentatus follows the opinion of Dr.Isabella Gordon who communicated to Richardson (1949c) that "Hemigrapsus sexdentatus cannot by priority retain its specific name and must now be known as H.edwardsii as proposed by Hilgendorf." The reasons for the priority are a consequence of uniting Brachynotus with Hemigrapsus. A northern hemisphere species described in 1826, Goneplax sexdentatus Risso 1826 = Brachynotus sexdentatus(Risso 1826) preoccupies the specific name sexdentatus which is then unavailable. But if the New Zealand species is placed in Hemigrapsus then this problem does not arise and presumably we should use H.sexdentatus. Clarification of this problem requires a clear definition of the limits of Brachynotus and Hemigrapsus(see Bennett 1964). Following the lead of R.Dell the spelling of the specific name has become 'edwardsi'

Type Locality

New Zealand

Distribution

Endemic to New Zealand. Hohoura Harbour to Stewart Island, Milford Sound, Puysegur Point.

Diagnosis (Fig. 62a-d)

Carapace polished, flattened, wider than long (ratio 1.15-1.2) and oblong in shape. Cardiac region well defined by grooves with a shallow groove extending inward from behind the last antero-lateral tooth. A strong broad, frontal groove extends back from the frontal margin, separating two broadly rounded protuberances lying above the margin. Antero-lateral carapace corners granulated and carrying 4-5 small protuberances. Frontal margin straight and produced into a raised low granulated ridge, ratio of frontal margin to CW is 0.45. Antennules are small and concealed by the ridge. Orbital margin deeply set, almost a right angle, post-orbital corner produced into a strong, sharp tooth. Eyestalks short and fat, prominent stridulating ridge beneath the eye, subhepatic region granular and shortly pubescent. Antero-lateral margin convex, raised as a low ridge, granulated and bearing two teeth, the first more prominent than the second.

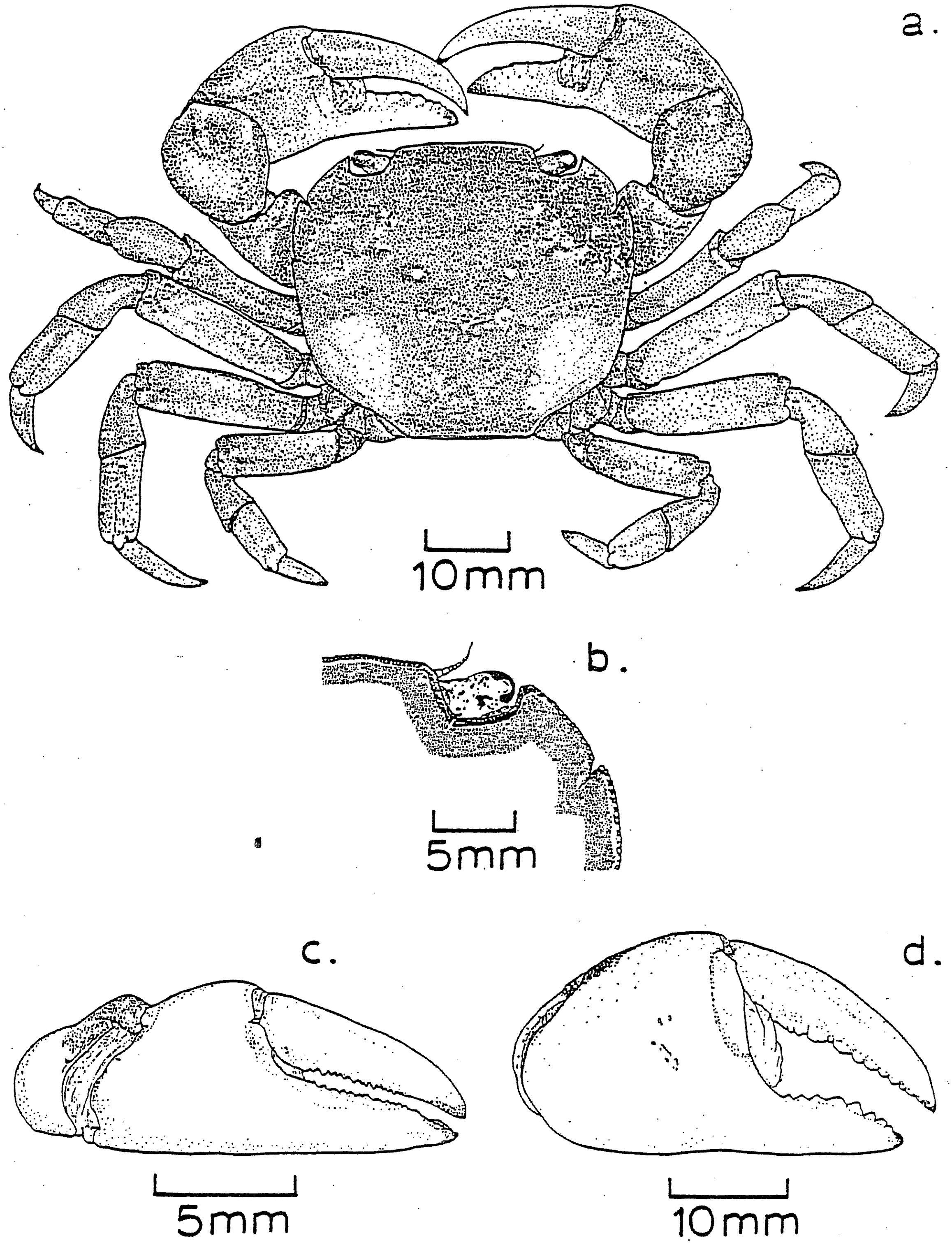


Fig. 62 - Hemigrapsus edwardsi: a - male, dorsal view; b - detail of orbital area, dorsal view; c - right chela, female, outer face; d - right chela, male, outer view (by J. Black).

Postero-lateral margins not ridged, slightly convergent, posterior margin straight. Chelipeds equal, well developed in the male, female smaller. Merus trigonal, innermost borders granulated, propodus much enlarged in the male, outer surface smooth and rounded, fingers comparatively thin, pointed, slightly downcurved, teeth, small regular, decreasing in size distally, fingers gaping at the base. Legs stout, segments laterally flattened, meri long, dactyls curved and sharp, second walking legs longest, fourth pair shortest. Fourth and fifth segments of the male abdomen are fused.

Colour

There is considerable variation in colouring but two types are recognizable: light and dark. Lighter crabs have either a grey or cream-coloured background with markings of light or dark chestnut-red. Darker crabs are marked with dark purple, sometimes almost a purplish black, and the legs are banded. Usually the front half of the carapace is more deeply pigmented than the rest. Eyestalks white, speckled with dark red, basal antennal segments banded, antennules pale green with dark red spots. Ventral surface white.

Size

Male 57mm CW, 47mm CL. Female 44mm CW, 38mm CL.

Habitat

H.edwardsi occurs on relatively sheltered rocky, stony or muddy shores, usually sheltering under rocks. Can live under slightly estuarine conditions, 14-15 ppt.

Depth

Extends from near high tide level down to about mid-tide level.

Breeding

At Wellington H.edwardsi is a late autumn-winter breeder with ovigerous females being recorded from March to August, and carrying eyed eggs as early as May (Wear 1970a). Near Portobello Begg (1980) found egg-bearing females as early as March and through to August when her study terminated. By May 96% of females were ovigerous. A similar pattern has been recorded at Kaikoura (J. Pringle, pers. comm.). Thus, H. edwardsi has a discrete late autumn-winter breeding season. The record of Wear (1970a) of an ovigerous female from Otago Harbour in December 1964 is exceptional and may have been the result of unusual environmental conditions. Thomson (1905) recorded egg hatching in August in Otago Harbour which is similar to Wellington. At Wellington the peak breeding period occurs in June-July when more than half the mature females were carrying eggs. At this time females were more abundant than males in the upper intertidal zone with mainly males present towards the mid-tide area. During other months, the sex ratio was about equal throughout the vertical range. Females carrying eggs without eyespots were recorded from March to July and females with more advanced eggs occurred from May to August. Eggs were incubated for about 6 weeks and females had only a single batch of eggs each year. A similar reproductive cycle was reported by Knudsen (1964) for H.nudus in Puget Sound, Washington. Wickham & Roe (1987) found that ovigerous H.nudus and H.oregonensis were infested with the egg-predator Carcinonemertes epialti. These nemerteans have not been reported from New Zealand as yet.

Begg (1980) found that the overall sex-ratio from December-August was 1.32 females/male but males predominated in the larger size classes. The smallest ovigerous female was 19 mm CW but at Wellington Wear (1970a) found an egg-bearing female of 16 mm CW. Most females do not mature until about 19 mm CW. Bennett (1964) gives an estimate of 26,000 eggs per female but does not specify female size. Large females undoubtedly have much larger clutches. Eggs freshly laid measure 0.37 x 0.33 mm and are light brown. Eggs about to hatch are almost transparent and measure 0.42 x 0.39mm. Egg size is very similar to H.nudus (Knudsen 1964).

Development and Growth

Five zoeal stages, first, third and fifth described by Wear & Fielder (1985). Wear (1970a) has recorded the pre-zoea which is very similar to H.crenulatus and lasts only about 15 minutes, and has described the stage one zoea larva. The first stage zoea was first described and figured by Thomson & Anderton (1921). During a survey of plankton of the Avon Heathcote Estuary from March to August 1982, Roper, Simons & Jones (1983) found very few H.edwardsi zoeae. The megalopa is unknown.

Recruitment must occur in spring and summer but little is known about adult growth and longevity. The study of H. edwardsi in Otago Harbour by Begg (1980) suggests that juveniles are recruited into the low-shore population and move higher up the shore as they grow larger. At Kaikoura Pringle (pers. comm.) found the crabs recruited in the spring grow very rapidly over the summer and reach maturity in less than 9 months, in the following winter.

Retention of larval stages and maximization of recruitment to the shore is a problem for all shore-living crabs. Shanks (1983, 1985) has shown that megalopae of Pachygrapsus crassipes, a Californian shore crab, have a strong tendency to cling to objects in the water and are transported shoreward by tidally forced internal waves.

Behaviour

H.edwardsi is a very agile rapidly moving crab although easy to handle. Males have very large chelae and are much more effective in crushing Lepsiella albomarginata and L.scobina than are females (Kitching & Lockwood 1974). Crabs emerge from crevices and under boulders to forage at night. At Kaikoura H. edwardsi seems to eat only drift algae such as Carpophyllum maschalocarpus. In Puget Sound, Washington, Knudsen (1964) found that H.nudus is herbivorous, eating mainly green algae, diatoms and desmids (see also Birch 1979).

Williams (1969) recorded locomotory activity of groups of male H.edwardsi (20-50mm CW) in simple tilting-box actographs under conditions of continuous dim red illumination. Activity shows a strong tidal rhythmicity with two peaks of activity every 25 hours (approx.). Activity peaks occurred at 11.5-13.0 hour intervals (mean period length 12.25 hours) with the median times of the peaks between 1.3 and 2.4 hours before times of high water on the shore from which the crabs came. Under these constant conditions the initial sharp rhythmicity fades slowly during the first 3 weeks but then is gradually re-established. After 5 weeks absence from a tidal environment the crabs exhibit a marked rhythm with normal tidal frequency but with median times of activity peaks occurring a short time after high water. Thus H.edwardsi is most active when the tide is in and remains quiescent, sheltering beneath rocks, while the tide is out. Under laboratory conditions the total amount of activity per peak seems to alternate with high levels of movement coinciding with what would be the hours of darkness or dawn in the natural environment. This may be caused by slight changes in temperature rather than changes in light. In winter, rhythmicity is not immediately apparent but can be detected after frequency analysis of the data. During winter the crabs move further down the shore to occupy the area around low water level. In spring they migrate back to the upper half of the littoral again and show stronger rhythmicity.

Thus H. edwardsi exhibits an endogenous circatidal activity rhythm with only a weak circadian component. Naylor & Williams (1984) showed that exposure to simulated high tide pulses before or after the 'expected' high tide resulted in slight phase delay or advance respectively. The circatidal rhythm depends mainly on repeated exposure to tidal variables for entrainment and each tide is able to adjust the behavioural rhythm only slightly from its endogenous pattern.

Behaviour of individual H.edwardsi has not been studied but Jacoby (1981) found 15 social and 12 maintenance behaviours in H.nudus from the coast of Washington. Social behaviours are used to defend food, space and mates and pairs of equal-sized crabs behave more aggressively than pairs of unequal-sized crabs. Resident crabs defend their space against invasion by non-resident crabs.

Ecology

Although H. edwardsi is found throughout the length of New Zealand, it is much more abundant on southern shores than in the north. In the northern part of New Zealand it is replaced by the xanthid crab, Ozius truncatus. At Kaikoura Cyclograpsus lavauxi occupies the upper shore and H. edwardsi occupies the middle region. Further south on the Catlins coast H. edwardsi occupies both the upper and middle shore levels and is very abundant.

The combined effects of temperature (5-25°C) and salinity (0-45 ppt) on survival of H.edwardsi have been investigated by Hicks (1973). Crabs collected in summer showed good survival from 15-45 ppt salinity at 5 and 15°C but at 25°C survival at 15 ppt salinity was reduced. Survival at 0 ppt was reduced to only 3 days at all temperatures. Similarly winter collected crabs also had poor survival at the lowest salinity. These crabs survived well at all temperatures when salinity was 15 ppt or greater. At the highest salinity (45 ppt) and temperature (25° C.) winter crabs had reduced survival. For both summer and winter crabs the dominant factor determining survival is salinity. Leader & Bedford (1978b)* examined composition of muscles and haemolymph and found that ion concentrations were similar to other crabs from the same habitat. H.edwardsi haemolymph is hyperosmotic to the external medium in dilute seawater but hyposmotic in more concentrated media (Phillips 1968). Bedford and Leader (1977) showed that H.edwardsi is imperfectly capable of regulating the composition of its haemolymph in the face of large changes in external concentration. Reduction of salinity by 75% (to approx. 9 ppt) resulted in reductions of the major inorganic ions in haemolymph - sodium (33%), potassium (35%), calcium (23%), magnesium (47%) and chloride (36%). Amounts of intracellular ions showed no change over the same range. Large amounts of free amino acid were lost from muscle tissues and the results suggest that changes in both haemolymph ion and muscle amino acid concentrations are involved in acclimation of H.edwardsi to low salinities. This crab is a typical euryhaline poikilosmotic animal so that when the external medium changes, corresponding, though lesser changes occur in haemolymph composition. Later Bedford & Leader (1978) showed that following transfer to hyperosmotic media, haemolymph approached a new equilibrium within 48 hours, suggesting that the crabs are very permeable to water and ions. High ion fluxes have been reported by O'Brien (1972). Intracellular readjustment to hyperosmotic stress was complete within 4 days. Pellegrino (1984) estimated percentage water content as 59% with a lethal water loss of 40% and he suggested that the integument is very permeable to water loss in air.

According to Graham (1939) H.edwardsi in Otago Harbour has relatively few fish predators. This crab was found in the guts of rig (Mustelus lenticulatus), red cod (Pseudophycis bacchus), sea perch (Helicolenus papillosus) and girdled parrot-fish (Pseudolabrus cinctus). Thompson (1930) also found that this crab was eaten by red cod in the Avon Heathcote Estuary. In the laboratory the cephalopods Octopus maorum and Robsonella australis will eat this crab (Pack 1982). Zoea larvae of H.edwardsi are eaten by kahawai (Arripis trutta) in Wellington Harbour (Baker 1971).

Based on laboratory observations Kitching & Lockwood (1974) proposed that H.edwardsi preys upon Lepsiella (which preys upon Chamaesipho columna) and may be responsible for thicker shells of snails on sheltered shores. This hypothesis is hard to accept because the stomachs of all H. edwardsi I have examined at Kaikoura contained drift algae such as Carpophyllum maschalocarpum. There was no evidence of any animal or mollusc fragments.

References

Batham (1956,1958), Bedford & Leader (1977), Begg (1980), Bennett (1964), Chilton & Bennett (1929), Dell (1963a, 1968a), Graham (1939), Hicks (1973), Kitching & Lockwood (1974), Knudsen (1964), Leader & Bedford (1978a,1978b), Miers (1876b), Naylor & Williams (1984), Pellegrino (1984), Phillips (1968), Richardson (1949a), Thompson (1930), Thomson (1905, 1912), Thomson & Anderton (1921), Todd & Dehnel (1960), Wear (1970a), Wear & Fielder (1985), Williams (1969).

Hemigrapsus crenulatus (H. Milne Edwards, 1837)
Hairy-handed Crab

Synonymy

Cyclograpsus crenulatus H. Milne Edwards, 1837; Trichodactylus granarius Nicolet, 1849; Hemigrapsus crenulatus Dana, 1852; Trichodactylus granulatus (for granarius) H. Milne Edwards, 1853; Heterograpsus crenulatus H. Milne Edwards, 1853; Lobograpsus crenulatus A. Milne Edwards, 1869; Heterograpsus crenulatus Miers, 1876b; Filhol, 1886; Heterograpsus barbimanus Cano, 1889 (not H.barbimanus Heller 1865); Hemigrapsus crenulatus Rathbun, 1898; Heterograpsus sanguineus Lenz, 1902; Hemigrapsus crenulatus Rathbun, 1910; Heterograpsus crenulatus Thomson, 1912; Hemigrapsus crenulatus Rathbun 1918a, Heterograpsus crenulatus Thomson & Anderton, 1921; Oliver, 1923; Hemigrapsus crenulatus Chilton & Bennett, 1929; Bennett, 1930; Brachynotus crenulatus Balss, 1930; Hemigrapsus crenulatus Porter, 1936a; 1936b; 1937; Richardson, 1949a; Garth, 1957; Dell, 1963a; Wood, 1963; Bennett, 1964; Batham, 1965; Garth, Haig & Yaldwyn, 1967; Dell, 1968a, Wood, 1968; Wear, 1970a; Hayward, 1974; Knox, Bolton & Hackwell, 1977; Knox & Bolton, 1978; Knox & Fenwick, 1978a; Knox, Bolton & Hackwell, 1978; Knox, 1983a; Wear & Fielder, 1985.

Type Locality

New Zealand. Milne Edwards did not specify the type locality of C.crenulatus (see Bennett 1964) and according to Garth, Haig & Yaldwyn (1967), he had access to Chilean as well as New Zealand material so that the type locality could equally well have been somewhere in Chile.

Distribution

Chile and New Zealand. Within New Zealand, Parengarenga Harbour to Stewart Island also Okarito, Westland and Long Sound, Fiordland.

There has been some discussion of the question of whether the New Zealand and Chilean specimens are conspecific. Rathbun (1918a) examined a male and female from Dunedin and compared them with Chilean specimens and considered them to be identical. Bennett (1930) questioned this opinion, suggesting that the wide range of habitats which H.crenulatus seemed to occupy might indicate that more than one species was involved. Further, Bennett (1964) gives the opinion of Dr.H.Balss that specimens from Stewart Island were different from the Chilean specimens because of differences in the sub-orbital stridulating ridge. They considered that the Chilean species should be called Hemigrapsus granarius (Nicolet 1849). However Garth (1957) examined 3 males and 1 female from Wellington and stated: "Only minute differences, such as amount of granulation and acuteness of anterolateral teeth, are discernable. This is the more remarkable considering the vast difference that separates the two populations. The male first pleopods correspond in detail." These specimens were later re-examined (Garth, Haig & Yaldwyn 1967) who stated: "The differences in the sub-orbital stridulating ridge suggested by Bennett as distinguishing the two forms appear no more than might be expected in a long series of specimens from either locality and the writer is inclined toward his earlier

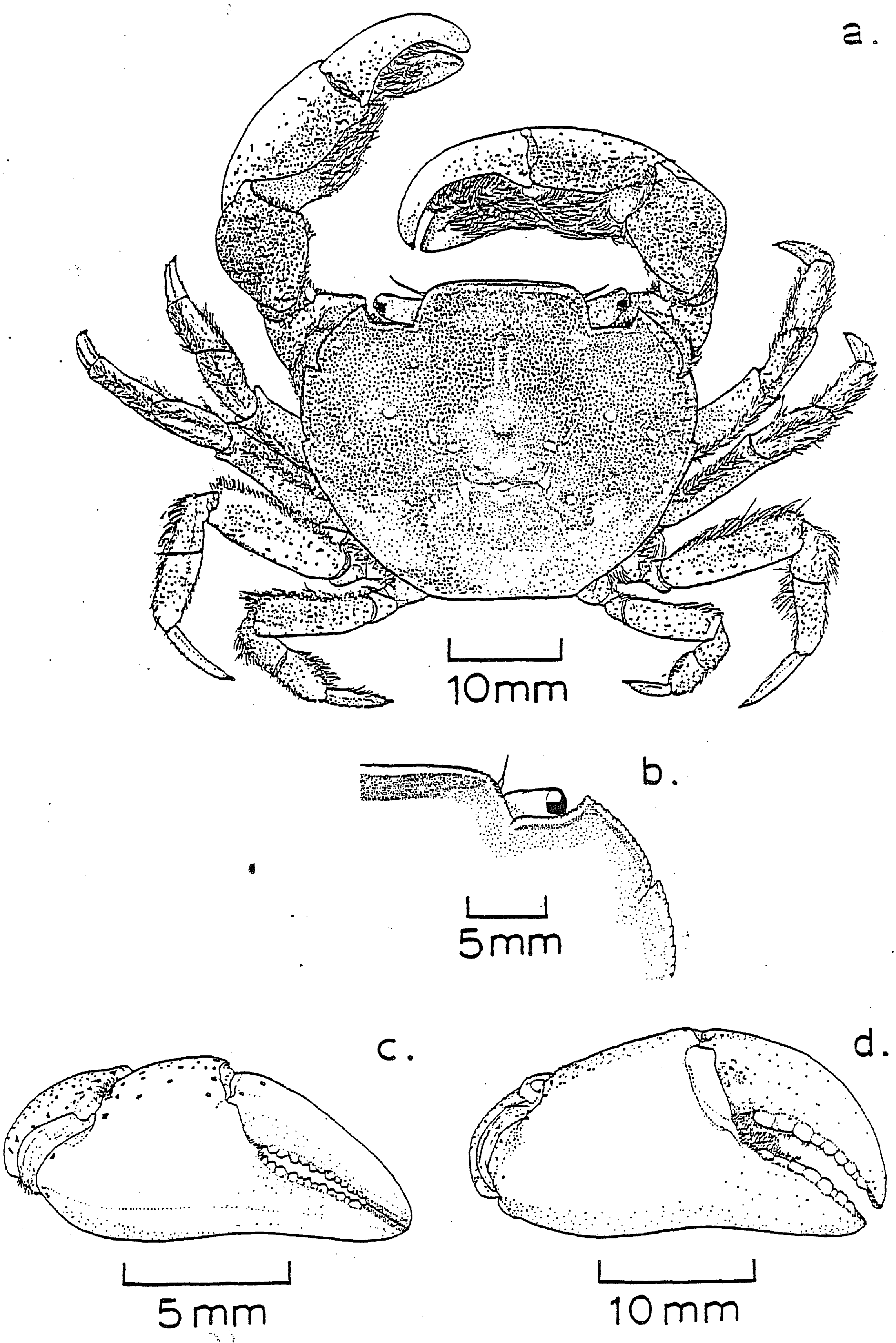


Fig. 63 - Hemigrapsus crenulatus: a - male, dorsal view; b - detail of orbital area, dorsal view; c - right chela, female, outer face; d - right chela, male, outer face (by J. Black).

opinion that the two are conspecific." Garth also states that if the two should later prove to be distinct there is no assurance that the name of crenulatus would remain with the New Zealand form because Milne Edwards did not specify a type locality. The Chilean species would become H.granarius (Nicolet 1849) and the New Zealand species would require a new name.

Diagnosis (Fig. 63a-d)

Carapace flattened, polished, wider than long (ratio 1.1-1.2) and distinctly oblong-shaped. Gastric and cardiac regions well defined, raised and separated by a distinct groove. Surface of lateral carapace margins minutely granulate. Carapace broadly convex laterally and antero-posteriorly, rising steeply from frontal margin and sloping more gradually posteriorly. A shallow, broad groove extends back from the frontal margin which is almost straight and rimmed and has a row of small granules close below the rim. Orbital margin deeply concave and produced at the post-orbital corner as a distinct tooth. Infra-orbital stridulating ridge continuously granulate in female but in male there is a smooth area separating off the outer part which is cut into two lobes. Antero-lateral margin runs almost straight back from the post-orbital corner and bears two small, blunt teeth. The margins of the orbit and antero-lateral border are minutely granulated. Posterolateral margins slightly convergent, posterior carapace margin straight. Chelipeds weakly developed, larger in male, merus sharply trigonal, margins with a distinct line of granules and a transverse row on the under surface. Outer surface of carpus and propodus rounded, fixed finger bent downward, inner surface of male propodus densely pilose, especially near bases of fingers. Granulated ridge on outer surface of propodus and fixed finger distinct. Fingers have 6-7 small, flattened teeth and only gape slightly at the base. Differences between male and female cheliped fingers are shown in Fig. 63c and d. First three pairs of legs as long as chelipeds, second pair longest, fourth pair shortest. Leg segments laterally flattened, margins carry long dense hairs, dactyls long and acute. Mature female abdomen of six segments plus telson occupies almost the entire ventral surface and is fringed with long hairs. Male abdomen narrow with faint movement between the fourth and fifth segments.

Colour

Carapace greeny-yellow with white patches, covered with tiny dark purple or reddish-brown spots. Marginal white band which also has dark tubercles. Eyestalks white, cornea black, antennules white with darker patches, antennae short and pale brown. Dorsal surface of cheliped carpus and propodus densely marked with dark purple-brown, fingers white with dark brown tips. Outer surface of propodus deep yellowish cream. Ventral surface white. Legs greeny-yellow with dark purple spots, fringed with short fine setae and some longer setae. Specimens from Chile are grey, grey-brown, green-brown and black.

Size

Male 37.5mm CW, 32.1mm CL. Female 26mm CW, 22.4mm CL. Smallest ovigerous female 9mm CW. Garth (1957) gave the following measurements for specimens from Chile: males 40mm CW, females 25.2mm CW, ovigerous females 8.8mm to 22.3mm CW.

Habitat

H.crenulatus seems to occur in a wide variety of habitats: under stones, burrowing in sand, mud, clay or earth, in sheltered marine or estuarine habitats. It occupies a similar habitat to Helice crassa.

H.crenulatus from Chile are found under stones in mid- and lower littoral (sparse in upper littoral), in holes in sand, among barnacles on piles, and in sheltered places often in proximity to fresh water.

Depth

Mid-tide level to 11m. (Supra-tidal records of H.crenulatus in burrows may well be based on mis-identification.)

Breeding

Ovigerous females have been collected at Paihia, Bay of Islands in December, at Wellington in October and November by Wear (1970a) and at Otago in January and February by Thomson & Anderton (1921). By late November H.crenulatus females at Wellington carry eggs at all stages of development. Females probably lay more than one batch of eggs per season as ovigerous females frequently have gravid ovaries. Immature eggs are light brownish-yellow and measure 0.28 x 0.26mm while mature eggs are almost transparent and measure 0.34 x 0.33mm with the remaining yolk light brown. One female of 15.6mm CW collected by Thomson and Anderton (1921) from Otago Harbour in January, carried 8,968 eggs with an average diameter of 0.26mm.

In a detailed study of the reproductive biology of H.crenulatus in the Avon-Heathcote Estuary, Clark (1987) found that ovigerous females occurred for 8-9 months from June to January/February, with over 50% of females ovigerous in October. Ovigerous females were absent from March to May. Gonad index changes and occurrence of females with stage 1 broods suggests that the long breeding season is the result of both asynchrony among females and second broods by some females, with or without an intervening moult. Although capable of transmoult sperm retention females which had the opportunity to mate after their first brood were more likely to produce a second successful brood. A cycle of oogenesis is completed within 16 weeks and eggs are incubated by the female for between 8-12 weeks. Successful brood development occurred between 18-36ppt salinity with development time increasing with decreasing salinity. The smallest ovigerous female was 9mm CW, carrying approx. 1500 eggs and brood size increased exponentially with a 26mm female carrying approx. 35,000 eggs. Male H.crenulatus are capable of mating all year round.

Collections from Chile suggest that females carry eggs from October to January and recruitment of young is evident by the end of March (Garth 1953, Garth, Haig & Yaldwyn 1967).

Wickham & Roe (1987) found that ovigerous H.nudus and H.oregonensis from California were infested with the egg-predator Carcinonemertes epialti. These nemerteans have not been reported from H.crenulatus in Chile or from New Zealand.

Development and Growth

Five zoeal stages described by Wear & Fielder (1985). Wear (1970a) has described the pre-zoea larva, which lasts only 5-10 minutes, and the first stage zoea. The megalopa is unknown. Zoeae are especially abundant in summer plankton samples taken in shallow water, especially harbours and adjacent to estuaries.

Relative growth of H.crenulatus from the Avon-Heathcote Estuary has been studied by Clark (1987). Maturation in males is marked by a change in cheliped allometry between 13-15mm CW, and in females by a change in abdomen allometry between 9-11mm CW. Male cheliped dactyl length is positively allometric both before and after the pubertal moult. Similarly, female abdomen width is positively allometric both before and after the pubertal moult while the male abdomen is negatively allometric throughout growth. In both sexes the sexually dimorphic character shows a sudden increase in size at puberty. After puberty female pleopod length is positively allometric while the male pleopod becomes negatively allometric.

A similar pattern of absolute growth is shown by both males and females. For males percentage growth increment increases from 16% to 20% at around the puberty moult and then decreases to 13% for the largest crabs. For females pre-pubertal growth increases from 17% to 20% and then declines to around 9%. Males have significantly larger growth increments than females, but there is no difference in length of intermoult periods. Males attain maturity in the 11th instar and pass through an estimated 19 instars to reach maximum size. Females attain maturity in the ninth instar and moult a total of 16 times to reach maximum size. Males could reach maturity in approx. 1.1 yr and live for nearly 5 yr if they reach maximum size, while females could reach maturity in approx. 0.8 yr and live for 3.5 yr to reach maximum size. The growth data suggest a sigmoid curve with the slope increasing initially and then decreasing following puberty. The size at which the sexes diverge is around 13mm CW. Growth of H.crenulatus follows an indeterminate pattern where maximum size is determined by how long the crabs survive. The largest crabs with missing limbs had new limb buds developing (Clark 1987).

Behaviour

Little is known about the behaviour of H.crenulatus. To some extent the micro-distribution at low tide reflects the presence of pools of water and stones or shells under which it can hide. Walker (1970) observed these crabs at Govenor's Bay feeding and moving shoreward with the incoming tide and retreating again as the tide dropped. They fed on organic matter disturbed by the rising tide. H.crenulatus is sometimes found in burrows under stones (see Wood 1968) but it is not clear whether these tunnels are made by the crabs themselves.

H. crenulatus is photonegative in both air and water and when offered different substrates of mud, sand and stones showed no evidence of a preference (Jones 1976). This result is surprising because the crab is most often found under stones in the Avon-Heathcote Estuary. Jones suggests that H. crenulatus buries in soft substrates rather than constructing permanent burrows. Clearly, further work on the substrate requirements of this species is necessary.

In September, Yaldwyn (1966) observed a pair of H.crenulatus from Wellington Harbour in copula. The female was slightly smaller than the male, who was underneath (at least part of the time) and who enclosed the female in his walking legs. The female's legs were stretched out laterally, not attempting to grip the male, while the male's chelipeds were held out aggressively over the anterior part of the female carapace. The female's chelipeds were folded under her and her abdomen was opened right back with the telson hooked on to the posterior edge of the male carapace. The male abdomen was opened out so that the ventral surfaces of the two crabs were closely opposed. The pair remained in this position for about 10 min and when they broke apart the male took up an aggressive stance, lying over the dorsal surface of the female. Thus H.crenulatus seems to mate when the female is in the hard-shell condition and there does not appear to be any courtship, although this point requires verification. Thompson (1930) also reported that all crabs found in copula, involved a male much larger than the female.

Observations on H. crenulatus with stage 4 broods show that shortly before hatching the female raised herself on the tips of her legs and flexed her body up and down and then beat her abdomen in a rhythmical fashion. Often the chelipeds were alternately dug into the brood to propel the newly hatched larvae into the surrounding water. Larvae were released over 0.5 to 6 hours and showed a strongly positive phototaxis (Clark 1987).

Ecology

In the Avon-Heathcote Estuary Clark (1987) found that H.crenulatus numbers at an intertidal site were lowest in the summer months when the sex ratio substantially favoured males and highest during winter when proportions approached 1:1. Overall the sex ratio favoured males, 1.48:1. Juveniles (<4mm CW) showed a male biased ratio (2.5:1) as did adults larger than 20mm CW. Size classes in between showed approx. equal numbers of males and females. These size-related sex ratios reflect the growth patterns of each sex. Juveniles were recruited into the population from October but recruitment continued until April as a result of the extended breeding season. Throughout the year the population was dominated by post-pubertal crabs (12-20mm CW). Recruits were absorbed into this group within a year and continued mortality of larger crabs produced a fairly stable population size-structure. Decrease in numbers of females in the intertidal during the summer may have been the result of female migration into sub-tidal areas.

The occurrence of H.crenulatus in estuaries has lead to a great deal of research on its adaptations to fluctuating salinity levels. Hicks (1973) investigated the combined effects of temperature and salinity on H.crenulatus in Wellington Harbour. Crabs collected in summer and winter were kept for 8 days at temperatures from 5-25^{o}C and salinities of 0-45 ppt. Winter acclimated crabs survived well at all temperatures and all salinities down to 15 ppt. At zero salinity they survived best at 15^{o}C in contrast to summer acclimated crabs which had very poor survival at all temperatures. Summer acclimated crabs exhibited a salinity optimum which decreased as temperature decreased.

H.crenulatus survival was best at medium to high temperatures in both seasons. With optimum conditions ranging from 6-23^{o}C, within a salinity of 12-42 ppt during the summer, this species is well adapted to the variations in habitat that occur. In winter the range of tolerance is widened even further. Burrowing by H.crenulatus may enable it to avoid detrimental combinations of temperature and salinity.

Jackson (1976) found that H.crenulatus can live in 10-160% seawater for at least 8 days without stress. From 10-65% haemolymph is hyperosmotic and from 90-140% it is isosmotic. Hoskins (1966) and Ayers (1968) obtained similar results. Jones (1976) recorded 90% survival in 10% seawater for 7 days and 55% survival in 1% seawater but activity was much reduced. Ion concentrations of muscle and haemolymph are similar to those in other crabs from the same habitat (Leader & Bedford 1978b).

Bloomfield (1982) examined the effects of season and salinity acclimation on crabs from the Avon-Heathcote Estuary which is colder and more dilute in winter than in summer. Winter collected crabs had a greater tolerance to dilute (1%) seawater than summer crabs. These crabs have a slower rate of sodium loss, a lower apparent water permeability and a 'stronger' regulation of blood osmotic pressure in 100% seawater, than summer crabs. In 1% seawater, winter crabs had an LT50 of greater than 12 days whereas summer crabs had an LT50 of only 48 hours. Both winter and summer crabs hyperosmoregulate in dilute (10%) seawater, but winter crabs regulate their blood osmotic pressure at a significantly lower concentration than summer crabs in 100% seawater. Using radioactve, tritiated water as a tracer, Bloomfield showed that water turnover rates of winter crabs were less than 2% per hour at 10% and 100% seawater, whereas turnover rates of summer crabs were 12% and 6% per hour for the same media. When H.crenulatus is transferred from 100% to 10% seawater, change in the haemolymph osmotic concentration is initially rapid: 50% of the change occurs in 6 hours, 94% in 24 hours with the remainder adjusting over a period of up to 5 weeks. The role of seasonal temperature changes in adjustment to dilute media is as yet unclear. Reed (1981) showed that exposure of H.crenulatus to 10% seawater caused a reduced permeability (perhaps resulting from structural changes to the gills) and an increase in respiration rate (perhaps resulting from the extra energy needed to maintain electrolyte balance). In 100% seawater approx. 40% of lost sodium ions are lost via the gills and approx. 60% via the urine. These studies confirm the findings of Hicks (1973) and Jones (1976) that H. crenulatus is a euryhaline crab.

Bull (1977) has conducted the only study of the physiological effects of sub-lethal levels of a heavy metal on a New Zealand crab. Heavy metals can form complexes with organic compounds and become fixed in tissues thus giving them a long biological half-life. Bull found that sub-lethal levels of mercury (0.1 and 1ppm) caused higher levels of mortality in dilute seawater. Gill epithelial layers were affected, with cell hypertrophy, decreased density and disruption of cellular details and an increased number of haemocytes in the gill lamellae. Exposure to mercury resulted in significant decreases in blood sodium levels below 80% seawater, but decreases in chloride ions were not significant. Sodium uptake rates, which were inversely proportional to body weight, were unaffected by exposure to mercury. Jennings & Rainbow (1979) found that 10ppm of cadmium was toxic for the portunid crab *Carcinus maenus*. Using radioactive cadmium they found that 59-80% of the cadmium uptake was adsorbed on to the body surface from seawater. When food was labelled, 16.9% of cadmium was found in the mid-gut gland and only 22% on the exterior. After 10 days in cadmium-free seawater crabs lost 69% of the accumulated cadmium. Internal cadmium was associated with protein (Jennings, Rainbow & Scott 1979). Equilibrium concentration for haemolymph cadmium was considerably less than the external medium (Wright & Brewer 1979).

In the Avon-Heathcote Estuary Jackson (1976) found that *H.crenulatus* collected inter-tidally were predominantly males while baited traps set in the sea yielded mostly females. This may be a seasonal phenomenon but in view of the uncertain lower depth limit it should be investigated further.

In Otago Harbour Graham (1939) stated that *H.crenulatus* was eaten by carpet sharks (*Cephaloscyllium isabella*), rig (*Mustelus lenticulatus*), red cod (*Pseudophycis bacchus*), rock cod (*Lotella rachinus*), sea perch (*Helicolenus papillosus*) and red gurnard (*Chelidonichthys kumu*). It was consumed in great quantities by especially red cod. Habib (1975) found that red cod from Banks Peninsula ate small quantities of *H. crenulatus* (1% of gut volume) as did red cod from off Otago Peninsula (0.11-0.23%). Thompson (1930) found that this crab was eaten by red cod, rig and also gulls (*Larus* spp.) in the Avon-Heathcote Estuary. Later Kilner (1974) found that *H. crenulatus* made up 1% of the volume of the food of sand flounder (*Rhombosolea plebeia*), see also Webb (1973a). It is also eaten by red cod, short-finned eels (*Anguilla australis*), yellow-bellied flounder (*R. leporina*), common sole (*Peltorhamphus novaezelandiae*), yellow-eyed mullet (*Aldrichetta forsteri*), kahawai (*Arripis trutta*), spotty (*Pseudolabrus celidotus*) and globefish (*Spheroides richei*) from the Avon-Heathcote Estuary (Webb 1973a, 1973b). Giant kokopu (*Galaxias argentius*) caught by M. Main in a stream flowing into Okarito Lagoon contained many *H.crenulatus*. Rig from Golden Bay and Kaikoura were also found to eat small quantities (King & Clark 1984, see also McCann 1953). These crabs are readily eaten by *Octopus maorum* in the laboratory (Pack 1982).

References

Ayers (1968), Bennett (1964), Bloomfield (1982), Bull (1977), Chilton & Bennett (1929), Clark (1987), Graham (1939), Hicks (1973), Hoskins (1966), Jackson (1976), Jones (1976), Kilner (1974), King & Clark (1984), Knox et al (1976), Knudsen (1964), Kuris & Mager (1975), Leader & Bedford (1978b), Pillay & Ono (1978), Reed (1981), Symons (1964), Thompson (1930), Thomson & Anderton (1921), Todd & Dehnel (1960), Walker (1970), Wear (1970a), Wear & Fielder (1985), Webb (1973a, 1973b), Wood (1968), Yaldwyn (1966).

Helice crassa Dana, 1851
Tunnelling Mud Crab

Synonymy

Helice crassa Dana, 1851; Helice lucasi H. Milne Edwards, 1853; Heller, 1868; Helice crassa Miers, 1876b; Helice lucasi Filhol, 1886; Helice crassa Thomson, 1912; Chasmagnathus subquadratus Thomson, 1912; Helice crassa Thomson & Anderton, 1921; Oliver, 1923; Helice lucasi Chilton & Bennett, 1929; Helice crassa Chilton & Bennett, 1929; Powell, 1937; Wood, 1963; Dell, 1963a; Bennett, 1964; Campbell & Griffin, 1966; Dell, 1968a; Wood, 1968; Wear, 1970a; Hayward, 1974; Knox, Bolton & Hackwell, 1977; Bolton & Knox, 1977; Knox & Fenwick, 1978a; Knox, Bolton & Hackwell, 1978; Knox, 1983a; Wear & Fielder, 1985.

Type Locality

H.crassa was described by Dana from Illawarra, New South Wales but this record is almost certainly incorrect (Campbell & Griffin 1966). Miers (1886) supposedly collected a small male from Sydney Harbour but gives no description and the habitat is wrong for H.crassa. Therefore this appears to be a mis-identification. These are the only records from Australia for H.crassa and both can be discounted. Therefore the type locality can only be given as 'New Zealand'.

Distribution

Endemic to New Zealand, North, South and Stewart Islands.

Diagnosis (Fig. 64a-b)

Carapace smooth, flattened, oblong-shaped, wider than long (ratio 1.2), anteriorly-posteriorly convex, more steeply at the front and gradually sloping towards the rear. Gastro-cardiac groove distinct leading to curved depression in the branchial areas and a curved depression directed forwards towards the antero-lateral corner. Postero-lateral carapace corners depressed. A broadly depressed frontal groove extends back from the frontal margin which is smooth, slightly concave and about one-third of the CW. Orbital margin unarmed, angled across the corner of the carapace and ending in a strong post-orbital tooth. Eyestalks short (20% of CW), not reaching to post-orbital corner. Lateral margins parallel and bearing two small teeth just behind the post-orbital tooth. Postero-lateral carapace corners angled and posterior margin slightly convex. Pterygostome with granules and setae. Chelipeds large, carpus inflated, rounded, superior inner corner produced as a broad lobe, propodus deep, outer surface flattened and rounded, inner surface concave, fingers long, down-curved and gaping basally. Walking legs shorter than chelipeds, last pair shortest and inserted sub-dorsally. All leg segments lack setal fringes, are laterally compressed, meri long, dactyli long, narrow and curved. Abdomen with six segments, telson small, triangular, fifth segment broader than fourth in the male.

Colour

Carapace grey, olive-green, blue-green to tawny brown, margins yellow. Chelipeds light yellow edged along the top with

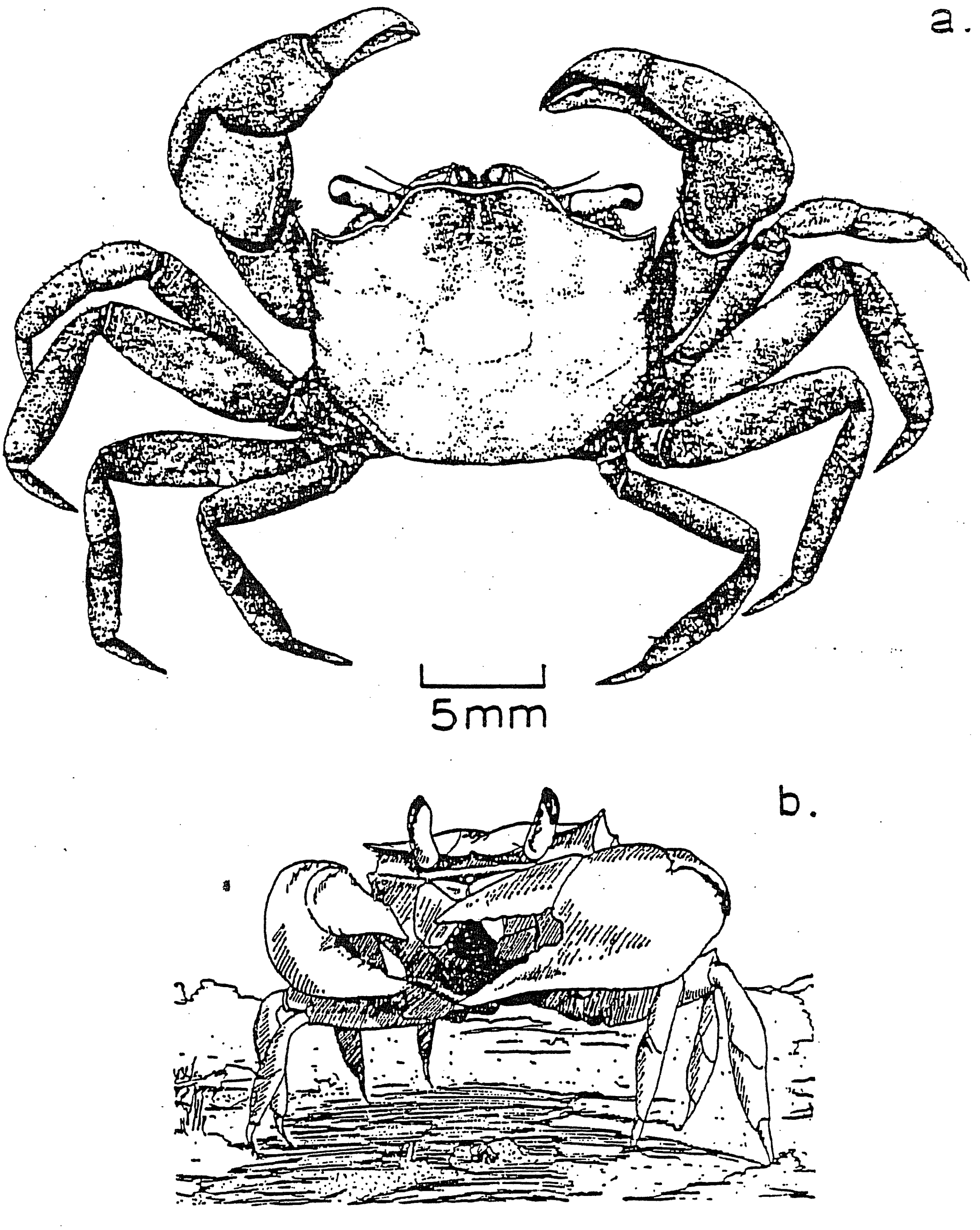


Fig. 64 - Helice crassa: a - male, dorsal view (after Jones, 1983); b - threat posture showing crab standing on 'tip-toes' (after Beer, 1959).

dark green, small patches of bright orange present in the joints. Antennae brown, antennules light purple, eyestalks pale green dorsally and white ventrally, cornea pale red, green, white wrap-around bands. Legs dark green with pale yellow margins. Ventral surface pale. Crabs about to moult are paler in colour (Nye 1977).

Size

Male 21.7mm CW. Female 20.9mm CW. Jones and Simons (1983) have shown that maximum size for both sexes is correlated with latitude, being smallest in the north and largest in the south of New Zealand. Nye (1977) found one female crab of 26mm CW at Papanui Inlet, near Dunedin.

Habitat

Enclosed beaches, sheltered harbours, lagoons, estuaries and mangrove swamps and penetrating areas where there is a strong freshwater influence. Constructs burrows in firm, well-drained sediment that is exposed to the air for more than six hours on each tidal cycle and also in firm, arid soil several metres above high tide level. Reported to climb mangrove trees (*Avicennia resinifera*) (Cox 1976).

Depth

Upper intertidal region.

Breeding

Female *H.crassa* mate in hard-shell condition (Nye 1977). Near Wellington ovigerous females have been collected from August to January (6 months) (Wear 1970a), Christchurch August to March (8 months) (Jones 1980) and near Dunedin from September to February (6 months) (Nye 1977). (A single ovigerous female was found in July by Nye and if included would make the breeding season 8 months). At all these places peak numbers of ovigerous females were recorded in November or December. Jones (1980) found in the Avon-Heathcote estuary that the sex ratio was biased in favour of males (1.48:1) and males were significantly more numerous than females in all sexable size classes from 4.1 to 18.0mm CW. This suggests that if sex is not environmentally determined and the primary sex ratio is equal then there must be differential mortality of males and females during the juvenile phase. However Nye (1977) recorded a 1:1 sex ratio for *H.crassa* at Papanui Inlet, near Dunedin. The smallest ovigerous female collected from the Avon-Heathcote estuary was 7.2mm CW while the smallest recorded from Papanui Inlet was 10mm CW. Wear (1970a) found that freshly laid eggs measured 0.26mm diameter and were brownish-yellow while mature eggs measured 0.32 x 0.31mm and were transparent or light grey-green. Jones (1980) recorded a similar initial egg-size in 1975-76 but a significantly smaller diameter (0.24mm) during 1976-7. In both years egg-size did not increase significantly during incubation although this may have been an artifact of preservation in ethanol. At Christchurch brood size increased linearly with CW and the smallest females (8.5mm CW) carried about 2,000 eggs while the largest females (16mm CW) carried 16,000 eggs. There was no signficant brood mortality during incubation. Most females collected from August to October had stage 1 eggs with only 10% having stage 2 eggs. Again during January there was a second smaller peak in new eggs. Stage 3 eggs first appeared in November and were last found in February.

Larger eggs produced in 1975-6 were incubated for approx. 90 days compared with approx. 60 days for smaller eggs produced during 1976-7. It is likely that incubation times will be shorter later in the breeding season. At Wellington incubation required 42 days although the temperature was not given. It is likely that H.crassa females produce 2 broods at the most during the season and the second brood can be produced without mating again (Nye 1977, Wear 1970a). At Papanui Inlet females exceeding 13mm CW were found carrying eggs more often than smaller crabs. In the laboratory females exceeding 15mm CW incubated 2 broods over the spring and summer with a break between broods of 30-112 days. One female incubated three broods in one breeding season (Nye 1977).

Jones and Simons (1983) made collections of H.crassa from 11 sites between 35°S (Mangonui Harbour) and 46°27'S (Oreti River Estuary) during November and December 1980 to investigate latitudinal variation in reproductive characteristics. Mean CW of ovigerous females (8.9-16.9 mm), CW of smallest (7.4-15.1 mm) and largest (11.7-19.6 mm) ovigerous females all increased and were significantly correlated with latitude indicating that size at puberty increased from low to high latitudes. Annala et al. (1980) found a similar relationship for final body size and size of maturity for female Jasus edwardsii in New Zealand. H.crassa egg numbers increased linearly with female CW and females of all sizes at Mangonui Harbour carried fewer eggs than females from southernmost sites. Intercept and slope values for the regression lines were correlated significantly with latitude and density but not with substratum. The major trend was an increase in egg numbers with increased latitude for crabs of similar sizes and a secondary trend of a decrease in egg numbers with increased density. Egg size and dry weight showed no distinct trends with latitude. However the heaviest eggs were found at the southernmost sites. These trends correlated with latitude are presumably a reflection of the effects of decreasing sea water temperatures on local life histories. The smaller brood size of northern females may be associated with more broods per season while greater brood size of southern females may be associated with fewer broods per season. Therefore despite differences in reproductive characteristics the output of offspring may be similar and unrelated to latitude. However more detailed demographic data are required to test this hypothesis. Eggs from southern females evidently contained more organic material and this may be necessary to sustain development over a longer incubation time or may enhance survival of planktonic larvae at colder temperatures.

Development and Growth

Five zoeal stages and megalopa (see Wear & Fielder 1985). Wear (1970a) has described the pre-zoea and first zoea larva of H.crassa. The pre-zoea cuticle is moulted within 10 minutes of hatching. Thompson (1930) found that megalopae were common in the Avon-Heathcote Estuary in February and March. During March-August 1982, Roper, Simons & Jones (1983) found small numbers of H.crassa zoeae in the plankton from this estuary.

Retention of cab zoeae in estuarine areas is a problem faced by species which are restricted to these habitats. Epifanio (1987) has suggested that vertical movements by the larvae and physical concentrating mechanisms associated with tidal fronts between less dense estuarine water and more dense oceanic water may be responsible for concentrating the larvae and retaining them close to the parental habitat.

Nye (1977) observed one female in the act of moulting. During the 5 minutes after the carapace split along the posterior margin, this crab pitched slowly forwards as more of the new soft carapace appeared. The new abdomen was then withdrawn and the crab fell onto its back bringing the flexed legs into view. The female immediately righted itself and moved off. Large crabs took approx. a week to harden and often ate part of their exuvia. In the laboratory females commonly moulted 3-6 weeks after their eggs hatched (average = 35 days) but some females carried another batch of eggs before moulting. All crabs larger than 11mm CW moulted in late summer (February-April) but more than half of these had also moulted during November-December. Five of 10 small crabs collected in October survived for a year and increased in size from an average of 2.8mm to an average of 7.8mm CW. A complete series of moult increments (and intermoult intervals) for a small crab (sex not given) initially 2.5mm CW were - 1.7mm (16+ days), 2.2mm (46 days), 0.8mm (112 days) and 0.8mm (125 days). The average moult increment was 1.38mm. The growth is similar to other Brachyura where percentage moult increments often decrease and intermoult intervals increase with size.

It seems likely that H.crassa reach maturity in the first year of life, perhaps producing only 1 brood in their first breeding season followed by 2 per season in the following years. If females grow to approx. 20mm CW then their maximum length of life may be as long as 5-6 years during which they might produce 10-12 broods. This would imply that the maximum number of offspring per female could be of the order of 100,000. However the average number of offspring per female must be considerably fewer.

Behaviour

Williams et al. (1985) compared field and laboratory activity patterns of H.crassa from Papanui Inlet, Otago Peninsula. Catches of crabs in pitfall traps at different shore levels suggest that crabs do not move far from the zone where they burrow, with the numbers caught more or less reflecting the relative density at each level. Catches during full moon spring tides in late January peaked during the 3 hours covering high tide, despite the fact that crabs were active on the surface (usually within 20-30 cm radius of the burrow) when the area was exposed to the air. Concurrent records of locomotor activity under constant laboratory conditions clearly showed circatidal rhythms with peak activity coinciding with the time of high water. In the field catch rate at high water does not vary with the day/night cycle even when high tides are around midday and midnight. However during neap tides, when the water barely reached most of the crabs, activity is still circatidal, but catch rates are only about 5% of the high water springs catch rate. Thus activity is related to tidal amplitude. The explanation of the apparent discrepancy between observations (see below) and trap catches when the habitat is exposed to air seems to require the assumption that when crabs are covered by water they exhibit more wide-ranging, exploratory locomotor activity.

Williams et al. (1985) found that the rhythm of groups of five H.crassa had a period of 24.8 hours. However when individual crabs are recorded separately none of them adopted this period. Two basic cyclic patterns were found: 25% of crabs displayed a unimodal pattern (period 26.5, SD=1.4 hours) while 68% displayed a bimodal pattern (period 25.7, SD=0.5 hours) with two peaks during this time. The other 7% were arrhythmic in constant conditions. The rhythms of individual crustaceans are typically very imprecise and only when studied as groups is any semblance of accurate timing seen (Palmer & Williams 1986a). Research on individual rhythm patterns of H.crassa led to the postulation of a dual clock hypothesis to explain the different cyclic patterns (Palmer & Williams 1986b, 1987).

Beer (1959) found that H.crassa was most active, burrowing and feeding, when exposed at low tide, although Fielder and Jones (1978) observed some crabs feeding while covered at high tide. Also some crabs who had burrows above high tide fed normally at this time. However most crabs emerged from their burrows within 10 minutes of being uncovered. Sea lettuce, Ulva lactuca, left by the receding tide and blocking burrow entrances was cleared away either by grasping the alga with the chelae and dragging it away, or pushing it away against folded chelae. After clearing the entrance most crabs cleaned themselves at the burrow entrance by pumping water from their branchial chambers across and through the mouthparts. Crabs then began feeding on the mud surface either on bleached or decomposing Ulva or fine particulate organic matter from the surface mud. Small strips of Ulva were torn off by opposing action of the chelae and inserted into the mouth by one chela. On a few occasions other encrusting algae were torn from rocks. When feeding on mud, crabs walked slowly forwards away from the burrow with chelae held vertically in front of them and probing the sediment. After a period of searching the crab began to pick up small pinches of surface sediment and transfer them to the mouthparts. Useful material is taken into the gut and waste accumulates at the bottom of the mouth-frame which is periodically wiped by a chela. When feeding on drier deposits these pseudo-faeces form small pellets. H.crassa seldom forages more than 200mm from its burrow. Beer (1959) also reported that H.crassa eats large pieces of dead organic matter, the bodies of dead lugworms, pieces of ascidians, etc. Nye (1977) maintained crabs in the laboratory by feeding them pieces of Chione stutchburyi.

In mangrove swamps this mud crab climbs up the trees to about 1m and feeds upon the film of mud on branches and leaves (Cox 1976). Climbing activity is restricted to the period immediately after high tide while trees are still wet and may also occur prior to high tide while the trees are still partially submerged. They are capable of scrambling rapidly among the branches and will drop to the mud below when disturbed. H.crassa burrow in firm, sandy mud and some shelter beneath stones (Nye 1977). Burrowing of H.crassa is very evident around the banks of the Avon-Heathcote Estuary where sandy, clay banks are riddled with holes which greatly weaken the stability of the bank. In spite of the glaring evidence of their handiwork there is scarcely a crab to be seen, the crabs appear to retire to lower levels when the tide is out. Many of the burrows intercommunicate making the residents extremely difficult to unearth. Thompson

(1930) observed that burrows often contain an assortment of rubbish, straw and even feathers with at least some of this being carried in by the crabs themselves. The terminal part of a burrow often slopes downward, holding 20-50mm of water at low tide. Thompson also recorded burrowing behaviour in the laboratory and found that the crabs were most active at low light intensity. Initially, the propodi and dactyli of the last three pairs of legs are thrust into the substrate and a lump is pulled away two or three times. Next the crab sinks into the depression it has made, broadens it by pushing back and forwards and uses the last three pairs of legs to pull out lumps of substrate which are dragged out. As the hole is extended the chelipeds are used to grub out the hole and each piece of substrate is laboriously pushed up the tunnel and rolled clear of the mouth. Thompson tried rolling a small stone down into the burrow and found that it was repeatedly removed. The addition of water accelerated the burrowing process. Most burrows have a narrow neck and widen out below the surface. H.crassa probably has an important influence on cycling of matter in the estuarine ecosystem, through its burrowing activity. Residence time in burrows affects the rate of burrowing and amount of material moved. H.tridens in Japan has very short residence times (generally one day) but this may be related to burrow collapse caused by tidal action (Takeda & Kurihara 1987). Burrow residence times of H.crassa are unknown. McKillup & Butler (1979) have investigated burrowing by the Australian grapsid Helograpsus haswellianus and have shown that the density of burrows does not exceed the level at which the substrate collapses. Generally there were more holes than crabs but at high density 2 or more crabs were found in some holes.

H.crassa is territorial and defends a small area around the burrow from intruders and seldom moves more than 600mm from its burrow (Beer 1959). When a wandering crab draws near another's burrow the occupier rushes out, or if feeding, runs to take up a position at the burrow entrance. If the intruder continues to approach the resident adopts a threat posture. Chelipeds are raised and held with fingers open revealing a colour pattern which accentuates their size. Legs are extended, the body is raised as high as possible and the chelipeds are raised and flexed so that the external surfaces are directed towards and abut against those of the rival. The outcome of the encounter was usually decided in a short time and the chance of success in a fight seemed to be an inverse function of the distance from the burrow entrance. Real fights, resulting in injury, were rare. One H.crassa male was seen to seize another by a cheliped, lift it bodily in the air, and thrust it onto the ground on its back. In other contests limbs were lost or thrown off. Both male and female H.crassa behave similarly when defending a burrow against an intruder of either sex. Males seemed readier to fight than females. This is in contrast to Macrophthalmus hirtipes where only males are involved. Fights of H.crassa occurred commonly on warm, sunny days and peak periods seemed to coincide with peak mating periods. At these times H.crassa males wander far from their burrows, engaging in a series of fights or raids on other burrows even to the extent of digging out the end-plug of blocked burrows to provoke the owner into defending its territory. Most fights are punctuated by short pauses during which feeding movements are performed without true feeding. These may be an example of a displacement activity - an irrelevant movement performed to relieve the 'tension'.

Mating in H.crassa was observed from August to May inclusive, with peak periods in October and May (Beer 1959). Copulation occurs on the surface of the ground or partly covered by water with the male flat on his back and the female uppermost (Nye 1977). Both crabs were always in the hard condition. Copulation was not preceded by any male courtship. The crabs began facing each other, the male pulled the female towards him and shuffled her into position above him as he fell back. The mean duration of 7 incompletely observed matings was 13 minutes (range 5-38 minutes). Males usually mated with smaller females (Nye 1977). Other grapsid crabs usually mate when hard and in all known cases the female was above the male (Hartnoll 1969). Christy (1987) classifies male competition for mates in H.crassa as involving only neighbourhoods of dominance which affect encounter rates with females rather than involving defence of resources or receptive females.

H.crassa reacts to any unusual movement within 6-10m by retreating quickly to its burrow. At first sign of disturbance crabs stop feeding and stand motionless. Such alert behaviour can be communicated to a large number of feeding crabs which do not detect the source of disturbance. These crabs may also be warned by the take-cover movements of other crabs. Some H.crassa may take cover in the nearest available burrow whether occupied or not. On one occasion Beer (1959) watched 4 crabs emerge from the same burrow.

When H.crassa is crouched close to the ground and partially buried all appendages are folded close to the body and the crab assumes as small and as flat a form as possible. Eyestalks are folded against the carapace and chelipeds are folded against the mouthparts. But when the same crab adopts a threatening posture the ventral surface is exposed, with every part unfolded and extended and the crab looks as big and obvious as possible. The light-yellow chelipeds contrast strongly with the background and the eyestalks are raised to their full height. Thus H.crassa has one set of colour patterns that aid in concealment and another set which clearly make it conspicuous (Beer, 1959).

Ecology

In the Avon-Heathcote estuary Jones (1980) found that juvenile H.crassa (<4.1mm CW) formed approx. 20-40% of the population over 20 months with the main recruitment period from February to April. The frequency of different sized males showed no clearly repeatable pattern over the study, sometimes unimodal, sometimes bimodal with the modal class being anywhere from 6 to 14mm CW. Similarly there was no seasonal pattern among non-ovigerous females. Ovigerous females of <14.1mm CW were present throughout the breeding season whereas larger ovigerous females were only collected from November to January. During the breeding season less than 15% of females <9.1mm CW were ovigerous, 35-55% of females 9.1-15.0mm CW were ovigerous and only one larger female was found with eggs. Somewhat similar results were reported by Nye (1977) although the data presented are very limited and difficult to interpret and it would appear that the frequency of small crabs (<6.0mm CW) was underestimated.

In their latitudinal survey Jones & Simons (1983) found that population structure was generally similar at all sites in November/December, 1980. Each population had few large crabs (>14.0mm CW), a frequency distribution skewed in favour of juveniles and small crabs and an unbiased sex ratio. The proportion of small crabs (<6.0mm CW) and of ovigerous females in each population was not correlated with latitude, substratum or crab density. However, the size of the largest males and females was significant, increasing from low to high latitude. Crab size was not associated with density or substrate. Density varied from 468 to 1848 crabs per m^2. and decreased significantly with increasing latitude and sediment particle size.

These results suggest that there may be little similarity of population structure of H.crassa between years but at least some similarity between sites at the same time. Whatever factors are important might be having the same effect at all sites but varying over time.

Distribution of H.crassa in the Avon-Heathcote estuary does not appear to be limited by the effects of salinity but more by the availability of suitable substrate for burrowing (Jones 1976). H.crassa was the only crab which extended into the Avon and Heathcote rivers and was concentrated in well-drained compacted sediments above mid-tide level (Jones & Simons 1982). Thus H.crassa usually occurs higher on the shore than Macrophthalmus hirtipes (see also Stephenson 1970, Williams et al. 1985) and is exposed to the air for from 5-9 hours per tidal cycle. Both juvenile and mature H.crassa are euryhaline and eurythermal and had low mortality after 7 days in salinities of 3.5-52.5 ppt at temperatures of 5-30°C. Mortality was high in all salinities at 35°C and at all temperatures in 0.35 ppt (Jones 1981). Juveniles showed widest salinity tolerance at temperatures closest to field temperatures at time of collection and lower and higher temperatures reduced the salinity range in which maximal survival was possible. No consistent effect of temperature on salinity tolerance of mature crabs was apparent. Bedford (1972) found that blood ion concentration is strongly regulated in media from freshwater to 80% sea water above which blood is isosmotic. Above 110% the blood ion concentration is slightly hyposmotic. Calcium ion concentration is strongly regulated but magnesium and potassium show very little regulation. Rate of loss of sodium ions increases as salinity is reduced suggesting that H.crassa is very permeable. (See also Barnes 1967a for comparative data on Australian grapsoid crabs.) Respiration is also affected by reduced salinity (Shumway & Jones 1981). By contrast stage I zoeae hatched at 20°C were stenohaline with 100% mortality in 24 hours at salinities less than 15 ppt (Jones 1980). The combination of wide salinity-temperature tolerances and the refuge of a burrow during extreme conditions allow H.crassa to occupy the most dilute regions of an estuary. In regions of low salinity ovigerous females congregate at highest shore levels, ensuring that larvae are released into salinities within their limited tolerance range. In areas of high salinity and little variation there is no concentration of ovigerous females at highest shore levels (Nye 1977).

H.crassa and Macrophthalmus hirtipes commonly occur together with H.crassa living higher on the shore, sometimes in a semi-terrestrial environment. Hawkins & Jones (1982) have shown that both these species have the same gill formula (16) but H.crassa has a significantly smaller gill area because of a reduction in the area of individual gill platelets. Both species carry water in their gill chambers when they emerge from their burrows but in H.crassa water expelled from the exhalant openings flows across the setose area on both the pterygostome and lateral surface of the branchiostegite and re-enters the gill chamber. H.crassa lacks any of the accessory respiratory structures that facilitate uptake of atmospheric oxygen by certain other high-shore crabs. Thus H.crassa must frequently return to the burrow to replenish their recirculatory system. Rates of oxygen consumption are consistently higher in semiterrestrial compared to aquatic brachyurans and Hawkins, Jones & Marsden (1982) found that H.crassa consumed more oxygen in both air and sea water than did M.hirtipes, thus confirming this pattern. In addition H.crassa was better able to utilize atmospheric oxygen. The burrow and respiratory adaptations enable this crab to live higher on the shore than M.hirtipes.

Beer (1959) reported unspecified predators catching this crab 'on numerous occasions' and suggested that kingfishers, herons, gulls and fish may be predators. Thompson(1930) observed gulls (Larus spp.) and kingfishers (Halcyon sancta) eating H.crassa from the Avon-Heathcote Estuary. Later Webb (1966, 1973a, 1973b) found that this crab was eaten by sand flounder (Rhombosolea plebia, see also Mundy 1968 and Kilner 1974), yellow-belly flounder (R.leporina), pufferfish (Contusus richei), and short-finned eel (Anguilla australis). H.crassa in the Ahuriri Estuary, near Napier are preyed upon by short-finned eels, long finned eels (A.dieffenbachi), yellow-bellied flounder, river flounder (R.retiaria), yellow-eyed mullet (Aldrichetta forsteri) and kahawai (Arripis trutta). Graham (1939) recorded H.crassa from stomachs of rig (Mustelus lenticulatus), red cod (Pseudophycis bacchus), rock cod (Lotella rachinus), sea perch (Helicolenus papillosus) and red gurnard (Chelidonichthys kumu) from Otago Harbour. Habib (1975) sometimes found large quantities (0.3-25% of gut volume) of this crab in red cod from Banks Peninsula and also in red cod from off Otago Peninsula. Davenport (1979) found that parore (Girella tricuspidata) commonly ate this crab in Whangateau Harbour. One fish (325mm SL) had 79 crabs in its gut! King & Clark(1984) also found that rig in Golden Bay ate small quantities of H.crassa, while in rig from Wellington it formed a major component of their diet. It is also readily eaten by Octopus maorum in the laboratory (Pack 1982).

Lichtwardt & Williams (1987) examined the resident gut mycoflora of several intertidal crabs and found that Taeniella carcini (Order Ekcrinales) was present in H.crassa from the Avon-Heathcote estuary. Lichtwardt (1986) summarized the biology of these hindgut fungi which seem to be commensalistic while Mattson (1988) found that the occurrence and abundance of these fungi was best explained by the feeding habits of the crab, those with fungi being herbivorous and/or detritivorous.

References

Annala et al. (1980), Barnes (1967a), Bedford (1972), Beer (1959), Campbell & Griffin (1966), Cox (1976), Fielder & Jones (1978), Graham (1939), Griffin (1971), Hartnoll (1969), Hawkins & Jones (1982), Hawkins, Jones & Marsden (1982), Jones (1976, 1980, 1981), Jones & Simons (1982, 1983), Kilner (1974), King & Clark (1984), Lichwardt & Williams (1987), Miers (1886), Mundy (1968), Nye (1977), Palmer & Williams (1986a,1986b,1987), Roper,Simons & Jones (1983), Shumway & Jones (1981), Stephenson (1970), Thompson (1930), Wear (1970a), Wear & Fielder (1985), Webb (1966,1973a, 1973b), Williams et al. (1985).

Cyclograpsus insularum Campbell and Griffin, 1966
Northern Smooth Shore Crab

Synonymy

Epigrapsus politus Lenz, 1901; Cyclograpsus lavauxi Chilton, 1910; Cyclograpsus whitei Chilton & Bennett, 1929; Dell, 1963a; Bennett, 1964; Cyclograpsus insularum Campbell & Griffin, 1966; Dell & Marshall, 1967; Dell, 1968a; Bacon, 1971b; Wear & Fielder, 1985.

Type Locality

Under basalt boulders on surf beach, Little Slope, Lord Howe Is.

Distribution

Lord Howe Is., Norfolk Is., Kermadec Islands, New Zealand. Within New Zealand North Cape to East Cape.

Diagnosis (Fig. 65a-e)

Carapace wider than long (ratio 1.2), flattened, surface very smooth, microscopically punctate, sometimes granulate laterally. A very faint granulate rim extends around lateral and frontal margins. Gastric and cardiac regions not defined, gastrocardiac groove shallow. Frontal groove absent, margin straight, curving abruptly downwards at right angles to rest of carapace, in anterior view frontal border is characterized by deep indentations for first antennae on either side of notched median ventral extension. Orbits very small, less than half frontal width, with outer angle not projecting, sub-orbital crest consisting of some 15 tubercles, largest beneath orbit, decreasing in size laterally. Eyes very small. Antero-lateral border strongly convex, usually twice microscopically interrupted by shallow grooves of which the more posterior is less distinct, sometimes absent. Postero-lateral margins almost straight, posterior margin straight. Cheliped carpus smooth, rounded, inner angle projecting sharply in smaller specimens but rounded in large specimens. Propodus devoid of granules or ridges, dentition of male fingers low, sometimes obsolete, dentition of female fingers distinct, regularly serrate. Legs robust, segments swollen. Second legs longest (a little more than 1.5 times CW), merus finely granulate especially on anterior and posterior borders, fourth legs shortest, all legs naked except for rows of sparse tufting on dactyli and scattered long bristles on posterior margins of propodi. Last leg with propodus little longer than broad, dactyl as long as propodus, twice as long as broad. No tufts of hair between bases of walking legs. Sternum hirsute between tip of abdomen and base of maxillipeds, hairs tending to form transverse parallel rows. Male abdomen evenly tapering from proximal border of third segment to distal quarter of sixth segment, then sharply incurving to the telson which is paraboloid, almost as long as broad.

Colour

Colour of carapace is always graded, without speckling or spots, the anterior half tends to be brown or purple grading into paler brown, with hints of grey or purple towards the back. Large specimens occasionally fawn coloured.

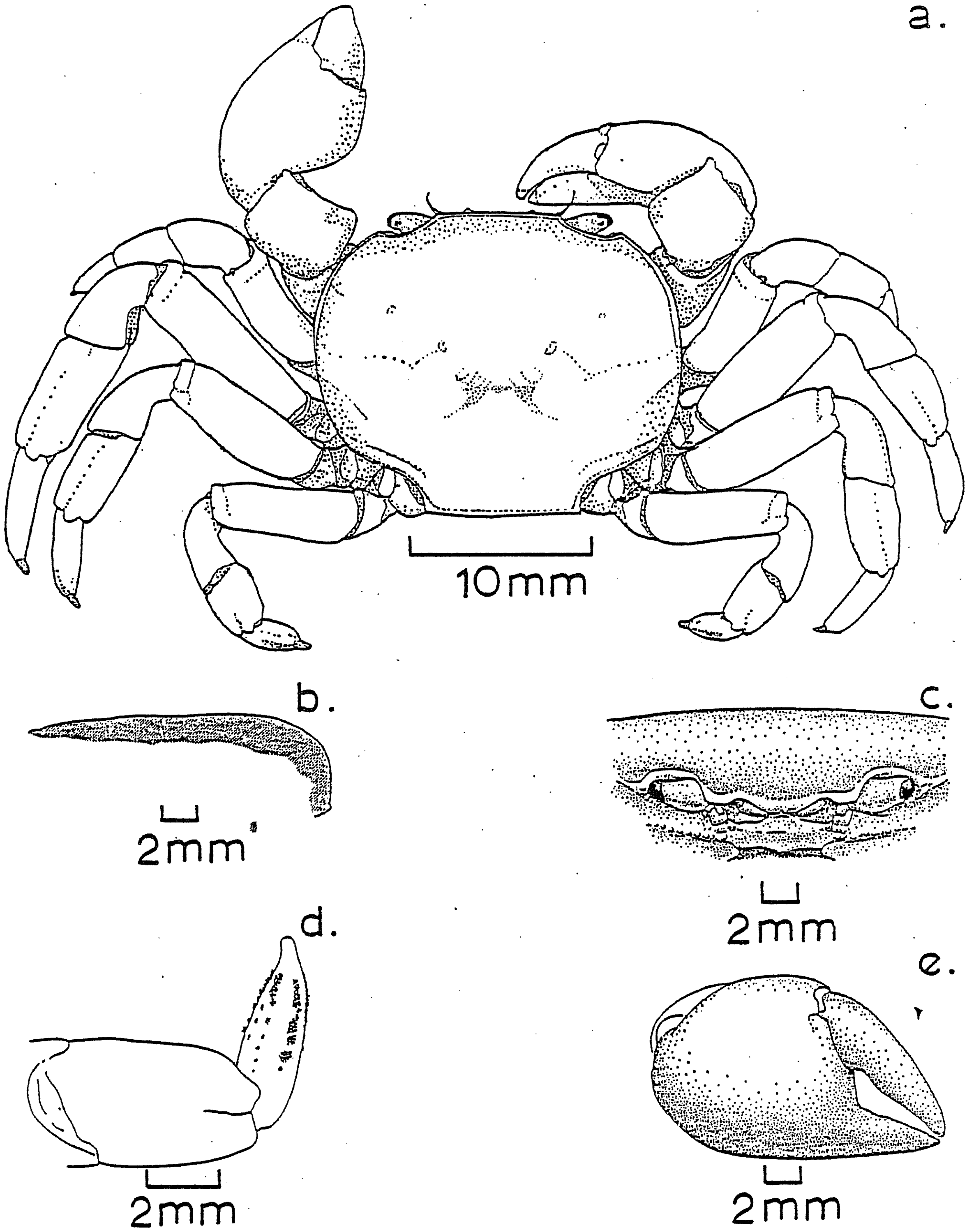


Fig. 65 - Cyclograpsus insularum: a - male, dorsal view (by J. Black); b - median longitudinal section of carapace; c - carapace, frontal view; d - right 1st walking leg, anterior view; e - right chela, male, outer face (after Campbell & Griffin, 1966).

Size

Male 22mm CW, female 18mm CW.

Habitat

Under boulders high on beaches (below EHWN) of open coasts where direct wave force is broken by offshore islands or extensive reefs, on substrates of smaller sand and silt content than C.lavauxi with which it overlaps.

Depth

EHWN down to mid-tide level.

Breeding

Ovigerous females have been collected at Whakatane in late August and September (Wear 1970a, Dell & Marshall 1967). Further north ovigerous females have been collected at Ti Point, Leigh in early June and from Bream Head and Taiharuru in July (Bacon 1971b). Considering the stages of egg development these records suggest that ovigerous females only occur for about 9 weeks at Whakatane (late August - late October) and probably only one brood is produced each season since spent females showed no sign of regenerating ovaries. Eggs freshly laid are larger than those of C.lauvaxi, measure 0.45 x 0.44mm and are dark purple. Eggs ready to hatch are 0.5 x 0.48mm and are coloured black by strong larval chromatophores and eyespots. Incubation period for the eggs is at least 7 weeks.

Development and Growth

Probably 5 zoeal stages, heavily pigmented (Wear & Fielder 1985). The pre-zoea, which lasts only about 15 minutes, and first stage zoea have been described by Wear (1970a). The megalopa is unknown.

Behaviour

Although C.insularum has a sub-orbital 'stridulatory' ridge of some 15 tubercles, it is not known whether this species is capable of sound production as has been suggested for C.lauvaxi (Bennett 1964).

Ecology

Although C.insularum had rarely been reported from New Zealand, Bacon (1971b) found that it was widespread in northern New Zealand and at one locality (Lady Alice Island, Hen and Chickens group) reached densities of $1000m^2$. Near Whakatane densities of $30\text{-}40m^2$ were common. Until recently C.insularum has been commonly confused with C.lavauxi.

References

Bacon (1971b), Bennett (1964), Campbell & Griffin (1966), Chilton (1910), Chilton & Bennett (1929), Dell (1963a,1968a), Dell & Marshall (1967), Wear (1970a), Wear & Fielder (1985).

Cyclograpsus lavauxi Milne Edwards, 1853
Smooth Shore Crab

Synonymy

Cyclograpsus audouinii Dana, 1852; *Cyclograpsus lavauxi* H. Milne Edwards, 1853; *Cyclograpsus whitei* H. Milne Edwards, 1853; *Cyclograpsus lavauxi* Miers, 1876b; Filhol, 1886; *Cyclograpsus whitei* Filhol, 1886; *Cyclograpsus lavauxi* Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Richardson, 1949a; Trevarthen & Kulka, 1950; Trevarthen, 1951; *Cyclograpsus chavauxi* Batham, 1956; 1958; *Cyclograpsus lavauxi* Dell, 1963a; Bennett, 1964; Campbell & Griffin, 1966; Dell, 1968a; Griffin, 1968c; Bacon, 1971b; Hayward, 1974; Marsden & Fenwick, 1978; Knox & Bolton, 1978; Marsden, 1981; Wear & Fielder, 1985.

Type Locality

New Zealand.

Distribution

New Zealand and Juan Fernandez, Chile. Within New Zealand Hohoura Harbour to Otago Peninsula, Dunedin, Hokianga Harbour to Westland.

Diagnosis (Fig. 66a-c)

Carapace wider than long (ratio 1.2-1.3), surface smooth or very weakly granular anterolaterally and close to frontal margin, a microscopically granular elevated ridge extending around margins. Regions poorly defined, gastrocardiac groove prominent which may be extended towards the lateral margin, midway between orbital margin and gastrocardiac groove is a shallow punctelation. Front well deflexed, barely visible in dorsal view, convex to weakly bilobate, median frontal groove prominent. Ratio of length of frontal margin to CW is 0.4. Orbits uniformly concave to subquadrate, junction with front sharp, posterior border transverse to sloping obliquely posterolaterally, outer angle a sharp tooth. Sub-orbital ridge strongly granular, granules 10-17 in number, usually 13-15, irregular in size. Antero-lateral margin convex, not interrupted by shallow grooves, postero-lateral margins sub-parallel, posterior margin straight. Cheliped merus borders minutely granulate, carpus smooth except for a minutely granular area at dorsomedial angle which is strongly produced. Propodus outer surface smooth, convex, upper and lower borders sub-parallel. Upper border convex, lower border slightly concave near the base of the finger. Inner face of propodus with a strongly granular, longitudinal medial ridge. Fingers gaping basally, dactyl curved strongly downward, dentition weak and uniform. Walking legs long, moderately robust, segments laterally compressed, second leg longest, first and third about equal and fourth leg shortest. Surfaces smooth, propodi dorsally felted, dactyli long and slender. Moderately long tufts of hair arising from between bases of first and second, and second and third legs, absent from between third and fourth. Anterior two segments of sternum very sparsely pubescent, second segment almost naked. Third segment of male abdomen convex laterally or with edges almost straight and widening slightly distally to just short of distal edge. Last segment much narrower than penultimate segment, wide basally, distally rounded.

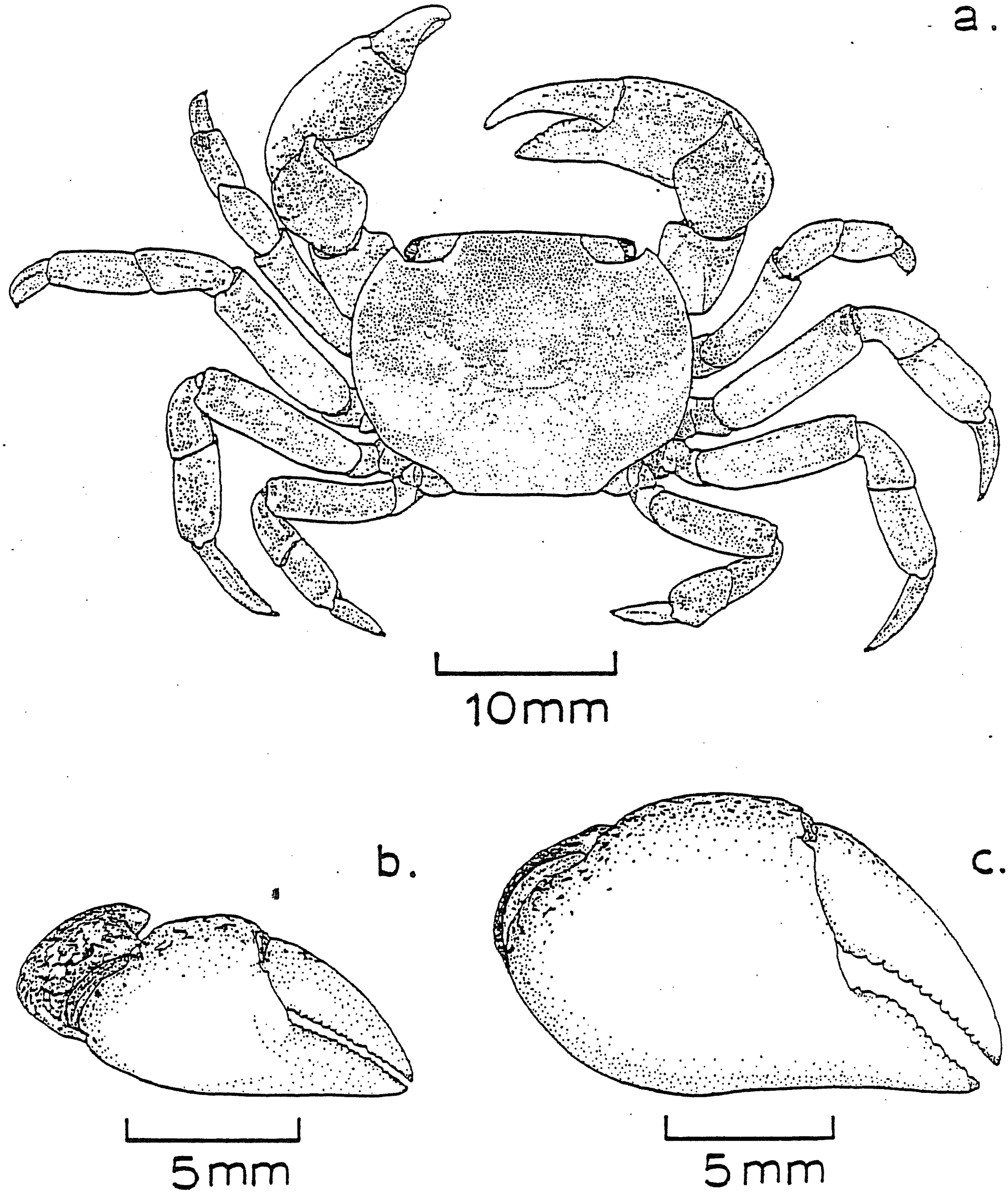


Fig. 66 - *Cyclograpsus lavauxi*: a - male, dorsal view; b - right chela, female, outer face; c - right chela, male, outer face (by J. Black).

Colour

Distinctly speckled in dark reddish-brown on a background varying through slate blue, bluish grey, fawn to yellowish brown. Legs with similar irregular mottling dorsally, ventral surface of legs and carapace, both outer and inner surfaces of chelae, pale.

Size

Male 28mm CW. Female 26mm CW (smallest ovigerous female 11.2mm).

Habitat

Upper half of the intertidal area, under stones on boulder beaches ranging from open, wave-exposed coasts to sheltered harbours. C.lavauxi is the most 'terrestrial' of New Zealand's crabs. This small crab usually outnumbers the larger H.edwardsi which lives lower on the shore.

Depth

At or about high tide level. Overlaps with C.insularum but zone of maximum density is higher on the shore.

Breeding

A pair were recorded near Godley Heads in copula in November 1927 by Chilton & Bennett (1929). As in C.punctatus (Broekhuysen 1941) and C.integer (Hartnoll 1965), mating probably involves hard-shell females and males. Ovigerous female C.lavauxi were found at Whakatane in December (Dell & Marshall 1967) and at Wellington from September to January but the peak of the breeding season extends from mid-October to late December. At Kaikoura females carrying eggs ready to hatch have been found in February. Eggs freshly laid are 0.32 x 0.31mm and are dark purple, becoming paler as development proceeds. Eggs ready to hatch are 0.38 x 0.35mm and are transparent with strong black eyespots (Wear 1970a). Egg size is very similar to C.integer (Hartnoll 1965). Thomson and Anderton (1921) reported that eggs hatch in December and January in Otago Harbour. With most crabs living high on the shore it seems likely that they will have a hatching rhythm which synchronizes larval release with spring tides.

Breeding and moulting of C.granulosus from Tasmania have been studied by Griffin (1969b). He found that in this species females are ovigerous from July to February, a similar length of time to C.lavauxi. Large female C.granulosus become ovigerous earlier than smaller ones and finish breeding later and may possibly breed twice each season. Moulting in adults occurs at the end of the breeding season and again prior to the next season for small adults. The post-breeding moult of males precedes that of females in the first four months of the year. In South Africa Broekhuysen (1941) found that ovigerous, female C.punctatus were present in all months except March-May but there were two main breeding periods with the main one from May-September and a minor period in January-February. Data on male gonad development suggests that mating occurs (between hard-shell crabs) one or more months prior to egg laying. During the breeding season new eggs tend to be produced in groups about 6-7 weeks apart but it is unclear whether these are produced by the same females or by different females commencing breeding at different times. Eggs are incubated for approx. 2 months. Examination of females carrying eggs showed that the majority had inactive gonads but a few had developing or nearly ripe gonads. It may be that a minority of females produce more than one clutch of eggs per breeding season. A similar situation was recorded by Hartnoll (1965) for C.integer from Jamaica. Although Wear (1970a) found that the ovaries of C.lavauxi females showed no sign of regeneration (suggesting that only one brood was produced per year), it is unclear how many females were examined. It may be that a few females are able to produce a second brood. The smallest female C.punctatus carrying eggs was only 6mm CW. This is similar to C.integer where females mature at about 7mm CW (Hartnoll 1965).

Begg (1980) found that the sex ratio in a population of C.lavauxi near Portobello was 1.37 females/male over the period December-August. In South Africa Broekhuysen (1941) also found more females than males (1.22:1) for C.punctatus. Development & Growth

Five zoeal stages described by Wear & Fielder (1985). The pre-zoea cuticle is moulted within 5 to 15 minutes of hatching and the first stage zoea has been described by Wear (1970a). The megalopa is unknown. Larvae are common in inshore plankton samples taken in spring and summer especially off stony beaches.

Moulting of C.lavauxi adult males and females seems to occur mainly from February to April, following the breeding season (Begg 1980), similar to C.granulosus (Griffin 1968b). In C.punctatus moulting usually occurs at night and crabs need access to both air and water to complete the process (Broekhuysen 1941). The new exoskeleton hardens in 1-2 days in small crabs but takes 6-7 days in large crabs. Percentage increase at each moult is reasonably constant (17-20%) up to 12mm CW for females and 15mm CW for males, but thereafter it declined to 5-6% at 25mm CW. Both males and females grow to a maximum size of around 33-34mm CW. The population was dominated by crabs of 8-19mm CW and continued growth and mortality produced a population structure which showed little variation from month to month. Intermoult intervals increased from around 26 days (5mm CW) to around 190 days (24-25mm CW). Crabs kept in the laboratory grew from 5-6mm to 19-20mm CW in 17-18 months. Thus most crabs in the population are in their first or second years. Large crabs may live up to 5 years but most die by the age of 2-3 years. More males than females reach the maximum age. In female C.integer there is no pubertal moult (Hartnoll 1965).

Behaviour

C.lavauxi is usually found under stones and has a curious habitat of using the last pair of legs to grasp stones. These legs are almost sub-dorsal in position and the crab backs up against a stone with these legs spread widely and the dactyls grasping the stone. The weight of the crab is supported by the other legs which hold the body well clear of the substrate. This may aid mobility and stabilize the crab against the effects of wave action. This is very similar to the behaviour of the xanthid crab, Ozius truncatus, which, in northern New Zealand, lives on the same shores as C.lavauxi although at a lower level. Ozius always uses this kind of behaviour during feeding.

When cornered C.lavauxi exhibits a striking aggressive posture when prodded (Campbell 1967). One or both chelipeds are raised, emphasizing their size and displaying the whiteness of the cheliped. Similar behaviour is seen in C.punctatus from South Africa (Alexander & Ewer 1969).

Although C.lavauxi is normally an algal-eater, when presented with a piece of mussel in the laboratory it is grasped by one cheliped and conveyed to the mouthparts which hold it while the chelipeds are pushed outwards, tearing the flesh. Sometimes a lateral tearing movement employing both chelipeds is used before food is transferred to the mouth. Feeding occurs both underwater and in air.

Three main body postures are observed:

1) 'flat', body horizontal, chelipeds folded and resting on ground, walking legs close to ground and parallel with it,
2) 'raised', body at an angle (up to 45°), hind part still on ground, chelipeds still folded and resting on ground, legs flat or flexed mid-way,
3) 'tip-toe', body horizontal or angled, lifted off ground, chelipeds still folded but held off the ground, walking legs extended with only dactyls touching the ground (Campbell 1967).

Chelipeds as well as legs are used to push stones away from the body, although it is unclear whether this is involved in foraging or burying. At Island Bay, Wellington, Pellegrino (1984) found that C.lavauxi dug cylindrical burrows 20-40mm deep under sheltering rocks. Often 3 or 4 crabs were found together. Alexander & Ewer (1969) describe the burrowing behaviour of C.punctatus from South Africa. Campbell (1967) monitored activity of C.lavauxi and found greatest activity during the hours of darkness and that activity was greatly reduced under constant bright light. This was confirmed by Begg (1980) who found a strong circadian influence on activity in summer, which is not too surprising considering that C.lavauxi spends a great deal of time out of the water and is adapted to live in the supralittoral fringe. Thus there is a single peak of activity every 24 hours, but in winter crabs were almost arrhythmic. Campbell also found a much higher level of activity when crabs were kept under water although the pattern of activity was still similar. Evidence from a study of gut contents also suggests that foraging activity may be related to ebb and flow of the tide.

Chilton & Bennett (1929) reported that the presence of C.lavauxi could be detected by 'clicking sounds' emanating from beneath boulders, sounding almost like 'distant artillery'! The paddle crab Ovalipes catharus and is the only New Zealand crab that is known to produce audible sounds. Bennett (1964) drew attention to the presence of the sub-orbital stridulatory ridge and the granulated ridge on the inner surface of the chela propodus although he believed that the propodal ridge did not act as the plectrum. Instead he claimed that the inner distal margin of the merus and the inner proximal upper margin of the carpus, and also the upper part of the inner distal surface of the propodus could be drawn across the ridge. However the merus does not seem to be long enough to engage the stridulatory ridge and there are no sharp edges on the upper part of the propodus. If this crab can produce sound the most likely structure is the inner margin of the carpus which in addition to engaging the stridulatory ridge, may also be able to rub against the antero-lateral border of the carapace. A simple explanation of Chilton & Bennet's observation may be that the sounds were produced by small gastropods (e.g. Melagraphia) being dislodged and falling among the boulders! Stridulatory ridges are also present in C.insularum, Hemigrapsus crenulatus and H.edwardsi but it is unknown whether these crabs are capable of sound production.

Ecology

Despite being very accessible for study, virtually nothing is known about the population ecology and feeding of C.lavauxi. At Kaikoura this crab eats a variety of seaweeds (Carpophyllum maschalocarpum, Glossophora kunthi, Halopteris paniculata, Hormosira banksi, Pterocladia sp. and Gracilaria sp.) foraging mainly at night (R.Dewa pers. comm.). C.lavauxi feeds on both drift and resident algae. In South Africa C.punctatus consumes the salt marsh plant Arthrocnemum pillansii as well as the alga Gracilosia sp. and some animal material (isopods, polychaetes) (Alexander & Ewer 1969). They also describe the gastric mill of this crab which has strongly developed teeth. In the Avon Heathcote Estuary Cyclograpsus lavauxi formed 15.8% of the total number of crabs collected, occurring under stones at high tide level, being absent from many areas because of the lack of suitable hard substrates (Jones, 1976). Bacon (1971b) recorded densities of over 30 per m^2 near Whakatane.

C.lavauxi is a semi-terrestrial crab and is often exposed to the air for long periods. Shanks (1982) found that small crabs from Governors Bay lost water faster than large crabs and that desiccation may set the upper limit of distribution. Lethal percentage water loss (LPWL) values are within the range 25-30% for both Governors Bay crabs (Shanks 1982) and crabs from Otago Harbour (Begg 1980). The time to reach LPWL at 70-80% relative humidity was 29.5 hours for small crabs and 42.4 hours for large crabs. Begg (1980) found that no small C.lavauxi were present at the top of the shore in summer but in winter all sizes were present (see also Pellegrino 1984). C.lavauxi is better adapted than Hemigrapsus edwardsi and Petrolisthes elongatus to tolerate aerial conditions having a lower rate of water loss and higher LPWL (Begg 1980, Shanks 1982, Pellegrino 1984). This is typical of semi-terrestrial crabs which have lower permeabilities than aquatic crabs (Herreid 1969).

When exposed to the air water was lost preferentially from the extracellular compartment and sodium and potassium ions were removed from the haemolymph to maintain osmotic equilibrium between intracellular and extracellular compartments. With increasing loss of body water the osmotic concentration of the haemolymph increased (Shanks 1982). Leader & Bedford (1978b) examined the composition of muscle and haemolymph of C.lavauxi and found that ion concentrations were similar to other crabs from the same habitat.

In the field crabs often rest on damp substrates and conserve branchial water by recirculation but in dry weather some are found to have air-filled branchial chambers (Innes et al. 1986). Fully hydrated C.lavauxi were found to have 62.3% of body weight made up of water but Shanks (1982) recorded 66% for crabs from Governors Bay. On warm, windy days emersed crabs undergo desiccation losing more than 17.5% of body water but they can tolerate comparatively large losses of body water (up to 36%). They found that desiccation had no significant effect on oxygen consumption even when up to 24% of body water had been lost. Resting rates of oxygen consumption were similar in air and water and the animals maintained a relatively high metabolic scope in both air and water. Aerobic scope is not reduced by desiccation. Waldron et al. (1986) investigated the effects of emersion and exercise on acid-base regulation in C.lavauxi. Concentration of oxygen is much higher (30%) in air than in water and conseqently ventilation rates in air-breathing crustaceans may be up to 4 times lower than in water. This can produce an elevation in blood carbon dioxide and affect the acid-base balance (respiratory acidosis). In C.lavauxi compensation may involve mobilization of calcium carbonate from within the animal. After 24 and 48 hours emersion blood pH returned to pre-emersion levels. Waldron et al. (1986) found that C.lavauxi exhibits characteristics of both terrestrial and aquatic decapods in its regulation of haemolymph acid-base status. Compensation mechanisms can restore pH to normal during aerial exposure but water is required for an efficient regulation after exercise. The quiescence of crabs under boulders during tidal emersion may be a partial consequence of this problem.

Thomson & Anderton (1921) recorded this crab from the stomachs of rig (Mustelus lenticulatus) and red cod (Pseudophycis bacchus) from Otago Harbour and Graham (1939) recorded it as being eaten by 6 other species of fish, but not from red cod. None of these predation records may be reliable because it is difficult to see how these fish could capture crabs which live so high in the intertidal zone. Habib (1975) found small quantities (0.2-0.3% of gut volume) of C.lavauxi in red cod from Lyttelton Harbour in May and July.

References

Alexander & Ewer (1969), Bacon (1971b), Begg (1980), Bennett (1964), Broekhuysen (1941), Campbell & Griffin (1966), Chilton & Bennett (1929), Dell (1963a, 1968a), Dell & Marshall (1967), Edmondson (1959), Gore & Scotto (1982), Graham (1939), Griffin (1968c,1969b,1971), Hartnoll (1965), Hiatt (1948), Miers (1876b), Pellegrino (1984), Shanks (1982), Innes, Forster, Jones, Marsden & Taylor (1986), Schaefer (1970), Thomson & Anderton (1921), Tweedie (1954), Waldron (1984), Waldron, Taylor & Forster (1986), Wear (1970a), Wear & Fielder (1985).

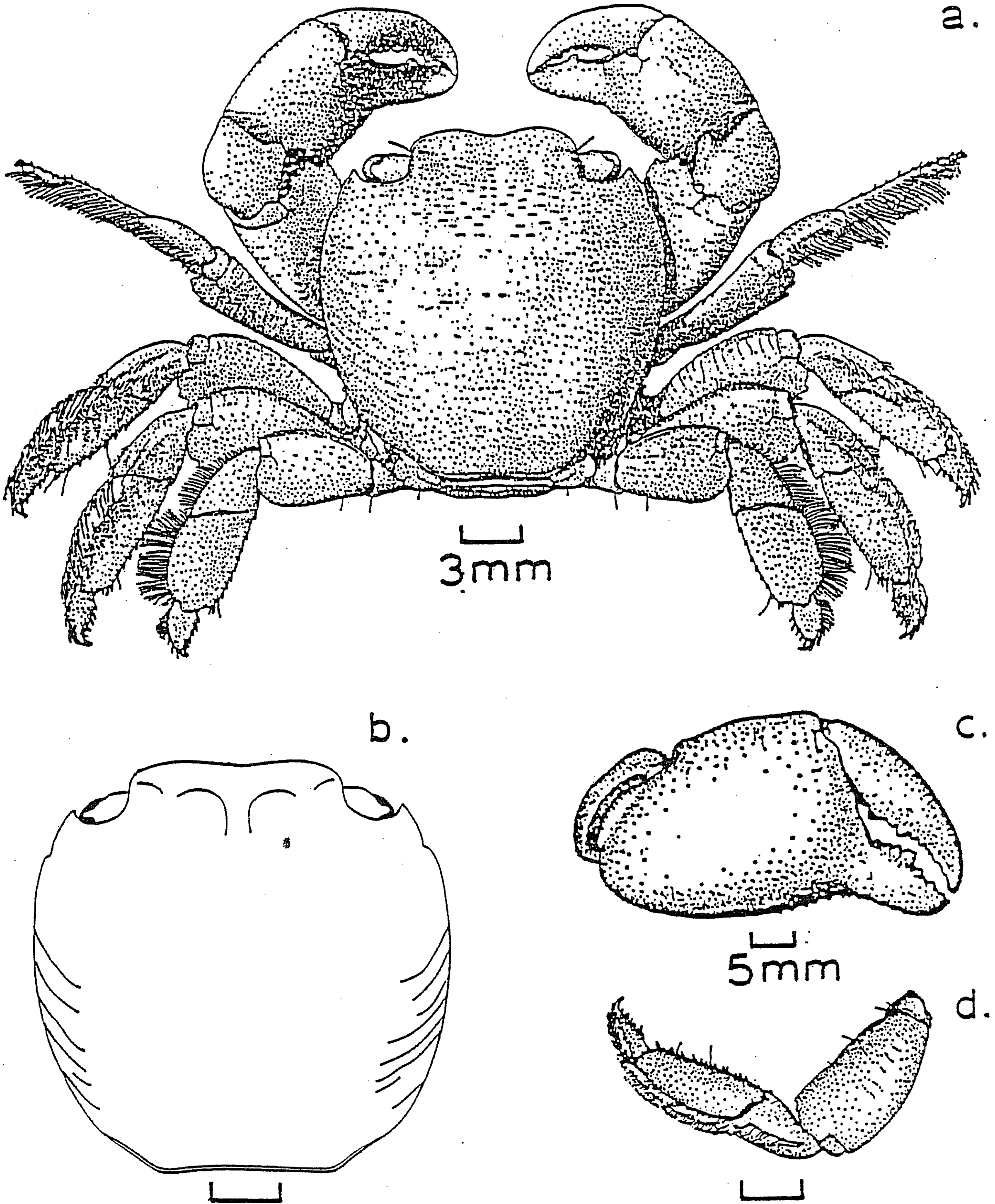


Fig. 67 - Planes cyaneus: a - male, dorsal view; b - carapace outline, dorsal view; c - right chela, male, outer face; d - right 2nd walking leg, male (after Chace, 1951).

subterminal tooth and a few posterior denticles which diminish in strength from first to last pair. Male abdomen narrowed beyond third segment, length of four distal segments about 1.26 times basal width of fourth segment. Terminal segment laterally convex, about 0.9 as long as basal width.

Colour

P.cyaneus has variable and protective colouration recorded as blue, bluish grey mottled with brown, yellowish clouded with brown and reddish brown. It is likely that *P.cyaneus* is capable of colour change in a similar manner to *P.minutus* (Hitchcock, 1941). Chromatophores of *P.minutus* are responsive to white, black, red, blue, yellow and green backgrounds but there is no immediate change in the general colour because of the extracellular pigment in the hypodermis and exoskeleton. Hitchcock suggests that colour can be changed only at the time of moulting and any crab that moves to a differently coloured background subsequent to hardening of the shell would cease to be protectively coloured.

Size

25mm CL. Ovigerous females 8.7 - 22.5mm CL (Garth 1957), 14.2 - 16.9mm CL (Chace 1966). Largest female 26mm CL.

Habitat

Oceanic, occasionally washed ashore attached to floating weed, flotsam and pieces of pumice. Also found clinging to turtles.

Depth

Surface of the ocean.

Breeding

Chace (1951) records ovigerous females off Baja California and Galapagos Islands in April and August. At St.Helena ovigerous females have been collected in February (Chace 1966). Ovigerous crabs do not seem to have been recorded from New Zealand.

Development and Growth

Muraoka (1973) has described the megalopa from *Sargassum* weed and floating timber in Sagami Bay, Japan (see Wear & Fielder 1985). Zoeal stages are unknown. Chace (1951) has examined some aspects of relative growth. Carapace width-length ratio remains fairly constant but legs become relatively shorter in larger crabs.

Behaviour

The normal habit of *P.cyaneus* is to cling to floating material on the surface of the ocean. Little is known about swimming ability or any other aspect of its behaviour.

Ecology

Crane (1937) examined stomach contents of a large ovigerous female taken from the tail of a green turtle and found that it contained finely digested animal matter that might have been excrement of the turtle.

References

Bennett (1964), Chace (1951,1966), Crane (1937), Chilton & Bennett (1929), Dell (1963a,1968a), Hitchcock (1941), Miers (1876b), Richardson & Morton (1948), Wear & Fielder (1985).

Planes marinus Rathbun, 1914

Synonymy

Planes marinus Rathbun, 1914; 1918a; Pachygrapsus marinus Chace, 1951; Edmondson, 1959; Dell, 1963c; 1964a; Planes marinus Chace, 1966; Dell, 1968a; Wear & Fielder, 1985.

Type Locality

West of Lower California, 23°49′N, 127°50′W.

Distribution

Indo-Pacific, Japan, west coast of North America, Australia, New Zealand and South Atlantic, St.Helena. Within New Zealand Kermadec Islands, Bay of Plenty to Cook Strait, Chatham Islands. The distribution of this oceanic crab is dependent upon the prevalence of flotsam or of floating or swimming organisms to which crabs may cling.

Diagnosis (Fig. 68a-d)

Carapace distinctly wider than long (ratio 1.07-1.16), subquadrate, convex antero-posteriorly and from side to side. Surface covered with punctae and fine reticulations, coarser striae cross the anterior half transversely and nearly all the branchial region obliquely. Frontal margin faintly bi-lobed, edge a raised finely granulated rim, frontal width slightly more than half CW. Orbits deeply set, almost a right angle, post-orbital corner produced as a distinct tooth, eyestalks short and fat. Antero-lateral margin convex with a blunt tooth behind the post-orbital tooth, postero-lateral margins nearly straight, convergent. Posterior margin short and almost straight. Chelipeds equal, massive, upper and lower margins of merus transversely striated, inner border irregularly denticulated. Outer surface of carpus finely striated, tooth at inner angle blunt. Surface of propodus nearly smooth, upper surface rounded, few inconspicuous granules near the lower margin. Fingers stout, not noticeably bent downward, prehensile edges narrowly gaping, irregularly dentate for their whole length. Legs short and stout, not noticeably flattened, dactyls short and stumpy, armed with coarse spines. Hairs on upper anterior margin of propodus of the first three pairs of legs are stout forming a dense growth without a natatory fringe. Proportion of length of three distal segments of second pair to CL ranges from 0.77 to 0.99. Male abdomen broadly triangular, length of four distal segments about 1.08 times basal width of fourth segment. Terminal segment broadly triangular, about 0.9 as long as basal width.

Colour

Dark reddish brown.

Size

20.8mm CW, 19mm CL. Ovigerous females 13.4-15.1mm CL (Chace 1966).

Habitat

Oceanic, occasionally washed ashore attached to floating weed and flotsam (fishing floats and mines), among goose-necked barnacles (Lepas spp.).

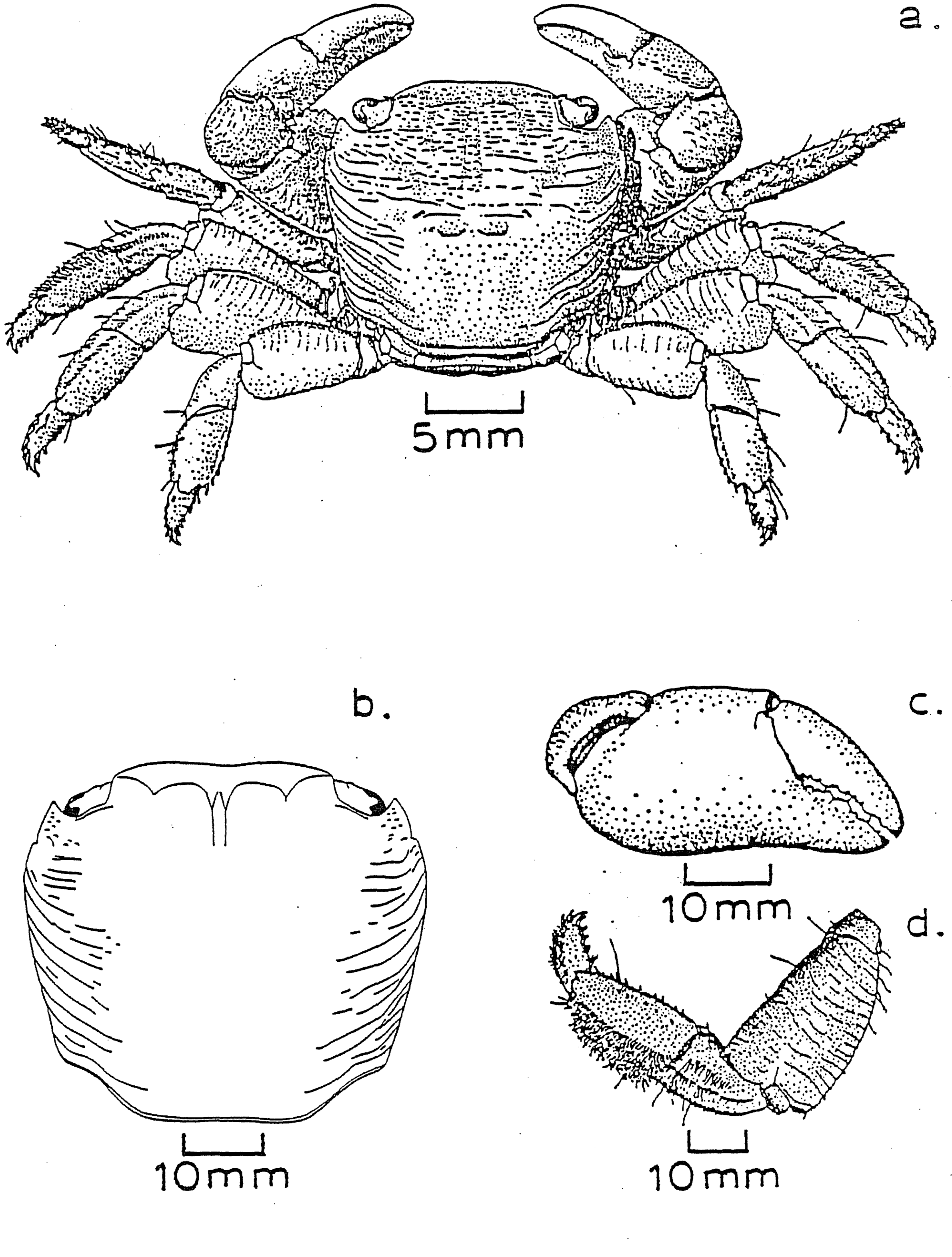


Fig. 68. Planes marinus: a - male, dorsal view; b - carapace outline, dorsal view; c - right chela, male, outer face; d - right 2nd walking leg, male (after Chace, 1951).

Depth

Surface of the ocean.

Breeding

Wear (1970a) recorded 27 ovigerous females with eggs in all stages of development, 3 males and numerous juvenile crabs on a rope and barnacle-covered glass fishing float washed up at Lyall Bay, Wellington in February 1965. Also Dell (1963c) found a similar float at Omaio Bay, Eastern Bay of Plenty carrying 18 males, and 8 females (2 ovigerous) in March 1962. Bennett (1964) reported 11 males and 9 females (1 ovigerous) collected from the Chatham Islands (incorrectly identified as *P.minutus*). The paucity of records for *P.marinus* makes it difficult to estimate the length of the breeding season. *P.marinus* may breed all year round as recorded for *P.minutus* by Lebour (1944).

Eggs freshly laid are dark brownish-purple and measure 0.3 x 0.29mm while mature eggs are 0.42 x 0.39mm with the remaining yolk coloured light brown. Incubation period is about 6 weeks and females lay more than one batch of eggs each breeding season. Wear (1970) found that females which shed their larvae all deposited a further batch of eggs within 12 hours.

Development and Growth

There are probably 5 zoeal stages (Wear & Fielder 1985). The megalopa is unknown. Wear (1970a) has described the pre-zoea, which lasts 15-20 minutes, and first stage zoea larva. Chace (1951) has examined some aspects of relative growth. Carapace width-length ratio remains fairly constant but legs become relatively shorter in larger crabs, as in *P.cyaneus*.

Behaviour, Ecology

Unknown.

References

Bennett (1964), Chace (1951, 1966), Dell (1963c, 1964a, 1968a), Edmondson (1959), Lebour (1944), Rathbun (1918a), Wear (1970a), Wear & Fielder (1985).

Pinnotheres atrinocola Page, 1983
Horse Mussel Pea Crab

Synonymy

Pinnotheres novaezelandiae Filhol, 1885d; Chilton, 1911a; Scott, 1961 (part); Bennett, 1964 (part); *Pinnotheres schauinslandi* Bennett, 1964 (part); *Pinnotheres novezelandiae* Takeda & Miyake, 1969; *Pinnotheres atrinocola* Page, 1983 (see for more detailed synonymy).

Type Locality

Whangarei Harbour, near High Island, 0-1m, from *Atrina zelandica*.

Distribution

Endemic to New Zealand. North and South Islands.

Diagnosis (Fig. 69a-g)

The following diagnosis refers to hard stage crabs. Carapace as wide as long, very smooth, convex, anterior and lateral margins rounded, posterior margin straight. Frontal and lateral margins without teeth, orbits barely discernable dorsally, eyes, antennules and antennae very reduced. Bases of third maxillipeds widely separated with only the palps meeting in the mid-line. Chelipeds small, propodus inflated with a continuous dorsal row of setae, tips of fingers hooked and pointed, movable finger with a strong distal tooth on the inner margin. Tips of fingers are crossed with movable finger tip inside the fixed finger tip. Legs short, first three pairs have long pinnate setae on carpus, propodus and dactylus which are flattened. Females have markedly asymmetrical legs. Abdomen six segments plus telson. Female abdomen very broad, covering almost the entire ventral surface. Terminal segment of hard-stage abdomen quadrate. First pleopod of hard stage male slender, strongly curved and sparsely setose. Male and female gonopores sternal.

Colour

Margins of male carapace pale orange, central regions have splotches of grey or cream separated by orange bands. An orange strip usually runs down the centre of the carapace. Chelipeds orange, interrupted by grey patches. Leg margins orange with medial grey areas or else banded orange and grey. Mature female unpigmented.

Size

Male 4.1-8mm CW. Female 10-19.9mm CW.

Habitat

Parasitic in horse mussel, *Atrina zelandica*, living within the mantle cavity. There are also records from *Modiolus areolatus* and *Chione stutchburyi*.

Depth

Intertidal down to 200m, in estuaries and off open coasts.

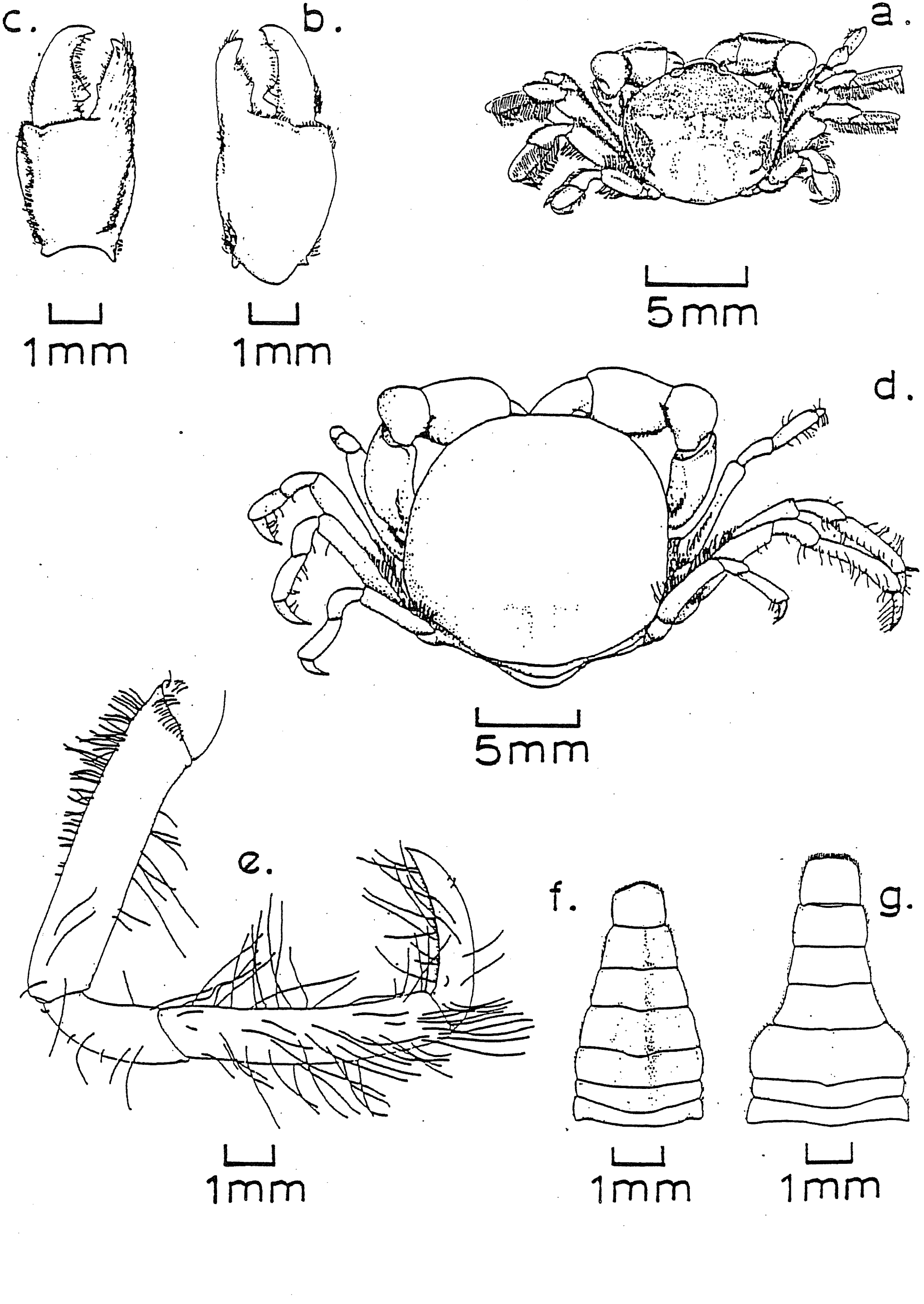


Fig. 69 - Pinnotheres atrinocola: a - hard-stage male, dorsal view; b - left chela, hard-stage male, outer face; c - left chela, hard-stage male, inner face; d - mature female, dorsal view; e - right 2nd leg, mature female, anterior view; f - abdomen, hard-stage female, ventral view; g - abdomen, hard-stage male, ventral view (after Page, 1983).

Breeding

Ovigerous females have been recorded in January, February, March, May, and December. First stage zoea are found in the Auckland plankton all year round but are more common during the warmer months from August-April.

Development and Growth

Pea crabs have a complex and unusual sequence of development. The first stage zoea of *P.atrinocola* has been described by Page (1983) but later zoeal stages are unknown. The 3 planktonic zoeal stages and the megalopa larvae are followed by the first crab instar (the 'invasive' stage) which is free living and invades the host. Males and females pass through a series of 'pre-hard' stages in the host before moulting into the first 'hard' stage which has a well calcified exoskeleton. At this stage males are sexually mature but the females moult through a further 4 'soft' stages and then become mature.

Behaviour

At Kaikoura, males have been captured at night in May when they are attracted to a light. They use their setose legs to swim actively up to the water surface and then descend into the depths again. The shape of the carapace and segments of the chelipeds allow them to reach right over the dorsal surface, like a spider crab. When observed in a dish they seem to do this quite often, rubbing the ventral margin of the propodus over the surface.

E. Grant-Mackie (pers. comm.) found a very low correlation ($r^2=0.15$) between crab and host (*Atrina zelandica*) size suggesting that crabs may leave their hosts to copulate and then return to different host mussels (see further discussion of mating strategies under *P.novaezelandiae*). C.Hay (pers. comm.) also found little correlation between crab and host size and that a single crab per host was the rule. This evidence suggests that *P.atrinocola* may have a different mating strategy from *P.novaezelandiae* involving temporary copulatory swarming of males and females.

Ecology

World-wide, pea crabs live in association with a wide range of marine invertebrates including molluscs, echinoderms and ascidians. They feed on food particles collected by their host and although often referred to as commensals they are essentially parasitic. Apart from stealing food, they induce formation of mantle lumps, cause gill and palp damage and reduce growth of their host (Christensen & McDermott 1958, Pearce 1966, Seed 1969, Kruczynski 1972,1975). The principal host of *P.atrinocola* is *Atrina zelandica* in which the incidence of the pea crab is very high. Waite (1909) and Stead (1971) found that incidence was almost 100% and Page (1983) found that 95.4% of a sample of horse mussels from Whangarei Harbour were infected. *Chione stutchburyi* is the only host that the two New Zealand species of pea crab are known to share but more work on other possible bivalve hosts is required to confirm this result. The exact identity of pea crabs which have been recorded in *Spisula aequilateralis*, *Mactra discors*, *Nemocardium pulchellum*, *Resania lanceolata*, *Tisostrea lutaria*, *Pecten novaezelandiae* and *Xenostrobus pulex* needs to be examined. At this stage it appears that *P.atrinocola* is much more host specific than *P.novaezelandiae*. Pea crabs presumably choose their host by its 'odour' and some valuable experiments about host specificity could be performed by offering crabs a choice of 'odours' from different hosts and recording their response.

P.atrinocola has a high (95%) incidence of bopyrid parasites which attach to the crab's gills (E. Grant-Mackie, pers. comm.). These have been described as a new species, Rhopalione atrinicolae Page, 1985.

References

Christensen & McDermott (1958), Dell (1968a), Griffin & Campbell (1969), Jones (1977a,1977b), Page (1983), Stead (1971), Waite (1909).

Pinnotheres novaezelandiae Filhol, 1885
Pea Crab

Synonymy

Pinnotheres pisum Heller, 1868; Miers, 1876b; Pinnotheres novaezelandiae Filhol, 1885d; Lenz, 1901; Pinnotheres schauinslandi Lenz, 1901; Chilton, 1911a; Pinnotheres pisum Oliver, 1923; Pinnotheres schauinslandi Chilton & Bennett, 1929; Pinnotheres novaezelandiae Young, 1929; Powell, 1937; Richardson, 1949a; Scott, 1961; Dell, 1963a; Bennett, 1964; Wear, 1965d; Dell, 1968a; Schmidt et al., 1973; Hayward, 1974; Jones, 1977a; 1977b; Knox & Fenwick, 1978b; Fenwick, 1978; Hickman, 1978; Page, 1983; Knox, 1983b; Wear & Fielder, 1985 (see Page 1983 for a more detailed synonymy).

Type Locality

Golden Bay, inside Mytilus edulis aoteanus.

Distribution

Endemic to New Zealand. North and South Islands, Stewart Island and Chatham Islands.

Diagnosis (Fig. 70a-g)

The following diagnosis refers to hard stage crabs. Carapace as wide as long, very smooth, convex, anterior and lateral margins rounded, posterior margin straight. Frontal and lateral margins without any teeth, orbits barely discernable dorsally, eyes, antennules and antennae very reduced. Bases of third maxillipeds widely separated with only the palps meeting in the mid-line. Chelipeds small, propodus inflated, without a continuous dorsal row of setae, tips of fingers hooked and pointed, movable finger with a strong distal tooth on the inner margin. Tips of fingers are crossed with movable finger tip inside the fixed finger tip. Legs short, without long setae on carpus, propodus and dactylus which are flattened. Last pair of legs shortest. Mature female has legs on both sides of similar length. Abdomen six segments plus telson. Female abdomen very broad, covering almost the entire ventral surface. Terminal segment of hard stage abdomen trapeziform. First pleopod of hard stage male is short, blade-like, slightly curved and densely setose. Male and female gonopores are sternal.

Colour

Hard stage colour pattern complex: anterior half of carapace orange-brown, with white spots and cream areas, posterior half with white spots on a mauve and yellow background. Chelae yellowish-brown. Legs brown with darker areas. Thoracic sternites creamy-yellow with brown patches along junctions between individual sternites. Mature female creamy-white all over.

Size

Male up to 11.3mm CW. Female 7.8-20mm CW. Size is positively related to host size.

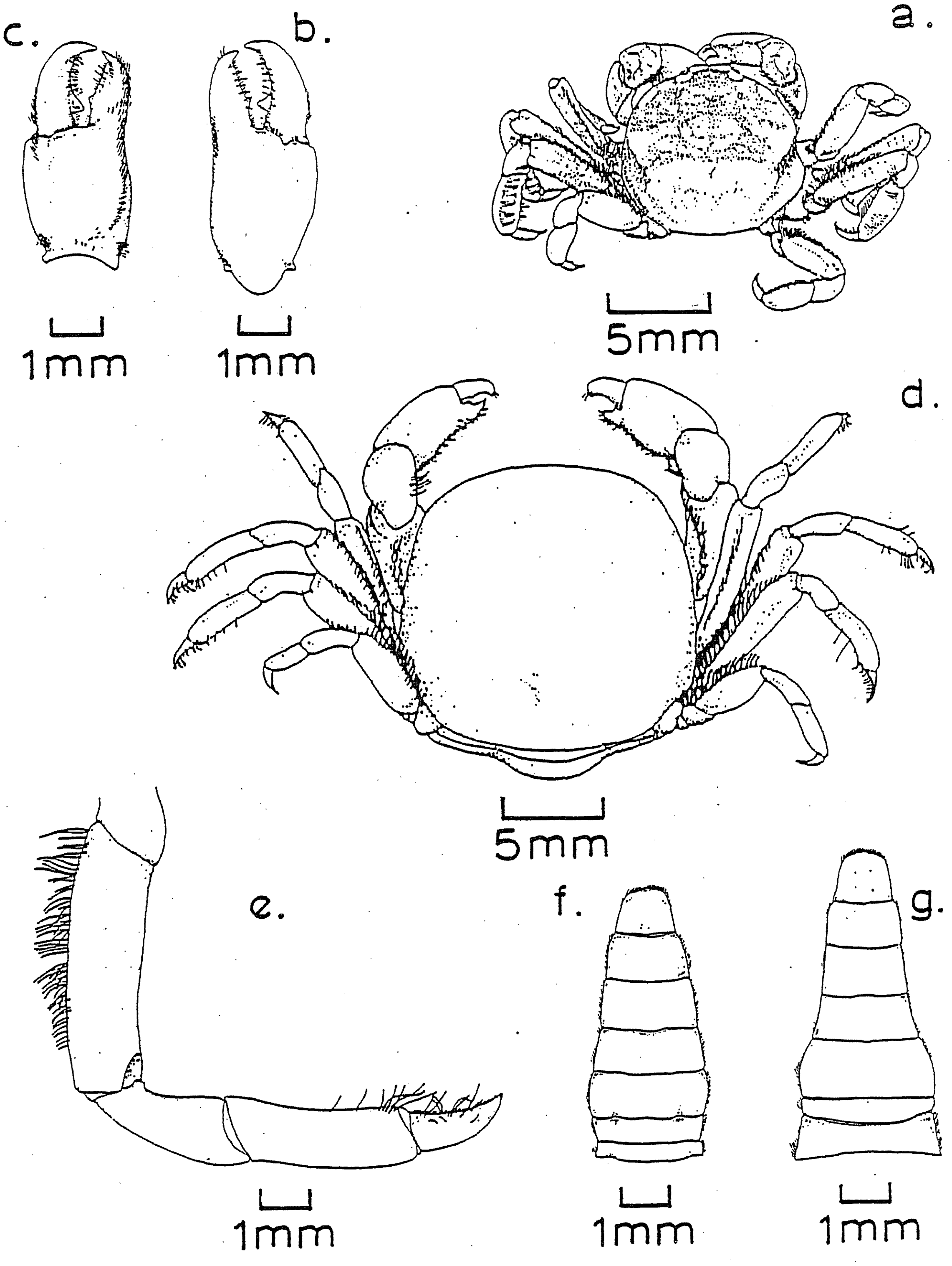


Fig. 70 - *Pinnotheres novaezelandiae*: a - hard-stage male, dorsal view; b - left chela, hard-stage male, outer face; c - left chela, hard-stage male, inner face; d - mature female, dorsal view; e - right 2nd leg, mature female, anterior view; f - abdomen, hard-stage female, ventral view; g - abdomen, hard-stage male, ventral view (after Page, 1983).

Habitat

Parasitic in Perna canaliculus (green lipped mussel) Mytilus edulis aoteanus, Aulacomya ater maoriana, Crassostrea gigas, Paphies ventricosa and Chione stutchburyi.

Depth

Intertidal and subtidal down to 30m. Estuaries and open coastline.

Breeding

Ovigerous females have been collected from Wellington Harbour in all months of the year (Jones 1977b). In Lyttelton Harbour ovigerous females collected in November were all carrying stage I eggs but their frequency gradually declined through to March when crabs carrying stage III eggs were most common (Baxter 1981). At Wellington Jones (1977b) recorded females with stage III eggs from August to March. The average diameter for stage I and II eggs from Lyttelton females was 0.3mm and egg numbers increased linearly with female CW. These females began breeding at CW 7.5mm when they carry about 2500 eggs and females of CW 14mm carry about 10,000 eggs. Comparison of regression lines relating egg numbers to female CW for stage I and stage III eggs showed no significant difference, suggesting that there is no appreciable egg mortality during development. Jones (1977b) caught 2 crabs in October 1974 which hatched their eggs and laid a second batch after 23 and 37 days. He suggested that incubation time was of the order of 2 months in summer water temperatures at Wellington.

Nemertean egg predators have been recorded from P.ostreum from North America (McDermott 1967) but these worms have not been found in New Zealand as yet.

First stage zoeae P.novaezelandiae are found in the Auckland plankton all year round but are more common during the warmer months from August to April (Page 1983). In the Avon-Heathcote Estuary new recruits were found in mussels in May (Baxter 1981).

Development and Growth

Three or possibly four zoeal stages before the megalopa. The first stage zoea has been described by Page (1983) and second and third stages by Wear & Fielder (1985). The megalopa is unknown. Jones (1977a) has described the different benthic stages of P.novaezelandiae: within the mussel Perna canaliculus there is an unknown number of pre-hard stages of both sexes, then a hard shell stage. Hard male crabs range in size from 3.2mm to 11.8mm CW and are sexually mature. Upon reaching this stage males continue to moult but do not change morphologically. By contrast females moult into a soft membranous stage and after 4 moults become sexually mature. Subsequent moults result in a size increase but no futher morphological change. Sexually mature females range in size from 9.3mm to 20.2mm CW. Scarcity of immature stages suggests that the crabs moult rapidly and reach maturity within one year (Jones 1977a). Mature females are found in mussels which are only 10 months old. Raft-grown mussels grow more than twice as fast as intertidal mussels and despite temperature differences, growth rates are similar in most parts of New Zealand, except at Bluff where growth is slower (Hickman 1979). Mussel growth is slowest in winter when condition index is also low (Hickman & Illingworth 1980). This research into the primary host for pea crabs suggests that raft-grown mussels should provide a better habitat than shore mussels but infection rates in these mussels is much lower than in shore mussels (see Ecology section, below).

Behaviour

In laboratory aquaria mature females are hostile towards one another and the stronger female will harass and eventually kill the other (Jones 1977b). It is therefore not surprising that females rarely occur together. Jones did not observe such hostility between males or between males and females.

Isolation of pinnotherids in separate hosts poses a problem for mating. There are a diversity of solutions to this problem:

1) temporary copulatory swarming of hard stage males and females in the water column followed by inseminated females re-entering the host,
2) hard stage females remain in their host and await the arrival of a male, or
3) male and female grow up in the same host and there is no need for a free-swimming stage.

In the first case multiple infections and a close correlation between crab and host size are not expected, in the second case multiple infections should be found occasionally and there should be a close size correlation between female crabs and their host, while in the third case multiple infections should be the rule and a close size correlation should be found. Jones (1977b) and Baxter (1981) both considered that P.novaezelandiae probably used the second of the above solutions with males being mobile and females sedentary. This interpretation is supported by evidence of low multiple infection rates and a good correlation between crab and host size (see below). However M.B.Jones captured 14 hard stage pea crabs in a light trap at Kaikoura in May 1981. The sex ratio was 1:1 and CW similar (3mm for males and 3.1mm for females) and this suggests that both sexes were swarming. It may be that these crabs were P.atrinocola which probably uses the first of the above mating strategies.

Ecology

P.novaezelandiae feeds on food particles collected by the host and although often referred to as a commensal it is essentially parasitic. The crabs cause erosion of gills and development of fibrous lumps or nodules on the mantle lip where the crab carapace rubs (Jones 1977b). There are no obvious structural differences between the same mouthparts from each developmental stage (Baxter 1981) suggesting that each stage feeds in the same manner. Incidence of this pea crab in Perna canaliculus is highly variable, ranging from 0-70.3% (Jones 1977b, Hickman 1978). Hickman (1978) found low infection rates, 0.2-3.6%, with only one mussel out of 6956 examined having 2 pea crabs (1 male and 1 female) in the same host. There was no significant effect on condition (proportion of meat in total weight) resulting from the presence of a pea crab. Also there was no apparent seasonal pattern in proportion of hosts infected. From December 1980 to May 1981 Baxter (1981) found that sub-tidal

P.canaliculus had infection rates of 25.1-37.2% (mean 29.9%) at a marine site but only 5.7-8.9% (mean 7.6%) nearby at the entrance to the Avon-Heathcote Estuary. Mature female CW increased linearly with mussel length but larger mussels were infected with fewer crabs than were smaller mussels. The host may live much longer than the parasite and larger mussels may be less susceptible to invasion. Out of 3672 mussels examined only 12 multiple infections were found, 2 involved 2 female crabs and the remainder involved at least 1 female and 1 hard stage male. But Jones (1977b) collected 8 male-female pairs in 173 mussels containing crabs as well as a pre-hard male pair,and one mussel containing 2 females.

Baxter (1981) found 2-2.3% infection of *A.maoriana* from the Avon-Heathcote Estuary and Lyttelton Harbour. Near Auckland Larcombe (1971) found less than 1% of *C.stutchburyi* contained pea crabs. Hard stage males and females have been taken free-living on *Corallina*, in subtidal algae and on wharf piles (Page 1983).

There are few reports of fish predation on *P.novaezelandiae*. Trevally (*Caranx lutescens*) and snapper (*Chrysophyrs auratus*) from the Hauraki Gulf eat small (0.2-0.8% of gut volume) numbers of this crab (Godfriaux 1969,1970a) as well as rig (*Mustelus lenticulatus*) from Golden Bay (King & Clark 1984). Habib (1975) recorded the occasional pea crab in red cod (*Pseudophycis bacchus*) stomachs from Banks Peninsula. Wear & Haddon (1987) found evidence of small males in the guts of the paddle crab (*Ovalipes catharus*). Zoea larvae of *P.novaezelandiae* are eaten by kahawai (*Arripis trutta*) in Wellington harbour (Baker 1971).

Ovigerous female *P.novaezelandiae* survived quite well for at least 8 days in salinities down to 14ppt but at lower salinities survival was drastically reduced (Baxter 1982). At salinities from 36 to 12ppt the crabs functioned as weak hyperosmotic regulators with haemolymph concentration declining as concentration of the external medium declined but always remaining above it. However it is the salinity inside the host rather than the external environment which is important and pea crab salinity tolerance only becomes critical if the host tolerance is outside the range of the crab. Salinities below 19ppt induce valve adduction in *Perna canaliculus* and hence the crabs are protected from the lower salinity extremes by the host response (Baxter 1981).

References

Baxter (1981,1982), Bennett (1964), Christensen & McDermott (1958), Dell (1963a,1968a), Hickman (1978), Jones (1977a,1977b), King & Clark (1984), Page (1983), Scott (1961), Wear (1965d), Wear & Fielder (1985).

Macrophthalmus hirtipes (Heller, 1862)
Stalk-eyed Mud Crab

Synonymy

Metaplax hirtipes Heller, 1862; Hemiplax hirtipes Heller, 1865; Miers, 1876b; Filhol, 1886; Miers, 1886; Macrophthalmus hirtipes Thomson, 1902; Hemiplax hirtipes Chilton, 1909; Tesch, 1918; Thomson & Anderton, 1921; Oliver, 1923; Chilton and Bennett, 1929; Powell, 1937; Richardson, 1949a; Ralph & Yaldwyn, 1956; Dell, 1963a; Bennett, 1964; Macrophthalmus (Hemiplax) hirtipes Barnes, 1967b; 1968b; Dell, 1968a; Barnes, 1970; 1971; Macrophthalmus hirtipes Knox & Bolton, 1978; Knox & Fenwick, 1978a; Knox, Bolton & Hackwell, 1978; Jones, 1983; Knox, 1983a; 1983b; Wear & Fielder, 1985.

Type Locality

Auckland Harbour. In 1853 Jacquinot described Cleistostoma hirtipes from Samoa and Chilton and Bennett (1929) and Bennett (1964) used the form Macrophthalmus hirtipes (Jacquinot 1853) implying that the Samoan and New Zealand species were synonymous although they admitted that this was highly unlikely. I do not think that this is very sensible and have therefore used Heller's name. Although Heller's locality records are highly unreliable I assume that this one is accurate! A problem could arise if it is shown that Jacquinot's and Heller's species belong to the same genus because the Samoan species would be hirtipes and the New Zealand species would be without a specific name.

Distribution

Endemic to New Zealand. North, South and Stewart Islands and according to Filhol, Campbell Island.

Diagnosis (Fig. 71a-c)

Carapace oblong, much wider than long (ratio 1.4-1.5). Convex antero-posteriorly, steep at front, more gradually sloping posteriorly, surface smooth. Gastro-cardiac groove distinct and connecting with a groove which runs irregularly to the base of the last antero-lateral tooth. Front almost straight, bearing two small lobes separated by a broad concavity, eyestalks long (25% of CW) and can be folded against front of carapace. Antennae about as long as eyestalks, antennules shorter. A strong, acute post-orbital tooth followed by two smaller lateral teeth. Posterior carapace margin straight. Chelipeds small, lightly built, fringed with long hairs, propodus inflated basally. Fingers long, narrow, inwardly curved and gaping. First pair of legs slightly longer than chelipeds, second and third pairs much longer and last pair similar in size to the first pair. Segments laterally compressed, merus of second pair spinous along its dorsal border, dactyli of all legs long and sharp, all segments fringed with long hairs. Last pair of legs inserted higher than the third pair and can fold over the other legs and on to the postero-lateral carapace corner. Abdomen of six segments plus telson which is small and triangular.

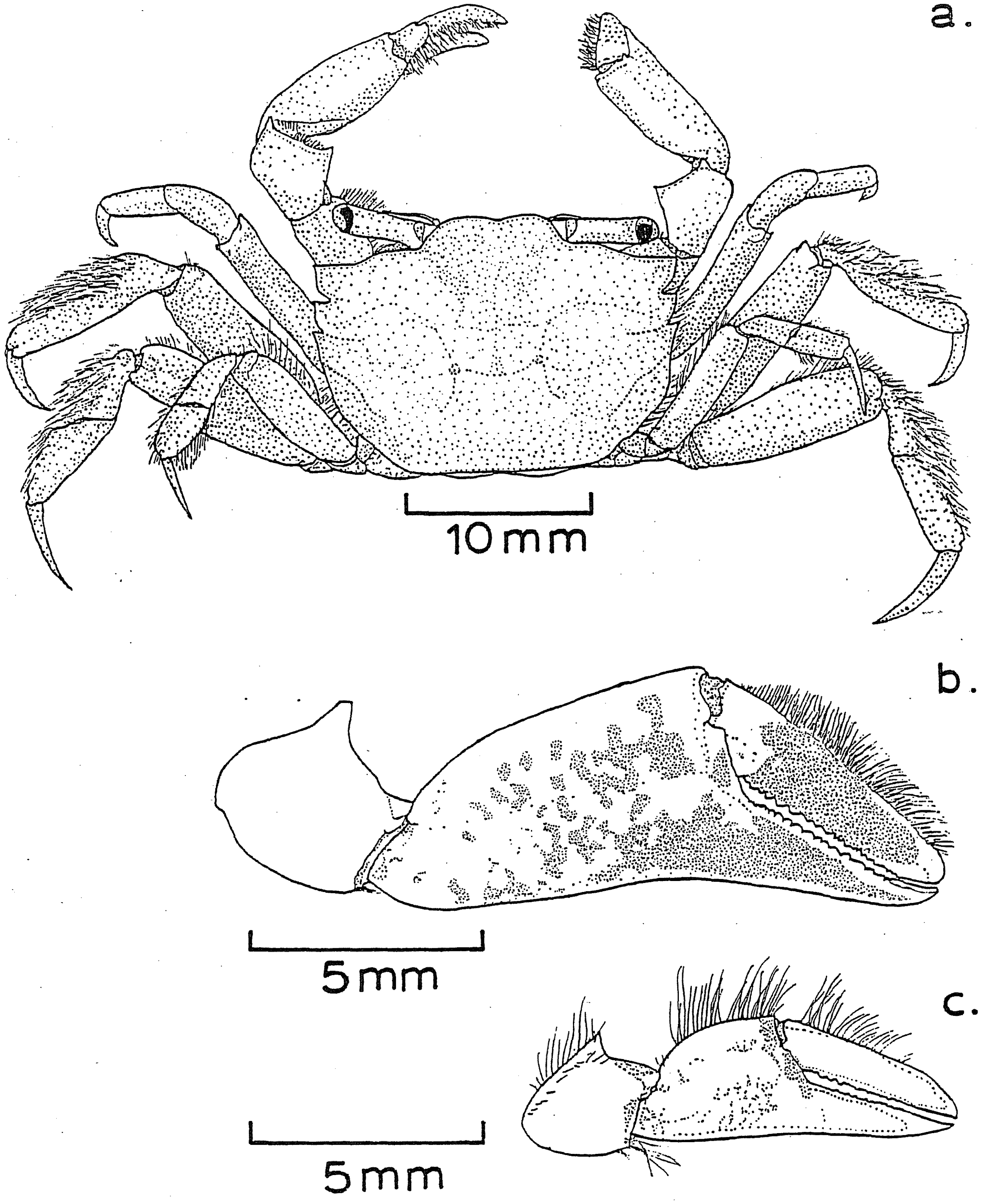


Fig. 71 - *Macrophthalmus hirtipes*: a - mature male, dorsal view; b - right chela, mature male, outer face; c - right chela, mature female, outer face (by J. Black).

Colour

Carapace deep green with scattered, dense, dark brown spots, margin dark brown. Eye stalks white with dark brown patches. Legs yellow-green and chelipeds deep red dorsally, white ventrally.

Size

Near Christchurch - male 24mm CW. Female 20mm CW. At Papanui Inlet, near Dunedin Nye (1974) recorded males up to 33mm CW. Barnes (1967b) gives maximum male CW as 30.2 and female CW as 29.25mm based on specimens from Westport, Christchurch and Dunedin.

Habitat

Common on the lower regions (below mid-tide level) of mud flats of harbours, lagoons and estuaries, living in temporary burrows in waterlogged sediments which are not exposed to the air for more than 8 hours. Small crabs live under shell debris or bury themselves in surface sediment, while larger crabs burrow.

Depth

Intertidal to 13m. Godfriaux (1969) found large numbers of M.hirtipes in stomachs of Hauraki Gulf snapper (Chrysophrys auratus) captured at depths down to 40m but it is not known whether the crabs live at this depth.

Breeding

Ovigerous M.hirtipes have been collected from late May to early March near Christchurch. At both marine (Governor's Bay) and estuarine (Avon-Heathcote Estuary) sites the sex ratio did not differ from 50:50 and up to 19.9mm CW males and females were equally frequent but in larger classes only males occurred. Females mature at 10-13mm CW and while carrying eggs under the abdomen the ovaries develop the next batch. During the breeding season females may produce 2-3 batches of eggs (Simons and Jones, 1981). In winter incubation time is of the order of 2.5-3 months at 10°C. Numbers of eggs increase exponentially with carapace width with the smallest females carrying around 300 eggs and the largest around 20,000 eggs. Females from an estuarine site carried significantly more eggs than females from a nearby marine site and this may reflect a higher level of food availability in the estuary. Comparison of regression lines for stage I and stage III eggs showed no significant difference, suggesting that there was no significant egg mortality at least in the estuarine population. Jones and Simons (1982) found that embryonic development proceeded normally at salinities as low as 18 ppt but at 11 ppt eggs did not hatch. Also at 18 ppt late-stage eggs were significantly larger than at 36 ppt. Wear (1968b) reported that eggs measure 0.25 x 0.24mm when freshly laid (dark brown in colour) while eggs ready to hatch measure 0.28 x 0.26 mm and are coloured light brown. Simons and Jones (1981) found that at both estuarine and marine sites eggs were larger than reported by Wear (1968) and that eggs laid in the first half of the breeding season (May-September) were significantly larger than those produced in the second half (October-February). During the latter part of the breeding season eggs from marine females were significantly smaller than eggs from estuarine females. Also there was some evidence of variation in egg size between seasons. These data indicate that we should be cautious in treating egg-size as a fixed quantity for each species as it is obviously responsive to environmental conditions such as food supply. In 1982, a survey of the Avon-Heathcote Estuary plankton from March to August resulted in very few zoeae (Roper, Simons & Jones 1983). Salmon et al. (1986) found hatching rhythms in fiddler crabs (Uca spp.). Most larval release occurred within one hour after high tide and peaks in larval density occurred semi-monthly during spring tides thus minimizing the risk of stranding on mudflats. Decapod crustaceans release larvae rhythmically in relation to lunar, light-dark and tidal cycles (Forward 1987). Christy (1986) found semi-lunar, tidal and diel timing of larval release by four species of intertidal crabs occurring together on the same exposed, cobble shore near Panama.

Development and Growth

There are 5 zoeal stages before the megalopa (see Wear & Fielder 1985). Wear (1968b) has described the pre-zoea larva and the first stage zoea. The pre-zoea is very short-lived (5-10 min.) and quickly moults to the first stage zoea. Zoea larvae of ocypodid genera show close affinities with those of Hymenosomatidae, Pinnotheridae and Grapsidae. Megalopa larvae of ocypodids are structurally modified in response to the specialized requirements of the beach-dwelling adults. Megalopae are provided with a thick cuticle and specialized grooves to allow close application of all appendages to the body. These provide protection against the desiccation, wave action and sand abrasion they are exposed to on sandy beaches.

Differential growth rates of secondary sexual characters of M.hirtipes have been studied by Simons (1981). Female chelae growth was negatively allometric (b=0.87) throughout post-larval life but there was a marked inflection in the relative growth of the male chela at 10-13mm CW. Before inflection growth was near isometric (b=1.0) but after inflection it was positively allometric (b=1.78). Male abdomen growth was negatively allometric (b=0.82) but female abdomen growth changed at around 11mm CW from being nearly isometric (b=1.07) to being positively allometric (b=1.4). Some large females with smaller abdomens than expected were infected with an undescribed epicarid isopod which retarded development of ovaries and abdomen. Comparison of estuarine and nearby marine M.hirtipes suggest that estuarine females mature at a smaller size. Male first pleopod length growth rate decreased gradually as small crabs grew until 10-12mm CW whereupon pleopod growth became negatively allometric (b=0.73). These changes in growth pattern are typical of the general pattern found in the subfamily Macrophthalminae (Barnes 1968c) and other brachyura (Hartnoll 1974) and are related to the onset of sexual maturity. Those structures affected are all involved in mating or brooding of eggs.

Behaviour

Williams et al. (1985) compared field and laboratory activity patterns of M.hirtipes from Papanui Inlet, Otago Peninsula. Catches of crabs in pitfall traps at different shore levels suggest that crabs do not move far from the zone where they burrow, with the numbers caught more or less reflecting the relative density at each level. Catches during full moon spring tides in late January peaked during the 3 hours covering high tide, despite the fact that crabs were seen on the surface (adults close to their burrows, but juveniles wandering widely) when exposed to air. Concurrent records of locomotor activity under constant laboratory conditions clearly showed circatidal rhythms with peak activity coinciding with the time of high water. In the field catch rate at high water does not vary with the day/night cycle even when high tides are around midday and midnight. Sometimes there was a slight increase at about the time of low water and if the total catch was divided into 'juveniles' (<12mm CW) and adults (>12mm CW) the low tide peak was composed mainly of juvenile crabs while the high tide peak was almost entirely adults. However, during neap tides the night-time catches were 3-4 times greater than during the day with most of the crabs caught during the day being juveniles and adults were only caught in large numbers during the night high tide. Activity in M.hirtipes is related to tidal amplitude but with a strong nocturnal influence. Macrophthalmus, living lower on the shore than Helice is less affected by the lunar cycle in tide height. The explanation of the apparent discrepancy between observations (see below) and trap catches when the habitat is exposed to air seems to require the assumption that when crabs are covered by water they exhibit more wide-ranging, exploratory locomotor activity. As Williams et al. (1985) suggest, the difference in activity between sexually mature and immature crabs in the field needs further investigation.

When activity rhythms of individual M.hirtipes were recorded none of them showed the group pattern mentioned above. The rhythms of individual crustaceans are typically very imprecise and only when studied as groups is any semblance of accurate timing seen (Palmer & Williams 1969a). Research on individual rhythm patterns of M.hirtipes led to the postulation of a dual clock hypothesis to explain these patterns (Palmer & Williams 1986b,1987).

In Governor's Bay, Christchurch, M.hirtipes emerge from their burrows 10-15 min. after the ebbing tide has passed with emergence often being preceded by a violent clearing of the burrow during which loose material is expelled from the entrance. After emerging they remain motionless for several minutes with eyestalks erect. M.hirtipes moves sideways across the mud while feeding and forages further from its burrow than Helice crassa (Fielder and Jones 1978). Crabs return to their burrows intermittently during feeding, probably to protect their burrows against trespassers. During feeding chelae are held horizontally so that down-turned fixed fingers can act as scraper-scoops. Small scoops of mud are conveyed to the upper mouth-frame by chelae working alternately. In soft slushy mud the setae fringing the fingers appear to act as a sieve concentrating food material. M.hirtipes also feeds on epiphytic algae growing on the shells of the mud snail Amphibola crenata which are very abundant in this habitat. Fragments of epiphytes are torn off by larger crabs using their chelae and subsequently eaten. This crab is a very adaptable and efficient feeder (Fielder and Jones, 1978). There is some disagreement about whether M.hirtipes is active when immersed (Beer 1959, Nye 1974, Fielder and Jones 1978) but the results of Williams et al. (1985) suggest that there is a high level of activity during submergence. Also activity seems to be influenced by temperature and perhaps other conditions. These points require further study.

Burrowing of M.hirtipes has been studied by Nye (1974) at Papanui Inlet, near Dunedin. Crabs begin to burrow by digging the tips of their right or left walking legs into the substrate, using them as a scoop with the other set of legs used to move the crab along. The shallow depression first formed was enlarged into a tunnel with excavated material deposited at the end of a tongue- or fan-shaped path (mean = 14.5cm long). Each burrow consisted of a single passage descending at an average angle of 36 ± 8.5^{o} (standard deviation). Most burrows (94%) had blind endings but 6% sloped up to the surface again and had 2 openings. Most burrows were curved (left or right) with only 25% being straight. The burrow entrance diameter averaged 2.6 cm and the average length was 17.3cm. Maximum depth below the surface averaged 6.0cm. Unfortunately Nye did not indicate how long burrows take to construct. Burrow openings were transient in the field, only 11% were in the same position 1 day later and none were in the same position 1 week later. Small crabs kept in a laboratory aquarium also had transient burrows: 62% lasted for less than 1 day, 28.5% were in the same position for 2 consecutive days and 9.5% were in the same position for 3 days. Although M.hirtipes does not attempt to cover its burrow entrance, many become concealed by sediment so that the number of burrows seen on the surface as the tide goes out is only a small fraction of the true number of crabs present in an area. If a crab was alarmed while away from its burrow it would quickly burrow in soft sediment. First the crab probed with the tips of legs and chelae, then pushed its body forwards and downwards into the substrate. Next the body was rocked backwards and upwards and sand was shovelled away from underneath with the chelipeds. This was repeated until the crab was hidden, with only the eyestalks protruding. Beer (1959) observed that crabs kept submerged on sand in the laboratory spent a large part of their time buried in this way. Both burrowing and burying are undoubtedly a protection against predators. The burrowing and social behaviour of the related M.latifrons from south-east Australia has been studied by Griffin (1968b).

M.hirtipes lives in quite dense concentrations but there is a minimum of social cooperation between them (Beer, 1959). Each crab defends a small area around its burrow from intrusion by other crabs. Crabs were marked with fingernail polish and records of their movements suggest that they wander over comparatively large areas utilizing and defending not one burrow, but any that happen to be at hand. It is most unfortunate that Beer did not include more precise and quantitative data about movements and use of burrows. When a wandering crab draws near another's burrow the occupier rushes out, or if feeding outside, runs to the burrow entrance. The defending crab adopts a characteristic threat posture - chelipeds are raised and held with fingers open to reveal a colour pattern which accentuates their size, and legs are spread to reinforce this impression. This may deter the intruder but if not, it also adopts a threat posture. The 2 crabs face each other and come together until their chelae touch. As they move closer together the combatants extend their chelipeds outwards to the maximum extent, meeting with the inner cheliped surfaces turned toward and abutting against those of their opponent. With legs also spread and their ventral surface close to the ground an impression of great width is reinforced. In this position mouthparts of the 2 crabs are brought close together and the 'blowing' or 'bubbling' of the breathing currents may play a part in this ritualized fighting. Several M.hirtipes were observed to hold this mutual threat position for over 5min. Unlike Helice crassa which tended to take less time to decide the issue, M.hirtipes individuals often took much longer with one contest lasting 70 min. The contest consisted of a series of mutual threatenings and pursuits in which the same crab was dominant throughout. Sometimes several crabs challenged a resident, pursuing it into the burrow and the conflict led to an epic struggle. Real fights, involving tearing with chelae, are reduced to a minimum. Unlike H.crassa ritualized fighting in M.hirtipes only occurred between males and, strangely, a crab which vigorously and 'victoriously' defended a burrow could often immediately wander away from it and apparently never return. These activities seem to be most common on warm, sunny days but peak periods of fighting and burrowing may coincide with peak mating periods. Most fights, whether on a territory or not, are punctuated by short pauses when crabs may perform feeding movements. These movements do not seem to be true feeding and they may in fact be displacement activities - ie. irrelevant movements which relieve the tension of the struggle. There is no evidence of interspecific agonistic behaviour towards H.crassa.

Beer (1959) also observed sexual behaviour in M.hirtipes from August to May (inclusive) with peaks in October and May. Copulation occurs on the surface and no courtship behaviour was observed. Without preliminary overtures the male seizes the female with his pincers and forces her to expose her ventral surface to his own. Sometimes the female struggles and escapes, but if the male is strong enough she becomes submissive. Christy (1987) classified this kind of male competition for mates as involving only search and interception which affect encounter rates with females rather than involving defence of resources or receptive mates. Thompson (1930) observed mating during April and June in the Avon-Heathcote Estuary. The male lay on his back with his abdomen inserted under the female's abdomen which curved over the dorsal surface of the male. The male's chelipeds enveloped the female tightly and one pair remained in this position for at least 18 minutes. Mating crabs were observed out of the water at low tide and in each case the male was much larger than the female.

Colouration of M.hirtipes is a combination of the need for concealment and conspicuousness (Beer, 1959). When trying to conceal itself the crab becomes as small as possible and all brightly coloured appendages are folded underneath leaving only the cryptically coloured parts exposed. But when disturbed by an intruder the crab orients in the direction of the disturbance, stiffens on outstretched legs with chelipeds spread and fingers gaping, thereby displaying all its brightly coloured parts (Thompson 1930). The crab moves as the source of disturbance moves so that the striking colour pattern is always on display. This behaviour is largely pure bluff since the crab could hardly inflict any significant damage on any attacker. If such intimidation fails the crab finally tries to run away and bury itself.

The behaviour of M.hirtipes is clearly a fascinating and entertaining subject and there is a great need to study its social behaviour in much greater detail. A future study should utilize marked crabs and labelled burrows and attempt to gather more quantitative data about burrowing, agonistic and mating behaviours. The work of Crane (1975), Christy & Salmon (1984) and Bertness & Miller (1984) is particularly relevant.

Ecology

Density of M.hirtipes seems to differ markedly between sites and times. Wood (1968) found a mean density of 26 crabs/m^2, Stephenson (1970) reported 11.1 crabs/m^2 from Porirua Harbour near Wellington in June while Simons and Jones (1981) reported densities in the Avon-Heathcote estuary of 25 (November) to 41.5 (March) and densities of 10.7 (June) to 37.8 (March). One sample taken by Nye (1974) at Papanui inlet, near Dunedin, suggested a density of approx. 88 crabs/m^2 in May. As noted earlier the number of apparent burrows on the surface is a poor indicator of the actual number of crabs present in an area.

The population biology of M.hirtipes at two sites (one estuarine and the other marine) near Christchurch shows some interesting differences (Simon and Jones, 1981). At the estuarine site peak recruitment occurred in summer (December) although some juveniles were present throughout the year. Following settlement the young crabs grew to form a modal peak at 4-6mm CW from February to June. This cohort overwintered as immature crabs (6-10mm CW) and became sexually mature (CW >9.9mm) during the next summer. There is probably a high level of mortality as relatively few mature crabs were present, with immature size classes dominating the population throughout the year. Few crabs grow larger than 20mm CW and these are all males. At the marine site there was no clearly defined recruitment peak. The population was bi-modal during autumn and winter (immatures, 4-6mm CW and matures 16-18mm CW) (see also Williams et al. 1985 who found a bi-modal structure in January, on Otago Peninsula). However in the following year the population was unimodal (8-10mm CW). The largest male was 23.6mm CW and the largest female 19.8mm CW. Average crab size was larger at the marine site but so were the seasonal fluctuations. Differences between the estuary and marine sites seem to reflect the more productive nutritional resources in the estuary - about 10 times more chlorophyll, higher ATP levels and higher micro-organism activity and productivity. A major element lacking in our knowledge about the population biology of M.hirtipes is the absence of any data about growth and age, and this makes it difficult to put the reproductive biology into perspective.

These may well be regional differences in M.hirtipes life history. In Japan Henmi (1987) found that more northern populations of M.japonicus matured at a larger size, had a longer life span, higher growth rate and smaller egg size than southern populations. Northern populations bred in summer while southern populations bred in winter.

The observed population differences between the estuarine and marine populations of M.hirtipes near Christchurch prompted Sin and Jones (1983) to investigate protein and enzyme variation insofar as it reflects genetic variation. Enzymes were extracted from either muscle or the hepatopancreas of single crabs. A survey of 24 loci revealed that 22 were common to both populations with 20 being monomorphic and 2 esterase loci were highly polymorphic (2 alleles each). The frequencies of the esterase-3 alleles were similar but frequency of the esterase-2 alleles in the estuarine population were significantly different from the marine population. There was a significant deficiency of esterase-3 heterozygotes in the estuarine population. Mean heterozygosity was 0.0401 at the marine site and 0.0171 in the estuary (not significantly different, $p>.05$). These values are similar to those reported for other decapod crustacea. These interpopulational genetic differences may reflect differences in environmental conditions. In the absence of knowing the population attributes of each individual we cannot know whether these genetic differences explain any of the observed population differences.

In the Avon-Heathcote estuary Jones (1976) found that M.hirtipes formed 15.2% of the 5 species of crabs collected and its absence from some parts of the estuary was related to lack of suitable soft substrate below mid-tide level or an inability to tolerate water of low salinity. In a later study Jones and Simons (1982) found that M.hirtipes was only half as abundant as Helice crassa, substrate preference was shown to be the most important factor influencing distribution, but lack of tolerance to salinities of less than 4 ppt prevents M.hirtipes from living at points close to freshwater input. Both of these species had similar sediment organic content and particle size requirements but M.hirtipes was found in waterlogged areas below mid-tide level, while H.crassa occurred above mid-tide level (see also Williams et al. 1985). M.hirtipes which has a significantly larger gill area (Hawkins and Jones 1982) is significantly less tolerant of desiccation than H.crassa. The blood of M.hirtipes was hyperosmotic to the surroundings at salinities of 10.5-23 ppt and isosmotic from 23-35 ppt. M.hirtipes seems to be excluded from drier, compact sediments by its burrowing behaviour which requires softer material, but this point requires further investigation. Also the lack of ability to retain and recirculate branchial fluid when in air may contribute to precluding it from dry high-shore areas (Hawkins and Jones 1982). M.hirtipes must rely on surface water to sustain its respiration during feeding excursions on exposed mudflats (Hawkins, Jones and Marsden 1982). The ecological distribution of the related M.latifrons in Tasmania has been investigated by Griffin (1971).

M.hirtipes collected near an old tannery which discharged into Otago Harbour contained high levels of chromium despite cessation of chromium discharge. Levels were higher in large crabs and the chromium was obtained by consumption of sediment and epiphytic bacteria which concentrate this element in an extra-cellular polymer layer (Bremer & Loutit 1987). This is a pathway by which chromium may enter marine food-chains. In another study Thrush (1987) found a positive correlation between zinc concentrations in M.hirtipes and sediment concentrations.

Predation of M.hirtipes in Otago Harbour by Patiriella regularis was reported by Crump (1969). Only 10-15% of the starfish were feeding on macroscopic food, a major part of which was M.hirtipes. Population density of the predator ranged from

0.1 to 1.98 per m^2. But when provided with live crabs in the laboratory the starfish did not eat any, suggesting that crabs fed on in the field were probably already dead from other causes (Crump 1969). Laboratory experiments showed that a food supply of freshly killed crabs gave superior body and gonad growth to a diet of fish, with food intake varying seasonally, being low during the colder winter months. Gonad development in crab-fed starfish was greater than in field animals. By contrast another starfish, *Coscinasterias calamaria* fed extensively on live *M.hirtipes* in all months (Crump 1969).

Several species of commercially important fish prey upon *M.hirtipes*: Thomson (1930), Otago Harbour:- rig (*Mustelus lenticulatus*) Graham (1939), red cod (*Pseudophycis bacchus*), red gurnard (*Chelidonicthys kumu*) Godfriaux (1969), Colman (1972); Hauraki Gulf and NW Bay of Plenty:- snapper (*Chrysophyrs auratus*, 23.2% of gut volume) Godfriaux (1970a), trevally (*Caranx lutescens*,4.7%), red gurnard (37.6%), and eagle ray (*Holorhinus tenuicaudatus*,1.3%) King & Clark (1984); Golden Bay, Kaikoura, Banks Peninsula, Wellington, Hauraki Gulf:- rig. Habib (1975) found *M.hirtipes* in red cod stomachs from Banks Peninsula in February(1.6%), May(0.4%), July(1.0%) and September(1.7%) and also in red cod from Otago Peninsula in November(0.27%) and February(0.16%). Sand flounder (*Rhombosolea plebeia*) in the Avon-Heathcote Estuary also ate this crab (2.1%) (Kilner 1974). Also in the Ahuriri Estuary, near Napier, Kilner & Akroyd (1978) found that *M.hirtipes* was preyed upon by the short-finned eel (*Anguilla australis*). Knight (1971) found this crab in stomachs of spotted stargazer (*Geniagnus novaezelandiae*). Beer (1959) recorded an *M.hirtipes* being eaten by *Hemigrapsus edwardsi* in Otago Harbour. It also seems that this crab would be a likely prey for kingfishers (*Halcyon sancta*), herons (*Egretta sacra* , *E.alba*) and gulls (*Larus* spp.) although this should be confirmed by a detailed study. *M.hirtipes* have been found in stomachs of Hector's Dolphin (*Cephalorhynchus hectori*) caught around Banks Peninsula.

Post-pleistocene fossils of *M.hirtipes* from Otago harbour have been reported by Glaessner (1960) as well as a large, extinct lower pleistocene species, *M.?major*, from the North Island.

References

Barnes (1967b,1968b), Bennett (1964), Beer (1959), Carpenter (1974), Chilton & Bennett (1929), Christy & Salmon (1984), Colman (1972), Crane (1975), Crump (1969,1971), Fielder & Jones (1978), Graham (1939), Griffin (1968b, 1971), Hartnoll (1974), Hawkins & Jones (1982), Hawkins, Jones & Marsden (1982), Jones (1976), Jones & Simons (1981,1982), Kilner (1974), King & Clark (1984), Knox et al. (1976), Nye (1974), Palmer & Williams (1986a,1986b,1987), Roper, Simons & Jones (1983), Simons (1981), Simons & Jones (1981), Sin & Jones (1983), Stephenson (1970), Thompson (1930), Wear (1968b), Wear & Fielder (1985), Williams et al. (1985), Wood (1968).

Amarinus lacustris (Chilton, 1882)

Synonymy

Elamena lacustris Chilton, 1882; *Hymenosoma lacustris* Chilton, 1883; Fulton & Grant, 1902; Hutton, 1904; Fulton & Grant, 1906; Chilton, 1906c; 1911b; 1914; *Halicarcinus lacustris* Kemp, 1917; *Hymenicus lacustris* Tesch, 1918; *Hymenosoma lacustris* Chilton, 1919; *Halicarcinus lacustris* Richardson, 1949a; Dell, 1963a; Holthius, 1968; Walker, 1969; Lucas, 1970; 1971; Melrose, 1968; 1975; Chapman & Lewis, 1976; *Amarinus lacustris* Lucas, 1980; Wear & Fielder, 1985; *Halicarcinus lacustris* Hutton, 1986.

Type Locality

Lake Pupuke, Auckland.

Distribution

Confined to north of North Island of New Zealand (not found south of Hamilton). Also south-eastern Australia (Victoria, South Australia, Tasmania), King Island, Norfolk Island and Lord Howe Island.

Diagnosis (Fig. 72a-d)

Carapace subcircular, flat or convex, grooves forming an H-shape with sides sub-parallel. Rostrum originating from carapace level, with almost straight basal suture. Rostrum simple, just longer than eyes, narrowing slightly distally, tip truncate, sharply deflexed. Ventral surface of rostrum not ridged. Chelipeds up to twice as long as CW, massive in large males, palm longer than carpus, rudimentary tooth rarely present on base of movable finger in male. Narrow linear gape present along proximal two-thirds of fingers in both sexes, distal one-third occluding and shallowly dentate. First two pairs of legs equal in length, as long as chelipeds, third and fourth pairs shorter. Leg segments slightly flattened, dactylus longer than propodus, sharply tapering, ending in tiny claw. Both edges of dactylus hairy, ventral edge with three or more rows of hairs but no teeth. Abdomen of five segments plus telson in both sexes. Whole crab setiferous.

Colour

Dark brown or red.

Size

Male 11mm CW. Female 7.5mm CW.

Habitat

Freshwater lakes and non-tidal rivers. *A.lacustris* is the only New Zealand freshwater crab.

Depth

Shallow water.

Breeding

Ovaries and testis develop prior to prepubertal moult and copulation can occur before this moult. Mating involves hard shell male and soft shell female. Ovigerous females carrying around 50 eggs have been collected from July to February. Eggs are a green colour and comparatively large (0.65 - 0.8mm diameter). Embryonic development is correspondingly long, 55

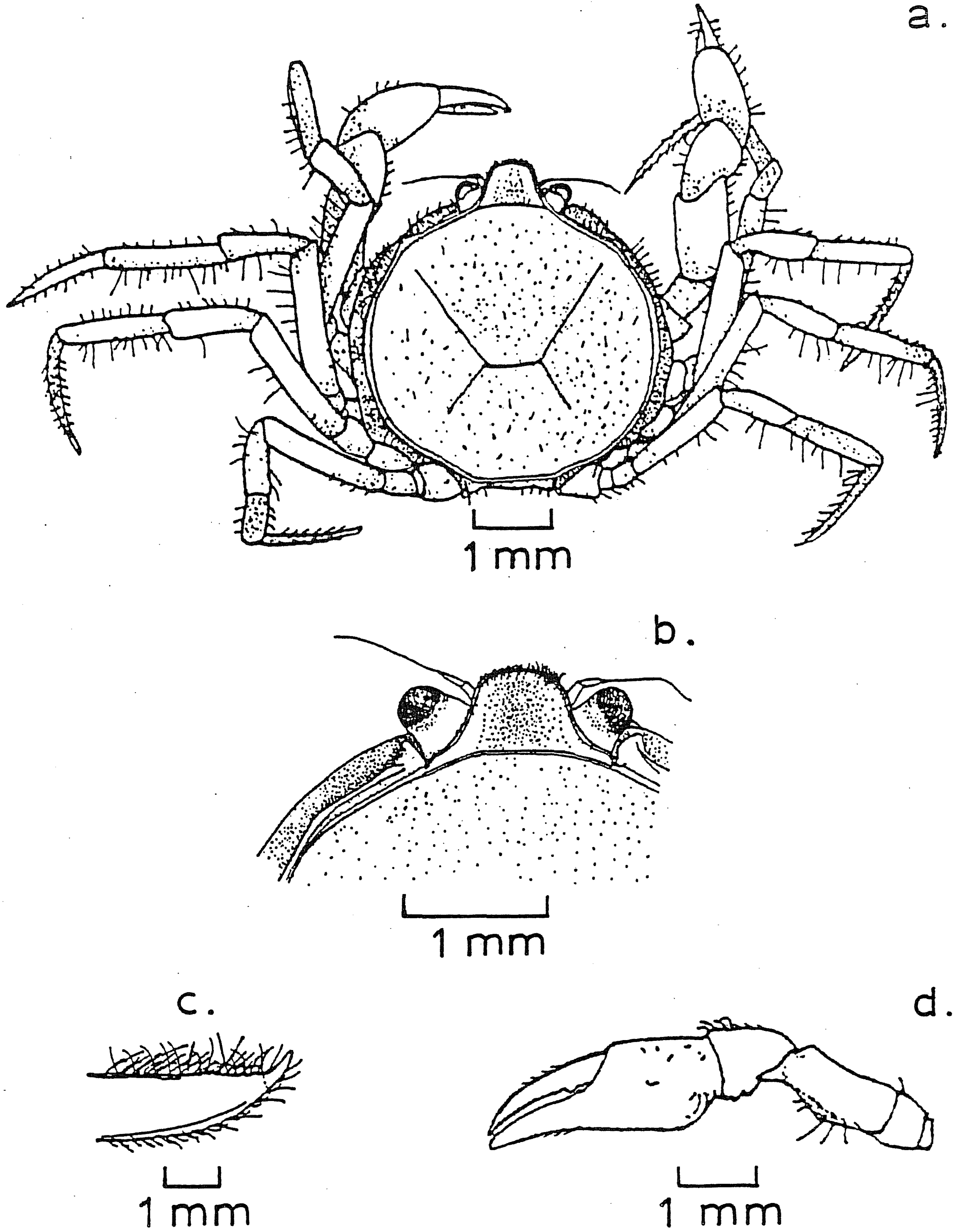


Fig. 72 - Amarinus lacustris: a - male, dorsal view; b - rostrum, male, dorsal view; c - tip of dactylus of 3rd walking leg, male, posterior view; d - left cheliped, male, outer view (after Melrose, 1975).

days. A female can produce several egg masses in quick succession without further copulation. Sperm are stored in spermathecae, an enlarged region of the genital duct. A mean of 2.6 broods per female was recorded (Lucas 1971).

Development and Growth

A.lacustris has no free-living larval stage and its development is direct. Late stage embryos are equivalent and similar to zoeal stages of species with indirect development. Hatching occurs before the first crab instar is reached and the free embryos remain among the maternal pleopods until moulting to juvenile crabs at CW 1.05mm. This moult is not synchronized within the brood, being spread over 2-6 days. There are 8 prepubertal instars for females which is a large number considering the small adult size. This results from proportionally smaller growth increments. At 20°C these moults take approx. 177 days after hatching. The female prepubertal moult is terminal (Lucas 1971).

Behaviour

May be found clinging to the stems and roots of aquatic plants in shallow swampy streams.

Ecology

Gut contents include both plant and animal material indicating omnivorous food habits. Crabs have been kept in captivity for up to 2 years but this species probably has a one year life cycle with a few crabs surviving to a second year. Recruitment occurs in late spring and summer. A.lacustris is found in salinities of 0.1-9.6 ppt but can survive several days in seawater (Walker 1969) A.lacustris occurs in freshwater on 6 land masses separated by many hundreds of kilometres of ocean. The evidence suggests a recent origin for this species in Australia and subsequent dispersal, perhaps by water fowl, to southern islands (Lucas 1980).

These small crabs are preyed upon by trout and the introduction of these fish into small lakes may have wiped out many populations (Chapman & Lewis 1976). They may also be eaten by freshwater crayfish (Paranephrops spp.).

References

Chapman & Lewis (1976), Lucas (1971,1980), Melrose (1975), Walker (1969), Wear & Fielder (1985).

Elamena longirostris Filhol, 1885

Synonymy

Elamena longirostris Filhol, 1885b; 1886; Borradaile, 1916; Tesch, 1918; Richardson, 1949a; Griffin & Yaldwyn, 1965; Melrose, 1968; Takeda & Miyake, 1969; Melrose, 1975; Lucas, 1980; Wear & Fielder, 1985.

Type Locality

East Coast of Stewart Island.

Distribution

Endemic to New Zealand. Off North Cape, and Wanganui, continental shelf off Banks Peninsula. Also Stewart Island.

Diagnosis (Fig. 73a-d)

Carapace almost exactly trigonal, dorsal surface not strongly convex, but nearly flat posteriorly. Marginal rim of dorsal surface distinct but not raised, lateral wall of carapace weakly expanded. A high tubercle directed obliquely upwards on marginal rim near first and second legs. Rostrum acute, triangular, extended strongly forwards and upwards. Chelipeds equal and slender. Fingers longer than palm, curved inwards near tips, cutting edges minutely serrated along entire length and tips are sharply pointed and crossing. Legs very long, dactyls depressed, slightly curved, both upper and lower borders densely fringed with short hairs or setae, two teeth near the small terminal claw. Abdomen of five segments plus telson in both sexes.

Colour

Pale brown, dorsal surface of carapace greyish and legs somewhat darker.

Size

Male 5.5mm CL. Female 11mm CL.

Habitat

Mud, sand and shell bottom, among sponges, bryozoans, red algae and detritus.

Depth

Shallow water, continental shelf to 116m.

Breeding

Ovigerous females have been collected in August and November to January. Newly laid eggs, opaque white, 0.37mm diameter, ready to hatch reddish black, 0.47-0.63mm.

Development and Growth

Three zoeal stages and first juvenile crab stage described by Wear & Fielder(1985).

Behaviour, Ecology

Unknown.

References

Lucas (1980), Melrose (1975), Takeda and Miyake (1969), Wear & Fielder (1985).

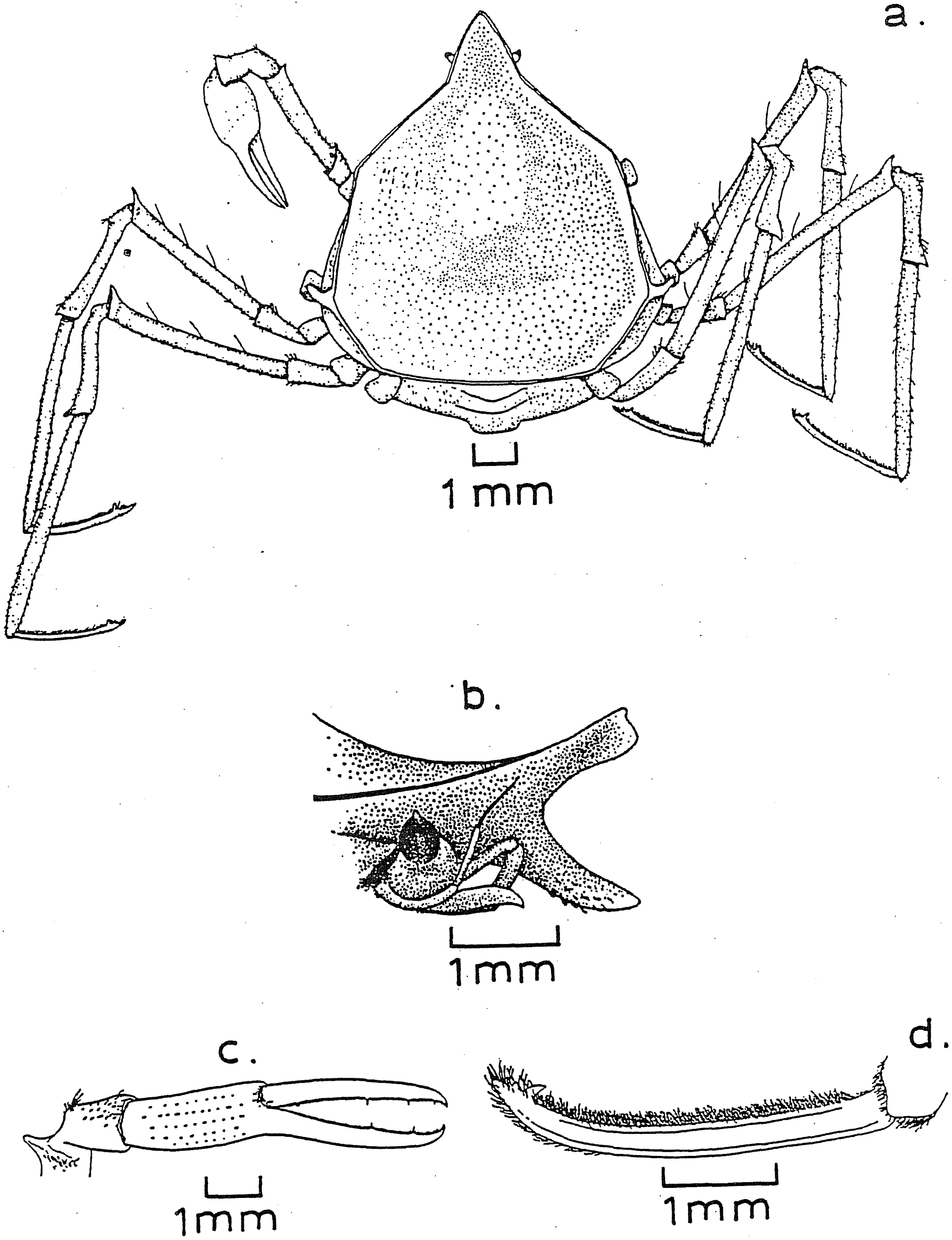


Fig. 73 - *Elamena longirostris*: a - male, dorsal view (after Melrose, 1975); b - lateral view of rostrum, female; c - right chela, female, outer view; d - dactylus of right 3rd walking leg, posterior view, female (after Takeda & Miyake, 1969).

Elamena momona Melrose, 1975

Synonymy

Elamena sp.nov. Melrose, 1968; Elamena momona Melrose, 1975; Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Chelsea Point, Waitemata Harbour.

Distribution

Endemic to New Zealand. Only known from Waitemata Harbour, near Wellington and Foveaux Strait oyster beds.

Diagnosis (Fig. 74a-e)

Carapace flat suboval, broader than long, without lateral angles. Rostrum fused with carapace, very short, shallowly rounded anteriorly. Ventral keel on rostrum square anteriorly, of equal depth throughout, not reaching below eyestalks in lateral view. Chelipeds small in both sexes. Chela of male little inflated, basal gape elongated, a small, square tooth on base of movable finger. Fingers slender, as long as palm. Tips of fingers in male spooned, hardly occluding at tips. Second pair of legs a little longer than the first, fourth pair shortest. Dactyli of legs as long as propodi, curving distally, ventral edge has single row of short hairs, two teeth distally. Abdomen of five segments plus telson in both sexes.

Colour

Unknown.

Size

Male and Female 9mm CW.

Habitat

Shell debris on mud and on rocky substrates among algae.

Depth

Shallow water.

Breeding

Ovigerous females have been collected in February, May and November. When newly laid, eggs are orange-yellow, 0.5mm diameter and 0.56 x 0.58mm when about to hatch.

Development and Growth

Three zoeal stages described by Wear & Fielder (1985). First juvenile crab stage unknown.

Behaviour, Ecology

Unknown.

References

Lucas (1980), Melrose (1975), Wear & Fielder (1985).

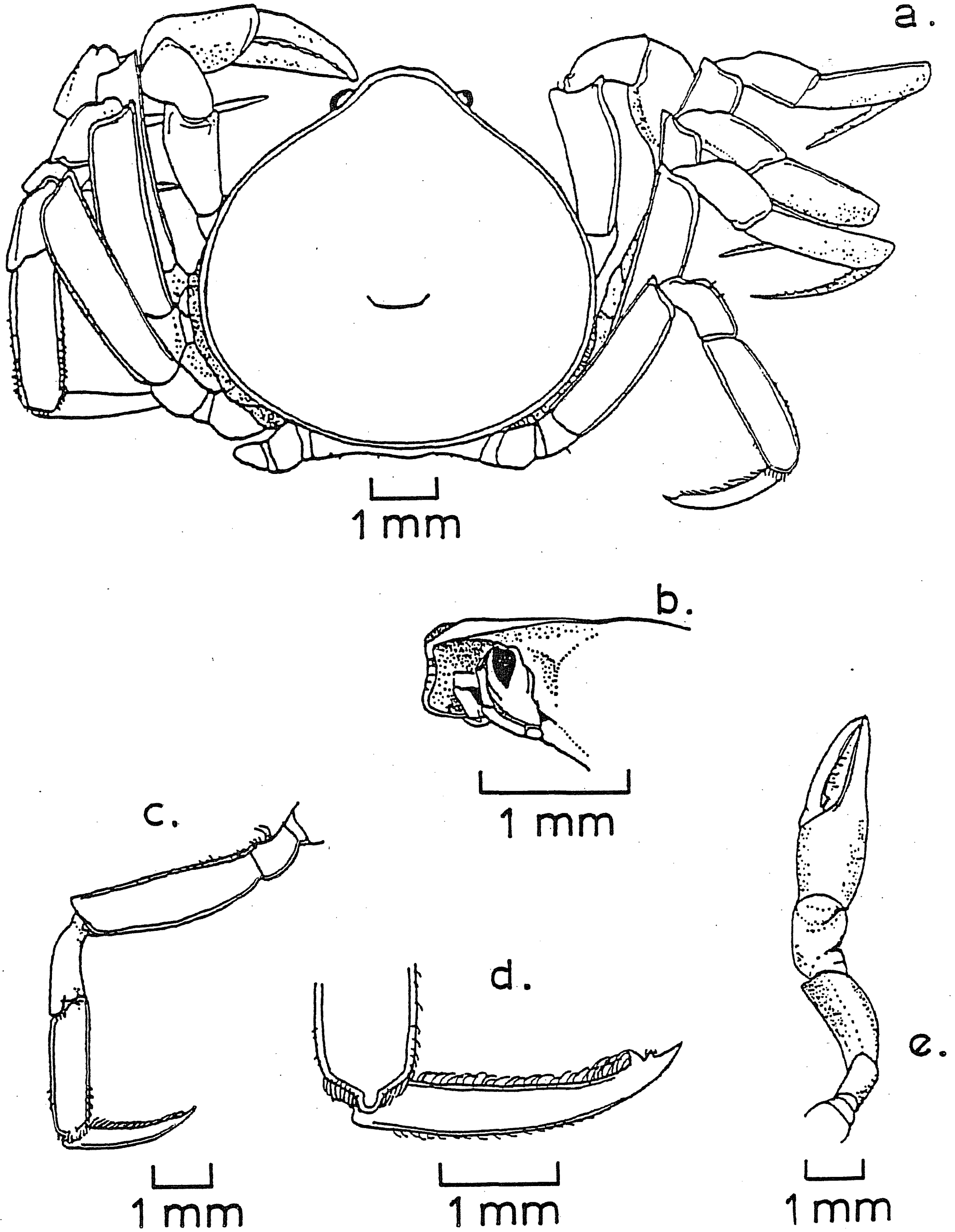


Fig. 74 - Elamena momona: a - male, dorsal view; b - lateral view of rostrum, male; c - left 3rd walking leg, male, posterior view; d - dactylus of left 3rd leg, male, posterior view; e - left cheliped, male (after Melrose, 1975).

Elamena producta Kirk, 1878

Synonymy

Elamena producta Kirk, 1878; Filhol, 1886; Elamena kirki Filhol, 1886; Elamena producta Lenz, 1901; Hutton, 1904; Elamena kirki Hutton, 1904; Elamena producta Chilton, 1906b; Chilton, 1911a; Thomson, 1912; Elamena kirki Tesch, 1918; Elamena producta Tesch, 1918; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Elamena kirki Chilton & Bennett, 1929; Elamena producta Young, 1929; Richardson, 1949a; Dell, 1960; 1963a; Melrose, 1968; Hayward, 1974; Melrose, 1975; Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Wellington, New Zealand.

Distribution

Endemic to New Zealand. Entire east coast of both North and South Islands. On west coast known from Kawerua, between Hokianga and Kaipara Harbours. Also Stewart Island and Chatham Islands.

Diagnosis (Fig. 75a-e)

Carapace subpentagonal in outline, flat or concave in large crabs. As wide as long, narrow in front. Margin of carapace raised upward into a sharp-edged wide rim. Rostrum semi-circular, fused with carapace, tipped by a small median peak indicating the end of the subrostral keel, downwardly deflexed anteriorly, rim ringed by short hooked setae. Ventral keel on rostrum large, thickened, subtriangular. Male cheliped less than twice as long as CW, massive. Female cheliped shorter, less massive. Fingers slender, spooned, as long as palm. Distinct dentation over distal two-thirds of fingers of females and young males, weaker dentation on margins of fingers in adult males, small rounded tooth at base of movable finger. Second pair of legs longest, fourth pair shortest. Dactyls flattened, ventral surfaces have a row of short hairs with two teeth distally. Abdomen of five segments plus telson in both sexes.

Colour

Carapace varying from blackish-brown to olive-brown, red-brown, purple, cream or white with no difference between the sexes. Striking white patches are present at base of last pair of legs. Legs are often purple-tinged and dactyls have two white bands. Cheliped fingers are white distally. Despite this very striking colouration it is strangely difficult to detect a specimen on the bottom of a sandy pool.

Size

Male 17.8 mm CW. Female 13 mm CW.

Habitat

Under large boulders in coarse sand or pebbles on bottom of pools in lower mid-littoral. Coralline turf usually present. Hard shores of moderate exposure. Often reported in shells of living paua (Haliotis iris). E.producta dies quickly (within 3 hours) when removed from water.

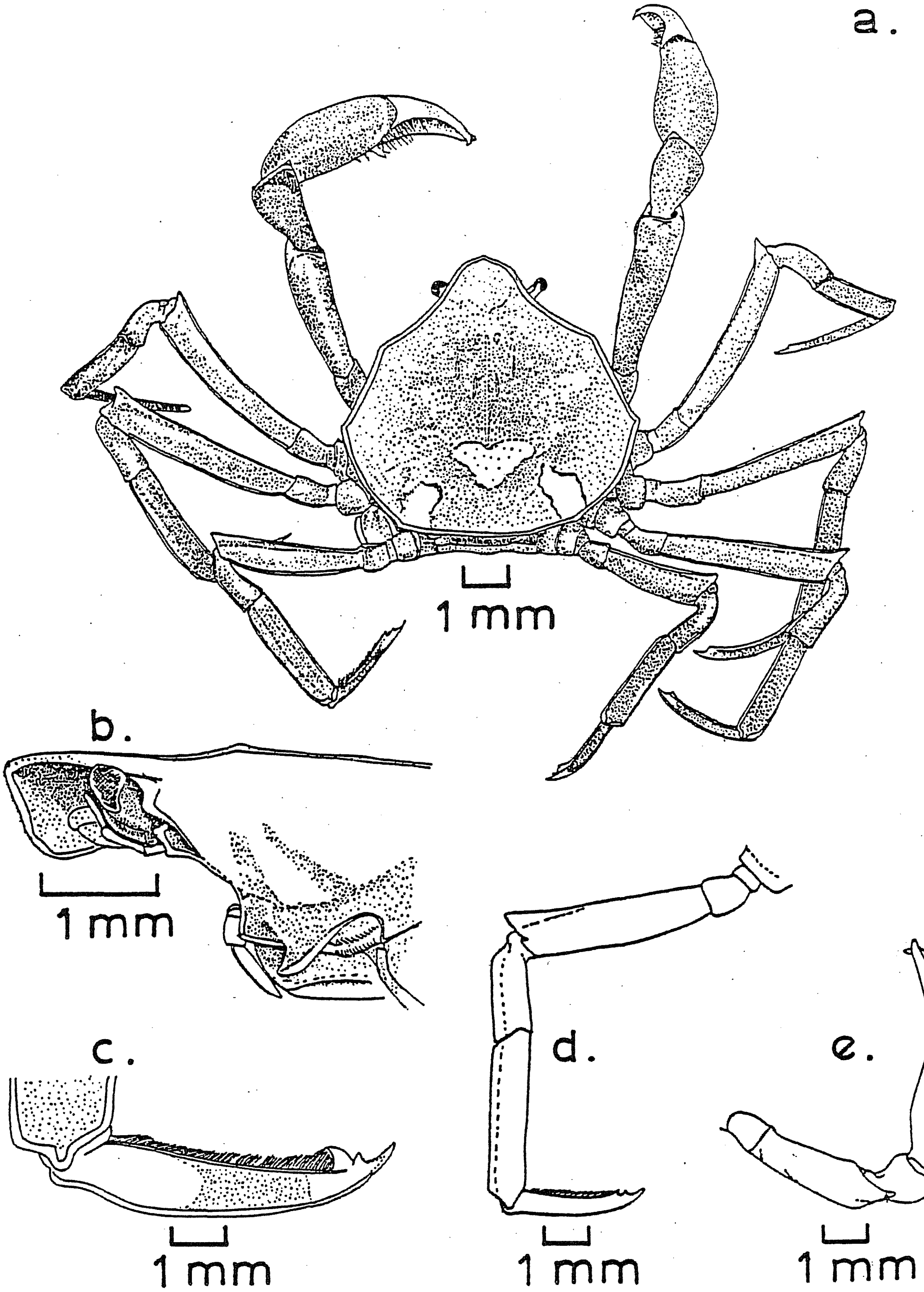


Fig. 75 - Elamena producta: a - male, dorsal view; b - lateral view of rostrum, male; c - dactylus of left 3rd walking leg, posterior view; d - left 3rd walking leg, male, posterior view; e - left cheliped, male (after Melrose, 1975).

Depth

Intertidal rock pools.

Breeding

Ovigerous females have been collected in January, May, July-December. Eggs newly laid, deep orange 0.5 x 0.6mm, near hatching, faint orange 0.55 x 0.6mm diameter.

Development and Growth

Three zoeal stages and first juvenile crab stage described by Wear & Fielder (1985).

Behaviour

When exposed from under a rock E.producta remains motionless for a while and then escapes. It will burrow backwards into the sand until partially covered. This crab has a very characteristic alarm reaction. Repeated prodding results in a posture with chelipeds spread and second walking legs pressed against them and finally with all the legs and chelipeds parallel and at right angles to the carapace. This posture is also adopted when it is dropped into the water, the crab turning over and over like a scrap of red algae drifting in the current. The alarm reaction is held for usually 30 seconds or a minute at the most. Both male and female E.producta have the same 'threat' posture : chelipeds are extended laterally and the fingers spread. The carapace is raised until it is almost vertical, supported by the legs.

Ecology

Not usually seen pursuing food like other more voracious hymenosomatids. In the laboratory it eats pieces of polychaetes held lengthwise in both chelae. Large talitrid amphipods or polychaetes are also eaten. No dead amphipods or polychaetes are accepted. Body usually clean of algal growth or sessile animals. Occasionally carry sponge or Spirorbis tubes.

Paua, Haliotis iris and occasionally H.australis, are host to E.producta but the association is not obligatory as the crab is often found free-living. The crab resides in the slot between the foot and viscera, its long flattened legs attach to the upper part of the foot muscle. Usually only one, but sometimes two or three crabs are found on a host (Poore 1969). Gut contents of the crabs revealed crustacean fragments, mostly parts of amphipods and free-living crabs have similar food in their gut. The paua seems neither to benefit nor suffer from the association.

Habib (1975) found that red cod (Pseudophycis bacchus) from Banks Peninsula ate E.producta in October (0.2% of gut volume), May (0.3%), and July (0.3%).

References

Dell (1963a), Lucas (1980), Melrose (1975).

Halicarcinus cookii (Filhol, 1885)

Synonymy

Hymenicus marmoratus Chilton, 1882; *Hymenicus cookii* Filhol, 1885a; 1886; Hutton, 1904; *Hymenicus marmoratus* Chilton, 1906b; *Hymenicus cookii* Tesch, 1918; *Hymenicus marmoratus* Young, 1929; Chilton & Bennett, 1929; *Halicarcinus cooki* Richardson, 1949a; Ralph & Yaldwyn, 1956; Dell, 1960; ?Hymenosomid Batham, 1965; *Halicarcinus cookii* Melrose, 1968; 1975; Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Cook Strait.

Distribution

New Zealand endemic. East coast of both North and South Islands, also Stewart Island, Chatham Islands.

Diagnosis (Fig. 76a-e)

Carapace octagonal, narrowing anteriorly, as wide as long, convex or flat, with narrow rim. Wide gastrocardiac groove always obvious. Anterolateral border markedly concave, suture between carapace and rostrum convex anteriorly. Carapace sides almost vertical and not inflated posteriorly. Two pairs of lateral teeth below the carapace rim. Rostrum short, trilobular, never projecting past eyes, forming a horizontal platform at same level as carapace. Median rostral lobe fractionally longer. Chelipeds not very massive, even in adult males, length nearly twice CW. Fingers longer than palm, slender, with simple dentation along entire inner edges in both sexes, the teeth enlarged distally. Male movable finger lacks usual large basal tooth. First two pairs of legs subequal in length but as long as chelipeds. Last two pairs of legs shorter, fourth pair shortest. Dactyls bear two irregularly arranged rows of sharply pointed teeth accompanied by short, fine setae. Male and female abdomens each of five segments plus telson.

Colour

Carapace colouration varies greatly and chromatophores react to light intensity. In males carapace is black or brown, usually with splotches of white, yellow, green or orange. In females the colour ranges from pure white through yellow-brown or reddish yellow and green, to pure black. A dark pigmented 'X-mark' is present behind the gastrocardiac groove. Antennules may be predominantly white, black or red, often contrasting strikingly with the carapace. The legs are commonly banded in both sexes. A striking distal white band is present on the propodus of all walking legs. Cheliped colouration is usually similar to the legs. Newly moulted crabs paler.

Size

Male 13mm CW. Females 8.5mm CW.

Habitat

Lives among seaweeds on rocky shores. Microhabitat is within finely divided algal fronds, in holdfasts and among *Corallina* and *Hormosira*. Colour pattern does not seem to be related to algal background.

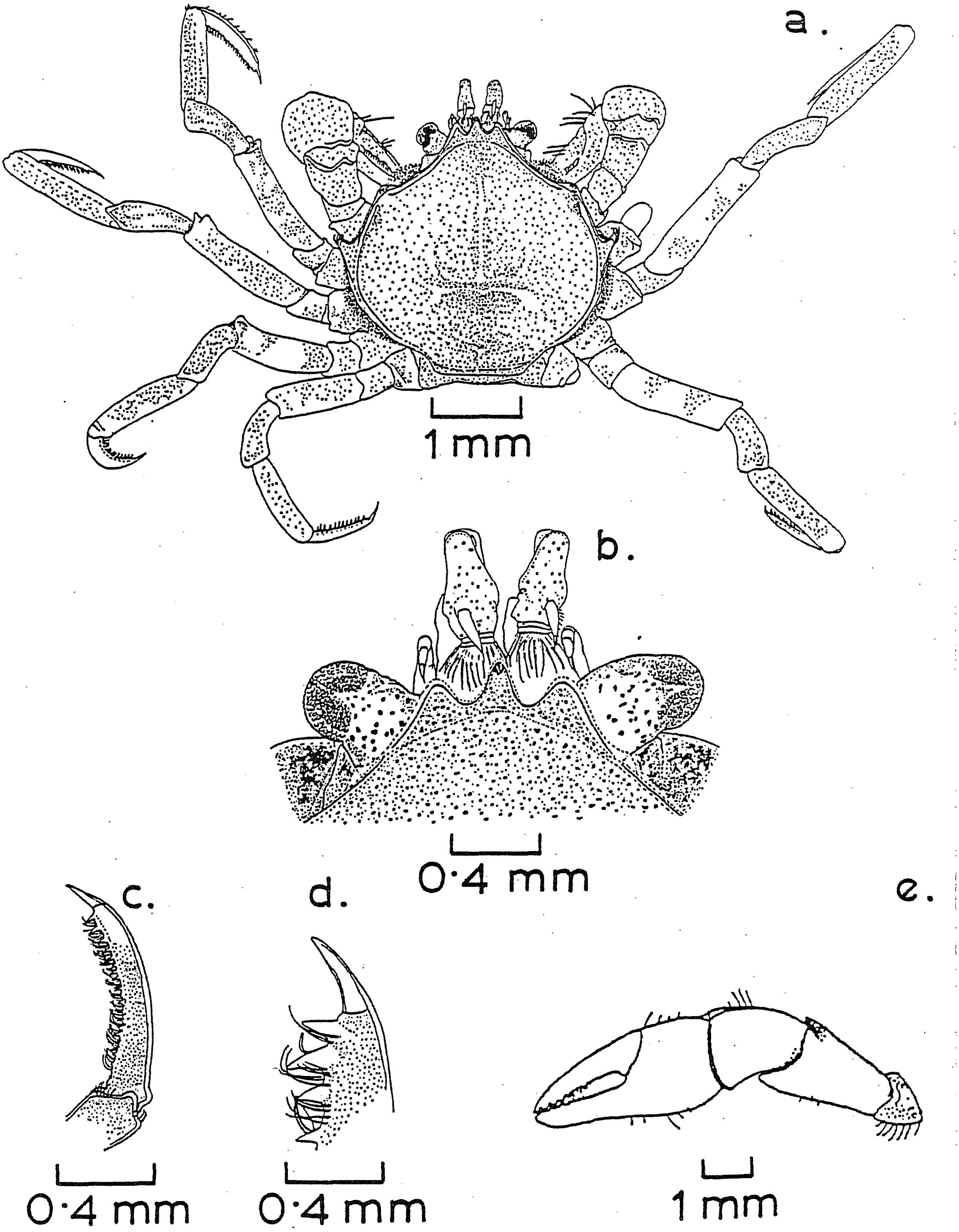


Fig. 76 - Halicarcinus cooki: a - male, dorsal view; b - rostrum, male, dorsal view; c - dactylus of 3rd walking leg, male, posterior view; d - tip of dactylus of 3rd walking leg, male posterior view; e - left cheliped of male, outer face (after Melrose, 1975).

Depth

Intertidal and sub-littoral shallow water.

Breeding

Mating involves hard shell crabs of both sexes. Eggs are faint yellow when new, becoming orange and faintly brown. Ovigerous females have been collected in most months. Females produce a new brood of eggs soon after hatching of the previous one. This results in a high proportion of ovigerous females all the time (Melrose 1975, Wear & Fielder 1986).

Development and Growth

Like other hymenosomatids H.cookii has 3 zoeal stages and no megalopa (Wear & Fielder). Melrose (1975) found that captive crabs moulted only once or twice, usually immediately after capture. Subsequent moulting appeared to be inhibited by laboratory conditions. Crabs 4-5mm CW gained approx. 0.5mm per moult. The modal size class in populations is usually between 3-5mm CW.

Behaviour

H.cookii has a strong, tactile response and the hooked claws give a tenacious grip on seaweed that prevents them being washed away. When dropped into water the legs and chelipeds are tightly folded underneath and this together with the colour pattern makes the crab resemble a piece of seaweed. When threatened larger males will stand up on their walking legs and brandish their unfolded chelipeds forward and upward. A crab lifted off a substrate will briefly remain immobile before running sideways or backing away. Normal locomotion involves both forward and sideways movements. Copulation involves the male clasping the female from underneath and continues for approx. 35 minutes.

Ecology

H.cookii is carnivorous, consuming polychaetes (Perinereis, Lumbriconereis and Neanthys) and especially amphipods (talitrids but not caprellids). The crab stands on 'tip-toes' with chelipeds raised and waved about alternately, the fingers opening and closing. An amphipod caught by the chela is stuffed into the mouthfield where it is dealt with by the mandibles and external maxillipeds. Movement of the prey seems to be essential to initiate grasping.

Carapace usually clear of settling organisms but occasional tubes of Pomatoceros caeruleus and algal sporelings at the 2-4 cell stage are present. H.cookii shows evidence of resistance to osmotic stress and can survive indefinitely in 50% seawater.

Godfriaux (1974a) found small numbers of H.cookii in the stomachs of tarakihi (Cheilodactylus macropterus) captured in the western Bay of Plenty. At Leigh Ozius truncatus will also eat this crab. In Otago Harbour Crump (1969) recorded the starfish Coscinasterias calamaria eating H.cookii. Paddle crabs (Ovalipes catharus) also eat H.cookii (Wear & Haddon 1987).

References

Cassie & Michael (1968), Godfriaux (1974a), Lucas (1971,1980), Melrose (1975), Wear & Fielder (1985), Wood (1968).

Halicarcinus innominatus Richardson, 1949

Synonymy

Cancer orbicularis Fabricius, 1775; Elamena quoyi H.Milne Edwards, 1853; Halicarcinus planatus Heller, 1858; Halicarcinus tridentatus Filhol, 1886; Halicarcinus huttoni Filhol, 1886; Halicarcinus planatus Chilton, 1906b; Halicarcinus planatus var. tridentatus Chilton, 1911a; Halicarcinus planatus Thomson, 1912; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Young, 1929; Balss, 1930; Richardson, 1949a; Halicarcinus innominata Richardson, 1949b, Garth, 1957; 1958; Halicarcinus innominatus Dell, 1960; 1963a; Melrose, 1968; Hayward, 1974; Melrose, 1975; Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Wellington Harbour.

Distribution

Tasmania and New Zealand mainland. Also Stewart Is. and Chatham Islands. Although this species has been recorded from Cape Maria van Diemen and around Auckland, it has not been recorded from around Leigh but is known from Kawerua on the west coast. Probably introduced into Tasmania, see Ecology section, below.

Diagnosis (Fig. 77a-d)

Carapace suboval, broader than long, with a wide rim. Carapace usually naked, deep grooves defining the regions. Rostrum short, not reaching the limit of the eyes, trilobular, all 3 lobes similar in shape and projecting straight forward bearing long tufts of hooked hairs. Frontal region completely separated from the gastric region. Two rudimentary lateral teeth sometimes present on the carapace margins. Chelipeds massive in adult males (length 1.5-1.8 times CW), slighter in females. Fingers longer than palm in both sexes. Deep linear gape in female, a pronounced basal gape in the male, dentation reduced in the male, movable finger has a square tooth basally, tips of fingers barely occluding at all. First two pairs of legs longer than chelipeds, last two pairs a little shorter. Stout dactyli, flattened, ventral edge has a central single row of blunt tubercles with the last two enlarged. Abdomen of five segments plus telson in both sexes.

Colour

Brown with green or black tints, banding on legs rare in mature males. Young specimens have pale yellow carapace flecked with black, orange and white chromatophores.

Size

Males 19mm CW. Mature females 7.5 - 15.5mm CW.

Habitat

Associated with the mussel Perna canaliculus on hard substrates, among seaweeds and fouling organisms on wharf piles and on keels of ships. Also under stones in the intertidal region.

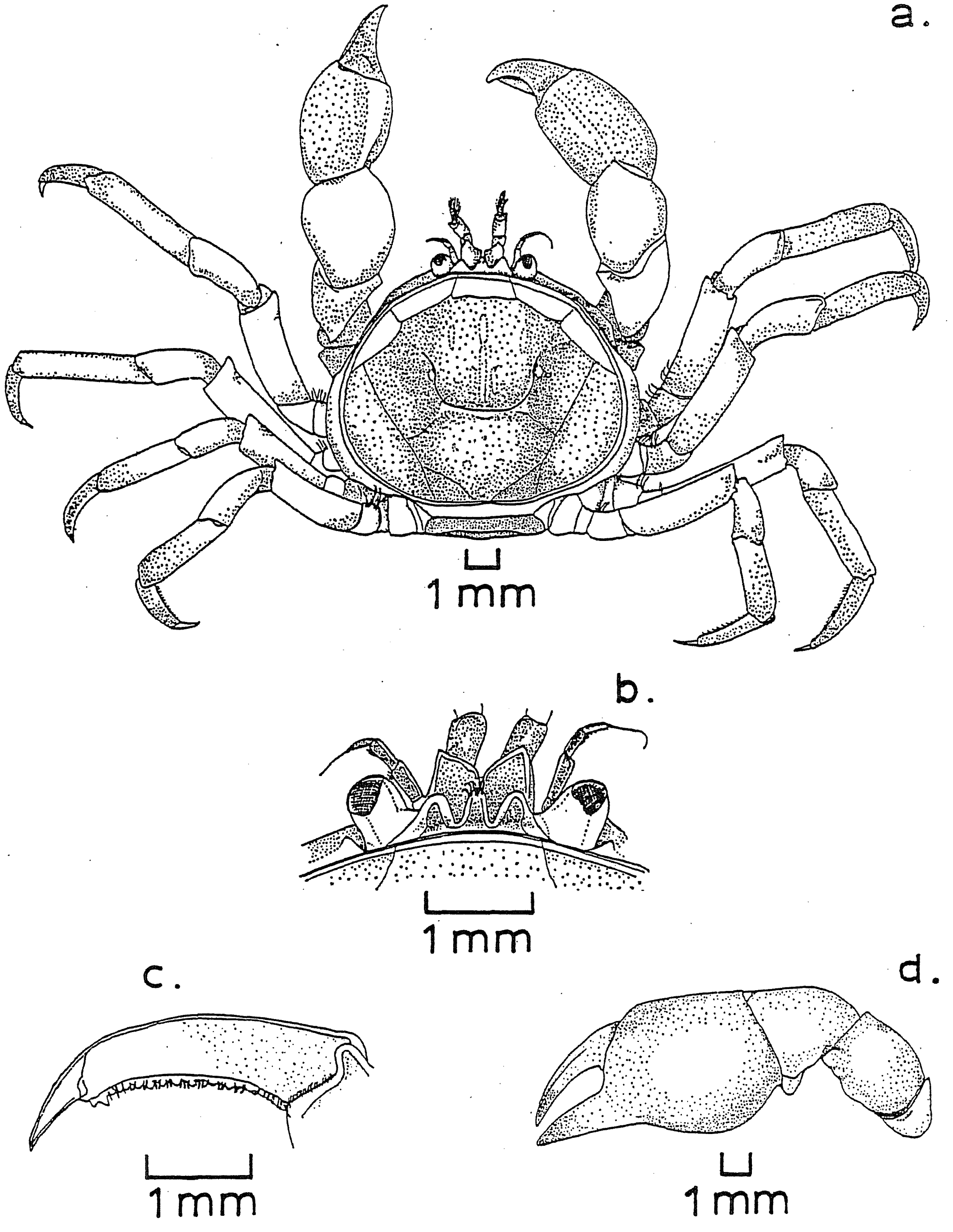


Fig. 77 - Halicarcinus innominatus: a - male, dorsal view; b - rostrum, male, dorsal view; c - dactylus of left 3rd walking leg, male, posterior view; d - left cheliped of male, outer face (after Melrose, 1975).

Depth

Intertidal, especially lower mid-littoral but also in rock pools with Perna.

Breeding

Ovigerous females have been collected in October, December, January, March to May. Eggs newly laid, yellow, 0.36 x 0.34mm, ready to hatch, black, 0.4mm diam. In a sample of 23 females collected in February at Kaikoura all but 3 immature crabs carried eggs (65% newly laid, 35% eyed).

Development and Growth

Probably 3 zoeal stages, zoea 1 described by Wear & Fielder (1985). Females at Kaikoura have a pubertal moult at 7-8mm CW.

Behaviour

When dropped in water H.innominatus floats with legs folded tightly and remains on the bottom upside-down for several minutes before scrambling upright and scuttling off. When threatened the crab rushes forward with chelae high and swinging from side to side, fingers opening and closing. This seems to be the most aggressive of the hymenosomatid crabs. When among mussels the crab hides beneath the valves with its back legs hooked under the edge of the valve. If a paua is present the crab will climb in between the shell and mantle, gripping the mantle edge and searching for food with the chelipeds.

On sand, without other cover, they will occasionally partially bury themselves. With chelae and legs spread they grasp the sand and pull downward, pushing back and forward until limbs and about half the carapace are covered.

Ecology

H.innominatus is a micropredator, consuming polychaetes, tiny bivalves (?Lasea sp.), microgastropods (?Littorina), crustaceans (amphipods, ostracods, other hymenosomatids) and fine organic debris. In the laboratory H.innominatus will eat pieces of mussel and paua and probably eats dead mussels on the shore. One specimen had an anemone, Actinothoe albocincta, on the carapace. Small, settled Perna were sometimes seen on the leg bases and carapace sides of larger crabs. One male had a large barnacle, Elminius modestus on its carapace.

H.innominatus is unique among Australasian marine hymenosomatids in having a trans-Tasman distribution. This is probably the result of man's transportation of the oyster, Ostrea angasi to Tasmania to improve the local oyster industry. The mussel, Perna canaliculus is present in Tasmania, probably introduced with the oyster as well sometime after 1885 (Lucas 1980).

Habib (1975) found that red cod (Pseudophycis bacchus) from Banks Peninsula ate H.innominatus in May (0.6% of gut volume). Also paddle crabs (Ovalipes catharus) from Brighton beach, Christchurch eat this crab.

References

Dell (1963a), Habib (1975), Lucas (1980), Melrose (1975), Wear & Fielder (1985).

Halicarcinus ovatus Stimpson, 1858

Synonymy

?Halicarcinus pubescens Dana, 1852; Halicarcinus ovatus Stimpson, 1858; ?Heller, 1868; ?Halicarcinus planatus Miers, 1876b; Halicarcinus ovatus Targioni-Tozetti, 1877; Hymenosoma planatum Haswell, 1882a; ?Halicarcinus huttoni Filhol, 1885c; 1886; ?Halicarcinus planatus Miers, 1886; Halicarcinus ovatus Miers, 1886; Stebbing, 1900; Fulton & Grant, 1906; Stimpson, 1907; ?Chilton, 1909; ?Chilton, 1911a; ?Halicarcinus huttoni Chilton, 1911a; Halicarcinus ovatus Kemp, 1917; Tesch, 1918; Hale, 1927a; 1927b; ?Chilton & Bennett, 1929; ?Balss, 1930; Lucas, 1971; Griffin & Yaldwyn, 1971; Griffin, 1972; Lucas, 1972; Melrose, 1975; Lucas, 1975; 1980. Not Halicarcinus ovatus Cano, 1888; Richardson, 1949b.

Type Locality

Port Jackson, Australia (no type specimens are extant, Lucas, 1980).

Distribution

Australia: Victoria, New South Wales, Western Australia, South Australia, Tasmania. ?New Zealand: Port Chalmers, Otago.

The specimen reported by Filhol (1886) as H.huttoni was collected by Quoy and Gaimard but the exact locality is not given. The inclusion of H.ovatus in the New Zealand fauna depends upon the synonymy of H.huttoni and H.ovatus. Given the absence of type specimens this cannot be resolved. The details of this complex problem are explained by Melrose (1975). No further specimens have been collected from New Zealand.

Diagnosis (Fig. 78a-e)

Carapace suboval, broader than long with an octagonally angled rim. Trilobular rostrum arising just below carapace rim, concavities between the lobules continuing under the rim. Lobules small, close together, median lobe a little longer than laterals, all directed straight forwards. Lower edge of rostrum with a central peak adjacent to the inter-antennular septum. Anterolateral border concave or straight, rim above rostrum straight, frontal region not produced. Two pairs of lateral teeth, first small, obtuse, marked by an angle in the carapace rim, second medium in size, acute projecting upward to the carapace rim. Postocular lobe and antennal spine both reduced, almost absent. Chelae of male large, greatly arched, inflated and deep, dentation reduced, basal gape shallow. Inner surface of propodus sparsely hairy. First pair of walking legs longest, longer than chelipeds, others successively shorter. Dactylus shorter than propodus, flattened, slender, curved, ending in long, strong claw, ventral edge with short, curved hairs either side between two very closely approximated rows of short teeth. Abdomen of five segments plus telson in both sexes. Lucas (1980) has detailed variation of the rostrum and legs of adults from different habitats.

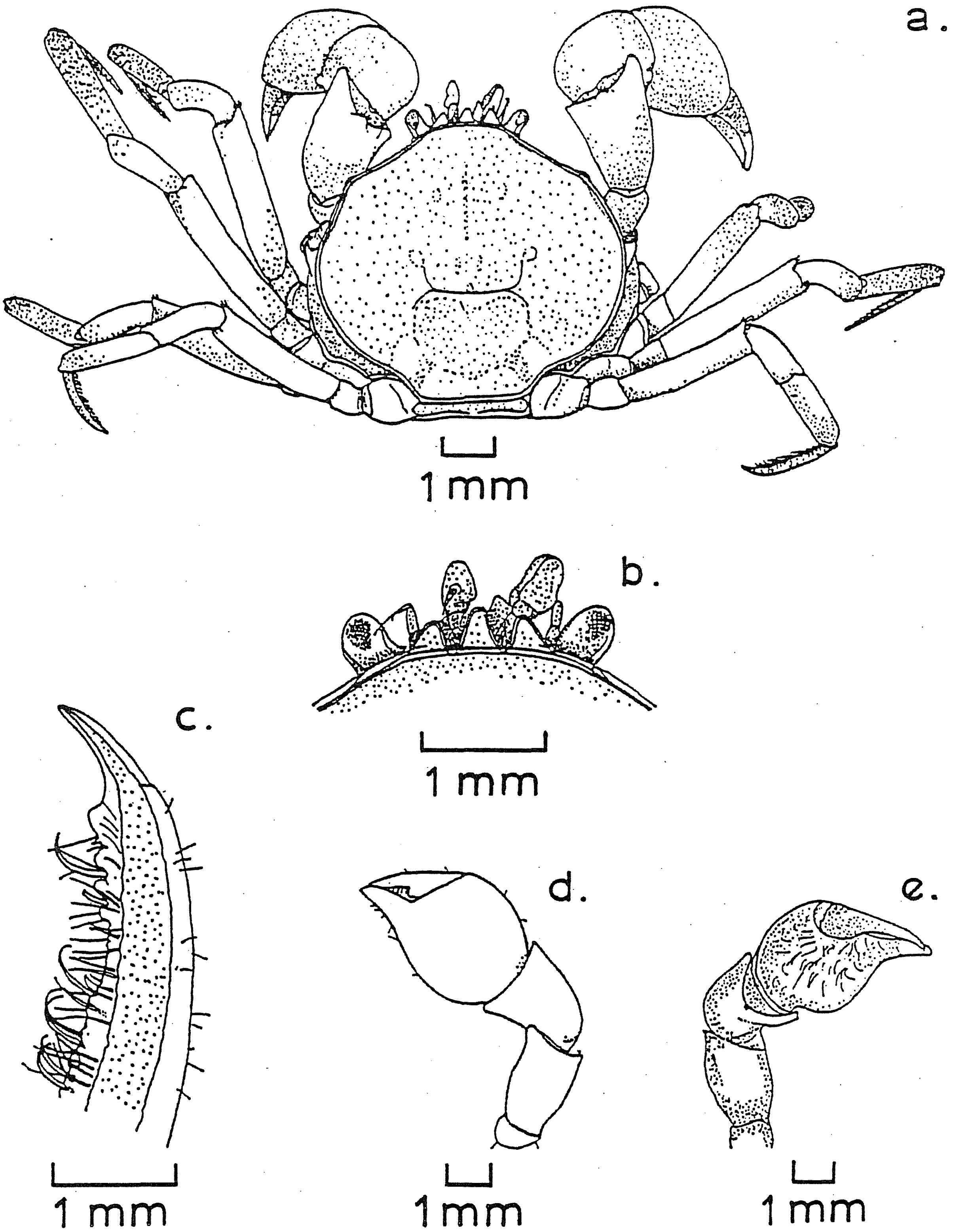


Fig. 78 - *Halicarcinus ovatus*: a - male, dorsal view; b - rostrum, male, dorsal view; c - tip of dactylus of left 3rd walking leg, male, posterior view; d - left cheliped, male, outer face; e - left cheliped, male, inner face (after Melrose, 1975).

Colour

Very variable: brown, red, orange, green, yellow, white and black splotches and mottling, pure white, brown, red-brown or black. Females more often having speckled coloration than the males.

Size

Male 7mm CW. Female 6.5mm CW.

Habitat

Marine, littoral and coastal sublittoral. Among Mytilus, under rocks in weed.

Depth

Intertidal, shallow water.

Breeding

Ovigerous females have been collected all year round at Perth, W.A. Egg diameter 0.29-0.37mm depending on origin of females (Lucas 1971). Females can mate when hard or soft-shelled and may extrude eggs within two days after the pubertal moult. Successive broods are produced rapidly with little delay in between and without the need to copulate. As a result a high proportion of females are always ovigerous. A 6.5mm CW female can produce approx. 850 eggs per brood (Lucas 1975). Like several other hymenosomatid species the eggs of H.ovatus are irrigated by a water current which flows over the eggs and forwards through the branchial cavities (Lucas 1980).

Development and Growth

Three zoeal stages, polymorphic, with variable carapacial spines (Lucas 1971). Megalopa absent, third zoea moults directly to first crab stage.

Behaviour

H.ovatus only swims as an escape reaction.

Ecology

Gut contents of hymenosomatid crabs suggests that they are omnivores and that plant detritus is a major component. In addition to detritus crustacean remains, including amphipods have been found in H.ovatus. This crab can capture live Artemia nauplii in the laboratory when they made contact with the legs (Lucas 1980).

References

Lucas (1971, 1972, 1975, 1980), Melrose (1975).

Halicarcinus planatus (Fabricius, 1775)

Synonymy

Caneer planatus Fabricius, 1775; Halicarcinus planatus White, 1846a; Miers, 1876a; Hodgson, 1902; Hutton, 1904; Chilton, 1909; ?Chilton & Bennett, 1929; Bennett, 1930; Halicarcinus ovatus Richardson, 1949a; Halicarcinus planatus Richardson, 1949b; Garth, 1958; Dell, 1963a; Bennett, 1964; Hartnoll, 1966; Garth, Haig & Yaldwyn, 1967; Melrose, 1968; Boschi, Scelzo & Goldstein, 1969; Melrose, 1975; Fenwick, 1975; Yaldwyn, 1975; Richer de Forges, 1977; Lucas, 1980; Wear & Fielder, 1985. (See Garth, 1958 and Melrose, 1975 for a complete synonymy.)

Type Locality

?New Zealand (see Garth 1958). This is unlikely to be true as H.planatus probably does not occur on the mainland.

Distribution

Circumpolar: Chile (38°S to 55°S), Falkland Islands, South Orkney, Prince Edward, Kerguelen, Macquarie, Campbell and Auckland Islands, off Gannett Island and ?Cook Strait, New Zealand.

Diagnosis (Fig. 79a-e)

Carapace suboval, broader than long, convex, with regions not usually obvious and entirely surrounded by a narrow rim. Gastrocardiac groove strongly deflexed centrally to form a shallow V. Short tridentate rostrum just reaching to the limits of the small eyes, teeth arising far apart, immediately below the carapace rim. Post-ocular lobe very reduced. Median rostral tooth shortest, lateral lobes sloping downward and outward. Two pairs of lateral teeth present well below the carapace rim, the first obtuse, the second acute. Chelipeds of male moderately inflated, basal gape narrow with a tiny tooth on the dactyl, teeth well developed on the distal third of the fingers. Chelipeds fairly massive in larger males. First three pairs of legs subequal, decreasing in size posteriorly, fourth legs shorter. Segments of legs stout, dactylus moderately curved, short, armed with two irregular rows of short, pointed teeth. Male and female abdomens each of five segments plus telson.

Colour

Slaty-blue, greyish brown, or reddish-brown, with banded legs.

Size

Male 23.5 mm CW. Female 19 mm CW. See Melrose (1975) for data showing tendency of size to increase in decreasing temperature.

Habitat

Sheltered shores, under stones and among algae, sub-tidal.

Depth

Most common in the intertidal but recorded down to 270 m (Garth 1958).

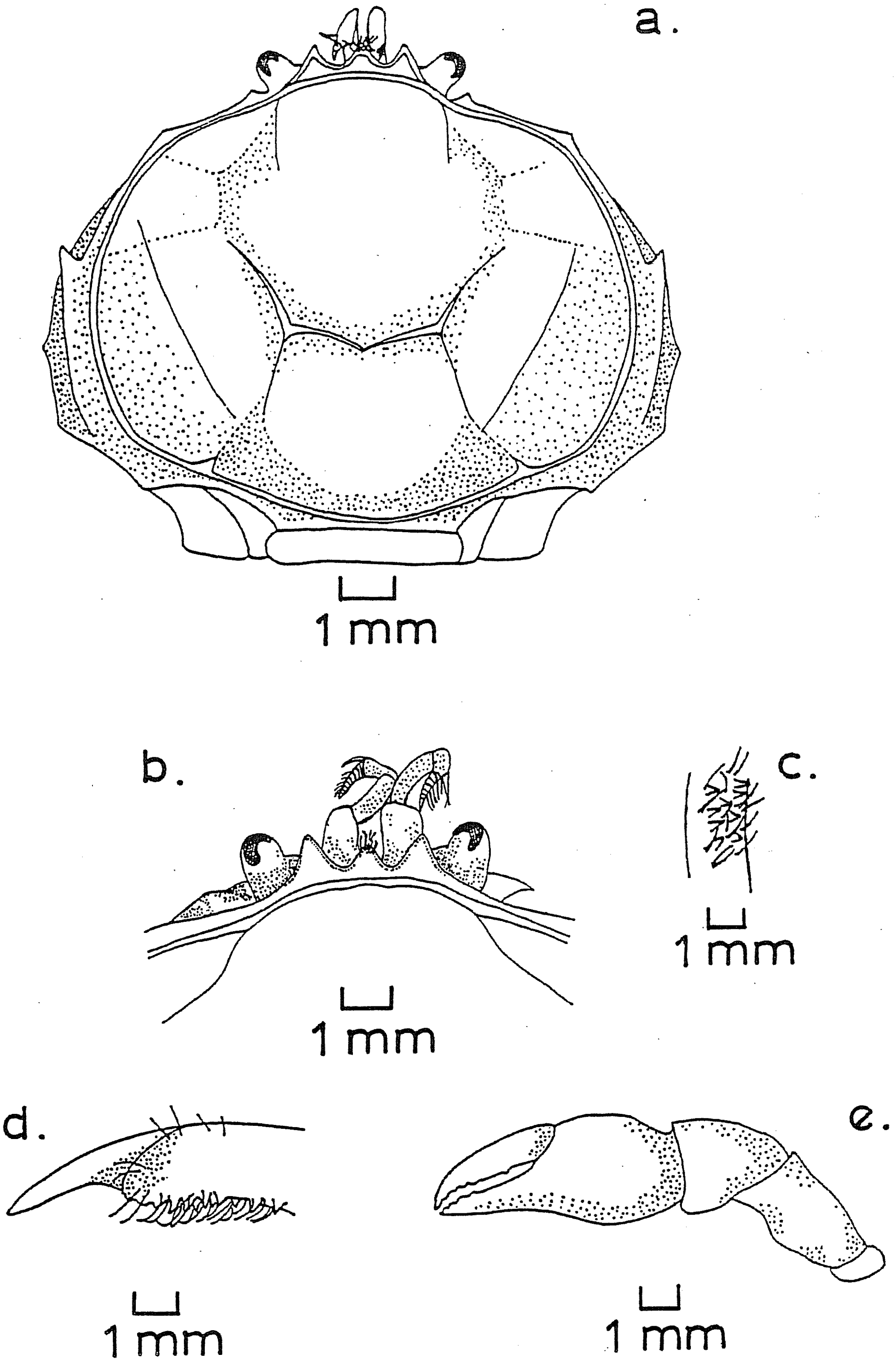


Fig. 79 - *Halicarcinus planatus*: a - male, dorsal view; b - rostrum, male, dorsal view; c - ventral edge of dactylus of left 3rd walking leg, male; d - tip of dactylus of left 3rd walking leg, male; e - left male cheliped, outer face (after Melrose, 1975).

Breeding

Mating involves hard shell crabs of both sexes (Richer de Forges 1977). Some females may copulate before their pubertal moult (i.e. <13mm CW). This is possible because their genital apertures are essentially in the mature condition. Similarly prepubertal males may also achieve successful copulation because the first and second pleopods are sufficiently large. At Kerguelen Island, almost all mature females were ovigerous throughout the autumn to spring breeding season. Ovigerous females from different parts of the species range have been collected in most months. H. planatus females produce comparatively large numbers of small eggs (Lucas 1980). A 13.7mm CW female had 1400 eggs but the exact egg size and colour has not been recorded.

Development and Growth

Wear & Fielder (1985) have described the three zoeal stages and first juvenile crab stage. There is no megalopa stage. Roberts (1972b) found that the occurrence of first stage zoea in the plankton was restricted to August-December with a peak in late September. The occurrence of gravid females as early as January-May suggests that egg development may require many months (8 months). If this is correct females could only produce a single brood of eggs each year. Zoeal development in the plankton may require a further 6 months (Richer de Forges 1977). Although Boschi et al. (1969) raised larvae at 11-13^{o}C and development was completed in about one month.

Richer de Forges (1977) has studied growth rate and relative growth of H.planatus at the Kerguelen Islands. Growth involves 11 instars and CW increases by about 0.5 mm/moult for juveniles rising to about 1.5mm/moult for crabs greater than 8mm CW and thereafter remains approximately constant. Intermoult interval is about 40 days when CW = 2.5mm, increasing linearly to 125 days when CW = 9.5mm. The terminal pubertal moult occurs when CW is about 14mm. Sexual identity of the crabs is not apparent until after the second moult. Percentage moult increments varies from 31.5% for juveniles (<2.5 mm CW) declining linearly to 11.6% for adult males and females >12 mm CW. The mean percentage moult increment was 22.6%. Moult increments may vary from place to place resulting in different maximum sizes being attained. Larger sizes tend to occur in colder waters (see Melrose 1975). Relative growth of abdomen width is positively allometric for immature females (b = 1.7) but isometric for males and mature females (b = 0.9-1.02). Cheliped propodus length is positively allometric for immature and mature males (b = 1.11-1.16) but isometric for immature and mature females (b = 1.039-1.084). Relative growth of propodus width and thickness tends to be positively allometric (b = 1.13-1.37) for both sexes.

Behaviour

Unknown.

Ecology

With the period of egg and zoeal development probably exceeding 12 months, recruitment at high latitudes does not occur until the following year and juveniles require almost a further year to reach sexual maturity after 11 pre-pubertal instars (Richer de Forges 1977). Thus reproduction occurs at approximately two years of age and females may only breed twice if they survive to the 3+ age group. It is likely that H.planatus is the longest-lived of all the hymenosomatids which usually have an annual cycle (Lucas 1980).

Richer de Forges (1977) recorded densities up to 150/m^2 and he suggested that in these sub-antarctic habitats H. planatus plays a significant role in food webs. At Kerguelen Island many teleost fish prey on this crab and sea birds which feed in the littoral zone may also eat them. H. planatus guts contain sand grains, shell fragments, remnants of algae, diatoms, polychaete setae and fragments of copepods and isopods which suggests that live prey are captured.

References

Boschi, Scelzo & Goldstein (1969), Fenwick (1975), Garth (1958), Hartnoll (1966), Lucas (1980), Melrose (1975), Richer de Forges (1977), Wear & Fielder (1985).

Halicarcinus tongi Melrose, 1975

Synonymy

Halicarcinus sp.nov. Melrose, 1968; Halicarcinus tongi Melrose, 1975; Lucas, 1980; Wear & Fielder, 1985 (list).

Type Locality

Great Barrier Island.

Distribution

New Zealand endemic. Recorded from Little Barrier Is., Port Jackson, Coromandel, Mayor Island, Bay of Plenty, off Gannet Is., Wanganui, Castlepoint, Wellington, Queen Charlotte Sound, Marlborough, Tasman Bay, Nelson, also Albatross Point, Antipodes Islands.

Diagnosis (Fig. 80a-d)

Carapace suboval, narrowing in front, longer than wide, gastrocardiac groove curved, short cervical grooves continuing curve forward. A pair of lateral angles below the carapace rim. Tridentate rostrum arising at carapace level, long, projecting well past eyes. Teeth narrow, blunt, median tooth slightly shorter, concavities between teeth almost reach suture at base of rostrum. Postocular lobe large and acute. Chelipeds not massive, half as long as CW. Fingers in both sexes dentate along most of length, complete occlusion in female, a tiny gape in male, small, square tooth on movable finger. First three pairs of legs longer than chelipeds (almost twice CW), fourth pair much shorter. Dactylus as long as propodus, strongly curved, flattened, very slender, ventral edge has single row of large, narrow, sharp, recurved teeth, increasing in size distally. Abdomen of five segments and telson in both sexes.

Colour

Greyish brown or yellow brown when preserved.

Size

Male and female 6.5mm CW.

Habitat

Unknown.

Depth

Deep water, 55-494m. This is the deepest record of any hymenosomatid species.

Breeding

Ovigerous females have been collected in November.

Ecology

A small male dredged off Little Barrier Is. in February, 1957 was attached to Aphanipathes.

References

Lucas (1980), Melrose (1975).

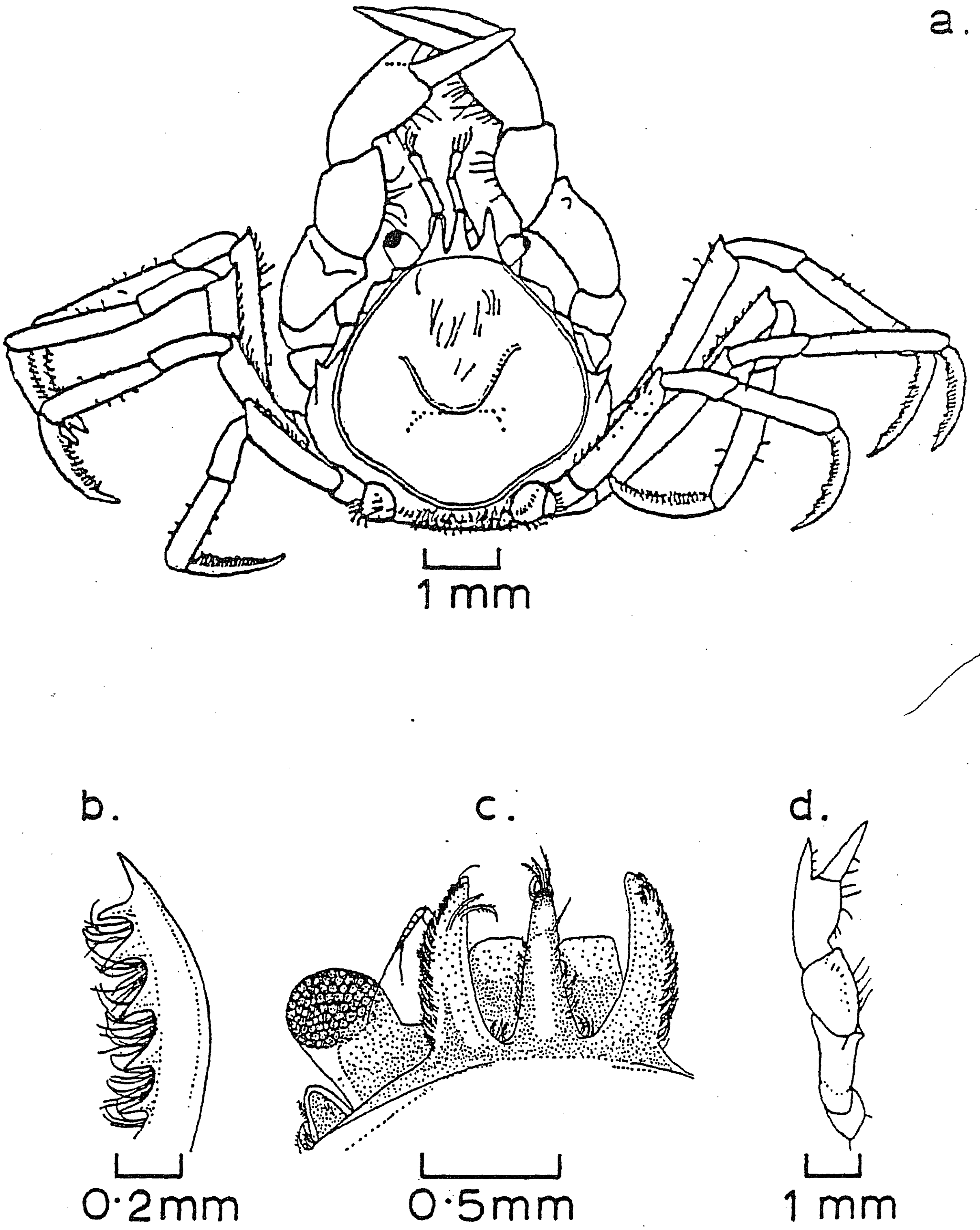


Fig. 80 - *Halicarcinus tongi*: a - male, dorsal view; b - tip of dactylus of left 3rd walking leg, male, posterior view; c - rostrum, male, dorsal view; d - left cheliped, male, outer face (after Melrose, 1975).

Halicarcinus varius (Dana, 1851)

Synonymy

Hymenicus varius Dana, 1851; Hymenicus novi-zelandiae Dana, 1851; Hymenicus varius Dana, 1852; Heller, 1868; Miers, 1876b; Hymenicus edwardsi Filhol, 1885a; Hymenicus edwardsi Filhol, 1886; Hymenicus varius Hutton, 1904; Thomson, 1912; Halicarcinus varius Kemp, 1917; Hymenicus edwardsi Tesch, 1918; Hymenicus varius Tesch, 1918; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Halicarcinus planatus Powell, 1936; Halicarcinus edwardsi Graham, 1939; Halicarcinus sp.15 Richardson, 1949a; Halicarcinus edwardsi Richardson, 1949b; Halicarcinus cooki Ralph & Yaldwyn, 1956; Halicarcinus varius Melrose, 1968; 1975; Lucas, 1980; Marsden, 1981; Wear & Fielder, 1985, Horn & Harms, 1988.

Type Locality

Bay of Islands, New Zealand.

Distribution

Endemic to New Zealand, North, South and Stewart Is. Also Chatham Islands.

Diagnosis (Fig. 81a-d)

Carapace subcircular, narrowing anteriorly, as wide as long, usually slightly convex. Carapace rim uninterrupted by angles, wide gastrocardiac groove always obvious, concave, upper surface of carapace sparsely covered with thin, curved hairs. Two pairs of lateral teeth on sides of carapace situated well below the rim. Suture between rostrum and carapace is straight. Rostrum originating at carapace level, forming a horizontal platform, sloping downward anteriorly. Apex of rostrum variable, being rounded or trilobular, with median lobe projecting further than laterals, not reaching past eyes. Deep ventral ridge along whole rostrum length. Postocular lobe long. Chelipeds hairy, almost twice CL in large males, only just longer than CL in small specimens. Fingers longer than palm, tapering distally, basal gape wide in both sexes, large basal tooth on movable finger in male, occluding along distal third where dentation is sharp. First three pairs of legs slender, hairy, longer than chelipeds (1.6-2.0 times CL), last pair shorter. Dactylus longer than propodus, very flattened, slender, ventral edge with very fine, small, pointed teeth in two very close rows, tooth adjacent to claws enlarged and recurved. Abdomen of five segments plus telson in both sexes.

Colour Carapace of large males predominantly dark brown, others pale green. White or yellow blotches at base of last pair of legs. Fingers of chelae white-tipped and there is a striking red or orange band. Legs brown and unbanded.

Size

Male 10.4mm CW. Female 9.8mm CW.

Habitat

In littoral zone H.varius is found in sheltered areas among algae (Carpophyllum, Sargassum, Hormosira), on rocks or under stones, in Zostera on harbour flats and in sandy areas. It is

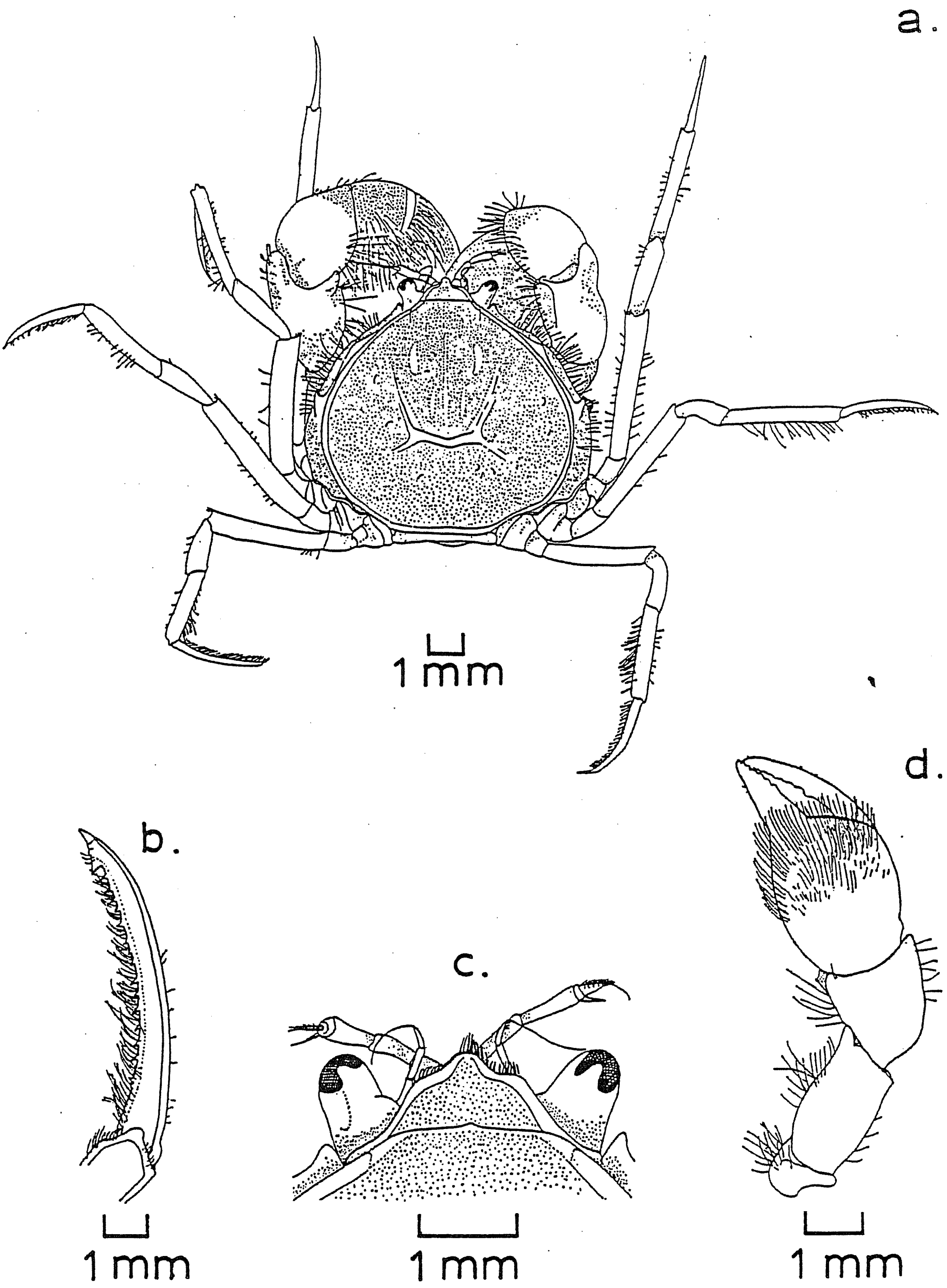


Fig. 81 - Halicarcinus varius: a - male, dorsal view; b - dactylus of left 3rd walking leg, male, posterior view; c - rostrum, male, dorsal view; d - left cheliped of male, outer face (after Melrose, 1975).

also common subtidally in Carpophyllum and associated with the bivalves Maoricolpus, Dosinula and Tawera. Not found where there is a high level of silt.

Depth

Intertidal to 30m.

Breeding

Ovigerous females have been collected January, February and April- December. Probably breeds all year round. Eggs newly laid, light olive-green, 0.26mm diam., ready to hatch, orange, 0.36mm.

Development and Growth

First zoea described by Wear & Fielder (1985). Complete larval development through three zoeae to juvenile crab recorded by Horn & Harms (1988). They found that larval development required 3-4 weeks at 16°C.

A female 18.6mm CW, collected at Kaikoura in December moulted overnight in the laboratory, increasing its CW by 14% and laid a clutch of eggs while still soft.

Behaviour

H.varius clings closely to seaweed but not as strongly as H.cookii or Neohymenicus pubescens. When dropped into water H.varius floats passively down with legs extended, swimming was rarely observed. Burrowing occurred by levering the hind part of the carapace into the sand using thrusting movements of the legs. Chelae are used very little in burrowing. When two males meet they adopt a threat posture with chelipeds extended outwards and fingers spread, sometimes grasping the opponent's chelae. Pursuit sometimes ensued (Melrose, 1975).

Ecology

H.varius reaches densities of 4-12 crabs per 0.1m^2 in summer, being most abundant in Zostera beds. There is a marked resistance to osmotic stress with some crabs surviving 2-20 days in fresh water. The burrowing habit helps H.varius to survive desiccation during tidal exposure. This crab eats amphipods, polychaetes and small shrimps. When starved they graze on fronds of Sargassum using chelae. Solitary bryozoans sometimes occur on the carapace.

References

Horn & Harms (1988), Lucas (1980), Melrose (1975), Wear & Fielder (1985), Wood (1968).

Halicarcinus whitei (Miers, 1876)

Synonymy

Halicarcinus depressus White, 1846a; 1847; Elamene whitei Miers, 1876a; 1876b; Elamena whitei Hutton, 1882; Filhol, 1886; Hutton, 1904; Tesch, 1918; Chilton & Bennett, 1929; Halicarcinus whitei Gordon, 1940; Richardson, 1949a; Melrose, 1968; 1975; Knox & Bolton, 1978a; Knox & Fenwick, 1978; Knox, Bolton & Hackwell, 1978; Lucas, 1980; Knox, 1983a; Wear & Fielder, 1985.

Type Locality

Bay of Islands, New Zealand.

Distribution

Endemic to New Zealand. North and South Islands and also Stewart Island.

Diagnosis (Fig. 82a-d)

Carapace suboval, longer than broad, narrowing in front, flat or convex, covered by felt of fine, short hairs. Gastrocardiac groove evident after removal of hairs. Sides of carapace very oblique and hairy in large males, branchiostegite projections large. Rostrum arising from upper carapace level, extending well past eyes, narrowing and deflexed. Rostrum trilobate, central lobe largest, postocular tooth large. Chelipeds of male large (length 1.5 - 2 times CW) and hairy, propodus as deep as long, pronounced basal gape and large square tooth on movable finger of male, distal third of fingers shallowly dentate. Linear gape of female fingers also large, lined with hairs. First three pairs of legs subequal, longer than chelipeds. Fourth legs much shorter. Dactyli very flat, slender, curved, tapering to long, terminal claw, ventral edge with single row of curved, sharp teeth, double row of curved setae either side of teeth. Abdomen of five segments plus telson in both sexes.

Colour

Carapace green, yellow, grey or brown sometimes finely speckled with white, black, cream or green. There may be a pair of small, white patches at base of last pair of legs and another white patch on the posterior margin. Distal half of dactylus of walking legs and chelipeds is white and a red basal band on cheliped fingers is common. There may also be dark bands on walking legs.

Size

Male 12.5mm CW. Female 11mm CW.

Habitat

Among Zostera on harbour flats, in sand of sheltered, open beaches and also in estuaries. Sediment particle size coarse to fine sand. Often found with H.varius but unlike this species never occurs in seaweed.

Depth

Intertidal, shallow water.

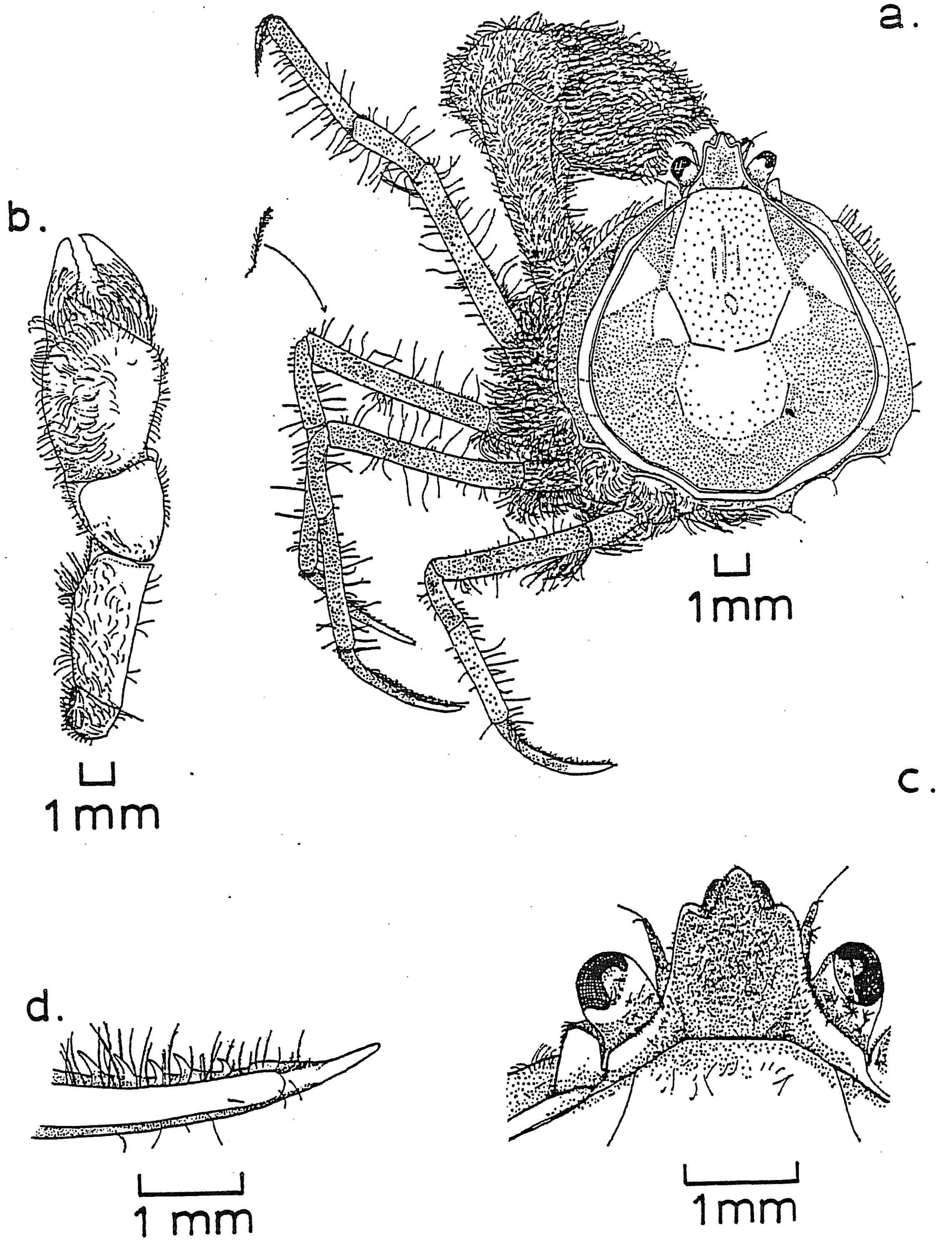


Fig. 82 - Halicarcinus whitei: a - male, dorsal view; b - left cheliped, male, outer face; c - rostrum, male, dorsal view; d - tip of left 3rd walking leg, male, posterior view (after Melrose, 1975).

Breeding

Ovigerous females have been collected in February, April-May, August, October-December. Eggs about to hatch, light green, 0.41mm diam.

Development and Growth

Probably 3 zoeal stages, first zoea described by Wear & Fielder (1985). First juvenile crab unknown. Moulting common in smaller specimens, especially after a large feed of worms. Moulting not observed in large males over 10mm CW.

Behaviour

Prodding the crab results in immobility, burrowing, or spreading of chelipeds. Cheliped-spreading resulted when two large males met. When dropped into water they float down with legs extended. Hairs on the carapace and legs trap debris which helps the crab blend with the surrounding bottom. *H.whitei* swims for short distances using leg movements similar to those used in walking. Burrowing is achieved slowly by pushing the rear end into the sand and with legs radiating outward it rocks back and forth until only the rostral end is exposed.

Ecology

Densities may reach $8m^2$ in summer (Melrose 1975). Wood (1968) found similar densities at Howick, Auckland (mis-identified as *H.cookii*). *H.whitei* is very tolerant of lowered salinities and can survive in freshwater for long periods. Also it is more resistant to desiccation than any of the other New Zealand hymenosomatid crabs. In the field this crab has been observed eating the polychaete *Perinereis*. It will also scoop up handfuls of sand and pass them to the maxillipeds. Starved crabs will readily eat *Zostera* or algae. *H. whitei* differs from *H.cookii* in consuming motionless food when contacted.

King & Clark (1984) found that rig (*Mustelus lenticulatus*) from Golden Bay ate small numbers of *H.whitei*. In the Avon-Heathcote Estuary Kilner (1974) found that sand flounder (*Rhombosolea plebeia*) ate this crab. Also parore (*Girella tricuspidata*) from Whangateau Harbour eat small numbers of *H.whitei* (Davenport 1979). In the Ahuriri Estuary, near Napier, Kilner & Akroyd (1978) found that short-finned eels (*Anguilla australis*), river flounder (*R.retiaria*), kahawai (*Arripis trutta*) and the cockabully (*Tripterygion nigripenne*) all preyed upon this crab. *H.whitei* is eaten by the paddle crab (*Ovalipes catharus*) (Wear & Haddon 1987).

References

King & Clark (1984), Kilner (1974), Kilner & Akroyd (1978), Lucas (1980), Melrose (1975).

Halimena aote~~o~~aroa Melrose, 1975

Synonymy

Gen.nov. sp.nov. Melrose, 1968; Halimena aoteoroa Melrose, 1975; Lucas, 1980, Lucas & Hicks, 1981; Wear and Fielder, 1985 (list).

Type Locality

Seal Reef, Kaikoura Peninsula.

Distribution

Endemic to New Zealand. Recorded at Goat Is., Leigh, Castlepoint, Cape Runaway, Lyttelton, Potato Point, Otago.

Diagnosis (Fig. 83a-d)

Carapace suboval, longer than broad (length 1.2-1.4 times CW), narrowing anteriorly, slightly convex dorsally and devoid of grooves. Rostrum as long as wide, tapering to narrowly rounded tip. There is a distinct groove between rostrum and carapace. Rostrum dorsally convex from side to side, curving steeply downward anteriorly, thickened ventrally but without keel. Chelipeds a little longer than CW, slender. Fingers without a gape, nearly twice as long as palm. Completely occluding. First pair of legs longest, fourth pair shortest. Dactyls flattened, tapering, ventral edge with row of curved hairs with a small blunt tooth distally. Abdomen of five segments plus telson in both sexes.

Colour

Similar to Elamena producta. Reddish-brown, ends of dactyli white. A dark stripe across the region of the suture at base of rostrum.

Size

Male 4.0mm CW. Female (ovig.) 6.2mm CW, immat. 3.8mm CW.

Habitat

Holdfast of Carpophyllum plumosum and among Caulerpa sp. and Cystophora torulosa.

Depth

Sub-littoral, shallow water.

Breeding

Unknown. A mature male has been collected (Lucas & Hicks 1981).

Development and Growth, Behaviour

Unknown.

Ecology

Unknown. Apparently a very rare species, only 5 have ever been collected. A 4mm CW male has been recovered from the stomach of a moki (Latridopsis ciliaris) at Kaikoura (C. Duffy, pers. comm.).

References

Lucas (1980), Lucas & Hicks (1981), Melrose (1975).

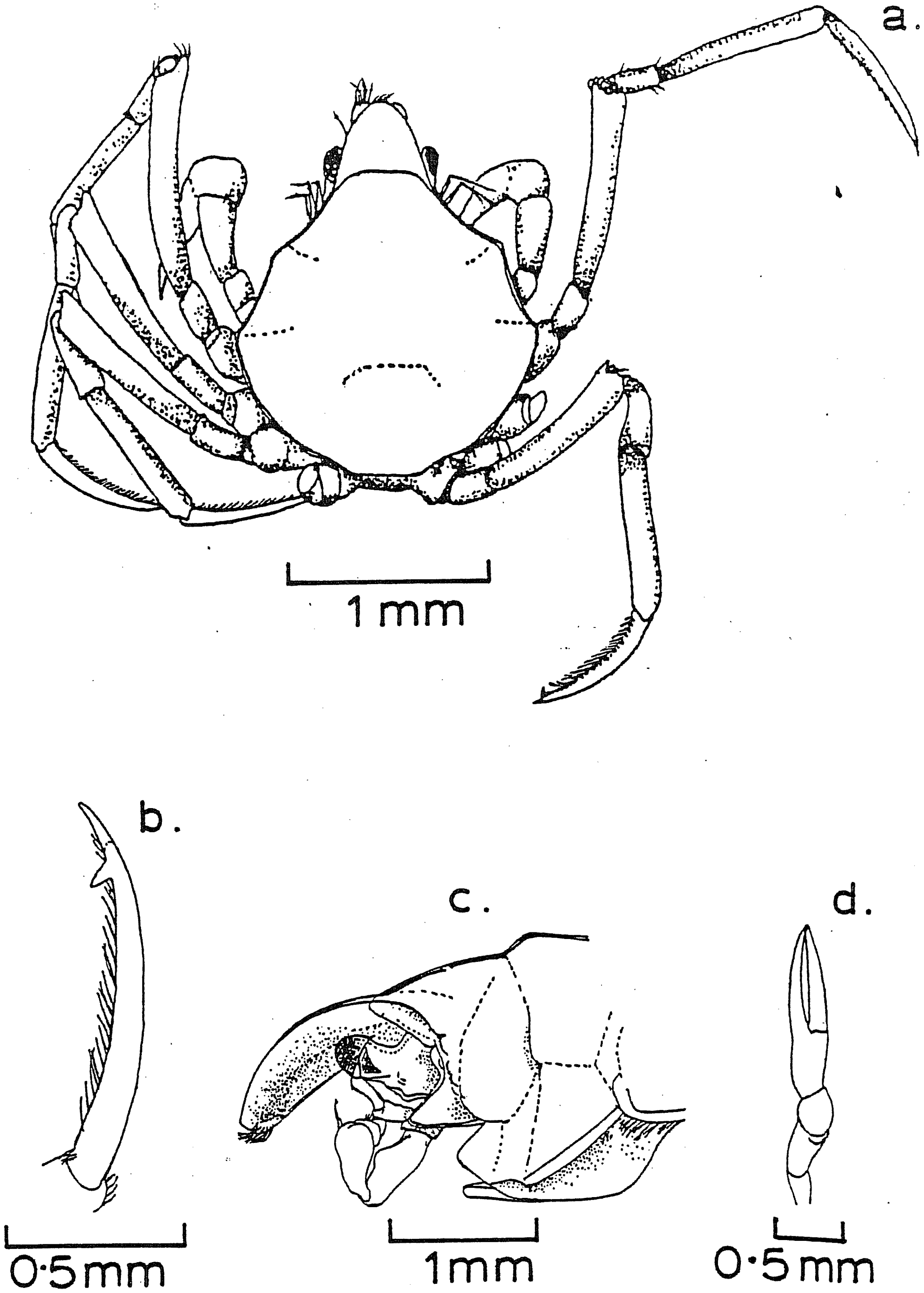


Fig. 83 - *Halimena aoteoroa*: a - immature male, dorsal view; b - dactylus of left 3rd walking leg of male; c - lateral view of rostrum, female; d - left cheliped, immature male, outer face (after Melrose, 1975).

Hymenosoma depressum Jacquinot, 1853

Synonymy

Hymenosoma depressa Jacquinot, 1853; Hymenosoma depressum Lucas, 1853; Hymenicus depressus Miers, 1876b; Filhol, 1886; Hymenosoma depressum Chilton, 1907; 1909; Thomson, 1912; Halicarcinus depressus Kemp, 1917; Hymenosoma depressum Tesch, 1918; Thomson & Anderton, 1921; "Hymenosoma" depressum Bennett, 1930; Hombronia depressa Graham, 1939; Richardson, 1949a; Dell, 1963a; Bennett, 1964; Melrose, 1968; Cyclohombronia depressa Melrose, 1975; Knox & Fenwick, 1978b; Probert et al., 1979; Hymenosoma depressum Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Auckland Islands, under stones.

Distribution

Endemic to New Zealand. North and South Islands : Leigh, Waiuku, Napier, Waikawa Beach, Palliser Bay, Kaikoura, Greymouth, Sumner, Blueskin Bay, Portobello. Also Auckland Islands.

Diagnosis (Fig. 84a-d)

Carapace suboval, slightly longer than wide, flattened or slightly convex, without distinct grooves or regions, with scattered, short, fine hairs. Rim minute, frontal regions prolonged, sides of carapace more densely setiferous. Rostrum arising at carapace level, small, bluntly pointed, not reaching past eyes, somewhat deflexed anteriorly. Edges have a row of short, straight, fine setae. Eyes close together, directed almost straight forward, hairy postocular lobe variable in size. Chelipeds short, not inflated, palm and fingers arched, hairy. Movable finger of male has a rounded proximal tubercle, rest of edge finely dentate. Distal half of fingers occluding, basal half with narrow linear gape. All legs very long, second and third pairs longest, fourth pair shortest, all fringed with long feathery hairs. Dactylus very slender, almost straight, tapering to a short claw, ventral edge with two fringes of hairs. Chelipeds and legs relatively much shorter in females. Abdomen of five segments plus telson in both sexes.

Colour

A pattern of black and yellow chromatophores linearly arranged behind the rostrum extending back to cardiac region, posteriorly chromatophores are mostly black. Eyestalks pale yellow, cornea translucent yellow with black spots, antennules banded yellow and black, antennae yellow. Chelipeds have scattered yellow and black chromatophores, base of dactyl yellow, fingers black. Legs black and yellow, propodal segments much darker, dactyls orange or yellow. This colour pattern is probably cryptic on sandy bottoms.

Size

Male 13mm CW. Female (ovigerous) 9.0mm CW.

Habitat

Under stones, among algae on sandy or silty bottoms.

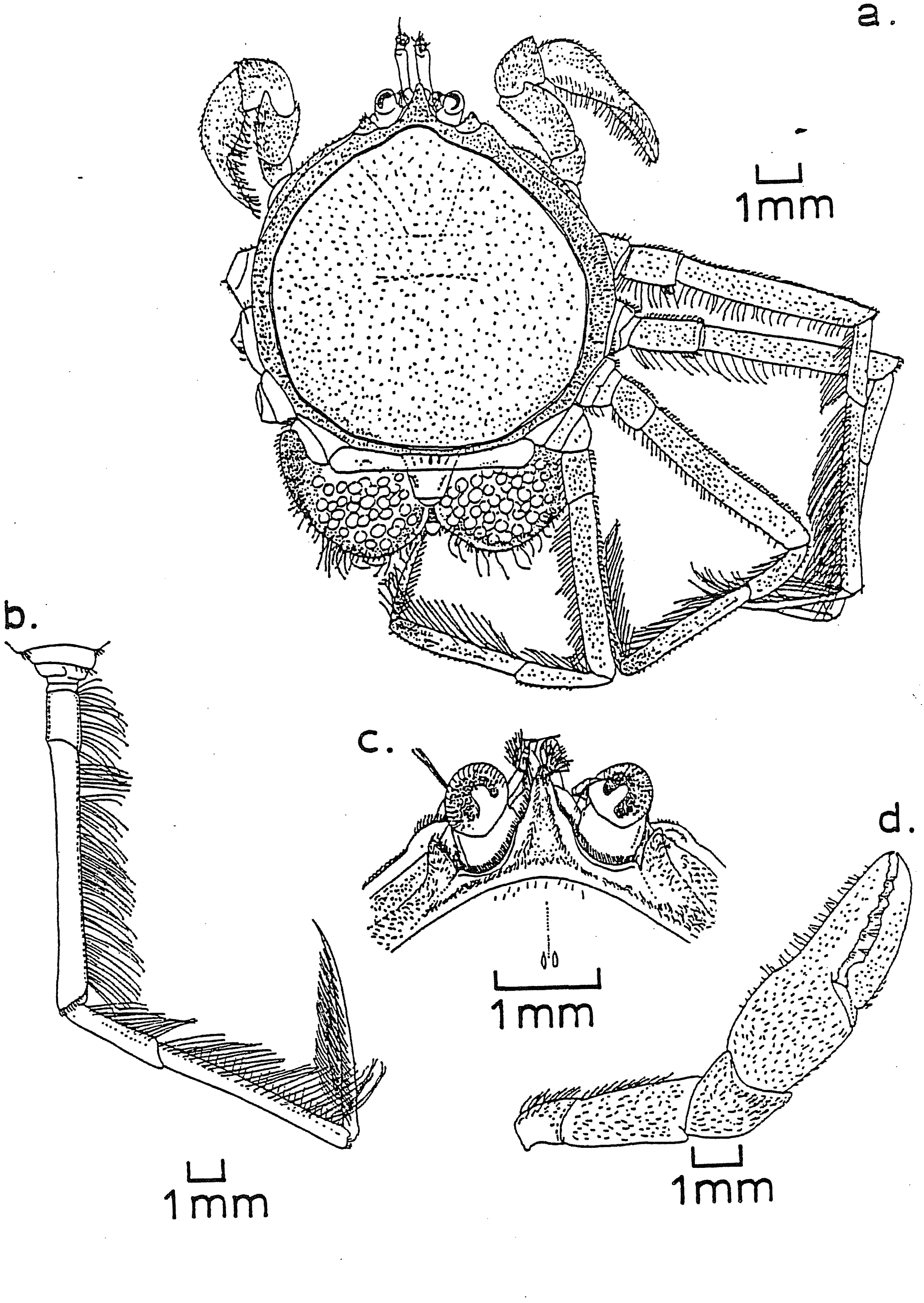


Fig. 84 - Hymenosoma depressum: a - female, dorsal view; b - left 3rd walking leg, male, posterior view; c - rostrum, male, dorsal view; d - left cheliped, male, outer face (after Melrose, 1975).

Depth

Intertidal - 10m.

Breeding

Ovigerous females have been collected in October and February. During a survey of the Avon-Heathcote Estuary plankton from March to August 1982, Roper, Simons & Jones (1983) found small numbers of H.depressum zoea.

A female carrying eggs captured in March from Brighton Beach was observed to alternately flex the pleopods on each side, swirling the eggs back and forward inside the abdominal cavity. A second batch of eggs was already present in the ovaries, suggesting another brood in quick succession. Another female kept in the laboratory laid a second brood without moulting.

In South Africa Broekhuysen (1955) found that H.orbiculare females were ovigerous from May to December. Smallest ovigerous female was 12.6mm CW and ovaries are well developed prior to the pubertal moult. Males probably mature at about the same size. Males with well developed gonads were present in most months with a maximum in April and few in December. For females the average interval between clutches of eggs was 23 days and the average length of each reproductive cycle was 66 days so that each female could produce 2-3 clutches in a breeding season without remating. Broekhuysen also demonstrated trans-moult sperm retention by females.

Development and Growth

Three zoeal stages and juvenile crab stage described by Wear & Fielder (1985).

Moulting and growth of H.orbiculare in South Africa has been investigated by Broekhuysen (1955). Small crabs, less than 12mm CW, show post-moult size increases of 22-24% while larger crabs have smaller increases, 15% (13-16mm CW) and 11% (17-22mm CW). After moulting the exoskeleton takes about 4 days to harden. Females larger than 14mm CW show a high frequency of moulting during March-May, just prior to the breeding season. As with other Brachyura the interval between moults increases with size: females - 40 days (5mm CW) to 128 days (17-22mm CW), males - 30 days (5mm CW) to 66 days (17-22mm CW). Rearing of small crabs suggests that those with CW of about 14mm are at least 8 months old. Most H.orbiculare probably do not survive more than about 18 months. Lucas (1980) notes that hymenosomatids show two different female growth formats: a pubertal, terminal moult as in Halicarcinus spp. or continued female growth after puberty as in Hymenosoma orbiculare and Elamenopsis lineata. Thus in H.obiculare both sexes have the same growth pattern and the larger size achieved by males is probably the result of shorter intermoult intervals rather than larger moult increments. Too little is known about H.depressum to say whether its growth format is the same as H.obiculare.

Behaviour

Mating of H.depressum has not been recorded but in H.orbiculare mating involves a hard male and soft, newly moulted female (Broekhuysen 1955). Prior to the female moult, the male holds the female beneath himself with his legs, with the female dorsal side upwards. After moulting the male holds the female on her back while copulation occurs, requiring about 30 min., and post-copulation guarding continues for about 24 hours while the female exoskeleton hardens.

Ecology

A female H.depressum collected off Brighton Beach, Christchurch, in March was found to have several small hydroid colonies around the carapace margin.

H.depressum has been recorded from guts of a large number of fish species and it forms an important part of their diet. Of the 52 species of elasmobranch and teleost fish which feed on crabs, 26 species contained hymenosomatids in their gut (Graham 1938, Godfriaux 1969). H.depressum occurred in guts of 23 fish species. In Hauraki Gulf snapper (Chrysophyrs auratus) this crab was most common (4.5% of gut volume) in fish from shallow muddy habitats near estuaries and more abundant in female fish than in male fish (Godfriaux, 1969). H.depressum is also eaten by Hauraki Gulf and NW Bay of Plenty trevally (Caranx lutescens), 0.5% (Godfriaux 1970a), and by rig (Mustelus lenticulatus) from Otago Harbour (Graham 1939). Webb (1973a) recorded this crab from stomachs of sand flounder (Rhombosolea plebeia), yellow-bellied flounder (R.leporina), common sole (Peltorhampus novaezelandiae), yellow-eyed mullet (Aldrichetta forsteri), kahawai (Arripis trutta) and pufferfish (Contusus richei) from the Avon-Heathcote Estuary. Also red cod (Pseudophycis bacchus) and short-finned eels (Anguilla australis) eat H.depressum (Webb 1973b). Paddle crabs (Ovalipes catharus) from Brighton Beach also eat this crab (see also Wear & Haddon, 1987). H.depressum has been recovered from stomachs of Hector's Dolphin (Cephalorhynchus hectori) caught around Banks Peninsula but these may have come from stomachs of their prey such as red cod.

References

Godfriaux (1969,1970a), Graham (1939), Lucas (1980), Melrose (1975), Roper, Simons & Jones (1983), Wear & Fielder (1985), Webb (1973a,1973b).

Neohymenicus pubescens (Dana, 1851)

Synonymy

Hymenicus pubescens Dana, 1851; 1852; ?Elamene quoyi H.Milne Edwards, 1853; Hymenicus pubescens Heller, 1868; Miers, 1876b; ?Hymenicus haasti Filhol, 1885a; Elamena quoyi Filhol, 1886; Hymenicus pubescens Hutton, 1904; Thomson, 1912; Halicarcinus pubescens Kemp, 1917; Hymenicus pubescens Tesch, 1918; Thomson & Anderton, 1921; Chilton & Bennett, 1929; Halicarcinus pubescens Richardson, 1949a; Melrose, 1968; Hymenicus pubescens Hayward, 1974; Halicarcinus pubescens Melrose, 1975; Neohymenicus pubescens Lucas, 1980; Wear & Fielder, 1985.

Type Locality

Bay of Islands, New Zealand.

Distribution

Endemic to New Zealand. North and South Islands as well as Stewart Island.

Diagnosis (Fig. 85a-d)

Carapace subcircular, as wide as long, convex, rim very thin. Whole body densely covered with hairs. Wide gastrocardiac groove strongly deflected backward centrally. Cervical grooves distinct, continuing anteriorly to base of rostrum. Lateral carapace teeth absent or vestigial. Rostrum arising at carapace level, simple, bluntly pointed, projecting past eyes, slightly deflexed, longitudinally ridged below. Suture between front and rostrum just convex. Chelipeds short in both sexes (1.2-1.5 times CW), segments in male moderately inflated. Fingers in both sexes shorter than palm : in male they are very broad with a large, short tooth on base of the movable finger, dentation rudimentary but fingers occlude almost completely when shut, in females fingers are slender, straight, occluding and dentation only on tips. First three pairs of legs as long as chelipeds, fourth pair shorter. Dactyli broad, considerably curved, both edges fringed with hairs, a single blunt tooth on ventral edge adjacent to the small claw. Abdomen of five segments plus telson in both sexes.

Colour

Grey-brown, yellow-brown.

Size

Male and female 6.5mm CW.

Habitat

Sheltered and moderately exposed rocky reefs. Found in Carpophyllum holdfasts, coralline turf, rock crevices and young crabs have been found floating off the coast among floating Sargassum weed. Common intertidally under rocks where it is exposed to the air regularly and recorded from shallow water dredging. In sandy-bottomed tide pools this crab is very hard to see because the dense coating of hairs traps mud, sand and shell fragments and obliterates the body shape.

Depth

Intertidal to 10m.

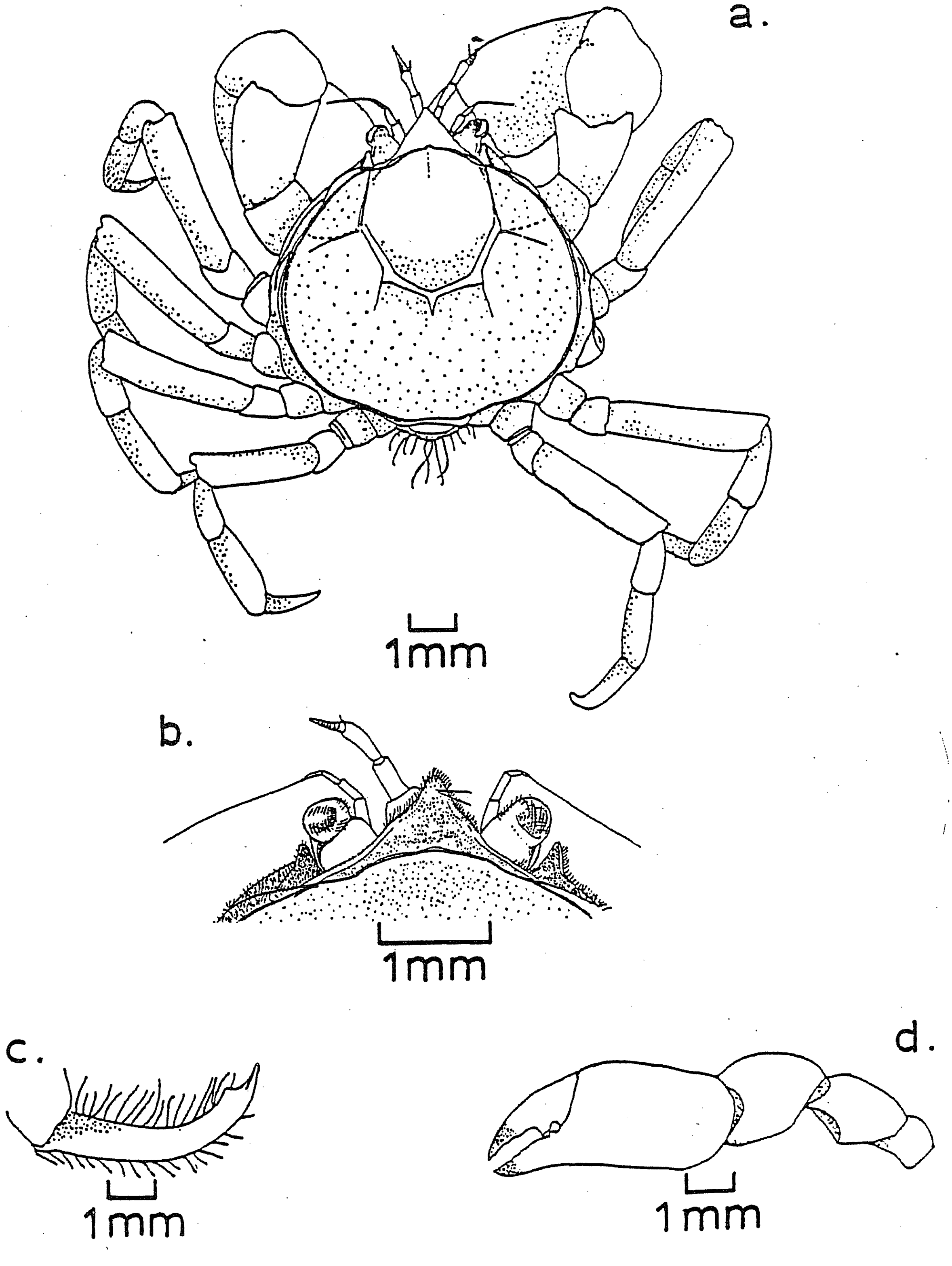


Fig. 85 - Neohymenicus pubescens: a - male, dorsal view, hairs not shown; b - rostrum, male, dorsal view; c - dactylus of left 3rd walking leg, male, posterior view; d - left cheliped, male, outer face (after Melrose, 1975).

Breeding

Ovigerous females have been collected January-March, June, November, December. Eggs ready to hatch, light orange, 0.5mm diameter. At Paihia, Bay of Islands, ovigerous females with new eggs (0.4mm diam.) have been collected in December. Females, 5.2mm CW, carried approx. 225 eggs.

Development and Growth

Melrose (1975) states that the zoeae of this species are strikingly different, having lateral expansions of the fifth segment and well developed dorsal and lateral spines. Three zoeal stages described by Wear & Fielder (1985) as well as the juvenile crab stage.

Kingsford & Choat (1985) found megalopae attributed to "Neohymenicus" associated with drift algae off the coast of Leigh in December.

Behaviour

N.pubescens are often observed on the underside of boulders, clinging to the boulder or other animals protected by the moist shelter. Movement is extremely slow and the crab shows a negative reaction to light. When dropped into water it floats passively downward with legs partially extended.

Ecology

At Leigh N.pubescens is most abundant from December to April, reaching a density of 2-6 per $0.1m^2$. On the shore near Paihia, where the Waitangi River meets the sea, even higher densities (up to 30 per $0.1m^2$) have been observed. This suggests that N.pubescens can withstand substantially lowered salinities. It can withstand short exposure to the air. This crab has not been seen catching prey or scooping up debris and is presumed to be predominantly a filter feeder. The mouthparts are extremely hairy and most of the time the crab remains motionless on a rock, with the maxillipeds open. At intervals the antennules are cleaned by the external maxillipeds and pieces of debris transferred to the mandibles. N.pubescens may also feed directly on sponges. Some crabs have small patches of sponge growing among the hairs on the carapace.

N.pubescens is preyed upon by paddle crabs (Ovalipes catharus) (Wear & Haddon 1987).

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