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The Marine Fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda)

by

R.G. WEAR and D.R. FIELDER

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CONTENTS

LIST OF FIGURES

LIST OF TABLES

The Marine Fauna of New Zealand: Larvae of the Brachyura (Crustacea, Decapoda)

by

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ABSTRACT

Some 74 species of Brachyura (including the Dromiacea) are known to belong to the New Zealand fauna. This report provides detail and illustrations of the larvae and larval development of 53 of these species.

The complete larval development, including the crab-like megalopa stage, is described for 25 species, while present coverage of the remaining 28 species still lacks either late zoea stages or the megalopa. Only the first stage zoea larva and the megalopa are figured here and descriptions are restricted to characters of immediate use in the recognition of species. Our treatment of the later zoea larval stages is confined to overall dimensions, key measurements, and comments relating to whether or not the species conform with a set pattern of morphological progression between successive instars.

Of the 21 recorded species for which we have no larval information, the great majority occur as adults in deep water on the northern or southern parts of the continental shelf or slope and are therefore infrequently caught. In ten of these cases, where congeners are available from beyond the New Zealand region, these have been illustrated and described briefly to demonstrate the larval characters which may be anticipated to occur in our representatives.

This paper collates all existing and new information and is intended to fill a gap in the literature available to practising planktologists. The format is therefore that of an "atlas" of the larvae of the New Zealand Brachyura, and the systematic section is introduced by describing and illustrating the life-history of *Cancer novaezelandiae* (Jacquinot, 1853) in full, to detail the descriptive anatomy and basic changes which occur typically in a zoea larval series and the subsequent megalopa. Keys to the zoea and megalopa larvae of the New Zealand Brachyura are provided. These are based on easily recognisable characters, for the most part exclusive for each genus and species. The likelihood of the larvae occurring in plankton samples is assessed for most species from what is known of their life-histories, larval morphology and habits. Affinities and possible evolutionary relationships of the larvae have not been treated in any detail.

Keywords: Crustacea, Decapoda, Brachyura, crab larvae, systematics, morphology, keys, marine fauna, New Zealand.

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GENERAL INTRODUCTION

Prior to 1965 the only published accounts of brachyuran larvae from New Zealand were those of Thomson and Anderton (1921), Gurney (1924), and Bennett (1964). Thomson and Anderton hatched the first zoea larval stages of *Ommatocarcinus huttoni* (as *O. macgillivrayi*), *Nectocarcinus antarcticus, Hemigrapsus edwardsi* (as *Heterograpsus sexdentatus*) and probably *Halicarcinus* sp. (as *Hymenosoma depressa*). Their figures, however, were little more than sketches and their descriptions were very incomplete. Gurney described and figured a number of non-brachyuran larvae from the plankton and one brachyuran, "Brachyura incertae sedis", which is probably a zoea larva of *Elamena producta*. Bennett described and figured the first zoea stage of *Pinnotheres novaezelandiae*, which had been hatched in the laboratory.

In 1965 Wear illustrated a number of larval decapods, including zoea stages and the megalopa of several crab species, which could be used as seasonal indicators in the plankton of Wellington Harbour. This study was followed by a number of detailed descriptions of the larval stages of New Zealand Brachyura in the families Xanthidae (Wear 1967, 1968a, 1970a), Ocypodidae (Wear 1968b), Grapsidae (Wear 1970b), Dromiidae (Wear 1970c, 1977), Dorippidae (Wear and Batham 1975), and Majidae (Webber and Wear 1982). Larvae of the following New Zealand crab species have been described from localities beyond New Zealand waters: *Homola orientalis* — Boas 1880; *Macropipus corrugatus* — Lebour 1928a; *Scylla serrata* — Raja Bai Naidu 1955, Ong 1964; *Latreillia australiensis, Paromola petterdi*, and *Lyreidus tridentatus* — Williamson 1965, 1967; *Halicarcinus planatus* — Boschi, Scelzo and Goldstein 1969; *Planes cyaneus* — Muraoka 1973; and*Portunus pelagicus* — Kurata and Midorikawa 1975, Shinkarenko 1979.

Some 74 species of Brachyura (including the Dromiacea) are known to belong to the New Zealand fauna. A further seven species are likely to be new records when studies on tentatively identified material are complete. Those recorded to the present belong to 48 genera and to 16 families. This report provides detail and illustrations of the larvae and larval development of 53 species (72% of the fauna) from 43 genera (90% of the fauna) representing all 16 families.

Detailed descriptions of the larvae of 34 species of New Zealand Brachyura have been published to date, and of these the complete life history, including the megalopa stage, is known from 14 species. This publication completes our morphological knowledge of the larval development of two species and adds substantially to that of a further six. Larvae of a further 14 species are described for the first time, including the complete life history of 11 species. In most cases, however, only the first stage zoea larva and the crab-like megalopa are figured, and only characters of immediate use in the recognition of species are emphasised in the descriptions. Our treatment of the later zoea larval stages is confined to overall dimensions, key measurements, and comments relating to whether or not the species conforms with what we have established as a set pattern of morphological progression between successive instars. More detailed descriptions of larvae recorded here for the first time may be published in due course. We are also aware of several larvae occurring in the plankton of New Zealand inshore waters which at present we are unable to tie up with any known adult. These have not been included in the present publication, but will be the subject of future work when their identity can be established by way of larval rearing.

Of the 21 recorded species for which we have no larval information, the great majority occur as adults in deep water on the northern or southern parts of the continental shelf or slope and are therefore infrequently caught. Among the shallow-water species the larvae of only five crabs are now unknown. Two of these occur only in southern New Zealand — the majid spider crab *Leptomithrax australis* and the swimming crab *Nectocarcinus bennetti*, and two are widely distributed but rarely captured — the small spider crab *Halimena aotearoa* (Hymensomatidae), and *Naxia huttoni* (Majidae). The fifth species, *Pinnotheres schauinslandi*, is a commensal pea crab (Pinnotheridae) of uncertain taxonomic status.

In ten cases where we have no larval information concerning the genera in which the New Zealand species have been placed, but where specific examples of either zoea or megalopa larvae are available from beyond the New Zealand region, these congeners are illustrated and described briefly to demonstrate larval characters which may be anticipated to occur in our representatives.

One of the major aims in compiling this paper, which collates all existing and new information, is to fill a gap in the literature available to practising planktologists. The format is therefore that of an "atlas" of the larvae of the New Zealand Brachyura, and the systematic section is introduced by describing and illustrating the life history of *Cancer novaezelandiae* (Jacquinot, 1853) in full, to detail the descriptive anatomy and basic changes which occur typically in a zoea larval series and the subsequent megalopa. Comprehensive keys to the zoea and megalopa larvae of the New Zealand Brachyura are provided. These are based on easily recognisable characters, for the most part exclusive for zoea and megalopa larvae of each genus and species.

For most species it has been possible to assess the

likelihood of the larvae occurring in plankton samples from what is known of their life histories, larval morphology, and habits.

Affinities and possible evolutionary relationships of the larvae have been treated only briefly by way of introduction to each family or group of families in the systematic section. Some of our intended comments in this regard have been obviated by a major paper by Rice (1980a) which appeared at the time that this present work was almost ready for publication. Workers in the field of crab zoea larval morphology and the bearing of the larval phase on the classification of the Brachyura should consult this excellent and very broad thesis, in which the positions of the more "primitive" crab-like groups especially, are described in considerable detail. It is the most definitive global treatment of brachyuran larval affinities published to the present time.

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We would like to acknowledge separate grants for travel provided by the New Zealand University Grants Committee in 1964, and by the Internal Research Committee of Victoria University of Wellington in 1965, 1968, and 1978. Financial assistance thus obtained enabled the first author to collect most of the material contributing to this study. The University of Queensland is acknowledged with thanks for allowing the second author to spend six months' study leave in New Zealand during the first half of 1978, when some of the manuscript was drafted and the format of this publication finalised between us.

We sincerely thank Dr John Yaldwyn, Director of the National Museum of New Zealand, for his interest and constant advice, especially in keeping us abreast of current work in the field of adult systematics and new records of decapod Crustacea from the New Zealand region as they became known. Previously published figures are acknowledged elsewhere, but we would like to convey our special thanks to all those authors who consented to reproduction of their work. We are extremely grateful to Mr M.P. Heasman of the Zoology Department, University of Queensland, and to Mrs A. Laviña of the Aquaculture Department, Southeast Asian Fisheries Development Centre (SEAFDEC), Philippines, who provided us with larvae of *Scylla serrata*; and to Mr G. Campbell, also of the Zoology Department, University of Queensland, for a reared larval series of *Portunus pelagicus*. We thank the Marine Biological Association of the United Kingdom for the loan of some of Lebour's material of *Ebalia* from their collections.

Other workers also contributed significantly to this work, and we wish to acknowledge the assistance of Dr R.V. Grace and Mr M. Thomson of Bioresearches Limited, Auckland, in their successful efforts to hatch the larvae of *Pyromaia tuberculata*; Mr E. Laviña of SEAFDEC, who provided us with a larval series of *Ovalipes catharus* reared during the course of his graduate studies at Victoria University of Wellington; and Mr P.E. Roberts, formerly of the Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, for the larvae of *Halicarcinus planatus*. The first author owes much to the inspiration provided by Dr Richard B. Pike during earlier years of this study, and to Mr Hugh Packer, who assisted with much of the larval rearing work completed over the summer of 1980–81.

Submission of this manuscript towards the end of 1980 was fortuitously delayed further by an opportunity for the first author to participate in r.v. *Tangaroa* cruise No. 1117 to the North Island shelf and slope, 9 January–3 February 1981, during which the larvae of three additional species were obtained and the life-history of a fourth species completed by subsequent larval rearing. We wish to thank the New Zealand Oceanographic Institute for the use of shipboard facilities and for the assistance provided by their technical staff. We also acknowledge assistance from staff of the National Museum of New Zealand, who were co-participants in this cruise.

The manuscript was nurtured through all stages of drafting to a form suitable for publication by Miss Nesta Black, to whom we are indebted for her great patience and considerable typing skill.

Finally, we express our gratitude to the staff of the Conservation Laboratory of the Alexander Turnbull Library, Wellington, and specifically to Mr Jeavons Bailey, for salvaging our working drawings and notes severely damaged by water and charring during a fire at the Victoria University Marine Laboratory, Island Bay, during November 1979. Without their skill and efforts many large gaps would exist, and publication would almost certainly have been delayed by several years.

METHODS

Published descriptions of larvae have been summarised as appropriate to our purposes and incorporated in the text. These are credited elsewhere. In the case of species described here for the first time, eggs being incubated by females were hatched in small sea-water aquaria and, where possible, zoea larvae were reared through to the megalopa in covered fingerbowls using newly hatched *Artemia* nauplii as food (*see* Appendix). Most species were hatched and reared by R.G.W. over the period 1964 to 1967, while working at the Victoria University Marine Laboratory at Island Bay, Wellington. Larvae were placed in 5% neutral formalin for long-term preservation and are now deposited, together with parent female crabs, in the collections of the National Museum of New Zealand, Wellington (NMNZ).

Drawings and measurements were made of preserved larvae using either a dissecting or compound microscope with a calibrated eyepiece graticule. All original drawings in this work were done by the first author.

Measurements of zoea larvae given in the text are defined as follows:

Total length[1]: from anterior margin of eye to tip of lateral cornu of telson with abdomen extended.

Carapace length: from anterior margin of eye to posterior margin of carapace behind posterior tubercle.

Carapace height: from ventral margin of carapace to its apex, excluding dorsal carapace spine.

Length of rostral spine: from ventral margin of eye to tip of spine.

Length of dorsal carapace spine: from junction of spine with carapace to tip of spine.

Length of lateral carapace spines[2]: from junction of spine with carapace to tip of spine.

Spine to spine length: from tip of rostral spine to tip of dorsal carapace spine.

Length of antenna 2 exopod: from tip of exopod (excluding distal setae) to point of junction with protopod.

Length of antenna 2 endopod: from tip of endopod to point of junction with protopod.

Length of antenna 2 spiniform process: from tip of process to point of junction with protopod.

Measurements used in descriptions of the megalopa larvae are defined as follows:

Carapace length: from the most anterior extremity of carapace (excluding spines) to its median posterior margin, but excluding the rostrum unless otherwise stated in the text.

Carapace width: across the widest (branchial) part of the carapace.

We would emphasise that for species newly described in this paper, all measurements of eggs, larvae, and of larval spines and appendages, are mean figures based on 10 or more larvae from each brood, and wherever possible more than one brood has been used. Such absolute figures can be subject to a maximum variation of $\pm 10\%$ within a given species over the extent of its range, except in the case of the families Hymenosomatidae and Pinnotheridae in which variation is considerably greater (*see* pp. 38 and 65). The length of spines relative to one another, however, remains constant for species irrespective of larval size unless otherwise indicated in the text. For larvae whose descriptions have been published previously and which are only briefly dealt with here, the measurements given are those of the original authors or have been calculated by us from published illustrations drawn to scale.

Terminology used in description of larval appendages follows that now generally accepted in the description of decapod larvae, except that the antennules (first antennae) and the antennae (second antennae) are termed antenna 1 and antenna 2 respectively, and the respective zoea larval stages are described as zoea I, zoea II *et seq.* Lebour (1928a) makes reference to three larval structures for which our terminology differs:

"Spinous process" of antenna 2 of zoea larvae is here termed the "spiniform process". "Spinous process" has been in general usage following Lebour, but is considered ambiguous as the adjective "spinous" can imply either that the structure as a whole is in the form of a spine, or that the structure is covered in spines. Although in the great majority of crab larvae this process is in the form of a spine, the spine may be either smooth, or lined with varying numbers of small spines or stout setae, according to the species. Use of the adjective "spiniform" removes the ambiguity and clears the way for more precise description of the variation in the ornamentation of this structure.

Lateral or dorsolateral "knobs" on the second and

1. This measurement is approximate only and given to the nearest 0.1 mm except in very small larvae. Very few larvae preserve with their abdomen perfectly straight and a more accurate measurement is therefore difficult to obtain.

2. Measurement of limited use since in late stage larvae the lateral spines are very broadly based, thus reducing the point of junction with the carapace to a close estimate only. We have not taken account of the horizontal distance between the tips of the lateral carapace spines as recommended by Rice (1979) due to the fact that the zoea carapace frequently inflates in preservative so as to produce an exaggerated measurement.

often subsequent zoea larval abdominal segments are here named "protuberances" since they are more often triangular, or spine-like, or strongly curved hook-like processes, rather than simple knobs.

"Feelers" frequently arising from the dactyl of pereiopod 5 of the megalopa larva are termed "long, terminally hooked setae", which more accurately describes their form rather than their improbable function as "feelers".

In the family Hymenosomatidae no true megalopa follows the zoea stages, and the name megalopa larva is not therefore used (*see* p. 37). Instead, this planktonic post-zoeal stage is termed the first juvenile crab.

The designation of higher taxa within the Brachyura follows the system of Balss (1957), with the reservation that the names used here have not been assigned taxonomic status. The terms Dromiacea, Oxystomata, Brachygnatha, Oxyrhyncha, and Brachyrhyncha are used merely to separate the families conveniently into the traditional order and groupings with which many workers are familiar.

CHECKLIST OF THE GENERA AND SPECIES OF NEW ZEALAND BRACHYURA

The following list includes all species of New Zealand Brachyura described up to the present, and named species are in each case followed by a summary of the larval stages described in this paper. Those marked with an asterisk are species from which the full larval life history is known. Species preceded by a dagger are those for which no larval knowledge is available, and where appropriate are followed by the name of the species from beyond the New Zealand region we have used as an illustration of the probable larval type.

	NMNZ Cr. No.
DROMIACEA	
Family HOMOLIDAE	
†**Paromola spinimana** Griffin, 1965	
Cf. *P. cuvieri* (Risso): zoea I	
Paromola petterdi (Grant, 1905): megalopa	
Latreillia australiensis Henderson, 1888: zoea I, megalopa	
Homola orientalis Henderson, 1888: zoea IV	
Cf. *H. barbata* (Fabricius): zoea I, megalopa	
Cf. *Homola* sp.: zoea II	
Family DROMIIDAE	
Petalomera wilsoni (Fulton & Grant, 1902): zoeas I & II, megalopa	2462
OXYSTOMATA	
Family TYMOLIDAE	
***Cymonomus bathamae** Dell, 1971: zoea I, megalopa	2463
†**Cymonomus aequilonius** Dell, 1971	
Family RANINIDAE	
***Lyreidus tridentatus** de Haan, 1841: zoeas I–VI, megalopa	2464
Family LEUCOSIIDAE	
Ebalia laevis (Bell, 1855): zoeas I–IV	2465
Cf. *E. tuberosa* (Pennant): megalopa	
†**Ebalia tuberculosa** (A. Milne Edwards, 1873)	
†**Merocryptus lambriformis** A. Milne Edwards, 1873	
†**Randallia pustulosa** Wood-Mason, 1891	
BRACHYGNATHA (OXYRHYNCHA)	
Family MAJIDAE	
Cyrtomaia hispida (Borradaile, 1916): zoeas I & II	2466
†**Platymaia maoria** Dell, 1963	
Pyromaia tuberculata (Lockington, 1877): zoeas I & II	2467
†**Naxia huttoni** (A. Milne Edwards, 1876)	
†**Achaeopsis ramusculus** (Baker, 1906)	
***Achaeus fissifrons** (Haswell, 1879): zoea I, megalopa	2468
†**Rochinia riversandersoni** (Alcock, 1895)	
Cf. *R. carpenteri* (Thomson): zoea I, megalopa	
†**Eurynome bituberculata** Griffin, 1964	
Cf. *E. aspera* Leach: zoea II, megalopa	
***Eurynolambrus australis** H. Milne Edwards & Lucas, 1841: zoeas I & II, megalopa	2469
***Notomithrax minor** (Filhol, 1885): zoeas I & II, megalopa	2471
***Notomithrax peronii** (H. Milne Edwards, 1834): zoeas I & II, megalopa	2470
***Notomithrax ursus** (Herbst, 1788): zoeas I & II, megalopa	2472
†**Leptomithrax australis** (Jacquinot, 1853)	
†**Leptomithrax garricki** Griffin, 1966	

	NMNZ Cr. No.
Leptomithrax longimanus Miers, 1876: zoea I	2473
Leptomithrax longipes (Thomson, 1902): zoeas I & II	2474
†**Leptomithrax richardsoni** Dell, 1960	
Leptomithrax tuberculatus mortenseni Bennett, 1964: zoea I	2509
†**Chlorinoides filholi** (A. Milne Edwards, 1876)	
Jacquinotia edwardsii (Jacquinot, 1853): zoeas I & II	2475
Family HYMENOSOMATIDAE	
***Amarinus lacustris** (Chilton, 1882): juvenile	
***Halicarcinus cookii** (Filhol, 1885): zoeas I–III, 1st juvenile crab	2476
Halicarcinus innominatus Richardson, 1949: zoea I	2477
***Halicarcinus planatus** (Fabricius, 1775): zoeas I–III, 1st juvenile crab	2478
†**Halicarcinus tongi** Melrose, 1975	
Halicarcinus varius (Dana, 1851): zoea I	2479
Halicarcinus whitei (Miers, 1876): zoea I	2480
***Hymenosoma depressum** (Jacquinot, 1853): zoeas I–III, 1st juvenile crab	2481
***Neohymenicus pubescens** (Dana, 1851): zoeas I–III, 1st juvenile crab	2482
***Elamena longirostris** Filhol, 1885: zoeas I–III, 1st juvenile crab	2483
Elamena momona Melrose, 1975: zoeas I–III	2484
***Elamena producta** Kirk, 1879: zoeas I–III, 1st juvenile crab	2485
†**Halimena aoteoroa** Melrose, 1975	
BRACHYGNATHA (BRACHYRHYNCHA)	
Family ATELECYCLIDAE	
†**Pteropeltarion novaezelandiae** Dell, 1972	
Trichopeltarion fantasticum Richardson & Dell, 1964: zoea I	2486
Family CANCRIDAE	
***Cancer novaezelandiae** (Jacquinot, 1853): zoeas I–V, megalopa	2487
Family PORTUNIDAE	
Macropipus corrugatus (Pennant, 1777): zoeas I, II, IV	2488
Cf. *M. holsatus* (Fabricius): megalopa	
***Nectocarcinus antarcticus** (Jacquinot, 1853): zoeas I–V, megalopa	2489
†**Nectocarcinus bennetti** Takeda & Miyake, 1969	
***Ovalipes catharus** (White, 1843): zoeas I–VIII, megalopa	2490
†**Ovalipes molleri** (Ward, 1933)	
***Portunus pelagicus** (Linnaeus, 1776): zoeas I–IV, megalopa	2491
***Scylla serrata** (Forskål, 1885): zoeas I–V, megalopa	2492
Family BELLIIDAE	
***Heterozius rotundifrons** A. Milne Edwards, 1867: zoeas I & II, megalopa	2493
Family XANTHIDAE	
***Ozius truncatus** H. Milne Edwards, 1834: zoeas I–IV, megalopa	2494
Pilumnopeus serratifrons (Kinahan, 1856): zoea I	2495
***Pilumnus lumpinus** Bennett, 1964: zoea I, megalopa	2496
***Pilumnus novaezelandiae** Filhol, 1886: megalopa	2497
Family GONEPLACIDAE	
†**Carcinoplax victoriensis** Rathbun, 1923	
Cf. *C. longimanus* (de Haan): zoea I, megalopa	
***Ommatocarcinus huttoni** Filhol, 1886: zoeas I–IV, megalopa	2498
Family PINNOTHERIDAE	
Pinnotheres novaezelandiae Filhol, 1886: zoeas I–III	2499
Cf. *P. ostreum* Say: megalopa	
†**Pinnotheres schauinslandi** Lenz, 1901 (uncertain status)	
Family GRAPSIDAE	
Leptograpsus variegatus (Fabricius, 1793): zoea I	2500
Planes cyaneus Dana, 1852: megalopa	
Planes marinus Rathbun, 1915: zoea I	2501
Hemigrapsus crenulatus (H. Milne Edwards, 1837): zoeas I–V	2502
Hemigrapsus edwardsi (Hilgendorf, 1882): zoeas I–V	2503
Cf. *H. sanguineus* (de Haan): megalopa	
***Helice crassa** Dana, 1851: zoeas I–V, megalopa	2504
Cyclograpsus insularum Campbell & Griffin, 1966: zoea I	2505
Cyclograpsus lavauxi H. Milne Edwards, 1853: zoeas I–V	2506
Cf. *C. cinereus* Dana: megalopa	
Plagusia chabrus (Linnaeus, 1764): zoeas I, V, XII, megalopa II	2507
Family OCYPODIDAE	
***Macrophthalmus hirtipes** (Jacquinot, 1852): zoeas I–V, megalopa	2508

GENERAL FEATURES OF REPRODUCTION AND LARVAL DEVELOPMENT IN THE NEW ZEALAND BRACHYURA

Breeding

Most New Zealand Brachyura show a seasonal breeding pattern with copulation occurring during winter or early spring, although some, notably those in the family Hymenosomatidae, breed throughout the year. In most species, female crabs are inseminated by the male whilst the former is in a newly moulted or soft-shelled condition. Sometimes breeding involves a period of precopulatory courtship in which the male protects and carries around the female of his choice until she actually moults. One of us (R.G.W.) has observed this behaviour in the swimming crab *Ovalipes catharus*; the male associates with the female for several days, with the male's walking legs used to hold the female carapace uppermost against his sternum leaving the chelipeds free for defence; the male loosens his grip on the female as she begins to moult and may even assist her to "undress" before grappling and turning her over for copulation.

Sperm are stored in the oviducts where they are able to remain viable for several months, usually in sufficient numbers to fertilise more than one batch of eggs. During spring months, eggs are fertilised as they pass down the oviducts, and after being extruded through the pair of female genital openings located in the sternal plate adjacent to the base of the third pereiopod, or in the coxa of the third pereiopod itself, they are attached to specialised egg-bearing setae on the abdominal pleopods by means of a tiny strand produced into a thin membrane encapsulating each egg. The mass of eggs is held beneath the female abdomen and incubated from six weeks to five or six months. From time to time the female aerates the egg mass by rhythmically beating her abdomen and cleans the eggs using her chelipeds, meticulously removing those which are moribund. If the first batch of eggs hatches in late spring, often a second batch is extruded without an intervening moult after being fertilised by sperm retained from the original insemination. This has been observed in the families Majidae and Hymenosomatidae. These eggs hatch towards the end of summer. Some species may have three or four batches of eggs in a single breeding season.

Incubation time varies between species and with water temperature. It is likely that incubation time for New Zealand Brachyura can be calculated according to the equation $D = a(T-\alpha)^{-2.3}$ derived by Wear (1974) for British decapods, where D = development time in days; a = a scaling constant reflecting the change in incubation period due to changes in temperature for a given species, thereby defining shifts along the development (D) axis; T = water temperature; α = zero in the case of cool temperate species. However, this work has not yet been repeated using New Zealand Brachyura.

Brachyuran larvae are usually able to swim quite actively, but their small size, never more than a few millimetres in length, means that fast absolute speeds are not possible. This in turn means that they fall easy prey to many kinds of larger carnivorous plankton-eating animals such as coelenterate medusae, ctenophores, and fish. Mortality is therefore very high, and as a partial counter to this, many eggs (up to three million per batch in the large portunid crab *Scylla serrata*) are hatched by each female during her reproductive life. On the other hand, some species have adopted the alternative of having fewer, larger and more yolky eggs, larger larvae on hatching, fewer larval stages, and an altogether shorter period of life in the plankton. A few species have gone as far as suppressing the planktonic phase altogether, and have very few eggs which hatch as juveniles. In one case (*Pilumnus novaezelandiae*) these are actually brooded and cared for by the parent female.

Larval Development

Brachyuran larval development can be divided into three basic phases.

With few exceptions the first free-living phase is the "pre-zoea", with the name implying nothing more than its position in ontogeny. This phase is non-planktonic and short-lived, with moulting occurring within about one hour of hatching from the egg. It is characterised by an enveloping pre-zoeal cuticular membrane which covers the whole larva, including its appendages, like a close-fitting cloak. This cuticle does not follow segmental indentations, and future larval structures such as spines and setae are usually invaginated beneath it and thus immobilised. In most New Zealand crabs, other than those of the family Hymenosomatidae and the more specialised or more recently evolved brachyrhynchous families Goneplacidae, Pinnotheridae, Grapsidae, and Ocypodidae, it is produced into delicate strap-like plumose processes arising from antennae 1 and 2 and from the posterior margin of the telson.

The second free-living phase is the "zoea" which swims actively by means of natatory setae on the exopods of maxillipeds 1 and 2. These larvae bear absolutely no morphological resemblance to their parents, and since they do not share the same habitat or habits as adult crabs, they are capable of undergoing adaptation and evolution in their own right. In fact, morphological relationships masked by specialisation among adult forms can often be demonstrated in their

larvae in cases where these have shared a common planktonic habitat throughout their evolution and have not been subjected to the same evolutionary pressures as the adults. An excellent example of this is *Eurynolambrus australis*. Larval affinities clearly support its present position in the family Majidae, rather than in the Parthenopidae in which the species was formerly included (Webber and Wear 1982).

Newly emerged larvae of most species find their way into the plankton where they may spend differing periods of time depending upon the number of zoeal 'stages' (genetically determined for the species) and the length of time spent in each stage. Duration of the zoea phase is also dependent on water temperature, availability of food, and probably also on salinity. Most laboratory rearing experiments by the first author during 1964–1968 were carried out at about 18°C, at which temperature the first two intermoults varied between six days and eight days, and subsequent intermoults were as short as five days. A very general estimate, based on laboratory work on a wide range of New Zealand species, is for an average planktonic life of seven days per zoea stage at 18°C, extending by one day for each 1°C drop in water temperature.

The "megalopa" phase is reached after a metamorphic moult from the final zoea larval stage. This larva is rather more crab-like in appearance, and swims by means of natatory setae on the abdominal pleopods. It is argued by some authors that the megalopa is post-larval rather than larval, but this is an academic point beyond the scope of the present paper. In the New Zealand Brachyura, and worldwide, there is usually only one megalopa stage, and this is also planktonic in many species. Our observations indicate that the duration of the megalopa stage can vary between eight days and 25 days within one species, and may well have a similar interspecific range. Our experience also suggests that megalopa larvae have some ability to delay metamorphosis until conditions are optimal, thus making laboratory-based estimates unrealistic for larvae in their natural habitat.

New Zealand species within each brachyuran family tend to undergo a similar number of zoea stages before metamorphosing to the megalopa. Thus the New Zealand representatives of the families Belliidae and Majidae have two zoea stages, those of the family Hymenosomatidae three zoea stages and no true megalopa, those of the family Xanthidae four zoea stages, while the species in the families Cancridae, Portunidae, Goneplacidae, Grapsidae, and Ocypodidae mainly have five zoea stages. *Lyreidus tridentatus* (Raninidae) has six zoea stages. Unfortunately, these generalisations do not always hold true. For example, in those families for which we have more than one species with larvae known, *Pilumnus novaezelandiae* (Xanthidae) and *Amarinus lacustris* (Hymenosomatidae) have no zoea larvae and eggs hatch as a megalopa or juvenile respectively; *Cymonomus bathamae* (Tymolidae) and *Pilumnus lumpinus* (Xanthidae) have only one very short-lived and rather atypical non-planktonic zoea; *Achaeus fissifrons* (Majidae) has one rather than two zoea stages; *Portunus pelagicus* (Portunidae) may have four rather than five zoea stages; and *Ovalipes catharus* (Portunidae) has eight zoea stages. *Plagusia chabrus* (Grapsidae) is known to develop giant larvae with 12 zoea stages before reaching the megalopa stage, possibly explaining why this species is rather more widely distributed than others of the New Zealand fauna except the Portunidae, which of course swim as adults.

LARVAE OF THE NEW ZEALAND BRACHYURA

Introduction

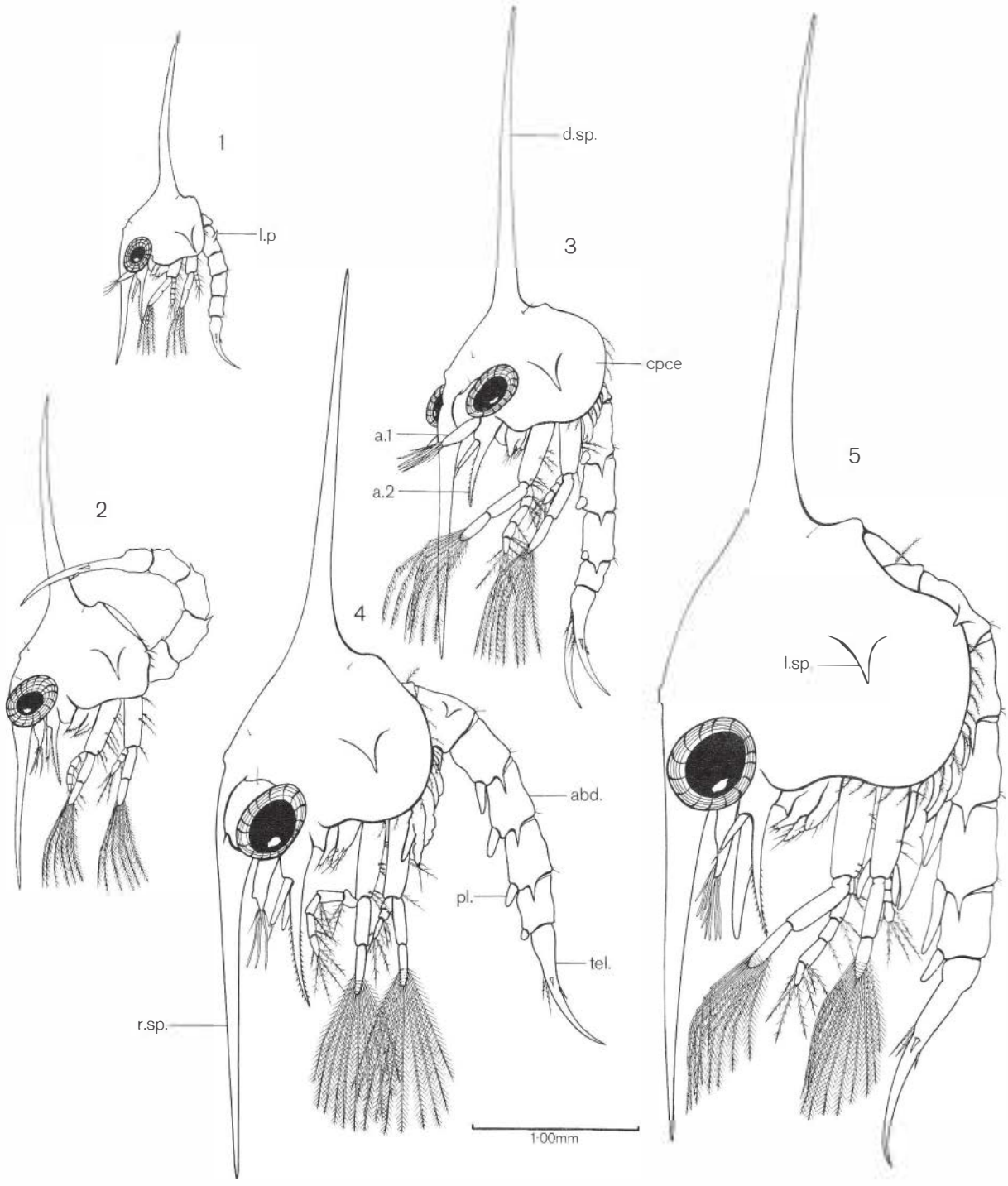
Cancer novaezelandiae (Jacquinot, 1853) is a relatively common shallow-water species endemic to New Zealand. Its larval life-history has not previously been described. However, its various larval stages possess most of the characters which occur in other New Zealand brachyuran larvae. We have therefore chosen this species as an example to introduce the detailed descriptive anatomy and the basic changes which occur typically in a zoea series and the subsequent megalopa. For the few species in which the developmental pattern differs from that described below, details are given in the appropriate sections.

The zoea stages

Figs 1–10 show lateral and posterior views of the five zoea stages which occur in *Cancer novaezelandiae*. All are drawn to the same scale to illustrate the relative sizes of each zoea stage. Figs 11–22 compare the appendages of the first and fifth zoea stages, and again these are drawn to the same scale as indicated. A shorter, but fully diagnostic description of the zoea stages of *C. novaezelandiae*, including key measurements not given below, is contained in the systematic section of this paper.

Cephalothorax

The carapace possesses very long dorsal and rostral spines (Figs 1–5), whilst the lateral spines (Figs 6–10) are much shorter. The eyes are relatively large and are stalked in all but zoea I, in which they are sessile (cf. Figs 6 and 7). Four small setae occur on the dorsal



FIGS 1–5: Family CANCRIDAE. *Cancer novaezelandiae* (Jacquinot, 1853). Complete larval development, consisting of 5 zoea stages, drawn to one scale, lateral views: 1, zoea I; 2, zoea II; 3, zoea III; 4, zoea IV; 5, zoea V. Abbreviations: a.1 - antenna 1; a.2 - antenna 2; abd. - abdomen; cpce - carapace; d.sp. - dorsal spine; l.p. - dorsolateral abdominal protuberance; l.sp. - lateral spine; pl. - pleopod; r.sp. - rostral spine; tel. - telson.

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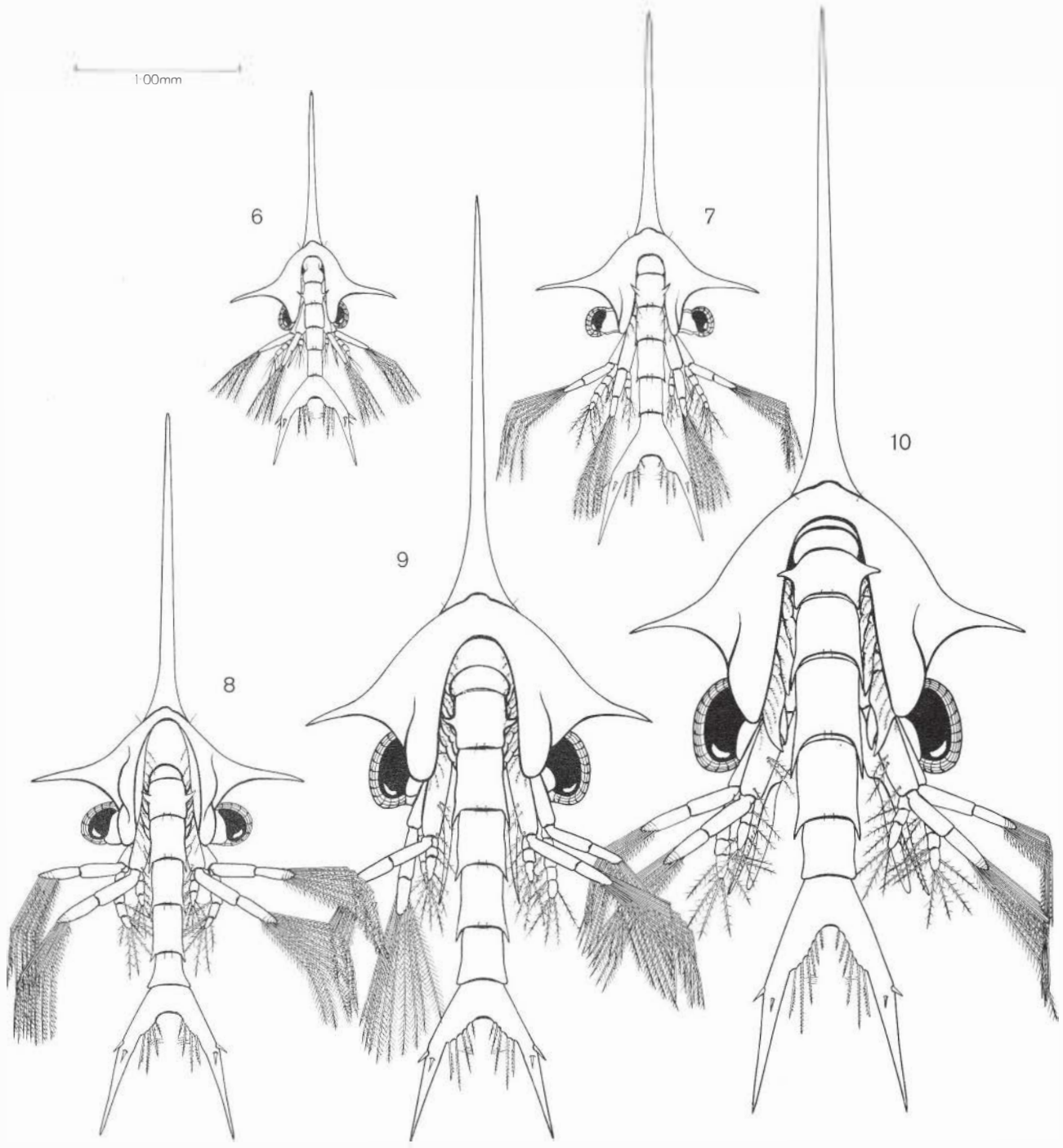

FIGS 6–10: Family CANCRIDAE. *Cancer novaezelandiae* (Jacquinot, 1853). Complete larval development, consisting of 5 zoea stages, drawn to one scale, posterior views: 6, zoea I; 7, zoea II; 8, zoea III; 9, zoea IV; 10, zoea V.

surface of the carapace, one above each eye and one at the base of the dorsal spine on each side. The posterior margin of the carapace has a fringe of plumose setae which arise from its inner surface and increase in number at each moult.

Cancer novaezelandiae is one among a substantial number of species of New Zealand Brachyura with zoea larvae in which the rostral, dorsal, and lateral carapace spines are all present. However, there are also a considerable number of species with zoea larvae in

which one or more of these carapace spines are absent. Virtually all possible combinations of presence/absence of rostral, dorsal, and lateral carapace spines are represented in the New Zealand fauna and, in addition, there are a few species known which have prominent spines in other positions on the carapace.

Cephalic Appendages

The cephalic appendages comprise antennae 1 and 2, a pair of mandibles, and maxillae 1 and 2.

Antenna 1 (Figs 1–5, 11, 12)

In early zoea stages antenna 1 is simple, unjointed, and armed with four or five terminal aesthetascs or slender, presumably sensory, spines (Fig. 11). In zoea V it is partly segmented, biramous, and bears two or more tufts of aesthetascs (Fig. 12).

Antenna 2 (Figs 1–5, 13, 14)

The protopod typically bears a long spiniform process, and an exopod (Figs 13, 14). The endopod develops as an unjointed rudiment in later stages, and can become almost as long as the spiniform process by zoea V (Fig. 14).

Mandible (Figs 15, 16)

Adapted for biting and crushing and usually developing both molar and incisor processes. A bud-like palp develops in zoeas IV and V (Fig. 16).

Maxilla 1 (Figs 17, 18)

In all zoea stages maxilla 1 comprises a flattened protopod giving rise to a jointed palp or endopod bearing a few plumose setae, and two endites each with basically two rows of stout plumose spines and setae, all curved towards the mouth. Maxillae 1 are principally manipulatory mouthparts.

Maxilla 2 (Figs 19, 20)

Characteristically maxilla 2 possesses a large, flat, plate-like exopod or scaphognathite, which has a few marginal setae in zoea I (Fig. 19), but many more by zoea V (Fig. 20). It also has four flattened inner lobes (endites) divided into two pairs separated by a deep cleft, and which all bear plumose setae or spines arranged similarly to those on the endites of maxilla 1. There is a palp (endopod), usually unjointed and bearing terminal and subterminal plumose setae arranged as illustrated in Figs 19 and 20. Maxillae 2 function as manipulatory mouthparts.

Thoracic Appendages

The functional thoracic appendages are restricted to maxillipeds 1 and 2, which are used in swimming.

Maxillipeds 1 and 2 (Figs 21, 22)

The short coxa articulates with a strong, rod-like, but somewhat flattened basis, which in turn gives rise to an exopod partly or completely divided into two segments bearing long, terminal, biplumose natatory setae. The endopod of maxilliped 1 (Fig. 21) is always somewhat longer than that of maxilliped 2 and comprises five segments each with a relatively constant arrangement and number of setae. That of maxilliped 2 (Fig. 22) is similarly conservative in its setation, but may be unsegmented or incompletely divided into three or four segments.

In zoea I of *Cancer novaezelandiae*, and of all known Brachyura with planktonic larvae, there are four natatory setae on maxillipeds 1 and 2, and in zoea II there are six setae (Figs 3, 7). In crabs with more than two zoea stages, zoea III has eight setae, zoea IV has 10 setae, and zoea V has 12. In effect, one additional pair of setae is added at each moult up to at least zoea V (Figs 1–10). There are relatively few exceptions to this rule. Among New Zealand Brachyura, zoea II of *Portunus pelagicus* (Portunidae) has eight rather than six setae, and zoeas II and III of *Ebalia laevis* (Leucosiidae) both have six natatory setae on the maxillipeds. This is also true for species of the genus *Ebalia* occurring beyond the New Zealand region. In general, the above setal pattern is a reliable indication of the particular stage a specimen has reached in a given larval series, but this does not follow in late stages of the New Zealand species *Ovalipes catharus* (Portunidae) and *Plagusia chabrus* (Grapsidae), where in the sixth and subsequent instars very many more setae are added at each moult.

Maxilliped 3 and Pereiopods

These remaining limbs are all rudimentary in the zoea stages although the buds of maxilliped 3 and pereiopods can usually be seen tucked under the carapace from zoea II or III onwards (Figs 3–5). In the last zoea stage, and sometimes in the penultimate stage, maxilliped 3 may be bilobed (Fig. 4), pereiopod 1 chelate and more or less jointed, and the remaining pereiopods may have segmental constrictions (Figs 4, 5). None of these, however, function as walking legs in any of the zoea stages.

Abdomen

The abdomen has five segments and a terminal telson in zoeas I and II (Figs 1, 2, 6, 7), but a sixth segment differentiates from the telson in later stages (Figs 3–5, 8–10). In New Zealand species of Brachyura with just two zoea stages, segment 6 separates in zoea II. In some families such as the Leucosiidae, Hymenosomatidae, and Pinnotheridae, only five segments are present throughout larval life.

Abdominal segment 2 has a pair of lateral protuberances (Figs 1–10). These occur in all known brachyuran zoea larvae and possibly act as a pivot for the abdomen, thereby accentuating the abdominal "whiplash" while feeding (*see* Herrnkind 1968). The extent of abdominal "whiplash" is indicated by comparing Fig. 2 with, for example, Fig. 5. In other New Zealand species similar protuberances may occur also on segment 3 or even segments 4 and 5. A pair of dorsal hairs are found near the posterior margin on segments 2–5 in *Cancer novaezelandiae* (Figs 6–10) and in all other larvae studied. Sometimes these are very fine and not readily seen with a stereomicroscope. The ventrolateral corners of segments 3–5 are produced

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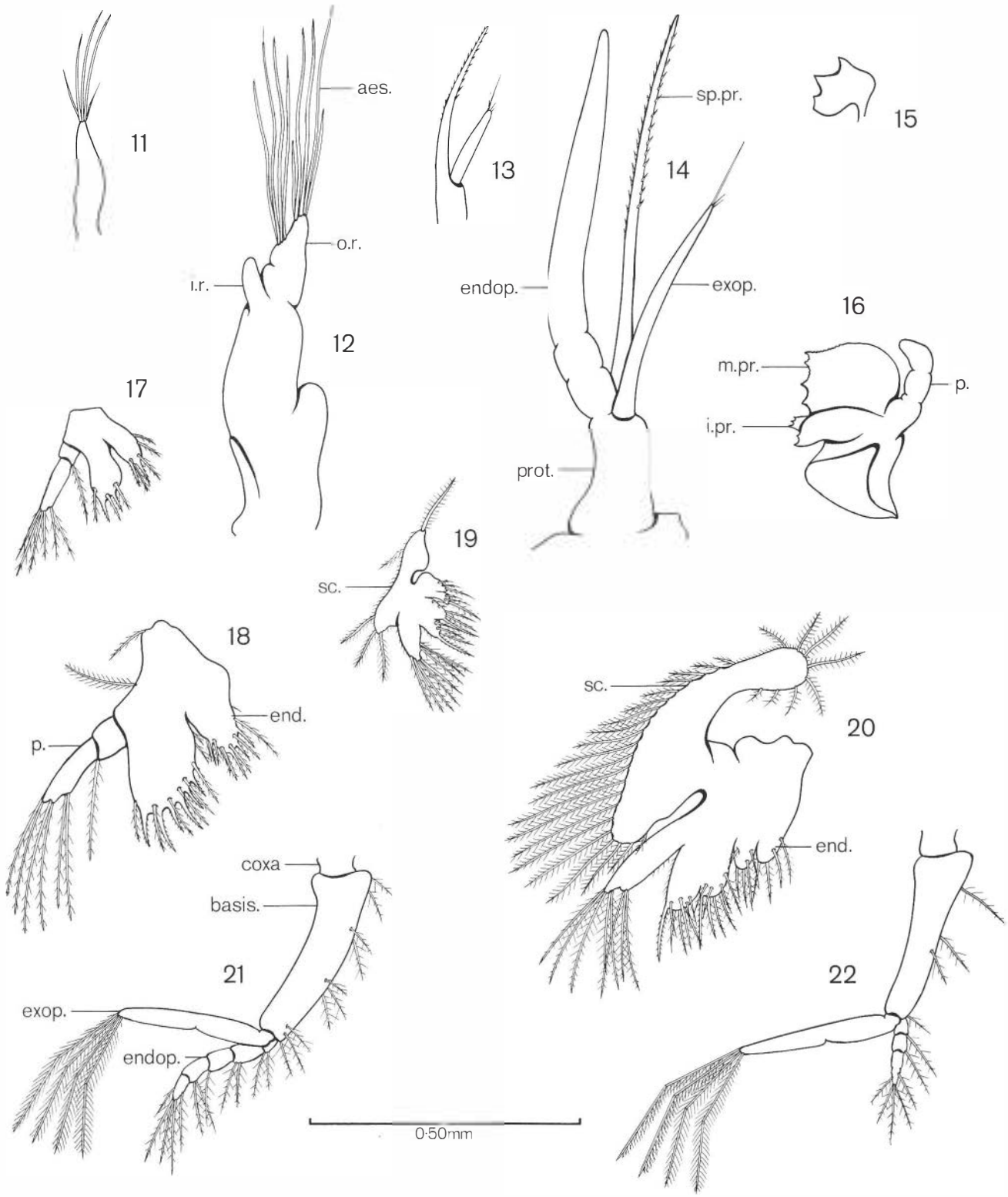


FIGS 11–22: Family CANCRIDAE. *Cancer novaezelandiae* (Jacquinot, 1853). Zoea larval appendages: 11, zoea I, antenna 1; 12, zoea V, antenna 1; 13, zoea I, antenna 2; 14, zoea V, antenna 2; 15, zoea I, mandible; 16, zoea V, mandible; 17, zoea I, maxilla 1; 18, zoea V, maxilla 1; 19, zoea I, maxilla 2; 20, zoea V, maxilla 2; 21, zoea I, maxilliped 1; 22, zoea I, maxilliped 2. Abbreviations: aes. - aesthetascs; basis - basipod; coxa - coxopod; end. - endite; endop. - endopod; exop. - exopod; i.pr. - incisor process; i.r. - inner ramus; m.pr. - molar process; o.r. - outer ramus; p. - palp; prot. - protopod; sc. - scaphognathite; sp.pr. - spiniform process.

into sharp spines which become more obvious in later stages, but these are not developed in zoea I of *C. novaezelandiae*.

Pleopods (Figs 3–5) are present as rudiments on segments 2–5, and by the final zoea stage they are long and biramous. These pleopod buds are non-functional as swimming organs, and have no setae. They do not occur on segment 1, or in zoea I of species with more than two zoea stages. Pleopods of segment 6 are destined to be the lateral elements of the tail fan (uropods) in the megalopa, and are always much smaller than those of preceding segments (Figs 4, 5). Some groups such as the Hymenosomatidae develop no pleopods at all.

The telson (Figs 6–10) is typically forked and in zoea I bears three pairs of plumose setae within the fork, arising from the posterior margin. The inner pair is provided with a tuft of rather longer spinules which possibly function as a locking device. An additional smaller pair of setae is usually added medially at each moult. Near the base of the lateral cornua three very small spine-like setae occur on each side (Fig. 6), with the first two located laterally and the third arising dorsally. The smaller of the lateral setae is lost after zoea stage I (Figs 7–10).

The megalopa

Figs 23–37 illustrate the megalopa of *Cancer novaezelandiae* and its appendages. A shorter, but fully diagnostic description, including key measurements not given below, is contained in the systematic section of the paper.

The megalopa (Figs 23, 24) swims orientated more or less horizontally with the abdomen extended to facilitate propulsion by synchronous beating of its setose pleopods. The maxillipeds now function as accessory mouthparts rather than as natatory organs, and have consequently lost their long, plumose setae. The body is flattened dorsoventrally, all adult appendages are developed, and its form is generally crab-like, except that the abdomen is relatively much longer than that of the adult and is usually extended. However, it can be flexed beneath the body.

In the family Hymenosomatidae no true megalopa follows the zoea stages. Instead the last zoea stage metamorphoses into a planktonic post-zoeal stage which lacks natatory pleopods or uropods and swims using the walking legs. It is termed the first juvenile crab.

Cephalothorax

In *Cancer novaezelandiae* the rostrum is rather long and directed anteriorly and the dorsal spine of the zoea is retained as a median spine directed posteriorly (Figs 23, 24). The carapace is smooth and relatively featureless apart from a depressed area immediately posterior to the rostrum. The eyes are large and on moveable stalks. In most other New Zealand species, the rostrum is directed downwards and is much smaller, and the posterior spine does not occur. Carapace hairs, tubercles, protrusions, and other topographical variations may also occur in other species.

The detailed structure of the megalopa appendages is more complex than in the zoea stages, but some generalisations can be made. Our comments are restricted mainly to differences from the condition already described for the zoea larvae.

Cephalic Appendages

Antenna 1 (Fig. 25)

Antenna 1 has a short, segmented peduncle swollen at its base to enclose a statocyst, and both the inner and outer rami are completely divided from the peduncle and bear aesthetascs.

Antenna 2 (Fig. 26)

Antenna 2 has a short, segmented peduncle giving rise to a slender, setose flagellum. In *C. novaezelandiae* this is not reduced, but in some species it may consist of just a few segments. There is no exopod.

Mandible (Fig. 27)

The mandible is provided with a segmented palp, with the terminal segment bearing a heavy tuft of stout setae.

Maxilla 1 (Fig. 28)

The endites now have many marginal plumose spines and setae, and the endopod (palp) is reduced from the condition seen in zoea V (Fig. 18).

Maxilla 2 (Fig. 29)

Maxilla 2 is dominated by a very large scaphognathite and by the four endite lobes, all with many marginal plumose setae arranged as illustrated. The endopod (palp) is reduced and usually lacks setae.

Thoracic Appendages

Maxilliped 1 (Fig. 30)

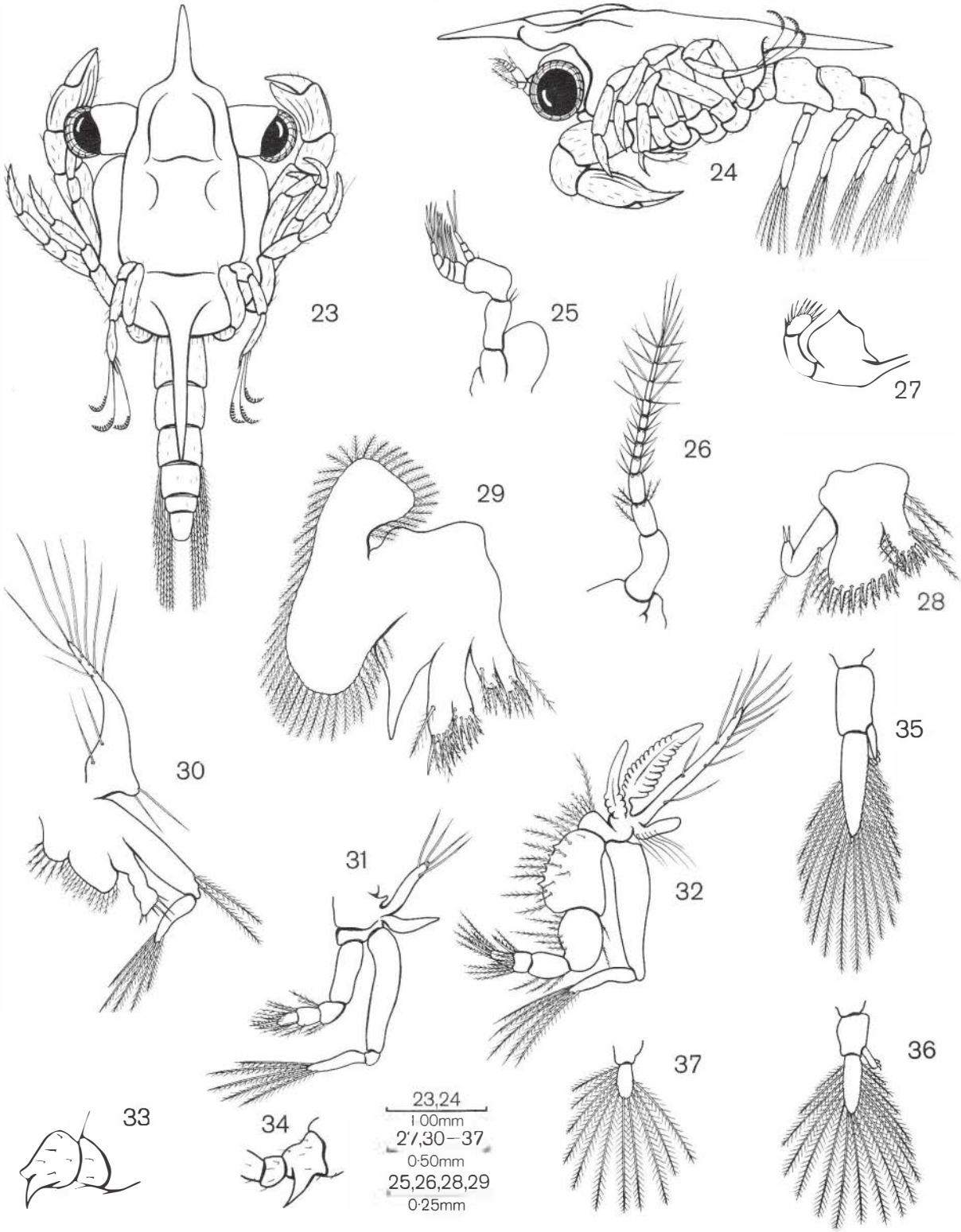
This has now developed two setose endites, one arising from the coxa and one from the basis, and a long, flattened epipod (gill cleaner) sparsely fringed with long, non-plumose setae. The endopod is reduced, usually segmented, and has just a few terminal setae. The exopod is of two, usually setose, segments, but the distal segment bears only five or six terminal plumose setae — reduced from the 12 setae characterising zoea V.

Maxilliped 2 (Fig. 31)

There are no endites, but a small epipod with terminal setae and bud-like rudiments of a podobranch and of a much smaller arthrobranch are present. These gills lack lamellae and are presumed not to be fully functional. The four-segmented endopod is more strongly developed and setose than in zoea V, but the exopod is of three segments and reduced, to a similar degree, to that of maxilliped 1.

Maxilliped 3 (Fig. 32)

Maxilliped 3 is very much more strongly developed than in the zoea larvae and this pair of appendages has assumed the adult form and function as mouth-



FIGS 23–37: Family CANCRIDAE. *Cancer novaezelandiae* (Jacquinot, 1853). Megalopa: 23, dorsal view; 24, lateral view; 25, antenna 1; 26, antenna 2; 27, mandible; 28, maxilla 1; 29, maxilla 2; 30, maxilliped 1; 31, maxilliped 2; 32, maxilliped 3; 33, basal segments of pereiopod 1; 34, basal segments of pereiopod 2; 35, pleopod 1; 36, pleopod 4; 37, uropod.

parts. A setose epipod, one podobranch, and two arthrobranchs with rudimentary lamellae are now present. The greatest development is seen in the endopod, which is now of five segments designated ischium (proximal), merus, carpus, propodus, and dactyl (distal) respectively, as in all decapod Crustacea. The entire structure is somewhat flattened, strongly setose, and in *C. novaezelandiae* it bears a row of teeth along the inner margin of the ischium.

Pereiopods (Figs 23, 24, 33, 34)

All pereiopods are sparsely covered with short setae, and pereiopod 1 is functionally chelate. A strong curved spine is present on the ischium of pereiopod 1 (Fig. 33), and on the basis of pereiopod 3 (Fig. 34). The dactyl of pereiopod 5 bears several long, curved, terminally hooked setae each equipped distally with a row of minute comb-like teeth. These setae were termed "feelers" by Lebour (1928a), but it is possible that they are used to clean the dorsal surface of the carapace and to keep it free from detritus and epiphytic or epizoic growth.

Abdomen

The abdomen (Figs 23, 24) comprises six segments and a telson, with the posterolateral spines characterising later zoea stages having been lost or modified as lateral pleural plates which overlie each following segment. Segments 2–5 bear functional, biramous, setose pleopods (Figs 35, 36) which decrease in size posteriorly (Fig. 24). The much smaller endopod bears several terminal hooklets which are probably used to grip those of the opposite member to synchronise swimming movements.

The pleopods of segment 6, or uropods (Fig. 37), are much smaller, uniramous, and are the lateral components of the tail fan. The telson in *C. novaezelandiae* is rounded posteriorly and lacks setae.

Identification of Species

In the following systematic treatment of the larvae of the New Zealand Brachyura we have used the general characters first suggested by Lebour (1928a) and which have proved adequate in the identification of larvae described subsequently. For zoea larvae these are:

1. The nature of the carapace and its armature;
2. The character of antenna 2;
3. The armature of the abdominal segments;
4. The character of the telson and its armature;
5. The number of zoea stages.

For megalopa larvae, the most important diagnostic characters are:

1. The general shape of the carapace and the presence or absence of tubercles or protuberances;
2. The nature of the rostrum;
3. The presence or absence of spines on the pereiopods and abdomen;
4. The presence or absence of long, terminally hooked setae on the dactyl of pereiopod 5.

Planktonic crab larvae are often brightly coloured in life, with each species having a distinctive pattern of red, orange, yellow, green, or black chromatophores which may expand or contract under the control of hormones influenced by the intensity of light and probably other factors. They quickly fade as soon as the animal dies and are therefore of limited use in taxonomic work. We have used details of the chromatophore pattern only on the few occasions where it is impossible to separate the larvae of different species by any other means.

Family and generic characters and comments applying to broader groupings are given only where such characters are considered to be of value for rapid identification to this level, and are constant so far as is known. The comments are thus restricted, and need not apply to other species occurring beyond the New Zealand region, although in most cases we have ensured that such diagnoses are true for all known species. For the most part, the following systematic treatment follows a generally accepted arrangement of families, and the genera are grouped, where relevant, in their respective subfamilies — although not in a formal manner. We have, however, tended to favour a progression of larval affinities between genera for ease of description and recognition of species.

Diagnostic Morphology of New Zealand Larvae

DROMIACEA

Zoea larvae rather more "anomuran" than brachyuran, with rostrum pointing anteriorly and with variable number of carapace spines; antenna 2 exopod a flattened setose scale; exopod of maxilliped 3 develops swimming setae after zoea I; setose uropods present in later larval stages with endopod and exopod of about equal size; telson triangular, becoming rectangular in later stages and not widely forked as the fourth process is not greatly enlarged; second telson process hair-like in all zoea stages; abdomen lacks dorsolateral protuberances on segment 2 and is held horizontally while swimming. A more detailed characterisation of dromiacean larvae and discussion of their relationships with those of other Brachyura appear in Rice (1980a). The larvae of this group are extremely variable and it is therefore unrealistic to list characters which would prove reliably diagnostic at the family level when considering the few species known to occur in the New Zealand fauna.

FAMILY HOMOLIDAE

Paromola Wood-Mason, 1891

Paromola petterdi Grant, 1905

SOURCE REFERENCES: Williamson (1965) — megalopa dredged off Port Hacking, N.S.W. Samuelson (1976)

— zoea I of *Paromola cuvieri* (Risso) from laboratory hatched eggs, as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island of N.Z.; continental slope. Also Australia.

BREEDING AND EGGS: No knowledge.

ZOEA LARVAL STAGES: No knowledge. Zoea I of *P. cuvieri* (Figs 38–40) is described and illustrated as an example of the genus.

Zoea with dorsal, rostral and lateral carapace spines. Total length about 2.3 mm — this species has large eggs (0.8 mm diameter) and consequently a relatively large first stage zoea larva; rostral spine straight and directed forwards; dorsal and lateral carapace spines short; posterior margin of carapace divided into a dorsal and a lateral lobe on each side and fringed with marginal teeth; antenna 2 exopod flattened and leaf-like (squamous) with several plumose setae on inner margin; five abdominal segments; abdominal segment 1 with several large plumose setae dorsally; telson triangular with a pronounced posteromedian notch, to each side of which are five posterior plumose setae and a posterolateral spine.

MEGALOPA (Figs 41, 42): Carapace length 4.0 mm; carapace width (excluding lateral spines) 3.7 mm; rostrum 1.4 mm long, slightly convex and directed downwards; dorsal spine 7.0 mm long, curved posteriorly; lateral spines 11.0 mm long; supraorbital spines 7.5 mm long, on either side of the rostrum and convergent, their tips apparently jointed; a small tubercle and a dome-like prominence occur between the rostrum and the dorsal spine; a second small tubercle occurs near the posterior margin of the carapace; a short, dorsally directed spine is present at the base of each supraorbital spine; dorsal surface of carapace with defined ridges; entire surface of carapace including spines covered with minute granules and very short hairs, posterior margin with some short setae; pereiopod 5 with one long, terminally hooked seta on the dactyl; abdominal segments 2–5 with biramous pleopods; abdominal segment 6 with setose biramous uropods, the endopod and exopod about equal in size; telson parallel-sided in its anterior half, tapering posteriorly, posterior margin with 7+8 plumose setae.

NOTES: The larval development of *P. petterdi* is known only from a single megalopa dredged from about 80 m depth near Port Hacking, New South Wales. Its identification is subjective and has not yet been verified. Rice (1971), however, discusses this identification in the light of the other similar megalopas taken from Japan.

Latreillia Roux, 1830

Latreillia australiensis Henderson, 1888

SOURCE REFERENCES: Williamson (1965, 1967) — zoea I from laboratory hatched eggs; megalopa from plankton.

ADULT DISTRIBUTION AND HABITAT: Northern half of North Island, N.Z.; outer continental shelf and continental slope. Also Australia.

BREEDING AND EGGS: Ovigerous females have been collected at all times of the year in Australian waters, but only in November in northern N.Z. Eggs, newly laid, white, 0.30 mm diameter; about to hatch, transparent, 0.40 mm diameter.

ZOEA LARVAL STAGES: Probably five or more stages; colour in life, mostly yellow.

Zoea I (Figs 43–45): Zoea with rostral carapace spine only. Total length 1.40 mm; rostral spine 0.29 mm long, extending anteriorly, straight; carapace with a posterolateral fold on each side, margins of fold and margins of carapace fringed with denticles in some specimens, no denticles in others (Fig. 45); length of antenna 2 exopod 0.08 mm; ratio of antenna 2 spiniform process to rostral spine and to antenna 2 exopod, *0.53 and 1* respectively; abdominal segments broader than long, segment 1 with tuft of six dorsal hairs, two shorter dorsal hairs on all others, small lateral spine arising just above posterior margin of segments 3–5; telson almost four times broader than long and with a shallow posteromedian notch, to each side of which are five posterior plumose setae and a posterolateral spine.

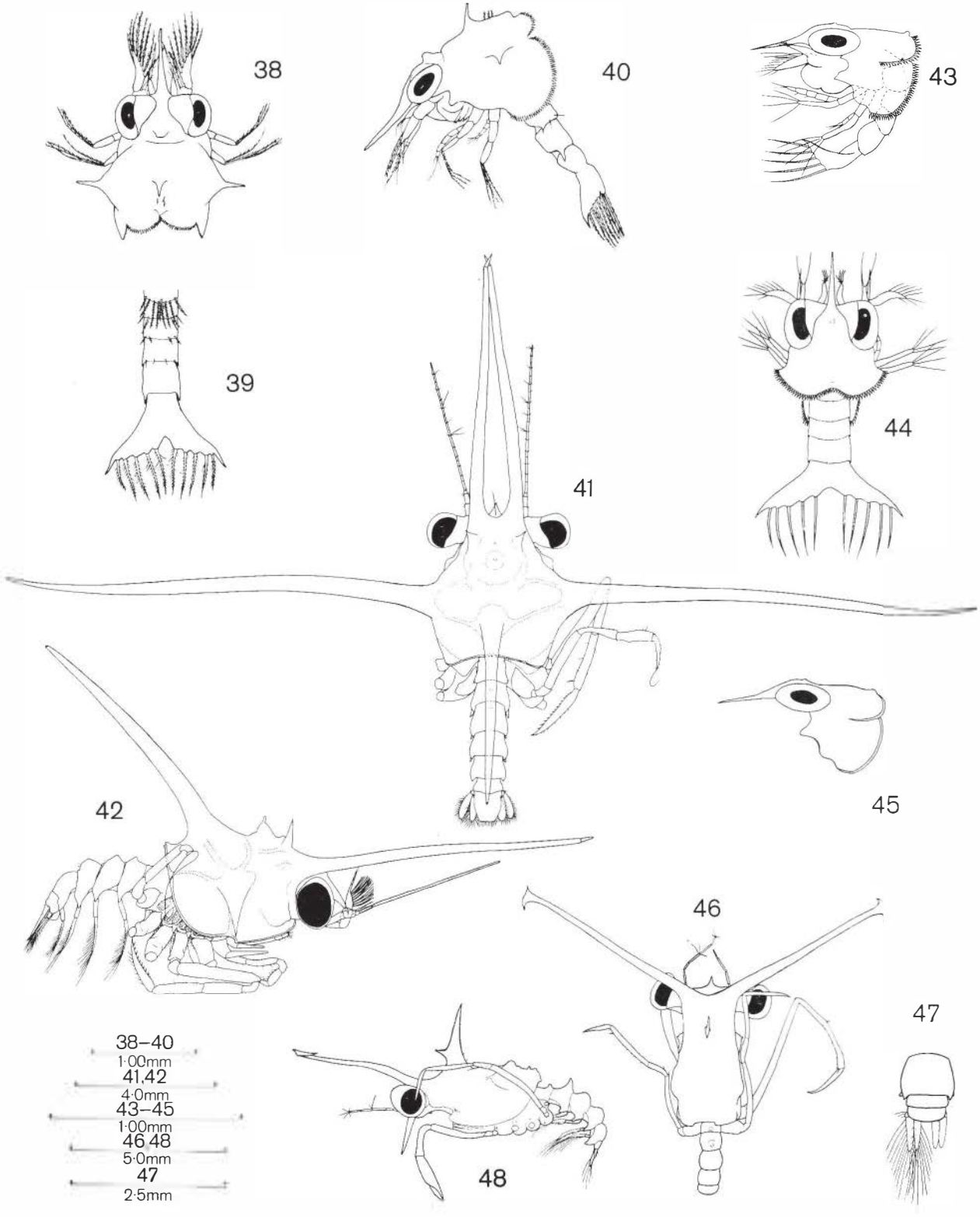
MEGALOPA (Figs 46–48): Carapace length (from sulcus between supraorbital spines to posterior margin) 3.9 mm; carapace width 2.2 mm; rostrum ventrally directed with broad base; very prominent and widely divergent supraorbital spines each ending in a hooked posterior spine and smaller anterior spine; prominent mediodorsal carapace spine with a smaller anteriorly-directed spine arising from its proximal half; posterior dorsal tubercle, and dorsal and dorsolateral carapace ridges defined; no long terminally hooked setae on pereiopod 5 dactyl; dorsal tubercle present on abdominal segments 1 and 2, pleura of segments 2–5 produced ventrally; biramous pleopods on abdominal segments 2–5; abdominal segment 6 with setose biramous uropods, the endopod and exopod about equal in size; telson without marginal setae or spines.

NOTES: The megalopa was described from a single specimen collected by a tow-net that touched bottom at 100 m depth. Its identification by Williamson (1967) cannot be verified. However, it conforms with the larval characters of *L. elegans* Roux and was taken from an area where adult *L. australiensis*, the only species of this genus found in Australian waters, was known to abound. In the light of this evidence Williamson considered the megalopa to belong almost certainly to this species.

Homola Leach, 1815

Homola orientalis Henderson, 1888

SOURCE REFERENCES: Boas (1880). Rice and von Levetzow (1967) — zoea IV from plankton. Rice (1964)



FIGS 38–48: Family HOMOLIDAE. *Paromola cuvieri* (Risso). Zoea I: 38, cephalothorax, dorsal view; 39, abdomen, dorsal view; 40, lateral view. After Samuelsen (1976). *Paromola petterdi* Grant, 1905. Megalopa: 41, dorsal view; 42, lateral view. After Williamson (1965). *Latreillia australiensis* Henderson, 1888. Zoea I: 43, lateral view; 44, dorsal view; 45, carapace lacking denticles, lateral view. Megalopa: 46, dorsal view; 47, posterior abdominal segments, dorsal view; 48, lateral view. Figs 43–45 after Williamson (1965), 46–48 after Williamson (1967).

— megalopa of *Homola barbata* (Fabricius) as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island of N.Z.; continental slope, but so far rarely captured. Indo-West Pacific.

BREEDING AND EGGS: No detailed knowledge of breeding in N.Z. waters. One ovigerous female collected in September.

ZOEA LARVAL STAGES: Probably five or more zoea stages. The larvae of *H. orientalis* are not known for certain. The figures drawn by Boas (1880) and reproduced here (Figs 49, 50) have been attributed to *H. orientalis* by Rice and von Levetzow (1967) on the basis of adult distribution. Consequently the descriptions of *Homola barbata* (Fabricius) zoea I (Fig. 51) by Rice and Provenzano (1970) and of *Homola* sp. zoea II (Fig. 52) by Rice and von Levetzow (1967) have also been used to provide what appear to be generic larval characters probably applicable also to this present species.

Zoea IV (Figs 49, 50): Zoea with dorsal, rostral and adrostral, and paired antorbital, postorbital, lateral and two pairs of posterolateral carapace spines. Carapace with posterolateral fold defined, with margins of fold and posterior carapace margin fringed with denticles (not figured by Boas 1880); abdominal segments with dorsal and lateral spines; telson broad, with 16 posterior setae and a posterolateral spine to either side of the midline and characteristic dorsal spines. These dorsal telson spines also are not figured by Boas (1880).

MEGALOPA: No knowledge. The megalopa of *H. barbata* (Fig. 53) is described and illustrated as an example of the genus.

Carapace setose with raised and tubercular areas, and with a well-defined groove separating the gastric and hepatic regions; rostrum directed downwards between a pair of strongly developed antorbital processes; pereiopod 5 with several long, terminally hooked setae on dactyl; abdominal segments unarmed, segments 2–5 with biramous pleopods, segment 6 with setose biramous uropods; telson fringed with posterior setae, and with numerous dorsal setae.

FAMILY DROMIIDAE

Petalomera Stimpson, 1858

Petalomera wilsoni (Fulton & Grant, 1902)

SOURCE REFERENCES: Wear (1965, 1970c, 1977) — zoea I from laboratory hatched eggs; zoea II and megalopa obtained from plankton.

ADULT DISTRIBUTION AND HABITAT: North Island and northern part of South Island, N.Z.; widely distributed and relatively common on rough bottoms between low tide and about 150 m, often found in association with sponges, bryozoans, and algae. Also Australia, South Africa, Japan.

BREEDING AND EGGS: Larvae occur in the Cook Strait inshore plankton throughout year, but more characteristically during spring and autumn. Ovigerous females have been collected in February and March. Eggs, newly laid, deep red, 0.75 mm diameter; about to hatch, light orange, 1.00 mm × 1.00 mm to 1.12 mm × 0.88 mm.

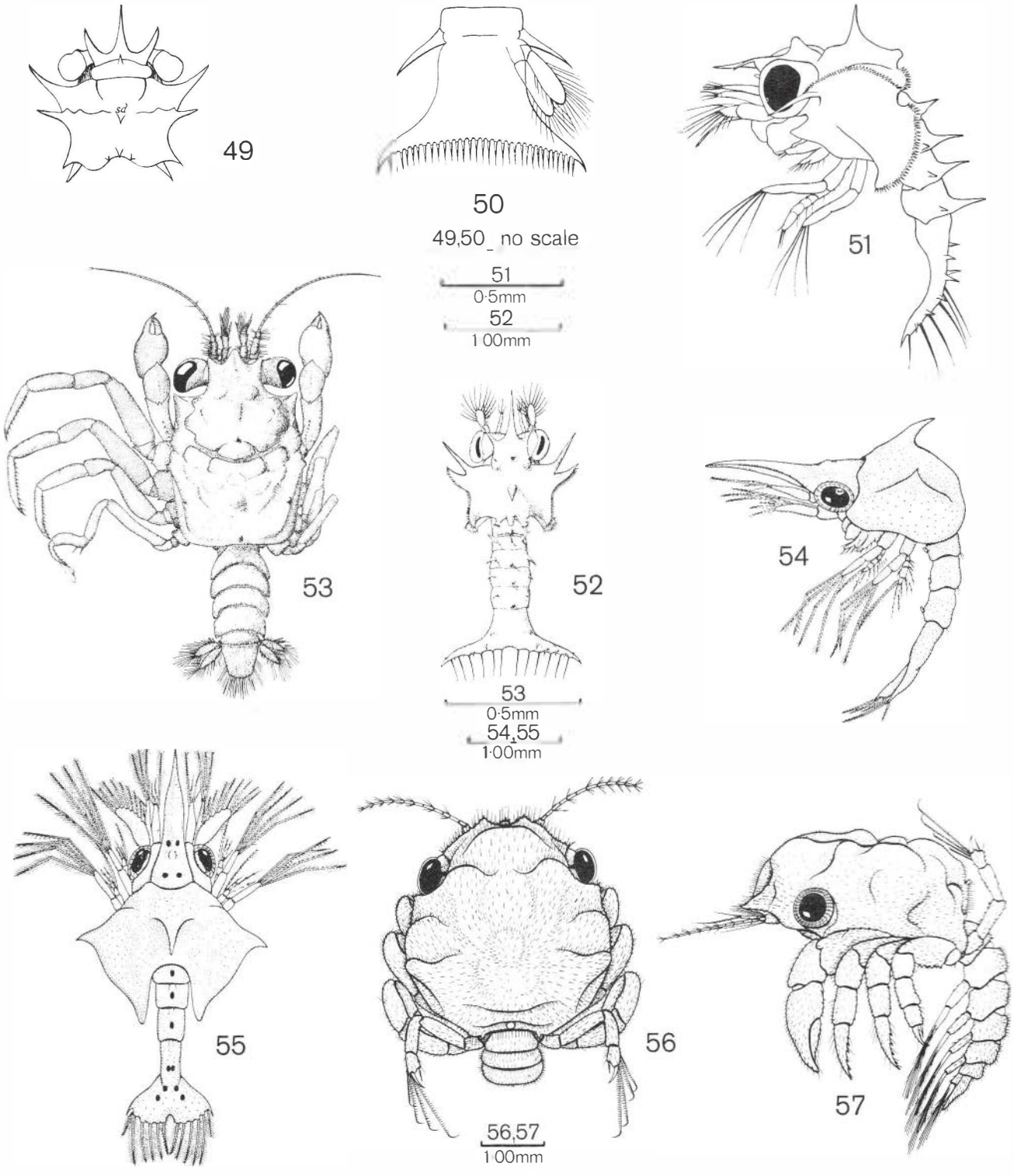
ZOEA LARVAL STAGES: Probably three or four zoea stages; colour in life, bright red, making them clearly visible in living plankton samples.

Zoea I (Figs 54, 55): Zoea with dorsal, rostral, and lateral carapace spines. Total length 4.0–4.8 mm; rostral spine 1.6 mm from tip to junction with carapace, separated from the carapace by a deep transverse groove and extending anteriorly with its tip slightly downturned; posterior carapace margin deeply cleft in midline but otherwise smooth; surface of carapace finely denticulate; dorsal carapace spine 0.4 mm long, broad at base, curved posteriorly; spine to spine length 2.63 mm; lateral carapace spines broadly based, wing-like and tilted upwards; length of antenna 2 exopod 0.44 mm; abdominal segments 2–5 with two posterior dorsal hairs but otherwise without spines, papillae or setae; pleopod rudiments may occur on abdominal segments 2–5; telson broad and spatuliform with small crescent-shaped notch in posterior midline, six posterior plumose setae and a posterolateral spine either side of central notch, and posterior margin fringed with fine hairs.

Zoea II: Total length 5.0–6.0 mm; rostral spine 2.0–2.3 mm from tip to junction with carapace; dorsal carapace spine 0.44 mm long and curved posteriorly; spine to spine length 3.13 mm; length of antenna 2 exopod 0.77 mm; maxilliped 3 with a functional natatory exopod.

MEGALOPA (Figs 56, 57): Carapace length 3.50 mm; carapace width 3.15 mm; carapace extensively grooved with raised areas, pubescent and granular, anterior and anterolateral margins armed with small spinules; rostrum very small or virtually absent, depressed between and below frontal carapace lobes; pereiopod 5 with four long terminally hooked setae on the dactyl and with dactyl terminating in a stout, curved spine opposing a smaller spine so as to appear chelate; abdominal segments without spines, segments 2–5 with biramous pleopods, segment 6 with uropods with the endopod reduced to a bud; telson sparsely setose.

NOTES: Stage II zoeas of *Petalomera wilsoni* were obtained from the plankton but none moulted to stage III in the laboratory. However, a third zoea stage, possibly the final one, was apparent beneath the stage II cuticle. To our knowledge the bright-red-coloured megalopas are rare in the plankton — the only occasion on which they have been captured remains the February 1969 record from a surface plankton haul taken close inshore among *Macrocystis* in the Cook Strait area (Wear 1977). Their planktonic existence



FIGS 49–57: Families HOMOLIDAE & DROMIIDAE. *Homola orientalis* Henderson, 1888. Zoea IV: 49, carapace, dorsal view; 50, telson, dorsal view. After Boas (1880). *Homola barbata* (Fabricius). Zoea I: 51, lateral view. After Rice and Provenzano (1970). *Homola* sp. Zoea II: 52, dorsal view. After Rice and von Levetzow (1967). *Homola barbata* (Fabricius). Megalopa: 53, dorsal view. After Rice (1964). *Petalomera wilsoni* (Fulton and Grant, 1902). Zoea I: 54, lateral view; 55, dorsal view. Megalopa: 56, dorsal view; 57, lateral view. Figs 54, 55 after Wear (1970c); 56, 57 after Wear (1977).

may be short-lived, since megalopas may be found also among *Macrocystis* holdfasts. Eleven megalopas and seven first stage juvenile crabs were found in a single holdfast washed up on Waikanae Beach, 3-8-74 (D.I. Bennett coll.).

The only other species of *Petalomera* with a known life-history, *P. lateralis* (Gray), has direct development (Hale 1925, Montgomery 1922), which is apparently common in dromiid crabs (*see* Wear 1967: 522).

OXYSTOMATA

Zoea larvae clearly "brachyuran" in their general facies and sharing more characters with those of the Brachygnatha or true Brachyura than with anomuran forms. The larvae show wide variation within the group, giving rise to the view expressed by Rice (1980a) and many other earlier workers that this assemblage of families is entirely unnatural. However, the zoea larvae fall within the scope of the diagnosis of a generalised brachyuran larva given earlier using *Cancer novaezelandiae* as an example.

FAMILY TYMOLIDAE

Use of the family name Tymolidae follows the suggestion of Gordon (1963) and its subsequent adoption as a taxonomic category by Williamson (1965) and Sakai (1976). Larvae of the previously used and broader family Dorippidae are unusual and distinctive, but can be divided into two groups defined by the tymolid crabs (larvae with squamous antenna 2 exopod and a flattened telson which may be described as primitive and "anomuran" in origin) and by the dorippid crabs (larvae which are rather more "brachyuran", with rod-like antenna 2 exopod and forked telson). All are more or less unique as a group, with their frequently exaggerated carapace armature and long and narrowly forked telson (*see* Wear and Batham 1975, Gurney 1942). Tymolid and dorippid zoea larvae are characterised by Rice (1980a), who also discusses their affinities.

Cymonomus A. Milne Edwards, 1880

Cymonomus bathamae Dell, 1971

SOURCE REFERENCES: Wear and Batham (1975) — zoea I from laboratory hatched eggs; megalopa characters from zoea about to moult. Dell (1971) — records of ovigerous females; fecundity; egg size.

ADULT DISTRIBUTION AND HABITAT: Southern half of South Island, N.Z.; occasionally taken by dredge in depths between 200 m and 800 m in association with sponges, molluscs and echinoderms. Endemic.

BREEDING AND EGGS: Ovigerous female collected in May. Eggs, newly laid, orange, 1.2 mm × 1.0 mm; about to hatch, 1.4 mm diameter.

ZOEA LARVAL STAGES: One, possibly two, zoea stages; colour in life, transparent.

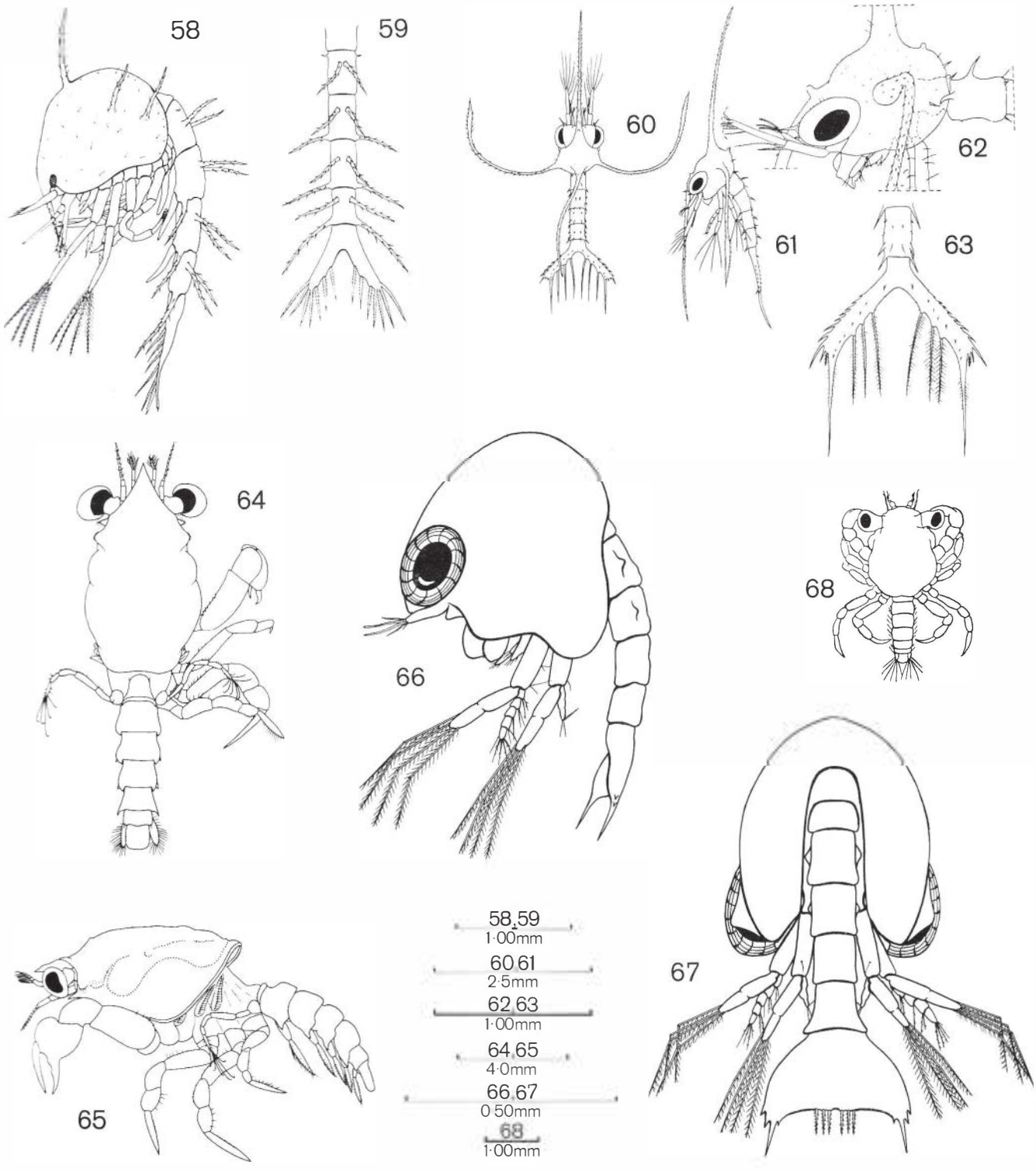
Zoea I (Figs 58, 59): Zoea with dorsal, rostral and two pairs of lateral carapace spines. Total length 3.3 mm; rostral spine 0.47 mm long, slender, straight, armed with dorsolateral spinules along distal half; dorsal carapace spine 0.67 mm long, curved slightly posteriorly and armed with small spinules; spine to spine length 1.97 mm; lateral carapace spines inclined strongly upwards and armed with small spinules; carapace with sparse covering of hairs; eyes very small; length of antenna 2 exopod 0.30 mm; pereiopods all present, well-developed and segmented; abdominal segments 2–5 each with a pair of slender dorsal spines and segments 3–5 with a pair of long posterolateral spines, the spines armed with spinules; abdominal segments 2–4 with pleopod buds, but uropod buds absent; telson broad and flattened with a deep median posterior notch, three posteromedial plumose setae and four slender posterior spines to either side of the notch, the spines and setae all of similar length, the spines possessing medial or ventral serrations.

MEGALOPA: Megalopa not seen, but some megalopa characters were observed in several zoea larvae about to moult. Rostrum short; carapace and abdomen without spines; dactyls of pereiopods with terminal claws; abdomen of five segments and a telson lacking posterior setae; three pairs of setose pleopods (segments 2–4); uropods absent.

NOTES: *Cymonomus bathamae* has few eggs, large in size, and development is partly abbreviated. The species may have only one zoea stage followed by the megalopa, or alternatively there may be a first zoea stage of very short duration which moults to a second stage zoea before advancing to the megalopa (Wear and Batham 1975). Larvae hatched in the laboratory are very weak swimmers and are not likely to occur in shallow-water plankton samples. The affinities and evolutionary significance of this most unusual larva are discussed in detail elsewhere (Wear and Batham 1975, Williamson 1974, Rice 1980a).

FAMILY RANINIDAE

Zoea larval carapace with rostral, dorsal and paired lateral spines, and also with many short spines, denticles and setae; abdomen spiny; telson somewhat flattened, often appearing as two narrow prongs, and armed with accessory anterolateral and dorsal spines; antenna 2 exopod flattened and scale-like as in the Anomura. Megalopa with forwardly directed rostrum (which may be quite long) but lacking other carapace spines; chelipeds with palm distinctly swollen; abdominal pleura with posteroventrally directed processes. Larval characters of the Raninidae are more fully summarised by Williamson (1965: 388), and zoea larval affinities of the family are discussed most recently by Rice (1980a).



FIGS 58–68: Families TYMOLIDAE, RANINIDAE & LEUCOSIIDAE. *Cymonomus bathamae* Dell, 1971. Zoea I: 58, lateral view; 59, abdomen, dorsal view. After Wear and Batham (1975). *Lyreidus tridentatus* de Haan, 1841. Zoea I: 60, dorsal view; 61, lateral view; 62, cephalothorax, lateral view; 63, telson, dorsal view. Megalopa: 64, dorsal view; 65, lateral view. Figs 60–65 after Williamson (1965). *Ebalia laevis* (Bell, 1885). Zoea I: 66, lateral view; 67, posterior view. *Ebalia tuberosa* (Pennant). Megalopa: 68, dorsal view. After Lebour (1928b).

Lyreidus de Haan, 1841

Lyreidus tridentatus de Haan, 1841

SOURCE REFERENCES: This study — two megalopas dredged over mud in 203–248 m in the Bay of Plenty, January 1979. Williamson (1965) — zoea stages I–V reared from laboratory hatched eggs; stage VI and megalopa from fish stomachs and by dredging respectively.

ADULT DISTRIBUTION AND HABITAT: Northern half of North Island, N.Z.; continental shelf and slope between 75 m and 220 m, usually dredged over muddy or sandy bottoms. Indo-Pacific.

BREEDING AND EGGS: No detailed knowledge of breeding in N.Z. Ovigerous females have been collected off Sydney from June to September. Eggs, newly laid, bright orange to red, 0.47–0.50 mm diameter; about to hatch, red, 0.65 mm × 0.60 mm.

ZOEA LARVAL STAGES: Probably six zoea stages; colour in life, bright red.

Zoea I (Figs 60–63): Zoea with dorsal, rostral and one pair of lateral carapace spines. Total length (from front of eyestalks to end of 4th telson process) 3.0 mm; rostral spine 2.0 mm long, very thin, with slight posterior curve on distal third; dorsal carapace spine 2.36 mm long, thin, with a slight posterior curve; spine to spine length 5.14 mm; lateral carapace spines 2.29 mm in length, curved ventrally, slightly expanded near tips; carapace spines all spinulated along their entire length; many denticles, long spines and short hairs on surface of carapace, anterior and posterior tubercles prominent in midline, small dorsolateral spines on each side near posterior margin, small lateral spine between large lateral spine and posterior carapace margin; length of antenna 2 exopod 0.42 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod (less setae), *0.09, 0.08, and 0.45* respectively; abdominal segment 1 with one pair of spines, segments 2–5 usually each with four or five pairs of smooth spines and one or two pairs of setae; telson broadly Y-shaped with two arms approximately at right angles to each other; each arm bearing eight small spines on the dorsal surface, seven or eight smooth anterolateral spines, three posteromedial plumed setae, and four posterior spines, the outer two spines smooth, the inner two plumed, the innermost much longer and more strongly developed than the others.

Zoeas II–VI: No measurements available (*see* Williamson 1965 for descriptions).

MEGALOPA (Figs 64, 65): Colour in life, bright red. Carapace length 7.1 mm; carapace width 4.3 mm, tapering anteriorly to forwardly directed rostrum; no other spines; anterior and posterior tubercles discernible but not prominent, the posterior tubercle a small, finger-like projection; carapace with a prominent postorbital process bearing a few setae, and a second less prominent tubercle with coarse granules behind this; remainder of carapace minutely granular and more or less smooth with a fairly well-defined branchial groove on each side; pereiopod 1 with propodus greatly swollen and broader than long; pereiopod 4 with dactyl somewhat flattened and sparsely setose marginally; pereiopod 5 bearing four or five long terminally hooked setae on dactyl plus four or five others graded to shorter length moving proximally; abdominal segments 2–5 bearing setose biramous pleopods and with ventrolateral margins extended into a broadly based spine on each side; uropods with endopod present as a small undivided protuberance and with two setae on protopod and about 32 setae on exopod; telson slightly longer than broad, subrectangular but rounded posteriorly.

FAMILY LEUCOSIIDAE

Usually four zoea stages and a megalopa. Zoea larvae globose, with no carapace spines in New Zealand species (subfamily Ebaliinae) and with only five abdominal segments in all stages; antenna 2 reduced to a small bud; telson spatulate with lateral teeth rather than being forked. Zoea larval characters of the family are synthesised and fully discussed by Rice (1980b). *See also* introductory comments to the family Pinnotheridae in this paper (pp. 64, 65).

Ebalia Leach, 1817

Ebalia laevis (Bell, 1855)

SOURCE REFERENCES: This study — zoeas I–IV collected from plankton. Lebour (1928b) — megalopa of *Ebalia tuberosa* (Pennant) as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, and probably also Stewart Island, N.Z.; continental shelf 10–120 m, usually over sand, shell, or pebble substrates. Endemic.

BREEDING AND EGGS: Ovigerous females have been taken in the Wellington area in December, January, May, and August, but records from a number of other localities include most other months of the year. Eggs, newly laid, light orange, 0.38 mm diameter.

ZOEA LARVAL STAGES: Four zoea stages; colour in life, red-orange.

Zoea I (Figs 66, 67): Zoea with no carapace spines; rostrum a tiny knob. Carapace globose and smooth, length 0.49 mm, height 0.53 mm; abdominal segments 2 and 3 each with small lateral protruberances; telson very broad, spatulate, the lateral cornua each with two lateral teeth and one inner tooth near base, three pairs of plumose setae centrally located between the widely separated cornua.

Zoea II: Carapace length 0.68 mm, height 0.68 mm; abdominal segments 2–5 with tiny pleopod buds, indistinct on segment 5; four lateral teeth on margins of telson, with lateral cornua reduced from zoea I.

Zoea III: Carapace length 0.75 mm, height 0.79 mm; maxillipeds 1 and 2 with only six rather than eight natatory setae on exopod; pleopod buds well-developed; lateral teeth on telson now absent.

Zoea IV: Carapace length 0.75 mm, height 0.80 mm; maxillipeds 1 and 2 with eight natatory setae on exopod; pereiopods well-developed, visible outside carapace and segmented; all pleopods now well-developed but still uniramous.

MEGALOPA: No knowledge. The megalopa of *Ebalia tuberosa* (Fig. 68) is described and illustrated as an example of the genus.

Carapace nearly smooth, longer than broad; rostrum not visible in dorsal view, but present as a shallow V-shaped structure declined at 90° (cf. Lebour 1928b); pereiopod 5 without long terminally hooked setae on dactyl; abdominal segments without armature, segments 2–5 with pleopods, segment 6 with uropods; uropod exopods with 6 setae; telson without setae.

NOTES: Larvae of *E. laevis* are often found in inshore plankton samples, but are weak swimmers and are found mainly at or near the bottom.

BRACHYGNATHA (OXYRHYNCHA)
FAMILY MAJIDAE

Zoea larvae typically brachyuran, with their general facies similar to those of *Cancer novaezelandiae* which were fully described earlier: antenna 2 rod-like with no primitive tendency towards flattening of the exopod; telson forked, with narrow cornua; carapace and abdomen lacking accessory spines beyond the usual complement. There are a number of characters which distinguish known New Zealand majid larvae from those of any other brachygnathous families: there are only two zoea stages (shared only with *Heterozius rotundifrons* (Belliidae)), with the bulky stage I zoeas hatching at an advanced stage of development, thus combining four maxilliped setae with an antenna 2 endopod bud and well-developed pereiopod buds; zoea II with six abdominal segments and six setae on the maxilliped exopod; megalopa larvae lack long terminally hooked setae on pereiopod 5 dactyl (also the case in *H. rotundifrons*, and probably in *Pinnotheres novaezelandiae* (Pinnotheridae)). A more comprehensive list of larval characters is given by Rice (1980a). *Achaeus fissifrons* has only one zoea stage which moults directly to a megalopa (*see* p. 30). This is the first record of a majid species with planktonic larval development varying from the normal two zoea stages.

Zoea larval affinities have been well covered in recent publications. Ingle (1979) provides a comprehensive account and discussion of majid subfamilial larval characters. Rice (1980a) takes Ingle's work and that of earlier authors into account and makes a number of tentative suggestions concerning the phylogenetic history of the family, comments about possible erroneous groupings of genera with little natural affinity in their zoea larval characters in the majid assemblage, and indicates a monophyletic origin for the group as a whole, with a series of independent lines of evolution towards an "advanced" condition apparent within the family. Affinities of the New Zealand larvae briefly described hereunder are discussed by Webber and Wear (1982).

Cyrtomaia Miers, 1886

Cyrtomaia hispida (Borradaile, 1916)

SOURCE REFERENCE:This study — zoeas I and II reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: Predominantly North Island of N.Z.; relatively common on continental shelf and slope, mainly in association with bryozoans and sponges on shell/sand or pebble substrates. Indo-West Pacific.

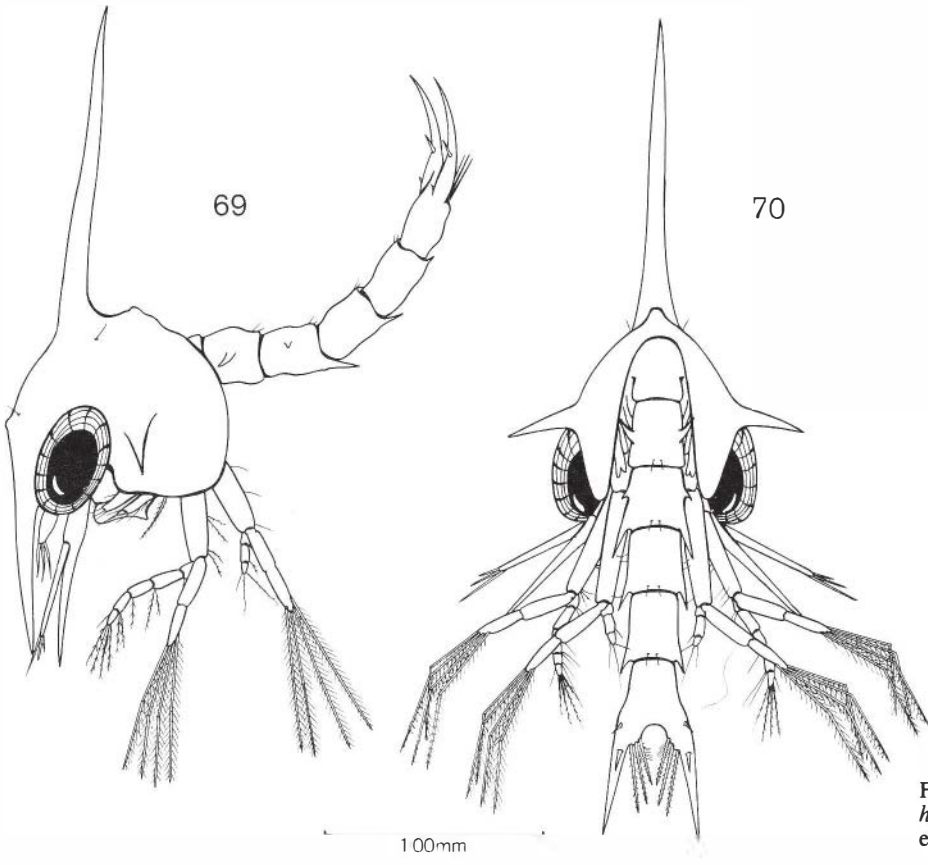
During NZOI cruise No. 1117 to northern New Zealand a number of specimens (ca 50) were dredged from 100 m to 200 m depth living on comminuted bryozoan and shell bottoms together with sponges, hydroids, gorgonian and solitary corals. None were found living in sand itself, as suggested by Griffin (1966) following Borradaile (1916).

BREEDING AND EGGS: Ovigerous females have been collected in northern New Zealand waters in January and February. Eggs, newly laid, 0.63 mm diameter, with red yolk; about to hatch, 0.72 mm diameter, with remaining yolk and larval eyespots coloured red.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, red with brownish-red eyes.

Zoea I (Figs 69, 70): Zoea with dorsal, rostral and lateral carapace spines. Total length 3.4 mm; rostral spine 0.80 mm long, straight; dorsal carapace spine 1.68 mm long, almost straight; spine to spine length 3.5 mm; lateral carapace spines slightly depressed, 0.32 mm long; length of antenna 2 exopod 0.53 mm, endopod a small bud; ratio of antenna 2 spiniform process (0.60 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.75, 0.36, and 1.13* respectively; dorsolateral protuberances on abdominal segments 2 and 3; abdominal segments 3–5 with ventrolateral spines decreasing in size posteriorly; telson with lateral cornua almost straight, a very small dorsolateral seta and a somewhat larger dorsal seta near the base of the cornu on each side.

Zoea II (measurements based on only four reared larvae): Total length 4.2 mm; rostral spine 0.96 mm long; dorsal carapace spine 1.44 mm long; spine to spine length 4.2 mm; lateral carapace spines strongly depressed, 0.38 mm long; length of antenna 2 exopod 0.48 mm, of endopod 0.30 mm; ratio of antenna 2 spiniform process (0.64 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.61, 0.44, and 1.33* respectively; abdominal segments 3–5



FIGS 69, 70: Family MAJIDAE. *Cyrtomaia hispida* (Borradaile, 1916). Zoea I: 69, lateral view; 70, posterior view.

with pleopod buds each about 0.3 mm long; uropod buds very small; telson with four pairs of setae posteriorly.

MEGALOPA: No knowledge.

Pyromaia Stimpson, 1870

Pyromaia tuberculata (Lockington, 1877)

SOURCE REFERENCES: Webber and Wear (1982) — zoea I from laboratory hatched eggs. This study — zoea II (4 specimens) from Auckland Harbour plankton, 19 July and 16 August, 1981.

ADULT DISTRIBUTION AND HABITAT: Northern half of North Island, N.Z.; in enclosed subtidal and shallow waters over mud or sand substrates; distribution so far restricted but probably spreading. Also Japan, and western U.S.A., where the species has been reported down to 650 m depth.

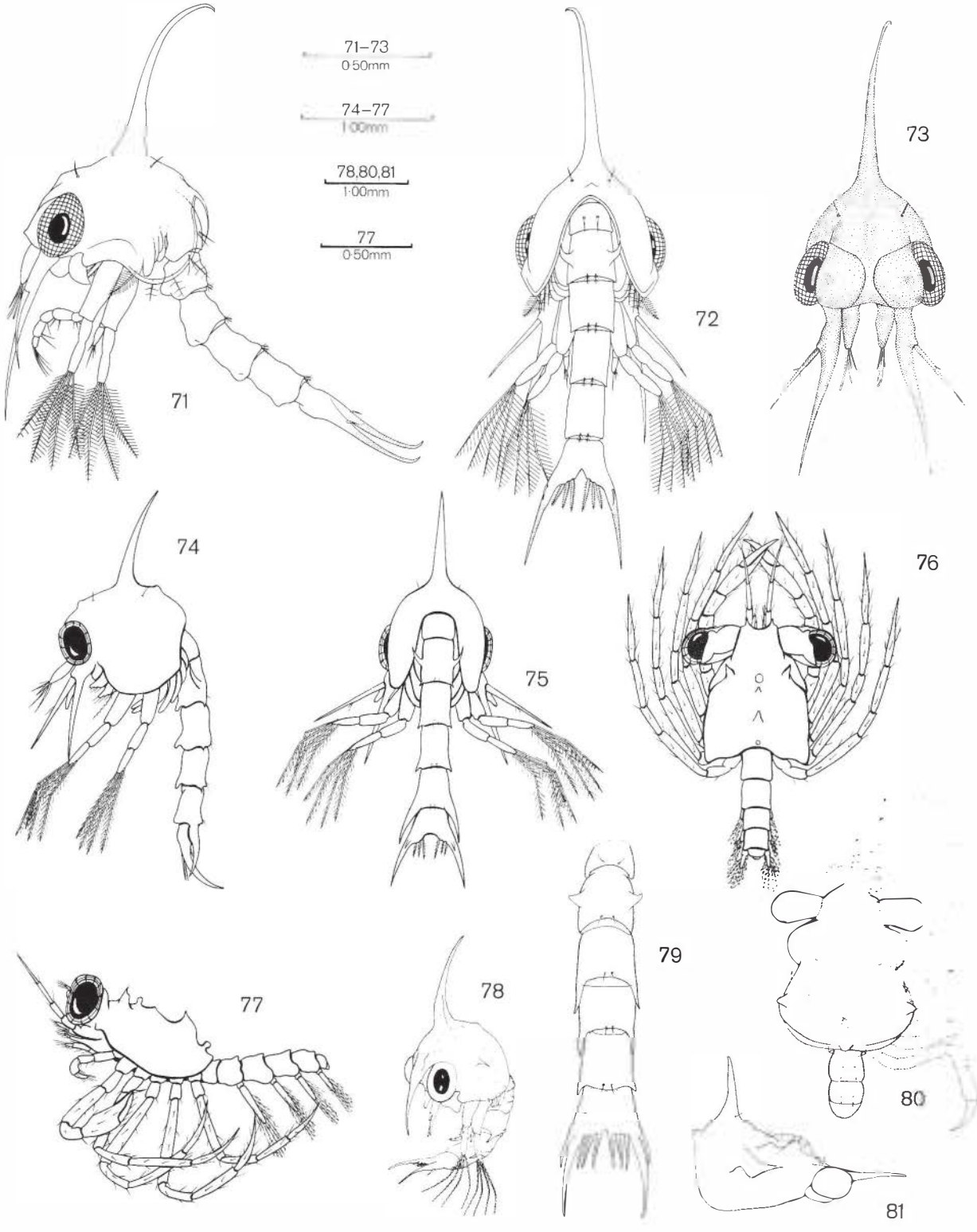
BREEDING AND EGGS: Ovigerous females have been collected in the Auckland area in April, May and June. Eggs, newly laid, red or orange-red; about to hatch, orange, 0.60 mm × 0.50 mm.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, not known.

Zoea I (Figs 71–73): Zoea with dorsal carapace spine only. Total length 1.9 mm; dorsal carapace spine 0.70 mm long, curved very strongly to be orientated posteroventrally near its tip in some cases; spine to spine length (tip of dorsal spine to ventral margin of eye) 1.15 mm; length of antenna 2 exopod 0.25 mm*; ratio of antenna 2 spiniform process (0.34 mm long) to dorsal carapace spine, and to antenna 2 exopod measured to its tip, *0.50 and 1.36* respectively; eyestalk with a distinct anterior papilla; dorsolateral protuberance on abdominal segment 2 only and with unusually fine tip, curved forward; abdominal segments 3–5 without ventrolateral spines; no lateral seta outside telson cornua, but a single small dorsolateral seta present at the level of the base of the cornu on each side.

Zoea II: Total length 2.6 mm; dorsal carapace spine 0.75 mm long; spine to spine length (tip of dorsal spine to ventral margin of eye) 1.35 mm; length of antenna 2 exopod 0.45 mm, of endopod 0.15 mm; ratio of antenna 2 spiniform process (0.60 mm long) to dorsal carapace spine, and to antenna 2 exopod measured to its tip, *0.80 and 1.33* respectively.

*Antenna 2 exopod has a central seta very much longer than the remaining two lateral setae and extending to about three-quarters the length of the spiniform process. This long seta is effectively contiguous with the exopod itself and has been included in the measurement, which would otherwise be 0.10 mm.



FIGS 71–81: Family MAJIDAE. *Pyromaia tuberculata* (Lockington, 1877). Zoea I: 71, lateral view; 72, posterior view; 73, carapace, frontal view. After Webber and Wear (1982). *Achaeus fissifrons* (Haswell, 1879). Zoea I: 74, lateral view; 75, dorsal view. Megalopa: 76, lateral view; 77, dorsal view. *Rochinia carpenteri* (Thomson). Zoea I: 78, lateral view (reversed from original); 79, abdomen, dorsal view. Megalopa: 80, dorsal view; 81, carapace, lateral view. After Ingle (1979). Reproduced by permission of the Trustees of the British Museum (Natural History).

MEGALOPA: No knowledge.

NOTES: Sakai (1976: 168–70) suggests that *Pyromaia tuberculata* has spread to Japan from the U.S.A. in recent years as larvae (presumably megalopas or juveniles) attached to the bottom of ships, and it is probable that the species reached New Zealand from the Northern Hemisphere by the same means. Our few late autumn and winter records of ovigerous females indicate that this crab has not modified its breeding pattern since its introduction from overseas, where ovigerous females are most abundant in spring and summer (Garth 1958).

Achaeus Leach, 1817

Achaeus fissifrons (Haswell, 1879)

SOURCE REFERENCE: This study — zoea I and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: Predominantly northern half of North Island, N.Z.; continental shelf and slope down to about 180 m, in association with extensive sponges and coralline algae (Griffin and Yaldwyn 1965). Indo-West Pacific with records in south-eastern Australia, Japan and perhaps also in the north-west Indian Ocean (Griffin 1966).

BREEDING AND EGGS: Ovigerous females have been collected in January, February, March, July, and September; eggs carried number between 20 and 30 only. Eggs, newly laid, 0.62 mm × 0.58 mm, with yolk colour yellow, orange, orange-brown; about to hatch, 0.61 mm × 0.67 mm, pale yellow.

ZOEA LARVAL STAGES: One zoea stage — the only species of the family Majidae with planktonic development recorded thus far as varying from the normal two stages; colour in life, pale reddish-yellow.

Zoea I (Figs 74, 75): Zoea with dorsal carapace spine only. Total length 2.9 mm; dorsal carapace spine 0.65 mm long, curved only slightly; spine to spine length (tip of dorsal spine to ventral margin of eye) 1.4 mm; length of antenna 2 exopod 0.65 mm (the form of antenna 2 necessitates the inclusion of the central seta in the measurement as with *Pyromaia tuberculata*); ratio of antenna 2 spiniform process (0.65 mm long) to dorsal carapace spine, and to antenna 2 exopod measured to its tip, *1 and 1* respectively; eyestalk lacking a distinct anterior papilla; pereiopod buds long and well-developed; dorsolateral protuberances on abdominal segment 2 only, long and with slender tips curved forward; short pleopod buds on abdominal segments 2–5; abdominal segments 2–4 with very short lateral spines, but those of segment 5 very strongly developed, about one-half the length of the telson and curved inward and ventrally; telson without lateral setae, but with a single dorsal seta present at the level of the base of the cornu on each side.

MEGALOPA (Figs 76, 77): Carapace length 1.0 mm; carapace width 0.7 mm; carapace with a large, median mesogastric tubercle, a large, median posterior (intestinal) tubercle, a single, broadly based cardiac spine, and a lesser spine in a metagastric position lying just behind the more anterior of the two tubercles; carapace also with a pair of broadly based protogastric spines, but otherwise lacking setae; frontal region with anterolateral corners produced into a sharp spine, otherwise concave anteriorly and without a rostrum; eyestalks with a small anterior papilla more easily seen when viewed ventrally; pereiopod 2 with a sharp ischial spine; pereiopod 5 with no long terminally hooked setae on dactyl; abdomen smooth, lacking spines or setae; abdominal segments 2–5 with pleopods (exopods all with eight setae), segment 6 relatively small with uropods absent; telson reduced to a tiny stump.

Rochinia A. Milne Edwards, 1875

Rochinia riversandersoni (Alcock, 1895)

SOURCE REFERENCE: Ingle (1979) — zoeas I and II, and megalopa of *Rochinia carpenteri* Thomson reared from laboratory hatched eggs, as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: Northern extremities of North Island, N.Z., and Kermadec Islands; continental slope, 428–1362 m, among pumice pebbles, small angular boulders, and coral (Yaldwyn and Dawson 1976). Indo-West Pacific.

BREEDING AND EGGS: No records of ovigerous females in New Zealand waters.

ZOEA LARVAL STAGES: No knowledge, but there are probably two zoea stages. Zoea I of *R. carpenteri* (Figs 78, 79) is described and illustrated as an example of the genus.

Zoea with dorsal, rostral and lateral carapace spines. Surface of carapace punctate; posterior carapace tubercle prominent; antenna 2 exopod about two-thirds the length of spiniform process, with one of its three terminal setae extending to a level slightly beyond the tip of the spiniform process; dorsolateral protuberances on abdominal segment 2 only, segments 3–5 with well-developed ventrolateral spines; telson cornua with a well-developed spine lateral to base but lacking axillary spines or setae.

MEGALOPA: No knowledge. The megalopa of *R. carpenteri* (Figs 80, 81) is described and illustrated as an example of the genus.

Rostrum long, slender, directed forwards; dorsal spine long, directed upward almost at right angles to the dorsal surface of the carapace, inclined only slightly backward; lateral spines reduced to a pair of triangular protuberances from branchial region; pereiopod 5 dactyl without long terminally hooked setae; abdominal segments 2–5 with pleopods, segment 6 with uropods; exopods of uropods with five plumose setae; telson almost semi-circular and lacking marginal setae.

NOTES: Records of *R. riversandersoni* thus far suggest that larvae may be restricted to the plankton of northern New Zealand. Good generic characters for the zoea larvae are likely to be the presence of lateral spines combined with the nature of the antenna 2 exopod and the absence of small axillary spines at the base of the telson cornua (cf. *Leptomithrax*, Figs 95, 96), and for the megalopa the presence and the configuration of carapace spines, especially the form and orientation of the dorsal spine.

Eurynome Leach, 1814

Eurynome bituberculata Griffin, 1964

SOURCE REFERENCE: Lebour (1928a) — zoeas I and II, and megalopa of *Eurynome aspera* Leach, as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island and South Island, N.Z.; continental shelf and slope, 60–260 m, on bottoms with sponges and on muddy sand with broken shell (Griffin 1966). Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in September and March.

ZOEA LARVAL STAGES: No knowledge. Probably two zoea stages. Zoea II of *Eurynome aspera* (Fig. 82) is described and illustrated as an example of the genus.

Zoea with dorsal and rostral carapace spines, lateral carapace spines absent; antenna 2 exopod no more than half the length of spiniform process; telson with two small spines lateral to the base of the cornu on each side, and 4+4 inner posterior setae.

MEGALOPA: No knowledge. The megalopa of *Eurynome aspera* (Fig. 83) is described and illustrated as an example of the genus.

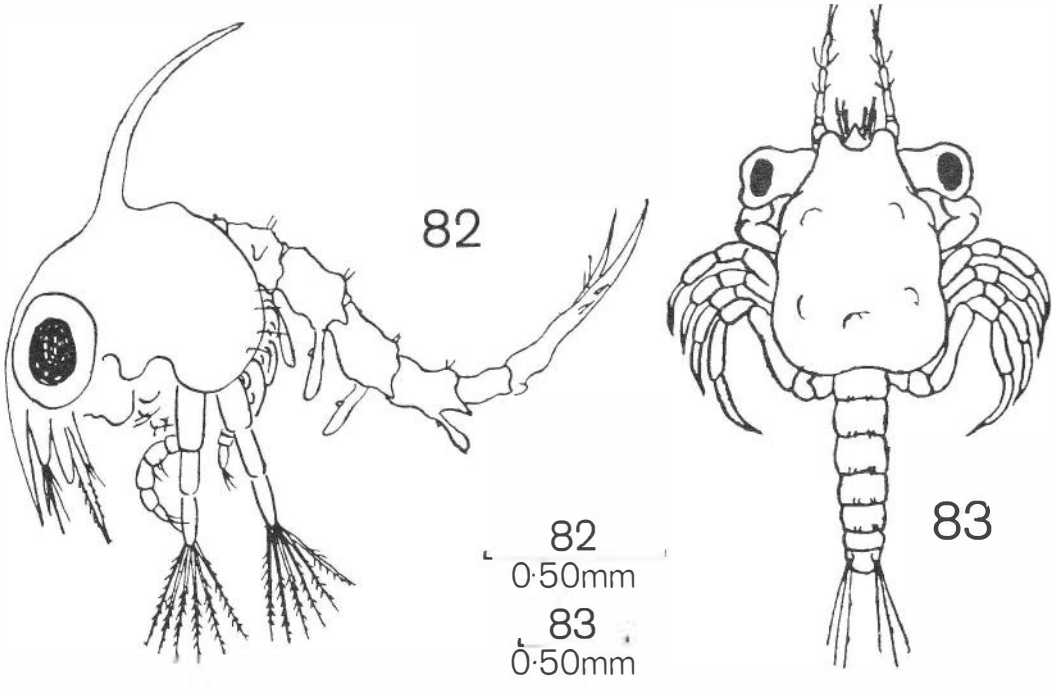
Rostrum a small spine inclined downwards at right angles; carapace with conspicuous dorsal protuberances but lacking accessory spines or setae; pereiopod 5 without long terminally hooked setae on dactyl; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopods with three setae; telson lacking setae.

Eurynolambrus H. Milne Edwards & Lucas, 1841

Eurynolambrus australis H. Milne Edwards & Lucas, 1841

SOURCE REFERENCE: Webber and Wear (1982) — zoea stages I and II, and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; littoral and sublittoral to about 80 m depth; common among and under small rocks covered with algae and bryozoans on moderately exposed coasts; also among *Macrocystis pyrifera* holdfasts (Webber and Wear 1982), and typically frequenting mostly muddy shores covered by scattered small stones or pebbles (Griffin 1966). Endemic.



FIGS 82, 83: Family MAJIDAE. *Eurynome aspera* Leach. Zoea II: 82, lateral view. Megalopa: 83, dorsal view. Figs 82, 83 after Lebour (1928a).

Inset 5*

BREEDING AND EGGS: Ovigerous females have been found in spring and early summer. Eggs, newly laid, bright orange, 0.65 mm diameter; becoming darker brown during incubation and increasing in size to 0.84 mm × 0.79 mm just before hatching.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, heavily pigmented olive green with large red subintestinal chromatophore on abdominal segment 4 diagnostic for this species. Larval chromatophores are fully described by Webber and Wear (1982).

Zoea I (Figs 84, 85): Zoea with dorsal and rostral carapace spines. Total length 3.0 mm; rostral spine 0.49 mm long, with slight posterior curve; dorsal carapace spine 0.58 mm long, curved posteriorly; spine to spine length 1.75 mm; length of antenna 2 exopod 0.26 mm; ratio of antenna 2 spiniform process (0.38 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.77, 0.65, and 1.46* respectively; antenna 2 spiniform process with distal half armed anterolaterally with two parallel rows of small spinules averaging 19 per 0.05 mm in each row, plus a few additional spinules between the rows; telson with lateral cornua curved upward only slightly, a large lateral spine and two tiny spines at the base of the cornu on each side.

Zoea II (Fig. 86): Total length 3.5 mm; rostral spine 0.55 mm long; dorsal carapace spine 0.61 mm long; spine to spine length 2.00 mm; length of antenna 2 exopod 0.28 mm, of endopod 0.19 mm; ratio of antenna 2 spiniform process (0.38 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.69, 0.62, and 1.36* respectively; antenna 2 spiniform process with spinules averaging 22 per 0.05 mm in each row; telson with 4+4 inner posterior setae, the two tiny lateral spines at the base of the cornu on each side now very indistinct.

MEGALOPA (Figs 87, 88): Carapace length 1.65 mm; carapace width 0.90 mm; surface of carapace uneven with slight lateral and median undulations and some fine setae, posterior margin with a thin fringe of plumose setae; rostrum short and depressed; pereiopods 2 and 3 each with a ventral ischial spine; pereiopod 5 with no long terminally hooked setae on dactyl; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopod about half the length of the protopod and bearing five long, plumose setae; telson with two small median setae.

NOTES: Zoea larvae of *Eurynolambrus australis* are sometimes common in inshore plankton samples in the Wellington area at or near the bottom, but occasionally occur in tows near the surface, especially at night. Megalopas are rarely captured in the plankton.

Eurynolambrus australis was previously placed in the family Parthenopidae. It was proposed by Krefft (1952) and later confirmed by Griffin (1966) that juvenile morphology and adult characters justify its inclusion in the Majidae. However, larval characters of the species suggest a closer relationship with *Notomithrax peronii, N. ursus* and *Leptomithrax longimanus* (subfamily Majinae) than its present position in the Pisinae permits (Webber and Wear 1982).

Notomithrax Griffin, 1963

Notomithrax peronii (H. Milne Edwards, 1834)

SOURCE REFERENCE: Webber and Wear (1982) — zoea stages I and II, and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal and shallow water, most commonly occurring in harbours and estuaries, and offshore in 2–3 m over sand or mud; adults are usually liberally camouflaged with green algae, particularly *Ulva*, as well as brown and sometimes red algae. Endemic.

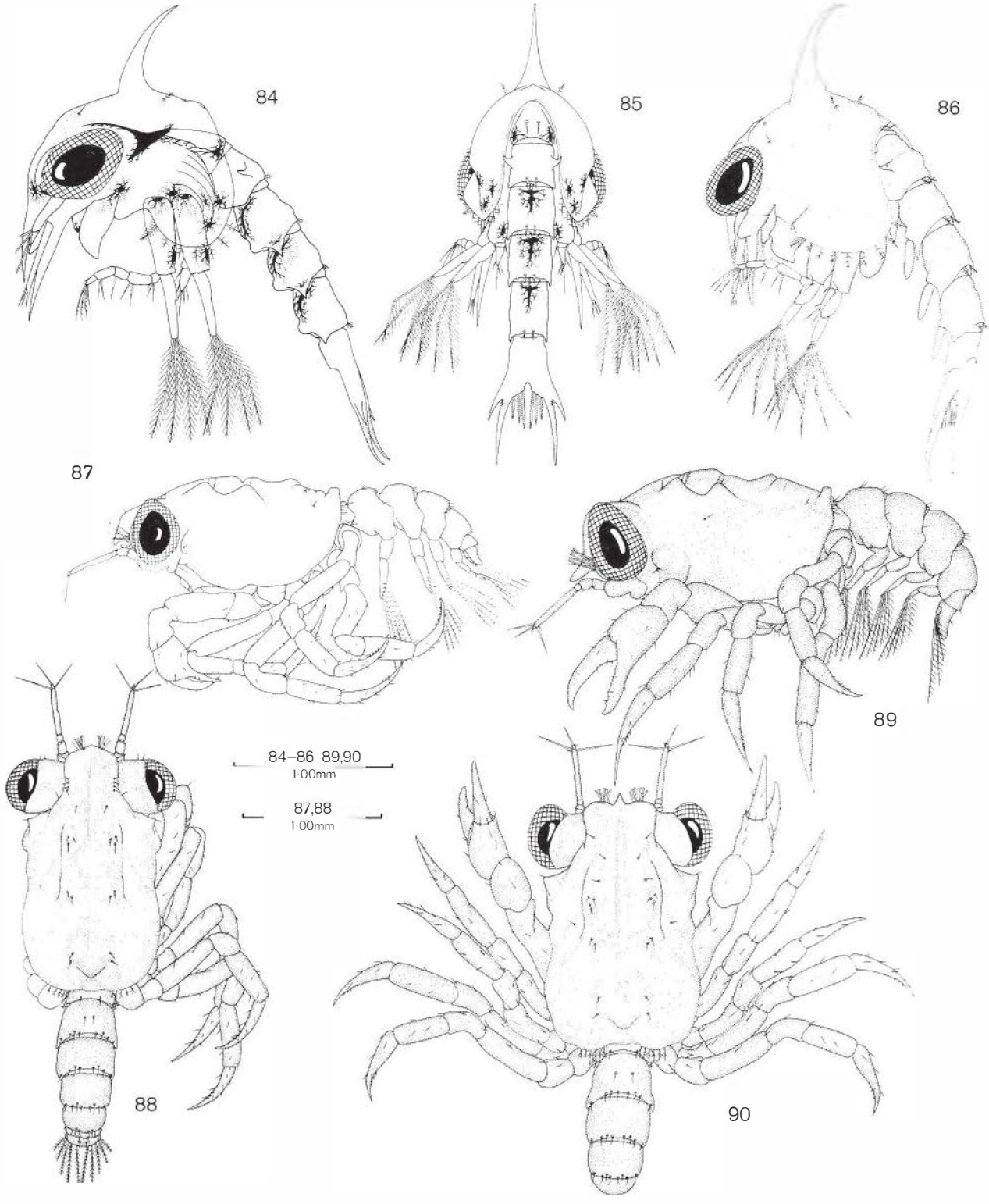
BREEDING AND EGGS: Ovigerous females have been collected from Wellington coasts from October to the end of March. Eggs, newly laid, bright orange; becoming brown when ready to hatch, then measuring 0.78 mm in diameter.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, olive green, but less heavily pigmented than those of *Eurynolambrus australis*. The zoea larvae have not been figured here due to their very close similarity to those of the former species. Larval chromatophores are fully described by Webber and Wear (1982).

Zoea I: Zoea with dorsal and rostral carapace spines. Total length 3.0 mm; rostral spine 0.39 mm long; dorsal carapace spine 0.55 mm long; spine to spine length 1.58 mm; length of antenna 2 exopod 0.25 mm, of endopod 0.13 mm; ratio of antenna 2 spiniform process (0.38 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.97, 0.69, and 1.52* respectively; antenna 2 spiniform process armed with two rows of spinules averaging 31 per 0.05 mm in each row; telson with lateral cornua curved upward only slightly, a large lateral spine and two small spines at the base of the cornu on each side.

Zoea II: Total length 3.50 mm; rostral spine 0.46 mm long; dorsal carapace spine 0.58 mm long; spine to spine length 1.61 mm; length of antenna 2 exopod 0.27 mm, of endopod 0.18 mm; ratio of antenna 2 spiniform process (0.40 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.87, 0.69, and 1.48* respectively; antenna 2 spiniform process with spinules averaging 30 per 0.05 mm in each row; telson with 3+3 inner posterior setae as in zoea I, the two smaller spines at the base of the lateral cornua now absent.

MEGALOPA (Figs 89, 90): Carapace length 1.65 mm; carapace width 0.98 mm; surface of carapace uneven with slight lateral and median undulations and some fine setae, posterior margin with a thin fringe of plumose setae; rostrum small and knob-like, directed anteroventrally; pereiopods 1, 2, and 3 each with a



FIGS 84–90: Family MAJIDAE. *Eurynolambrus australis* H. Milne Edwards & Lucas, 1841. Zoea I: 84, lateral view; 85, posterior view. Zoea II: 86, lateral view. Megalopa: 87, lateral view; 88, dorsal view. Figs 84–88 after Webber and Wear (1982). *Notomithrax peronii* (H. Milne Edwards, 1934). Megalopa: 89, lateral view; 90, dorsal view. After Webber and Wear (1982).

ventral ischial spine; pereiopod 5 with no long terminally hooked setae on dactyl; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopod about one-third the length of protopod and with four long plumose setae; telson broader than long.

NOTES: Larvae of *Notomithrax peronii* occur mainly in shallow-water plankton samples taken at or near the bottom.

Notomithrax ursus (Herbst, 1788)

SOURCE REFERENCE: Webber and Wear (1982) — zoea stages I and II, and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal and continental shelf down to about 75 m depth, and a common inhabitant of lower tidal rock pools. Adults are usually well camouflaged by a thick covering of red and small brown algae. Also south-east Australia.

BREEDING AND EGGS: Ovigerous females have been taken in N.Z. from August through to early March, but the breeding season may be longer. Eggs, newly laid, bright orange; becoming brown just before hatching, when they measure 0.75 mm × 0.70 mm.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, olive green. The zoea larvae have not been figured due to their very close similarity to those of *Eurynolambrus australis* and *Notomithrax peronii* (*see* Figs 84–86). Larval chromatophores are fully described by Webber and Wear (1982).

Zoea I: Zoea with dorsal and rostral carapace spines. Total length 3.0 mm; rostral spine 0.44 mm long and almost straight; dorsal carapace spine 0.63 mm long, with pronounced posterior hook distally; spine to spine length 1.77 mm; length of antenna 2 exopod 0.31 mm, of endopod 0.41 mm; ratio of antenna 2 spiniform process (0.42 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.95, 0.67, and 1.35* respectively; antenna 2 spiniform process armed with two rows of spinules distally, the spinules averaging seven per 0.05 mm in each row; telson with lateral cornua strongly curved dorsally, a large lateral spine and two small spines near the base of the cornu on each side.

Zoea II: Total length 3.50 mm; rostral spine 0.55 mm long, dorsal carapace spine 0.75 mm long; spine to spine length 2.10 mm; length of antenna 2 exopod 0.34 mm, of endopod 0.20 mm; ratio of antenna 2 spiniform process (0.50 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.91, 0.67, and 1.47* respectively; antenna 2 spiniform process with 11 spinules per 0.05 mm in each row; median posterior telson notch with a small stout seta occurring centrally.

MEGALOPA (not figured): Carapace length 1.70 mm; carapace width 1.1 mm; surface of carapace uneven with slight lateral and median undulations and some fine setae, posterior margin with sparse fringe of setae; rostrum as in *N. peronii* and directed anteroventrally; pereiopods 1 and 2 each with a ventral ischial spine; pereiopod 5 lacking long terminally hooked setae on dactyl; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopod not jointed to protopod but fused with it to form a short, tapered appendage supporting four plumose natatory setae; telson small, broader than long.

NOTES: Zoea larvae of *Notomithrax ursus* occur chiefly in shallow-water plankton tows taken near the bottom or at night, but planktonic megalopas have not been found. All the larval stages are very difficult to distinguish from those of *N. peronii*, from which they differ significantly only in fine details of the appendages, mainly of antenna 2 and mouthparts. Such fine distinctions are beyond the scope of this paper, but are fully outlined and illustrated in Webber and Wear (1982).

Notomithrax minor (Filhol, 1885)

SOURCE REFERENCE: Webber and Wear (1982) — zoea stages I and II, and megalopa reared from laboratory hatched eggs.

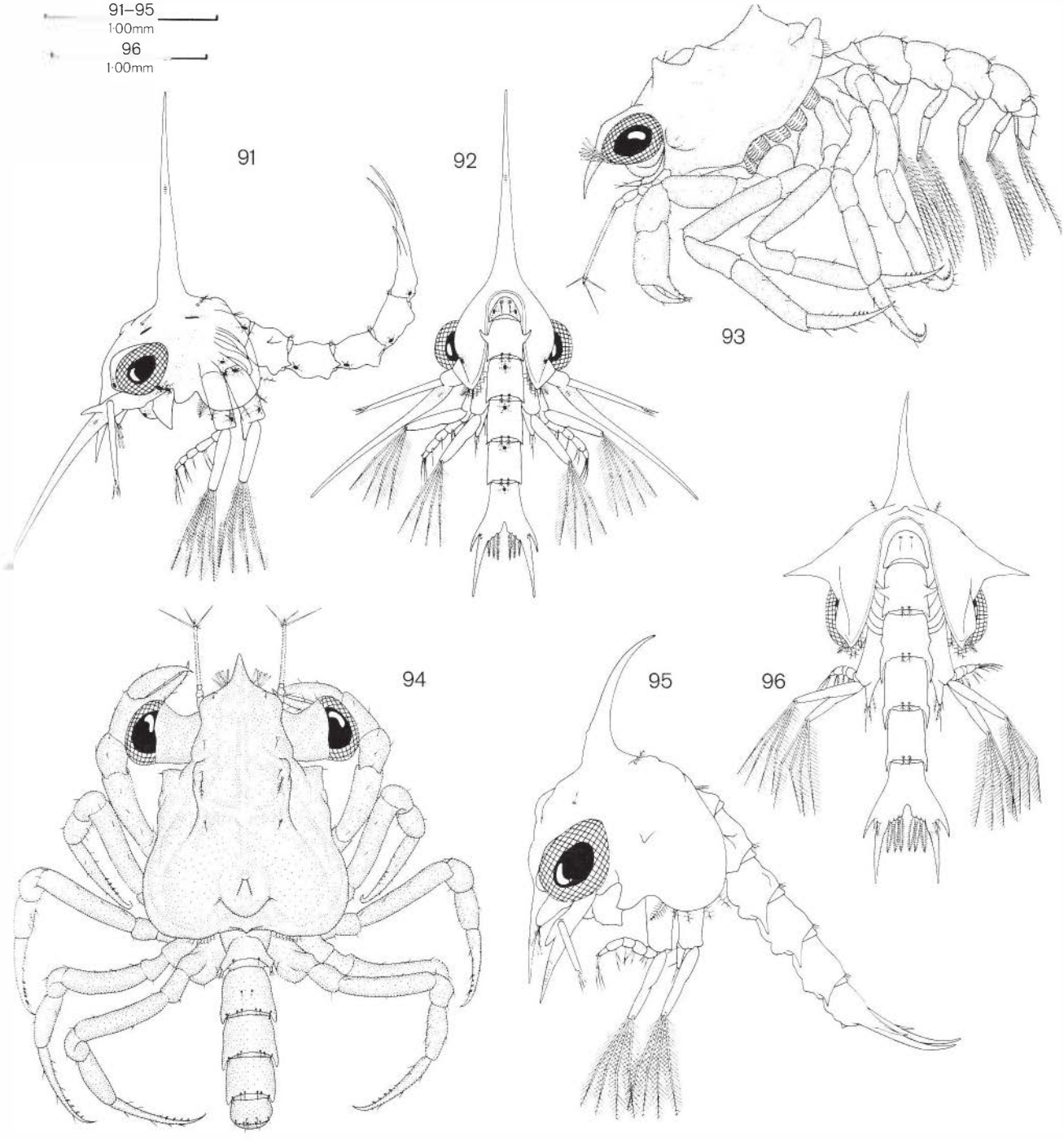
ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, N.Z., but apparently absent from the Chatham Islands; common on sandy or muddy substrates between the sublittoral and about 40 m depth; adult carapace adornment more frequently of sponge than of algal material. Also eastern Australia.

BREEDING AND EGGS: Our records and those of Griffin (1966) indicate that ovigerous females occur from September through to April, but the breeding season is undoubtedly longer (*see* NOTES below). Eggs, newly laid, bright orange, 0.60 mm × 0.56 mm; about to hatch, light orange to transparent, 0.63 mm × 0.61 mm.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, almost transparent or light yellow-green. Larval chromatophores are fully described by Webber and Wear (1982).

Zoea I (Figs 91, 92): Zoea with dorsal and rostral carapace spines. Total length 2.8 mm; rostral spine 0.45 mm long, straight; dorsal carapace spine 1.24 mm long, straight; spine to spine length 2.25 mm; length of antenna 2 exopod 0.32 mm, of endopod 0.43 mm; antenna 2 spiniform process very long (0.84 mm) with ratio to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *1.87, 0.67, and 2.63* respectively; antenna 2 spiniform process unarmed; telson with lateral cornua only slightly curved upward, a stout lateral spine and two very small spines at the base of the cornu on each side.

Zoea II: Total length 3.2 mm; rostral spine 0.55 mm long; dorsal carapace spine 1.40 mm long; spine to



FIGS 91–96: Family MAJIDAE. *Notomithrax minor* (Filhol, 1885). Zoea I: 91, lateral view; 92, posterior view. Megalopa: 93, lateral view; 94, dorsal view. Figs 91–94 after Webber and Wear (1982). *Leptomithrax longipes* (Thomson, 1902). Zoea I: 95, lateral view; 96, posterior view. After Webber and Wear (1982).

spine length 2.56 mm; length of antenna 2 exopod 0.46 mm, of endopod 0.18 mm; ratio of antenna 2 spiniform process (0.94 mm) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *1.71, 0.67, and 2.04* respectively.

MEGALOPA (Figs 93, 94): Carapace length 1.65 mm; carapace width 1.15 mm; surface of carapace uneven, with acute lateral and median undulations and processes and some fine setae, posterior margin with a fringe of fine setae; rostrum sharply pointed and only

slightly depressed; pereiopod 2 only with a ventral ischial spine; pereiopod 5 with no long terminally hooked setae on dactyl; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopod bearing four setae; telson longer than broad, with a small posteromedian lobe.

NOTES: Zoea larvae of *Notomithrax minor* occur inshore and in harbour surface and mid-water plankton samples during all months of the year, but are most abundant during spring and summer. Breeding therefore occurs throughout the year, at least in the Wellington area from which regular plankton samples have been taken. They are usually the most common majid species caught and this is thought to be due to the floatation afforded by their well-developed antennal and carapace spines relative to their overall size, which allows the larvae to maintain a position in the surface layers. Megalopa larvae have not been identified from plankton samples.

Leptomithrax Miers, 1876

Leptomithrax longimanus Miers, 1876

SOURCE REFERENCE: Webber and Wear (1982) — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, N.Z., but apparently absent from the Chatham Islands; present in shallow water and occasionally in rock pools, but much more common offshore, chiefly between 20 m and 200 m depth over muddy or sandy bottoms in association with polychaetes, bivalve molluscs, sponges, and bryozoans; carapace of adults often adorned with serpulid worm tubes, and sponges, frequently also mud. Endemic.

BREEDING AND EGGS: Ovigerous females have been recorded in October, November, December, March and April. Eggs, newly laid, bright orange, 0.60 mm diameter; about to hatch, orange brown to transparent, 0.63–0.65 mm diameter.

ZOEA LARVAL STAGES: Two zoea stages. The zoea larvae are very similar to those of *Eurynolambrus australis, Notomithrax peronii* and *N. ursus* and have not been figured.

Zoea I: Zoea with dorsal and rostral carapace spines. Total length 3.0 mm; rostral spine 0.44 mm long, with a distinct curve posteriorly in distal one-third; dorsal carapace spine 0.62 mm long, with marked posterior curve; spine to spine length 1.75 mm; length of antenna 2 exopod 0.27 mm; ratio of antenna 2 spiniform process (0.38 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.84, 0.63, and 1.41* respectively; maxilliped 2 endopod of one segment only; antenna 2 spiniform process armed with tiny spinules in two rows distally, the spinules averaging seven per 0.05 mm in each row; telson with one stout lateral spine and two minute spines near base of cornu on each side.

MEGALOPA: No knowledge.

NOTES: The unsegmented endopod of maxilliped 2 is the only feature clearly distinguishing preserved zoea larvae of this species from those of *Eurynolambrus australis, Notomithrax peronii* and *N. ursus* without resorting to very fine microscopic detail of antenna 2 and the mouthparts. Larvae have not been identified from the plankton.

Leptomithrax longipes (Thomson, 1902)

SOURCE REFERENCE: Webber and Wear (1982) — zoea stages I and II reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: South Island as far north as Cook Strait, Stewart Island, Chatham Islands, and Auckland and Campbell Islands; most records are from the north and east of the South Island and from Foveaux Strait offshore between 20 m and 80 m depth, chiefly on muddy or sandy bottoms in association with sponges, anemones, bryozoans and polychaetes; adults are almost always thickly covered with epizooites such as sponges, hydroids, anemones, polyzoans, and tubicolous polychaetes, which generally obscure the carapace (Griffin 1966). Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in September, November, January, February and March. Eggs orange, but no measurements are available.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, not known.

Zoea I (Figs 95, 96): Zoea with dorsal, rostral and lateral carapace spines. Total length 3.2 mm; rostral spine 0.57 mm long, straight; dorsal carapace spine 0.87 mm long, angled posteriorly; distal two-thirds of dorsal and rostral spines sparsely spinulated; spine to spine length 2.20 mm; lateral carapace spines 0.23 mm long, projecting horizontally; length of antenna 2 exopod 0.18 mm; ratio of antenna 2 spiniform process (0.32 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.56, 0.37, and 1.78* respectively; antenna 2 spiniform process armed with two rows of spinules along its distal half, the spines averaging eight per 0.05 mm in each row; abdominal segment 3 with a pair of dorsolateral knob-like protuberances in addition to the usual strongly developed pair on segment 2; posterolateral spines on abdominal segments 3–5 strongly developed; telson with a large lateral spine and two smaller spines at the base of the cornu on each side, the smaller spines robust and about one-half the length of the lateral spine.

Zoea II: Total length 3.6 mm; rostral spine 0.69 mm long; dorsal carapace spine 0.95 mm long, with tiny spinulations which are very sparse and inconspicuous; spine to spine length 2.75 mm; lateral carapace spines similar to zoea I but broadly based and difficult to

measure accurately; length of antenna 2 exopod 0.27 mm, of endopod 0.18 mm; ratio of antenna 2 spiniform process (0.36 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.52, 0.38, and 1.33* respectively; antenna 2 spiniform process with 10 spinules per 0.05 mm in each row; small spines at the base of the telson cornua now little more than one-quarter the length of lateral spine.

MEGALOPA: No knowledge.

Leptomithrax tuberculatus mortenseni Bennett, 1964

SOURCE REFERENCE: This study — zoea I hatched from eggs of 3 ovigerous females collected 22 January 1981, 37°35.4′S, 178°52.9′E, Ranfurly Bank, 34–54 m.

ADULT DISTRIBUTION AND HABITAT: Northern part of North Island (Hauraki Gulf to Cape Maria van Diemen — Griffin 1966) and Kermadec Islands; relatively common among sponges and bryozoans on rough bottoms between 10 and 100 m depth. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in November, January and February. Eggs, newly laid, orange, 0.60 mm diameter; ready to hatch, 0.78 mm × 0.72 mm.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, dark olive green to orange-yellow with a light green tinge when the chromatophores are contracted. Zoea I larvae are very similar to those previously described for *Eurynolambrus australis, Notomithrax peronii, N. ursus* and *Leptomithrax longimanus* and have not been figured (*see* Figs 84–86 for *E. australis*). Zoea II was not obtained for study.

Zoea I: Zoea with dorsal and rostral carapace spines, lateral spines absent. Total length 2.8 mm; rostral spine 0.40 mm long, curved slightly posteriorly; dorsal carapace spine 0.50 mm long, curved strongly near its base but relatively straight over its distal two-thirds; spine to spine length 1.55 mm; length of antenna 2 exopod 0.29 mm, the shortest of the three terminal exopod setae little more than one-half the length of the longest seta, length of endopod bud 0.14 mm; ratio of antenna 2 spiniform process (0.47 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *1.17, 0.94, and 1.62* respectively; telson with a large lateral spine and two smaller spines at the base of the cornu on each side, the smaller spines each about one-half as long as the lateral spine, but the anterior small spine rather more robust.

MEGALOPA: No knowledge.

NOTES: Although the zoea larvae of *Leptomithrax tuberculatus mortenseni* are very similar in their general facies to those of *L. longimanus, Eurynolambrus australis, Notomithrax peronii* and *N. ursus*, they can be readily distinguished from these by the relative lengths of the terminal setae on the antenna 2 exopod and of the lateral telson spines described above, at least in the first zoea stage.

Jacquinotia Rathbun, 1915

Jacquinotia edwardsii (Jacquinot, 1853)

SOURCE REFERENCE: Webber and Wear (1982) — zoea I hatched from an ovigerous female; zoea II from plankton.

ADULT DISTRIBUTION AND HABITAT: Southern half of South Island, Stewart Island, and Auckland and Campbell Islands; continental shelf and slope to 550 m depth, sometimes abundant in shallow water at certain times of the year and subject to migratory movements and periodic swarming (*see* Ritchie 1970). Endemic.

BREEDING AND EGGS: Ovigerous females have been caught in November and January, but eggs are probably incubated throughout the winter to hatch between mid-October and mid-November. Eggs, newly laid, orange-yellow, mean diameter 0.94 mm; swelling to 1.0 mm × 1.4 mm when ready to hatch.

ZOEA LARVAL STAGES: Two zoea stages. The zoea larvae are very similar to those of *Eurynolambrus australis* (*see* Figs 84–86) although somewhat larger; colour in life, not known.

Zoea I: Zoea with dorsal and rostral carapace spines, lateral spines absent. Total length 4.2 mm; rostral spine 0.45 mm long, straight; dorsal carapace spine 0.80 mm long, curved posteriorly; spine to spine length 2.4 mm; length of antenna 2 exopod 0.20 mm, of endopod 0.15 mm; ratio of antenna 2 spiniform process (0.35 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.78, 0.44, and 1.75* respectively; antenna 2 spiniform process armed with two rows of stout spinules distally; telson with a stout lateral spine and two thinner spines at the base of the cornu on each side, the thinner spines two-thirds the length of the lateral spine.

Zoea II: Total length 4.6 mm; rostral spine 0.50 mm long; dorsal carapace spine 0.85 mm long; spine to spine length 2.5 mm; length of antenna 2 exopod 0.25 mm, of endopod 0.25 mm; ratio of antenna 2 spiniform process (0.40 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod *0.80, 0.47, and 1.60* respectively; small spines at base of telson cornua now about half the length of lateral spine.

MEGALOPA: No knowledge.

FAMILY HYMENOSOMATIDAE

A discrete and easily identifiable family with three zoea stages followed by the juvenile stage which lacks natatory pleopods or uropods. The true megalopa larva is absent in all species, but since the very long-legged and "spidery" juveniles are able to swim using their walking legs, and are often caught in plankton samples, they are included in this paper where known.

Zoea larvae of New Zealand hymenosomatid spe-

cies are very small; the carapace smooth, globose, and sometimes higher than long, especially in later stages, mostly with a rostral spine only, but occasionally with a short and stout dorsal spine and a pair of short and stout lateral spines (one N.Z. species), or with a long rostral spine and paired lateral spines (one N.Z. species); antenna 2 spiniform process very short and exopod reduced to a very small spine or seta; maxilla 2 with coxal and basal endites undivided; exopods of maxillipeds 1 and 2 with seven natatory setae in stage II, and usually nine setae in stage III; abdomen of five segments in all zoea stages, and in the first juvenile crab. Abdomen of the zoea larvae of two basic types: (a) very small and slender; telson much longer than broad and wider anteriorly, terminating in a narrow and short fork spreading no more widely than the abdomen itself; inner and outer margins of lateral telson cornua fringed with very small spines or setae and lateral telson margins similarly armed; telson with three pairs of close-set posterior setae within the fork, with the outer pair longest and usually inclined posterolaterally; pleopod buds absent in zoea stages II and III; (b) abdomen as in (a) but with segments 4 and 5 extended laterally, segment 5 into a broad plate overlapping the telson on each side. Rice (1980a) lists the family larval characters based on five genera with species described from beyond the New Zealand region, and gives further diagnostic information on the mouthparts.

Lucas (1980) has reviewed and revised the systematics of the family Hymenosomatidae, which now includes 10 genera and 64 species. Lucas also uses supporting evidence from the larval phase in his revision and summarises larval characters for species belonging to the genera *Hymenosoma* Desmarest, *Elamena* H. Milne Edwards, *Halicarcinus* White, *Trigonoplax* H. Milne Edwards, *Elamenopsis* A. Milne Edwards, *Amarinus* Lucas, and *Neohymenicus* Lucas, with general characters of the larvae of *N. pubescens* supplied from the draft manuscript of this present work. Larval characters occurring in worldwide representatives of the family Hymenosomatidae conform generally with those given above for New Zealand species, except that there is rather more variation in the degree of development of carapace spines among species not represented here. The very "advanced" features of hymenosomatid larvae, including the tendency to reduce the carapace and abdominal armature, the reduction in relative length of the telson forks and the simplification of cephalothoracic appendages, seem to ally them, at least superficially, with the most advanced catametopous families, such as the Pinnotheridae and the Leucosiidae (Wear 1967), rather than with the similarly advanced Majidae which have abbreviated their zoea larval development by loss or combination of early zoea stages instead of losing the later ones including the megalopa (Rice 1980). (*See also* introductory comments to the family Pinnotheridae, pp. 64, 65).

Individual specific descriptions of the larvae supplement the above general diagnosis for the 11 New Zealand species in five genera described here, and these common features are not repeated unless necessary. It should be noted that measurements of both the eggs and larvae are subject to variations of up to 20% from the mean figures given in the text. Hymenosomatid larvae are common in inshore plankton samples but are found mainly near the bottom, probably due to the absence of long carapace spines, and, consequently, limited powers of floatation and orientation in swimming. The exception is *Hymenosoma depressum*, whose larvae are often found in surface layers.

Amarinus Lucas, 1980

Amarinus lacustris (Chilton, 1882)

SOURCE REFERENCES: Chilton (1915), Lucas (1971, 1980), Melrose (1975).

ADULT DISTRIBUTION AND HABITAT: Northern parts of the North Island, N.Z., as far south as Auckland; confined to freshwater lakes and non-tidal rivers. Also Australia, Lord Howe Island, Norfolk Island.

BREEDING AND EGGS: Ovigerous females have been collected in N.Z. during August. No information on eggs is available.

LARVAL STAGES: No free-living larval stages; late stage embryos are equivalent to the zoea stages of species with indirect development. Hatching occurs before the first crab instar is reached, but the free larvae remain among maternal pleopods until they moult to juvenile crabs.

NOTES: This species has up till recently been placed in the genus *Halicarcinus* White, but is now included in the new genus *Amarinus* Lucas, 1980.

Halicarcinus White, 1846

Halicarcinus cookii (Filhol, 1885)

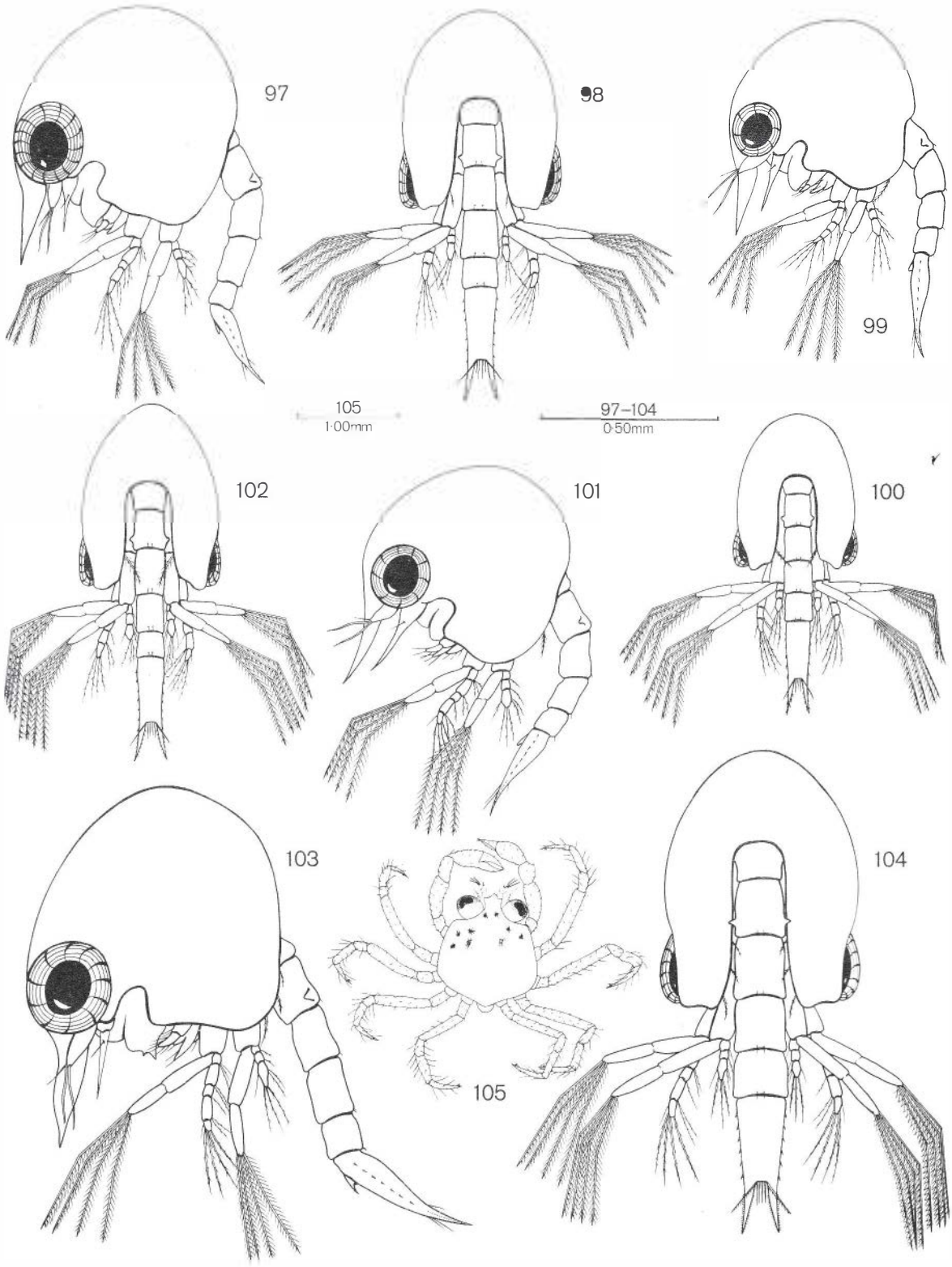
SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs; zoea stages II and III from plankton; first juvenile crab reared from planktonic stage III zoeas. Melrose (1975) — notes on breeding.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; very common and widespread in the littoral zone, mainly among finely divided algal fronds and holdfasts. Endemic.

BREEDING AND EGGS: Probably breeds throughout the year with peaks of egg production in spring and midsummer. Eggs, faintly yellow when newly laid, become orange and finally brown when about to hatch.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, translucent orange to almost transparent.

Zoea I (Figs 97, 98): Zoea with rostral carapace spine only. Carapace length 0.55 mm; carapace height 0.54 mm; rostral spine 0.24 mm long, straight and



FIGS 97–105: Family HYMENOSOMATIDAE. *Halicarcinus cookii* (Filhol, 1885). Zoea I: 97, lateral view; 98, posterior view. *Halicarcinus varius* (Dana, 1851). Zoea I: 99, lateral view; 100, posterior view. *Halicarcinus whitei* (Miers, 1876). Zoea I: 101, lateral view; 102, posterior view. *Halicarcinus planatus* (Fabricius, 1775). Zoea I: 103, lateral view; 104, posterior view. 1st juvenile crab: 105, dorsal view. Fig. 105 after Boschi, Scelzo and Goldstein (1969).

angled slightly forward, its length about equal to the vertical eye diameter; carapace with single plumose seta originating from near the inner posteroventral margin on each side; telson with a pair of weakly developed anal spines, and with several small lateral marginal spines.

Zoea II: Carapace length 0.75 mm; carapace height 0.94 mm; rostral spine 0.36 mm long; abdomen length 1.00 mm; pereiopods present as slender buds.

Zoea III: Carapace length 0.95 mm; carapace height 1.20 mm; rostral spine 0.38 mm long; abdomen length 1.30 mm; maxilliped exopods occasionally with eight natatory setae, but more usually with nine; pereiopods well-developed and partly segmented.

FIRST JUVENILE CRAB (not figured): Carapace length 1.25 mm (including rostrum of 0.25 mm); carapace width 1.10 mm; carapace without sharp angles laterally in postorbital and branchial regions; rostrum pyramidal and of three acute lobes, with central lobe the longest and bearing an apical tuft of strong, curved setae; distance between lateral margins of the eyes 0.75 mm; abdomen 0.65 mm long and setose dorsally; pereiopods hairy, pereiopod 3 the longest (2.70 mm); pereiopods 2–5 with terminal spine and two subterminal spines on dactyl.

NOTES: Specimens of the juvenile crab were unfortunately destroyed during a fire at the Victoria University Marine Laboratory during November 1979, and before they could be drawn for inclusion in this work.

Halicarcinus innominatus Richardson, 1949

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs. Melrose (1975) — figure of incompletely hatched zoea and appendages.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal and shallow water, associated with mussel clumps, seaweeds, and fouling organisms on wharf piles and on the keels of ships. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in October, December, January, March, April and May (Melrose 1975). Eggs, newly laid, yellow, 0.36 mm × 0.34 mm; about to hatch, black, 0.4 mm diameter.

ZOEA LARVAL STAGES: Probably three zoea stages; colour in life, black to olive green. Larvae have not been figured due to their close similarity with those of other species (*see* Figs 99–102 for *H. varius* and *H. whitei*).

Zoea I: Zoea with rostral carapace spine only. Carapace length 0.62 mm; carapace height 0.62 mm; rostral spine 0.20 mm long, straight and not angled forward, its length about equal to the vertical eye diameter; carapace with single plumose seta originating from near the inner posteroventral margin on each side; telson with a pair of weakly developed anal spines and with several very small lateral marginal spines.

FIRST JUVENILE CRAB: No knowledge.

Halicarcinus varius (Dana, 1851)

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs. Wear (1965) —zoea I figured.

ZOEA LARVAL STAGES: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; widespread in the intertidal and in shallow water, usually in sheltered conditions in association with algae. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected from the Wellington area in January and February, and from April through to December, and the species apparently breeds year round. Eggs, newly laid, light olive-green, 0.26 mm diameter; about to hatch, orange, 0.36 mm diameter.

ZOEA LARVAL STAGES: Probably three zoea stages; colour in life, black.

Zoea I (Figs 99, 100): Zoea with rostral carapace spine only. Carapace length 0.49 mm; carapace height 0.48 mm; rostral spine 0.22 mm long, straight but angled slightly anteriorly, its length about one and one-half times the vertical eye diameter; carapace with single plumose seta originating from near the inner posteroventral margin on each side; telson with a pair of weakly developed anal spines, and with several very small lateral marginal spines.

FIRST JUVENILE CRAB: No knowledge.

Halicarcinus whitei (Miers, 1876)

SOURCE REFERENCE: This study — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, N.Z.; not recorded from the Chatham Islands by Melrose (1975); usually in shallow sandy inshore areas and intertidally in estuaries; often found on *Zostera* flats. Endemic.

BREEDING AND EGGS: Ovigerous females have been caught in February, April, May, August, October, November and December (Melrose 1975) and may well breed throughout the year. Eggs, about to hatch, light green, 0.41 mm × 0.42 mm.

ZOEA LARVAL STAGES: Probably three zoea stages; colour in life, blackish yellow.

Zoea I (Figs 101, 102): Zoea with rostral carapace spine only. Carapace length 0.54 mm; carapace height 0.56 mm; rostral spine 0.26 mm long, slender and curved anteriorly, its length about one and one-half times the vertical eye diameter; carapace with single plumose seta originating from near the inner posteroventral margin on each side; telson with a pair of weakly developed anal spines and with several very small lateral marginal spines.

FIRST JUVENILE CRAB: No knowledge.

Halicarcinus planatus (Fabricius, 1775)

SOURCE REFERENCES: Boschi, Scelzo and Goldstein (1969). Roberts, P.E. (unpublished) — zoea I from laboratory hatched eggs; zoea stages II and III from plankton.

ADULT DISTRIBUTION AND HABITAT: N.Z. subantarctic islands; intertidal and continental shelf, and can be very common in shallow water. Also South America.

BREEDING AND EGGS: Ovigerous females have been collected from January through to May, and in August and November (Melrose 1975). No information is available on egg size or colour.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, chocolate brown.

Zoea I (Figs 103, 104): Zoea with rostral carapace spine only. Carapace length 0.72 mm; carapace height 0.72 mm; rostral spine 0.33 mm long, straight with slender point but rapidly thickening to give distinctive "humped" appearance; carapace with at least three plumose setae originating from near the inner posteroventral margin on each side; telson with a pair of prominent anal spines and with several small lateral marginal spines.

Zoea II: Carapace length 0.75 mm; carapace height 0.90 mm; rostral spine 0.40 mm long; at least four plumose setae originating from near the inner posteroventral carapace margin on each side.

Zoea III: Carapace length 1.13 mm; carapace height 1.28 mm; rostral spine 0.50 mm long; at least six plumose setae originating from near the inner posteroventral carapace margin on each side; maxilliped 1 with eight natatory setae; maxilliped 2 with nine natatory setae.

FIRST JUVENILE CRAB (Fig. 105): Carapace length 1.0 mm; carapace width 1.0 mm; rostrum well-defined, narrow and trilobed, with central lobe longest and lacking an apical tuft of curved setae; carapace smooth (from figure of Boschi *et al.* 1969) but pereiopods setose or hairy; pereiopods 2–5 each with a strong subterminal spine.

NOTES: The southern subantarctic distribution suggests that the larvae of *Halicarcinus planatus* are unlikely to occur in plankton samples taken in New Zealand mainland waters. At Campbell Island the larvae of this species are often abundant (P.E. Roberts pers. comm.).

Neohymenicus Lucas, 1980

Neohymenicus pubescens (Dana, 1851)

SOURCE REFERENCE: This study — zoea stages I, II, and III, and first juvenile crab reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, N.Z.; not recorded from the Chatham Islands by Melrose (1975); common from the intertidal to relatively deep water on sheltered and moderately exposed reefs. Endemic.

BREEDING AND EGGS: Ovigerous females have been caught in January, February, March, June, November, and December (Melrose 1975). Breeding probably occurs throughout the year. Eggs, about to hatch, light orange, 0.50 mm diameter.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, yellow-brown to olive-green with vivid blue eyes.

Zoea I (Figs 106, 107): Zoea with short and stout dorsal, rostral and lateral carapace spines. Carapace length 0.48 mm; carapace height 0.60 mm; rostral spine 0.31 mm long, straight; dorsal carapace spine 0.22 mm long, broadly based and arising in line with the anterior margin of the carapace or tilted slightly forward; spine to spine length 1.14 mm; lateral carapace spines 0.23 mm long and at right angles to the carapace (Fig. 107); carapace usually with five plumose setae spaced along inner posterolateral margin on each side; abdominal segment 4 laterally inflated posteriorly; segment 5 rather more inflated, with the lateral wings overlapping the telson by one-eighth its length; telson with fringe of small setae laterally.

Zoea II: Carapace length 0.75 mm; carapace height 0.80 mm; rostral, dorsal and lateral carapace spines each 0.30 mm long; spine to spine length 1.40 mm; maxillipeds 1 and 2 exopods with seven natatory setae, but one is usually much smaller than the others.

Zoea III: Carapace length 0.85 mm; carapace height 0.90 mm; rostral, dorsal and lateral carapace spines each 0.30 mm long; spine to spine length 1.50 mm.

FIRST JUVENILE CRAB (Figs 108, 109): Carapace length (including rostrum) 1.13 mm; carapace width 1.00 mm; carapace sparsely setose and with relatively sharp postorbital and branchial angles; rostrum 0.37 mm long, tapered with rounded tip, not lobed, and provided with long setae distally; distance between lateral margins of the eyes 0.65 mm; pereiopods hairy, pereiopod 3 the longest (2.40 mm); pereiopods 2–5 with a subterminal spine.

NOTES: Lucas (1980) has established *Neohymenicus* as a monotypic genus with *N. pubescens* as the type species on the basis of both adult and larval characters.

The zoea larvae of *N. pubescens* show considerable variation in size and in the degree of development of carapace spines. Stage I larvae hatched from a female captured in Whangaroa Bay, Northland, possessed dorsal and lateral carapace spines measuring just 0.13 mm (cf. about 0.2 mm in most specimens from the Wellington area). Stage I larvae sorted from plankton samples taken in Auckland Harbour have rostral and lateral spines 0.13 mm long but the dorsal spine is reduced to a rounded knob. In all areas females collected showed no significant differences from the

description of the conspecific *Halicarcinus pubescens* published by Melrose (1975).

Hymenosoma Desmarest, 1825

Hymenosoma depressum (Jacquinot, 1853)

SOURCE REFERENCE: This study — zoea I from laboratory hatched eggs; zoea stages II and III, and first juvenile crab from plankton.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Auckland Islands, and probably also Stewart Island, N.Z.; not recorded from the Chatham Islands by Melrose (1975); intertidal and shallow water, chiefly in sandy areas. Endemic.

BREEDING AND EGGS: Ovigerous females have been caught in October and February.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, red to translucent black.

Zoea I (Figs 110, 111): Zoea with rostral and lateral carapace spines, this combination of spines being immediately diagnostic. Carapace length 0.50 mm; carapace height 0.50 mm; lateral carapace spines 0.38 mm long, tending dorsolateral in origin and angled upwards; rostral spine 0.43 mm long, slender, curved anteriorly over proximal half and recurved posteriorly towards its tip; posterolateral carapace margins with 10–11 small teeth; telson with numerous small setae along lateral margins.

Zoea II: Carapace length 0.63 mm; carapace height 0.63 mm, lateral carapace spines 0.75 mm long; rostral spine 0.66 mm long.

Zoea III: Carapace length 1.19 mm; carapace height 1.19 mm; lateral carapace spines 0.88 mm long; rostral spine 0.88 mm long; maxilliped 1 exopod with eight plumose natatory setae, maxilliped 2 exopod with nine setae.

FIRST JUVENILE CRAB (Figs 112, 113): Carapace length (including rostrum) 1.60 mm; carapace width 1.60 mm; carapace with sparse covering of hairs, almost perfectly circular in outline and very flat dorsally; rostrum small, triangular with rounded tip; distance between lateral margins of the eyes 0.80 mm; pereiopods very long and slender (pereiopod 3 being 3.2 mm long) and generally setose; distal segments of pereiopods 2–5 with distinctive, long and evenly spaced, plumose setae along lateral margins; pereiopods 2–5 lack subterminal hook-like spines.

NOTES: This species has been the subject of considerable indecision with regard to its generic status, being originally described as *Hymenosoma depressa* (Jacquinot, 1853) and subsequently variously assigned to the genera *Hymenicus, Hymenosoma, Hombronia*, and finally to a new genus *Cyclohombronia* Melrose, 1975. Lucas (1980) has declared *Cyclohombronia* a junior synonym of *Hymenosoma*, and the name *Hymenosoma depressum* for this New Zealand species is followed here.

Elamena H. Milne Edwards, 1837

Elamena longirostris Filhol, 1885

SOURCE REFERENCE: This study — zoea stages I, II, and III and first juvenile crab reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, and Stewart Island, N.Z.; not recorded from the Chatham Islands by Melrose (1975); shallow water and continental shelf to 116 m depth, found mainly among sponges, bryozoans, red algae, and detritus. Endemic.

BREEDING AND EGGS: Ovigerous females have been recorded in August, November, December and January. Eggs, newly laid, opaque white, 0.37 mm diameter; about to hatch, reddish black, 0.47–0.63 mm diameter.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, almost black with dark red tinge, heavily pigmented. Measurements given in the following description relate to a larval series from the Marlborough Sounds only (*see* NOTES below).

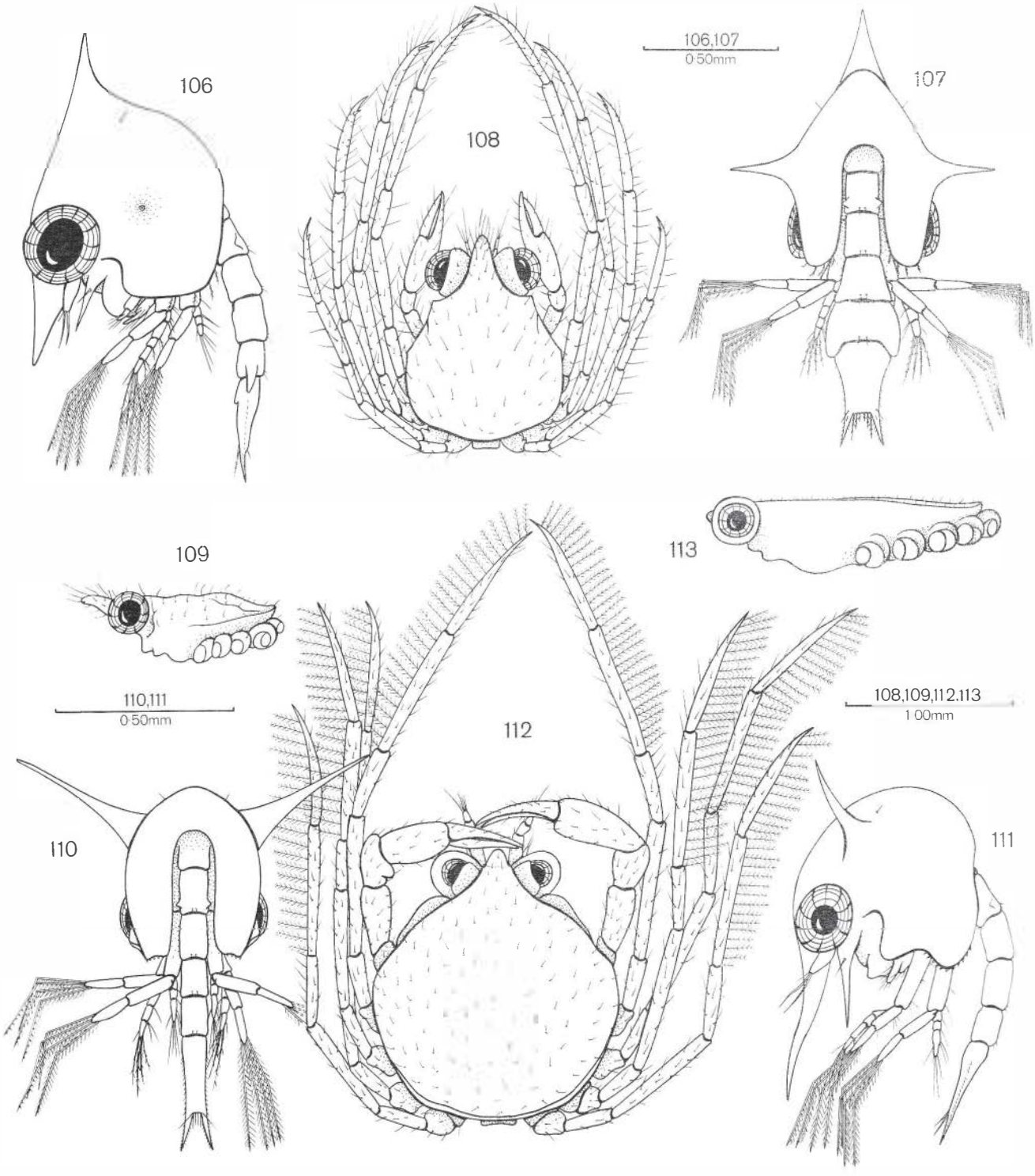
Zoea I (Figs 114, 115): Zoea with rostral carapace spine only. Carapace length 0.80 mm; carapace height 0.85 mm; rostral spine 0.22 mm long, stout, straight with pronounced anterior hump; carapace with four plumose setae arising from above the posterolateral margin on the inside of the carapace on each side; abdominal segments 4 and 5 laterally inflated with lateral wings of segment 5 overlapping telson by about one-third its length; lateral telson setae very difficult to see except for one close to the base of the lateral cornua.

Zoea II: Carapace length 0.96 mm; carapace height 1.15 mm; pereiopod buds all present.

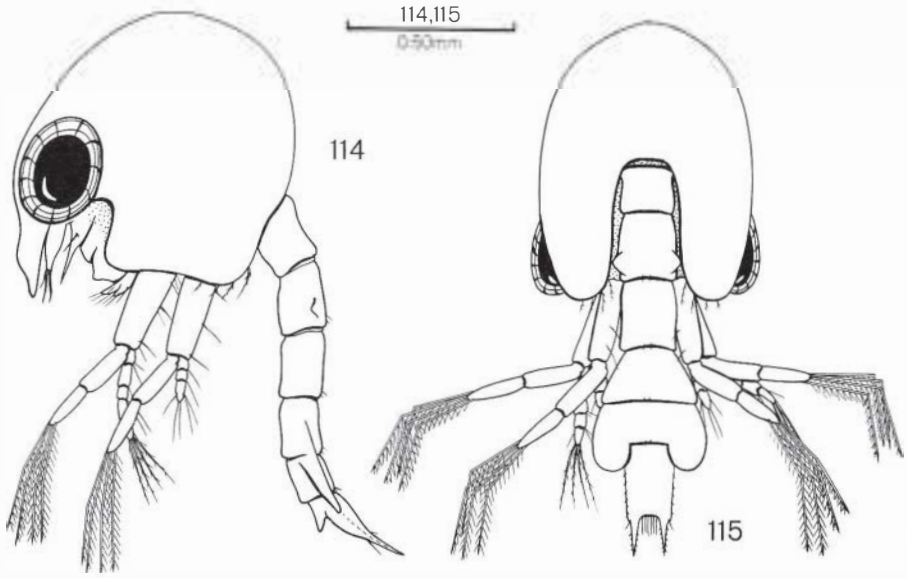
Zoea III: Carapace length 1.22 mm; carapace height 1.38 mm; maxillipeds 1 and 2 exopods usually with eight and nine setae respectively, but sometimes with eight and ten setae; pereiopod buds very long, almost one-half as long as the abdomen.

FIRST JUVENILE CRAB (Figs 116, 117): Carapace length (including rostrum) 1.95 mm; carapace width 1.40 mm; carapace smooth except for a small median posterior tubercle, not markedly scalloped in dorsal outline but with nevertheless well-defined postorbital and branchial angles; sharp, forwardly directed branchial spine present; rostral region long and almost parallel-sided, with a well-defined anterior orbital angle on each side, inclined slightly upward; rostrum itself with a trilobed keel; distance between lateral margins of the eyes 1.0 mm; walking legs very long (pereiopod 3, 5.3 mm) and sparsely setose; dactyls of pereiopods 2–5 each with a curved subterminal spine and a row of strong setae.

NOTES: The larvae of *Elamena longirostris* are about 20% smaller in the northern than in southern parts of its range, although in all other respects they are iden-



FIGS 106–113: Family HYMENOSOMATIDAE. *Neohymenicus pubescens* (Dana, 1851). Zoea I: 106, lateral view; 107, posterior view. 1st juvenile crab: 108, dorsal view; 109, carapace, lateral view. *Hymenosoma depressum* (Jacquinot, 1853). Zoea I: 110, posterior view; 111, lateral view. 1st juvenile crab: 112, dorsal view; 113, carapace, lateral view.



FIGS 114, 115: Family HYMENOSOMATIDAE. *Elamena longirostris* Filhol, 1885. Zoea I: 114, lateral view; 115, posterior view.

tical. Zoea I larvae from the Marlborough Sounds and from Papanui Canyon off Otago are all similar in size. Zoea II larvae from Whangaroa Harbour (carapace length 0.80 mm, height 0.85 mm) are about the same size as zoea I larvae from the South Island localities, and zoea III larvae from Whangaroa Harbour (carapace length 0.96 mm, height 1.15 mm) the same as zoea II from the Marlborough Sounds. However, first stage juvenile crabs from Whangaroa Harbour are less than 5% smaller than their southern counterparts.

Elamena momona Melrose, 1975

SOURCE REFERENCE: This study — zoea stages I, II, and III reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, N.Z.; not recorded from the Chatham Islands by Melrose (1975); continental shelf, occurring over shell and mud bottoms and on rocky substrates among algae in relatively shallow water. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in February, May, and November. Eggs orange-yellow, 0.50 mm diameter when newly laid and 0.56 mm × 0.58 mm when about to hatch.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, yellowish black and relatively heavily pigmented.

Zoea I (Figs 118, 119): Zoea with rostral carapace spine only. Carapace length 0.75 mm; carapace height 0.83 mm; rostral spine 0.27 mm long, straight with only a small anterior hump; carapace with four plumose setae arising from above the posterolateral margin on the inside of the carapace on each side; abdominal segments 4 and 5 laterally inflated with lateral wings of segment 5 overlapping telson by about one-third its length; small lateral telson setae often difficult to see except for one close to the base of the lateral cornua.

Zoea II: Carapace length 0.8 mm; carapace height 1.15 mm; rostral spine 0.31 mm long.

Zoea III: Carapace length 1.00 mm; carapace height 1.35 mm; rostral spine 0.35 mm long.

FIRST JUVENILE CRAB: No knowledge.

Elamena producta Kirk, 1879

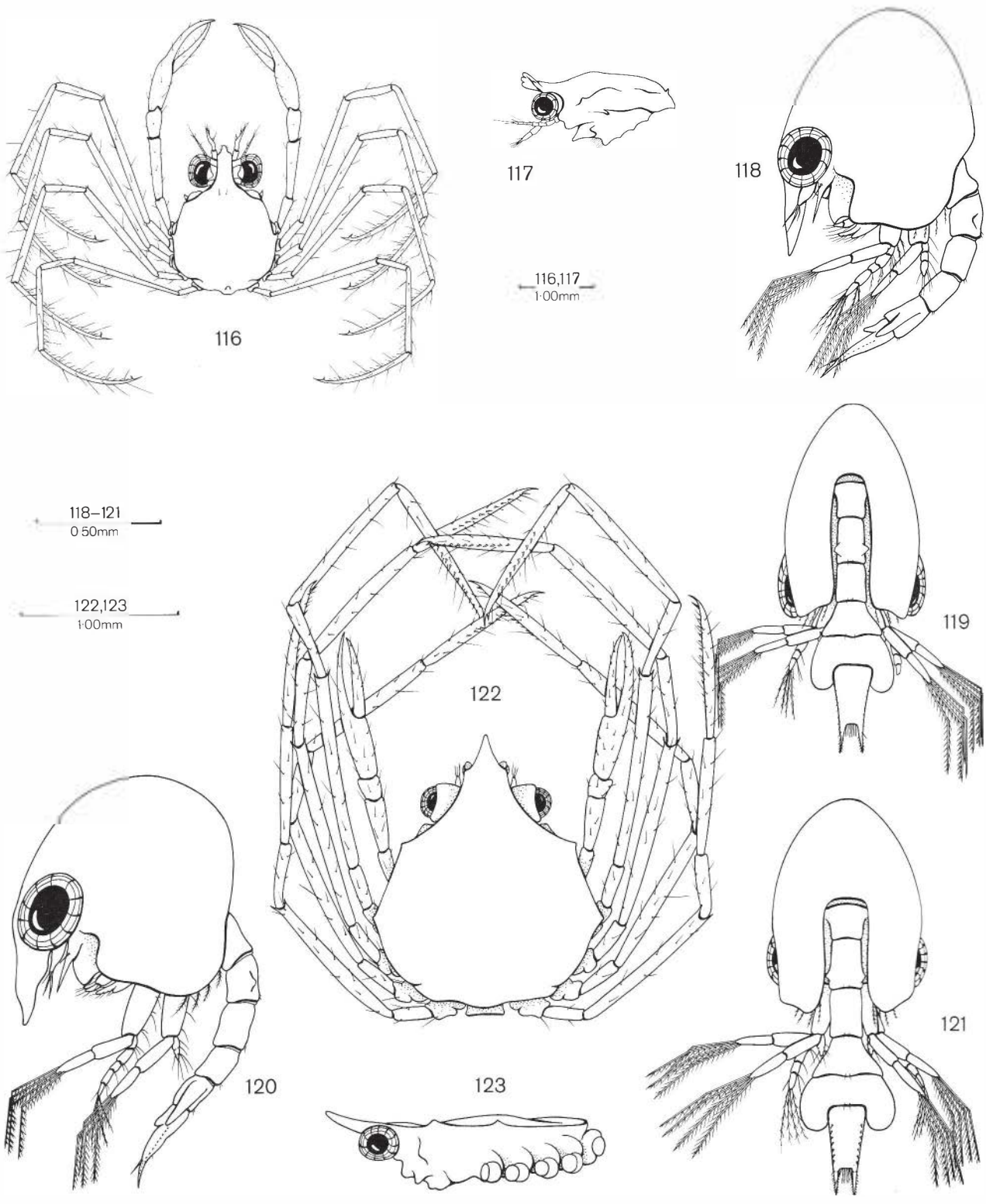
SOURCE REFERENCES: This study — zoea stages I, II, and III and first juvenile crab reared from laboratory hatched eggs. Gurney (1924: 195–6, fig. 78) — zoea III figured and described briefly.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; widely distributed on rocky shorelines in the intertidal and in shallow water; also under large boulders in coarse sand and among pebbles on the bottoms of pools in the lower mid-littoral; often reported in the shells of living *Haliotis iris* (paua) on more exposed Wellington coasts. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in the Wellington area in January, May, July, August, September, October, November, and December. The species apparently breeds throughout the year. Eggs, newly laid, deep orange, 0.50 mm × 0.60 mm; near hatching, faint orange, 0.55 × 0.60 mm.

ZOEA LARVAL STAGES: Three zoea stages; colour in life, yellow.

Zoea I (Figs 120, 121): Zoea with rostral carapace spine only. Carapace length 0.63 mm; carapace height 0.66 mm; rostral spine 0.23 mm long, robust, with anterior and posterior humps; carapace usually with four plumose setae arising from above the postero-



FIGS 116–123: Family HYMENOSOMATIDAE. *Elamena longirostris* Filhol, 1885. 1st juvenile crab: 116, dorsal view; 117, carapace, lateral view. *Elamena momona* Melrose, 1975. Zoea I: 118, lateral view; 119, posterior view. *Elamena producta* Kirk, 1879. Zoea I: 120, lateral view; 121, posterior view. 1st juvenile crab: 122, dorsal view; 123, cephalothorax, lateral view.

lateral margin on the inside of the carapace on each side; abdominal segments 4 and 5 laterally inflated with lateral wings of segment 5 overlapping telson by about one-third its length; telson with many very small lateral marginal setae.

Zoea II: Carapace length 0.93 mm; carapace height 1.10 mm; rostral spine 0.34 mm long.

Zoea III: Carapace length 1.30 mm; carapace height 1.31 mm; rostral spine 0.38 mm long; maxilliped 1 exopod with eight natatory setae, maxilliped 2 exopod with nine setae.

FIRST JUVENILE CRAB (Figs 122, 123): Carapace length (including rostrum) 1.70 mm; carapace width 1.50 mm; carapace smooth and distinctly scalloped in dorsal outline with well-defined postorbital and branchial angles, but lacking a branchial spine or a posterior tubercle; rostrum subtriangular, very broad with a defined anterior orbital angle on each side, inclined slightly upward, but without a ventral keel; distance between lateral margins of the eyes 0.80 mm; walking legs very long (pereiopod 3 being 4.2 mm) and sparsely setose; dactyls of pereiopods 2–5 each with a subterminal spine and a single line of smaller spines spaced along distal half.

BRACHYGNATHA (BRACHYRHYNCHA)

Brachyrhynchous zoea larvae are a heterogeneous assemblage with respresentatives showing almost all possible combinations of larval characters within the true brachyuran framework. Family characters within the group are not well-defined, but generally most can be identified to the level of species, genus, and often subfamily with relative ease. New Zealand brachyrhynchous larvae, as a group, show most of the larval characters exhibited by *Cancer novaezelandiae* described earlier as a generalised brachyuran larval series: there are four or more zoea stages; rostral, dorsal, and lateral carapace spines are usually present; natatory setae on the maxilliped exopods increase from four in zoea I by the addition of two further setae at each moult; the telson is widely forked with narrow cornua; pleopod and uropod buds are present in later zoea stages; and there is a true megalopa with long terminally hooked setae on the dactyl of pereiopod 5. The only aberrant families are perhaps the Belliidae as defined by Guinot (1976), which has zoea larvae with a greatly exaggerated antenna 2 spiniform process, and a megalopa with greatly reduced antennae and without long terminally hooked setae on the pereiopod 5 dactyl; and the Pinnotheridae, which show rather more affinity with zoea larvae of Leucosiidae and Hymenosomatidae (*see* Rice 1980a).

Several New Zealand brachyrhynchous crabs have abbreviated development with no zoea stages, or just one, but anomalies shown in their larval characters tend to be a manifestation of hatching at a late stage in development or a telescoping effect, and are thus applicable to individual species rather than to higher taxa.

FAMILY ATELECYCLIDAE

Zoea larvae of this family are highly variable and for the purposes of discussion Rice (1980a) has treated the three subfamilies (Atelecyclinae, Acanthocyclinae, and Thiinae) recognised by Balss (1957) separately. Their larval affinities are by no means clear. In the one atelecyclid species known from New Zealand waters (Atelecyclinae) development is abbreviated.

Trichopeltarion A. Milne Edwards 1880

Trichopeltarion fantasticum Richardson & Dell, 1964

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs. Richardson and Dell (1964) — records of ovigerous females with data on egg colour and dimensions.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Chatham Rise, N.Z.; continental shelf and slope, 20 m to about 800 m depth with most specimens captured between 300 m and 600 m. Endemic.

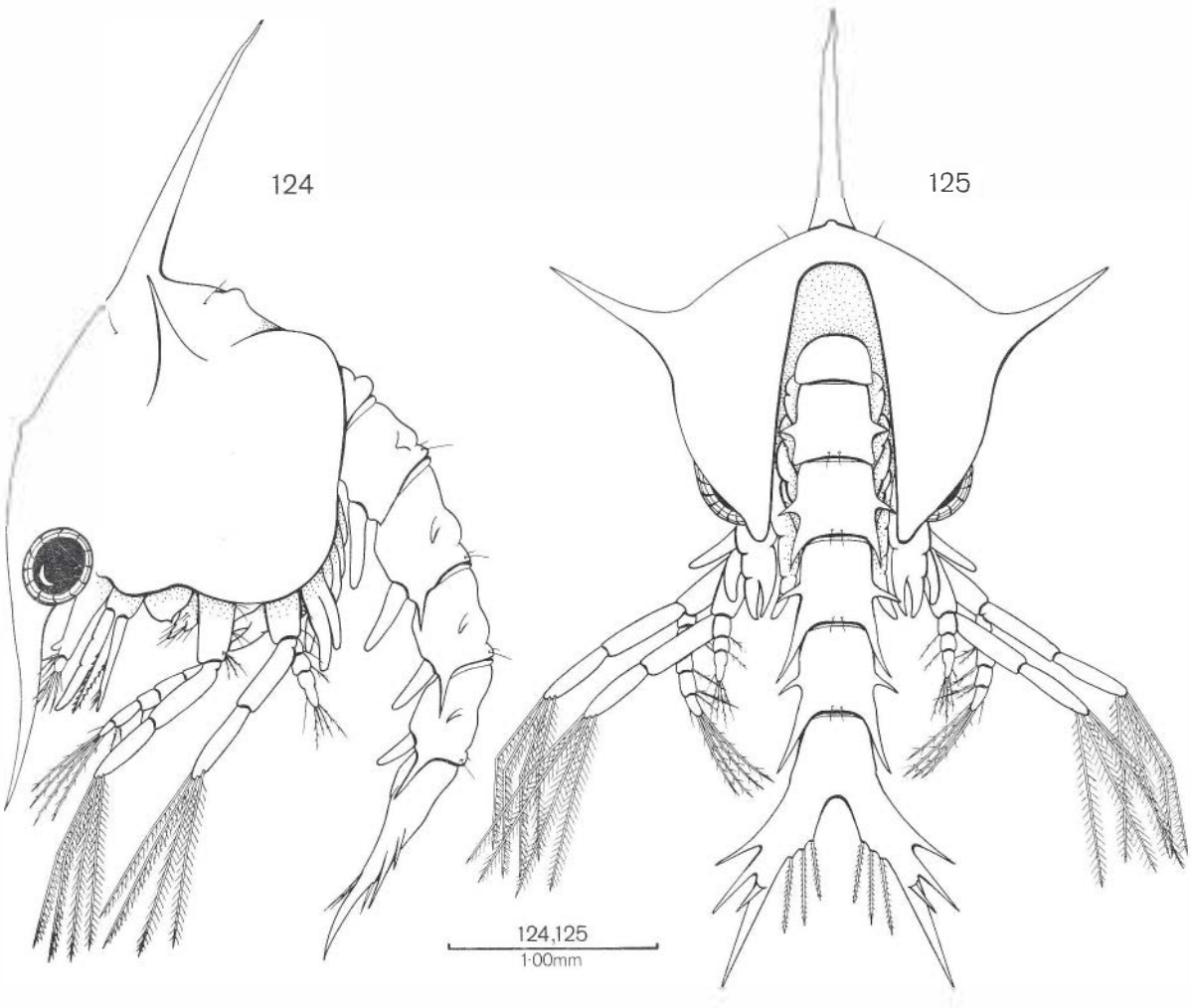
BREEDING AND EGGS: Ovigerous females have been collected in June and October. Eggs, newly laid, dark maroon or dull red-orange (Richardson and Dell 1964), 1.44 mm × 1.33 mm; about to hatch, almost transparent, 1.75 mm × 1.65 mm.

ZOEA LARVAL STAGES: Probably only one zoea stage; colour in life, not known.

Zoea I (Figs 124, 125): Zoea with dorsal, rostral and lateral carapace spines. Total length 4.4 mm; rostral spine 0.96 mm long, curving anteriorly over distal half; dorsal carapace spine 1.37 mm long, straight but tilted posteriorly; spine to spine length 3.92 mm; lateral carapace spines 0.65 mm long, inclined anteriorly and markedly upward (Fig. 125); carapace with small well-defined frontal and dorsal tubercles; length of antenna 2 exopod 0.44 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.51, 0.36, and 1.11* respectively; maxilliped 3 and pereiopods well-developed with pereiopod 1 chelate; abdominal segment 2 with usual lateral protuberances, segments 3–5 with a pair of posteriorly curved dorsolateral spines and strongly developed ventrolateral spines; pleopods present on abdominal segments 2–5; telson Y-shaped with a deep median posterior notch, two well-developed spines lateral to cornu on each side and a large seta arising dorsally from each cornu near its base, three pairs of setae inside cornua slender and plumose.

MEGALOPA: No knowledge.

NOTES: The larvae of *Trichopeltarion fantasticum* are large, heavily built, and are very poor swimmers. They are unlikely to be found in plankton samples, as it is probable that they are relatively short-lived and remain at or near the bottom in offshore waters.



FIGS 124, 125: Family ATELECYCLIDAE. *Trichopeltarion fantasticum* Richardson & Dell, 1964. Zoea I: 124, lateral view; 125, posterior view.

FAMILY CANCRIDAE

Five zoea larval stages with dorsal, rostral and lateral carapace spines; lateral spines protruding horizontally with the larva appearing almost precisely cruciform in posterior view; dorsal and rostral spines very long, almost straight and running through one vertical plane in lateral view. Megalopa with a long and well-developed rostral spine and median posterior carapace spine aligned horizontally, this combination being characteristic of the family; long, terminally hooked setae present on the pereiopod 5 dactyl.

The above diagnosis applies to the New Zealand species only, and also to most zoea larvae of the genus *Cancer* described from elsewhere. Relationships within the group and the affinities of this family with other groups are discussed by Rice (1980a), who points to complex relationships with the Portunidae and possible derivation from, or close to, the Polybiinae (Portunidae).

Cancer Linnaeus, 1758

Cancer novaezelandiae (Jacquinot, 1853)

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs; zoea stages II–V and megalopa from plankton. Wear (1965) — megalopa larva figured.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, Chatham Islands, and Auckland Islands; shallow water to continental shelf, usually occurring on sandy bottoms and particularly common in harbour areas. Probably endemic.

BREEDING AND EGGS: Ovigerous females have been

collected in the Wellington area in January and May. Eggs, newly laid, orange, 0.38 mm diameter; about to hatch, orange, 0.40 mm diameter.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, very light pink. The larvae of this species are fully described in the introductory section but no measurements are given. The following diagnosis is here reduced to the format used for other species.

Zoea I (Figs 1, 6, 11, 13, 15, 17, 19, 21, 22): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.4 mm; rostral spine 0.6 mm long, smooth, with very slight anterior curve; dorsal carapace spine 1.0 mm long with very slight posterior curve; spine to spine length 2.07 mm; lateral carapace spines 0.32 mm long, at 90° to carapace but slightly downturned at tips; carapace with small frontal and dorsal tubercle, posterior margins with one or two plumose setae protruding from beneath; length of antenna 2 exopod 0.15 mm; ratio of antenna 2 spiniform process (0.30 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.52, 0.31, and 2.07* respectively; dorsolateral protuberances on abdominal segment 2 only; telson Y-shaped with large lateral cornua curved dorsally, a seta lying laterally at base of cornua, a second smaller seta located laterally posterior to first seta, a third seta arising dorsally from base of cornu on each side.

Zoea II (Figs 2, 7): Total length 2.06 mm; rostral spine 1.0 mm long; dorsal carapace spine 1.29 mm long; spine to spine length 2.96 mm; lateral carapace spines 0.43 mm long; length of antenna 2 exopod 0.20 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.37, 0.29, and 1.85* respectively; posterior carapace margin with four or five plumose setae; abdominal segments 3–5 now with a pair of ventrolateral spines; second lateral telson seta now absent.

Zoea III (Figs 3, 8): Total length 2.9 mm; rostral spine 1.43 mm long; dorsal carapace spine 1.8 mm long; spine to spine length 3.96 mm; lateral carapace spines 0.49 mm long; length of antenna 2 exopod 0.2 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.28, 0.22, and 2.0* respectively; posterior carapace margin with many plumose setae; abdominal segments 2–5 with small pleopod buds; single median, dorsal, plumose seta on abdominal segment 1; abdominal segment 6 now separated but no uropod buds or ventrolateral spines present.

Zoea IV (Figs 4, 9): Total length, 3.9 mm; rostral spine 1.97 mm long; dorsal carapace spine 2.30 mm long; spine to spine length 5.55 mm; lateral carapace spines 0.48 mm long; length of antenna 2 exopod 0.32 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.38, 0.33, and 2.24* respectively; abdominal segment 6 now with uropod buds.

Zoea V (Figs 5, 10): Total length 5.8 mm; rostral spine 1.97 mm long; dorsal carapace spine 3.0 mm long; spine to spine length 6.76 mm; lateral carapace spines 0.47 mm long; length of antenna 2 exopod 0.43 mm; ratio of antenna 2 spiniform process (0.73 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.37, 0.24, and 1.75* respectively.

MEGALOPA (Figs 23–37): Carapace length (excluding rostrum) 2.50 mm; carapace width 1.75 mm; rostrum narrow and pointed, 0.75 mm long, extending anteriorly; posterior spine 1.50 mm long, extending posteriorly behind carapace in same plane as rostrum; dorsum of carapace with large depression behind rostrum; posterior carapace margin fringed with short hairs; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods; uropod exopod bearing 11 plumose setae; telson rounded posteriorly and naked.

NOTES: Larvae of *Cancer novaezelandiae* are relatively common in plankton samples taken from Wellington Harbour, where the first two or three zoea stages may be quite abundant in near-surface layers during September and October (Wear 1965). Later zoea stages are infrequently caught, but the megalopa is a particularly strong swimmer and is also common in surface tows.

FAMILY PORTUNIDAE

Species with at least three zoea stages, mostly five, and up to eight stages. Zoea larvae with dorsal, rostral and lateral carapace spines, the dorsal spine curved backwards; antenna 2 exopod about one-half to one-third the length of spiniform process; dorsolateral protuberances usually present on abdominal segments 2 and 3 (absent from segment 3 in the subfamily Carcininae); ventrolateral spines on abdominal segments 3–5 in later stages; mouthpart characters are listed by Rice (1980a). Megalopa larvae lacking a dorsal carapace spine; rostrum directed either anteriorly or vertically downward; abdominal segment 5 usually with a pair of posterolateral spines; pereiopod 5 with long terminally hooked setae on the dactyl. Beyond this, larval characters at the family level are difficult to generalise since there is considerable variation within the group.

Diagnoses of larvae described from the three subfamilies Carcininae, Polybiinae, and Portuninae are given in Rice and Ingle (1975) and are further elucidated by Rice (1980a) in view of more recent work. Rice suggests that zoea larvae of the Carcininae and Portuninae are significantly more advanced than those of the Polybiinae and can be quite readily derived from this latter group. In the adults, this implies two distinct evolutionary trends from a polybiinid-like ancestor, one involving a loss of swimming specialisations and leading to the Carcininae, and the other involving

increased specialisation and leading to the Portuninae (Rice 1980a).

New Zealand genera covered in this present work fall into all three subfamilies: Carcininae (*Nectocarcinus*), Polybiinae (*Macropipus, Ovalipes*) and Portuninae (*Portunus, Scylla*). Significant departures from previously established subfamily characters are found in two species. In *Nectocarcinus antarcticus*, which has five rather than four zoea stages, the zoea larvae have lateral spines, there is a tendency to lose ventrolateral abdominal spines in later stages, and dorsolateral spines are present on abdominal segment 5, while the megalopa has short coxal spines on pereiopods 2 and 3 and posterolateral spines on abdominal segment 5. In *Ovalipes catharus*, which has eight rather than five zoea stages, all except the first lateral accessory telson setae are lost from zoea V onward (*see* Rice and Ingle 1975, Rice 1980a).

Nectocarcinus A. Milne Edwards, 1860

Nectocarcinus antarcticus (Jacquinot, 1853)

SOURCE REFERENCE: This study — zoea I from laboratory hatched eggs; megalopa from the plankton.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, Chatham Islands, and the N.Z. subantarctic islands; shallow water to continental shelf and slope; widespread and abundant, especially in southern regions. Endemic.

BREEDING AND EGGS: Ovigerous females have been caught in August, October, November, January, April and May. This suggests that ovigerous females may be found in most months of the year. Eggs, newly laid, pale orange-yellow, 0.42 mm × 0.35 mm; about to hatch, transparent to light yellow, 0.49 mm × 0.42 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, faint pink.

Zoea I (Figs 126, 127): Zoea with dorsal, rostral and lateral carapace spines. Total length 2.0 mm; rostral spine 0.53 mm long, curved slightly posteriorly and with sparse armature of tiny teeth in distal half; dorsal carapace spine 0.63 mm long, curved slightly backwards; spine to spine length 1.67 mm; lateral carapace spines 0.17 mm long, declined ventrally; carapace with frontal and posterior dorsal tubercles, the latter being ill-defined; length of antenna 2 exopod 0.18 mm, central terminal spine very robust and about as long as exopod itself; ratio of antenna 2 spiniform process (0.32 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.62, 0.52, and 1.8* respectively; dorsolateral protuberances on abdominal segment 2 only; ventrolateral corners of abdominal segments 2–5 extended as short spines; abdominal segment 5 with a pair of large dorsolateral spines; telson cornua very long, with a row of setae on inner and outer margins, a lateral spine and a dorsal spine at base of cornu on each side.

Zoea II: Total length 2.4 mm; rostral spine 1.0 mm long, smooth; dorsal carapace spine 1.1 mm long, armed with sparse complement of stout setae protruding from the spine at right angles; spine to spine length 2.90 mm; lateral carapace spines 0.20 mm long; three small frontal setae present above each eye; length of antenna 2 exopod 0.32 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.42, 0.38, and 1.32* respectively; abdominal segments 3–5 with short ventrolateral spines, those of segment 2 now absent.

Zoea III: Total length 3.2 mm; rostral spine 1.40 mm long; dorsal carapace spine 1.40 mm long; spine to spine length 3.60 mm; lateral carapace spines 0.21 mm long; length of antenna 2 exopod 0.49 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.40, 0.40, and 1.15* respectively; pleopod buds present on abdominal segments 2–5; all accessory ventrolateral abdominal spines now absent.

Zoea IV: Total length 4.2 mm; rostral spine 1.60 mm long; dorsal carapace spine 1.60 mm long; spine to spine length 4.00 mm; lateral carapace spines 0.21 mm long; length of antenna 2 exopod 0.63 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.44, 0.44, and 1.11* respectively.

Zoea V: Total length 4.8 mm; rostral spine 1.80 mm long; dorsal carapace spine 1.80 mm long; spine to spine length 4.60 mm; lateral carapace spines 0.22 mm long; length of antenna 2 exopod 0.7 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.5, 0.5, and 1.28* respectively; only 10 and 11 natatory setae on exopods of maxillipeds 1 and 2 rather than the usual formula of 12 and 12 respectively for a stage V zoea.

MEGALOPA (Figs 128, 129): Carapace length 2.11 mm; carapace width 1.57 mm; carapace sparsely setose; rostrum directed ventrally; pereiopods 2 and 3 with short ventral coxal spines; pereiopod 5 with three long terminally hooked setae on slightly expanded and flattened dactyl; abdominal segment 5 with a pair of strong posterolateral spines; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods; uropod exopods each with 12 plumose setae; telson almost square and lacking setae.

NOTES: *Nectocarcinus antarcticus* is frequently the most abundant brachyuran larva occurring in offshore near-surface plankton samples, especially during the spring and summer months. The megalopa is a strong swimmer and is usually found together with the zoea larvae, sometimes in monospecific swarms. They are particularly attracted to light, and great numbers can be collected at night in this way. One of us (R.G.W.) collected an abundance of larvae representing all zoea larval stages, the megalopa, and juvenile crabs using

a dip net at night off the Portobello wharf in Port Chalmers, November 1969.

Ovalipes Rathbun, 1898

Ovalipes catharus (White, 1843)

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs; zoea stages II–VIII and megalopa from the plankton. Mr E. Laviña (unpublished data) — zoea stages I–VIII and megalopa reared in the laboratory.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; very common in harbours and estuaries, and from the surf zone down to about 100 m depth off open sandy coasts. Also eastern and southern Australia.

BREEDING AND EGGS: Ovigerous females have been caught in the Wellington area from July to April, with the peak of the breeding season being from November through to February or March. Eggs, newly laid, yellow, brown-orange or light brown, 0.30 mm × 0.29 mm; about to hatch, black, 0.37 mm × 0.38 mm.

ZOEA LARVAL STAGES: Eight zoea stages; colour in life, transparent to blackish to the naked eye with red chromatophores clearly visible in later stages. The following descriptions are a little more extensive than for other species, since the larvae possess unusual combinations of characters and some unique features, mainly in consequence of the species having extended larval development.

Zoea I (Figs 130, 131): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.4 mm; rostral spine 0.33 mm long, almost straight; dorsal carapace spine 0.58 mm long, with strong posterior curve; spine to spine length 1.26 mm; lateral carapace spines 0.24 mm long, almost at 90° to carapace or directed slightly downward; carapace with frontal and posterior tubercles; length of antenna 2 exopod 0.09 mm; ratio of antenna 2 spiniform process (0.20 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.61, 0.34, and 2.2* respectively; ventrolateral corners of abdominal segments 2–5 extended slightly as short, three-toothed angular lobes; paired lateral protuberances on abdominal segments 2 and 3; telson with one large lateral spine, one small lateral seta, and one dorsal seta, at the base of the cornu on each side.

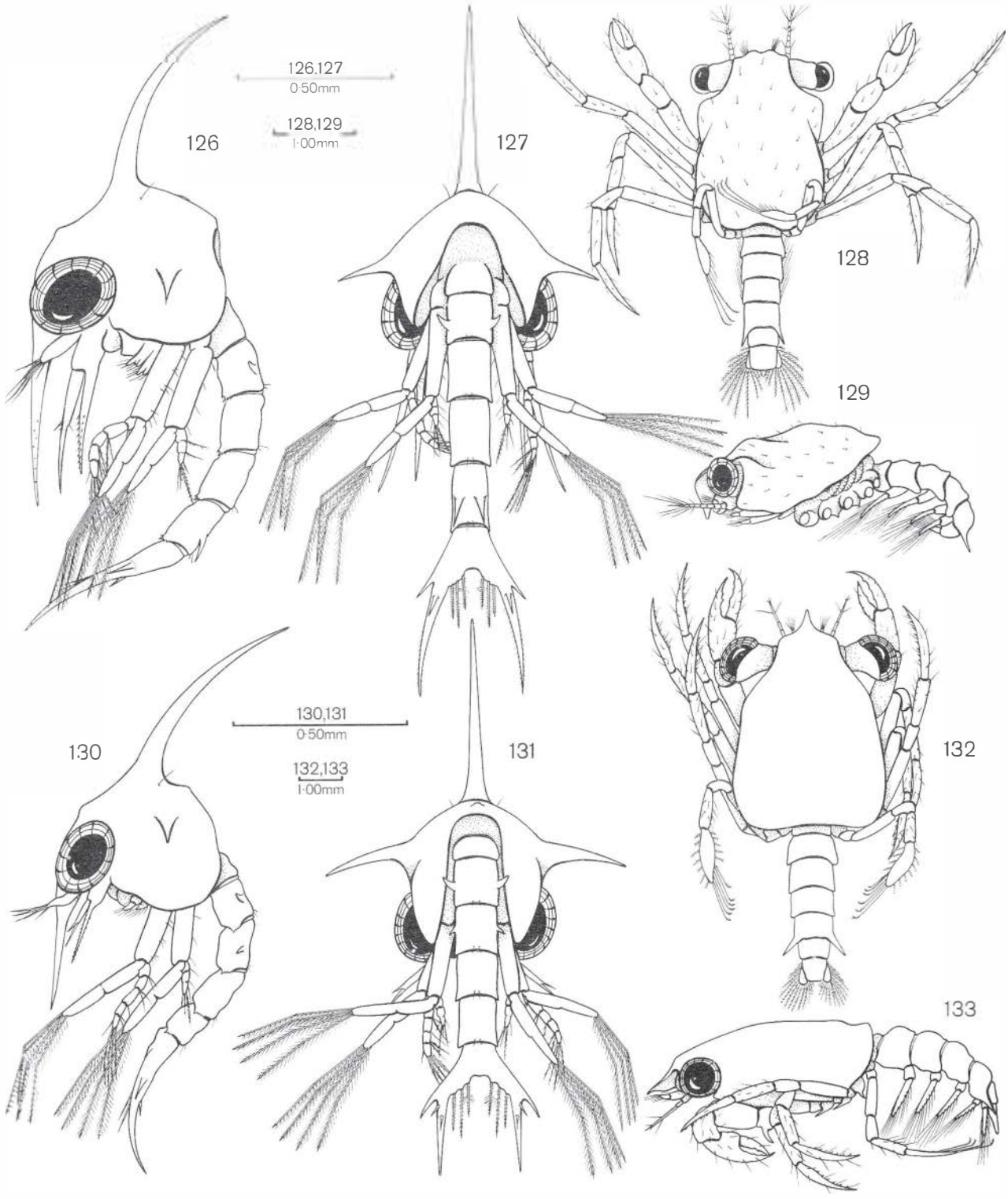
Zoea II: Total length 1.75 mm; rostral spine 0.50 mm long; dorsal carapace spine 0.76 mm long; spine to spine length 1.92 mm; lateral carapace spines 0.28 mm long; length of antenna 2 exopod 0.11 mm; ratio of antenna 2 spiniform process (0.28 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.56, 0.37, and 2.55* respectively; abdominal segments 3–5 with a pair of ventrolateral spines decreasing in size posteriorly.

Zoea III: Total length 2.4 mm; rostral spine 0.64 mm long; dorsal carapace spine 1.00 mm long, now only slightly curved; spine to spine length 2.52 mm; lateral carapace spines 0.28 mm long; length of antenna 2 exopod 0.13 mm; ratio of antenna 2 spiniform process (0.35 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.55, 0.35, and 2.69* respectively; telson with 5+5 or 5+4 inner posterior setae; telson seta in axilla of large lateral spine and cornu now very tiny and hair-like.

Zoea IV: Total length 3.2 mm; rostral spine 0.96 mm long; dorsal carapace spine 1.36 mm long, straight, provided with tiny denticles along its distal half; spine to spine length 3.40 mm; lateral carapace spines 0.28 mm long, declined ventrally; length of antenna 2 exopod 0.20 mm, endopod not yet developed; ratio of antenna 2 spiniform process (0.42 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.44, 0.31, and 2.10* respectively; pleopod buds not yet developed; telson with 5+5 inner posterior setae; axillary lateral telson seta absent.

Zoea V: Total length 4.0 mm; rostral spine 1.28 mm long; dorsal carapace spine 1.96 mm long; rostral and dorsal spines both with denticles along distal half or two-thirds, those on rostral spine appearing as small tooth-like spines; spine to spine length 4.72 mm; lateral carapace spines 0.29 mm long, markedly depressed; length of antenna 2 exopod 0.22 mm, endopod a tiny bud; ratio of antenna 2 spiniform process (0.45 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.35, 0.23, and 2.04* respectively; maxilliped 1 exopod with 12 large and two small natatory setae; maxilliped 2 exopod with 16 setae, four of which are very small; pleopod buds and uropod buds present, but small; telson with 6+6 inner posterior setae; lateral telson spine now in dorsolateral position, with both small setae at base of the lateral cornua now absent.

Zoea VI: Total length 5.3 mm (range 5.0–5.8 mm); rostral spine 2.09 mm long (range 1.92–2.20 mm); dorsal carapace spine 2.40 mm long (range 2.32–2.56 mm), sometimes curved slightly forwards over its length, with strong red chromatophore present in tip; spine to spine length 6.00 mm (range 5.60–6.60 mm); lateral carapace spines 0.35 mm long, but broadly based and difficult to measure accurately; length of antenna 2 exopod 0.49 mm, of endopod bud 0.28 mm; ratio of antenna 2 spiniform process (0.70 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.35, 0.29, and 1.43* respectively; maxilliped 1 exopod with 18 or 19 setae, maxilliped 2 exopod with 20 or 21 setae, on both maxillipeds the setae extend around the entire margin of the distal exopod segment, and decrease in length moving proximally; pereiopod buds still small, not protruding below ventrolateral carapace margins; pleopod buds about 0.14 mm to 0.10 mm in length; telson with 6+6, 6+7, or 7+7 inner posterior setae



FIGS 126–133: Family PORTUNIDAE. *Nectocarcinus antarcticus* (Jacquinot, 1853). Zoea I: 126, lateral view; 127, posterior view. Megalopa: 128, dorsal view; 129, lateral view, pereiopods removed. *Ovalipes catharus* (White, 1843). Zoea I: 130, lateral view; 131, posterior view. Megalopa: 132, dorsal view; 133, lateral view.

and with one further slender plumose seta sometimes arising from medial margin of cornu about midway along its length; dorsolateral telson spine near base of cornu now rather small.

Zoea VII: Total length 6.4 mm (range 6.2–6.8 mm); rostral spine 2.88 mm long (range 2.80–3.00 mm); dorsal carapace spine 3.61 mm long (range 3.40–3.80 mm); spine to spine length 8.93 mm (range 8.50–9.20 mm); lateral carapace spines 0.45 mm long; length of antenna 2 exopod 0.67 mm, rather different in structure than in earlier stages and now bears two short setae at its tip, the long terminal seta either lost or having become part of the exopod itself; antenna 2 endopod 0.70 mm long; ratio of antenna 2 spiniform process (0.70 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.25, 0.20, and 1.07* respectively; maxilliped 1 exopod with 24 setae, maxilliped 2 exopod with 26 setae; pereiopod buds protrude below ventrolateral carapace margins; pleopod buds 0.21 mm long (segment 2) to 0.14 mm long (segment 5); uropod buds 0.10 mm long; telson with 7+8 or 8+8 inner posterior setae.

Zoea VIII: Total length 7.2 mm (range 7.0–7.5 mm); rostral spine 2.88 mm long (range 2.80–3.00 mm); dorsal carapace spine 3.47 mm long (range 3.40–3.60 mm); spine to spine length 8.60 mm (range 8.20–9.00 mm); lateral carapace spines 0.45 mm long; length of antenna 2 exopod 0.70 mm, structure as in zoea VII; antenna 2 endopod 0.84 mm long, segmented beneath cuticle; ratio of antenna 2 spiniform process (0.93 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.32, 0.27, and 1.33* respectively; maxilliped 1 exopod with 24 setae, maxilliped 2 exopod with 26 or 28 setae; pereiopod buds very large, partly segmented; pleopod buds 0.25 mm long (segment 2) to 0.21 mm long (segment 5); uropod buds 0.12 mm long; telson with 8+ 8 inner posterior setae, and with one medial cornu seta on one side of the telson in one of the specimens studied; living tissue withdrawn from telson plate in all three specimens examined, with characters of the megalopa abdomen clearly visible.

MEGALOPA (Figs 132, 133): Reared larvae are coloured black in life. Carapace length (including rostrum) 4.65 mm (range 4.40–4.80 mm); carapace width 2.75 mm (range 2.60–3.00 mm); carapace smooth and without hairs, setae or prominent tubercles; rostrum sharply pointed in dorsal view and declined at an angle of about 45°; pereiopod 1 with a strong ischial spine curved posteriorly; pereiopods 2 and 3 with a straight basial spine directed forwards; pereiopod 4 with a small basial spine curved slightly posteriorly; proximal pereiopod segments smooth, propodus and dactyl of each pereiopod only sparsely setose; dactyls of pereiopods 2–4 with a row of small ventral spines; pereiopod 5 dactyl markedly flattened and with six or seven long, terminally hooked setae; abdominal segment 5 with a pair of strongly developed spines originating and directed posterolaterally; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods; exopod of uropods with 22–24 plumose setae, protopod with two lateral setae; telson rounded and lacking posterior setae.

NOTES: The life history of *Ovalipes catharus* is unusual in that the zoea phase is exceptionally long. These larvae are rare in the inshore shallow-water and harbour plankton in spite of the abundance of adults of this species nearby. A larval series of 16 specimens representing stages V to VIII were identified from an Agassiz trawl sample taken in a depth of 527–680 m off Hicks Bay near East Cape in January 1979. It must be assumed, therefore, that the larvae live offshore in deeper water, perhaps near the bottom in late zoea stages, and migrate inshore in the megalopa stage when they may occur in surface plankton samples.

Portunus Fabricius, 1798

Portunus pelagicus (Linnaeus, 1776)

SOURCE REFERENCES: This study — zoea stages I–IV and megalopa reared from laboratory hatched eggs. Aikawa (1937) — zoea I and megalopa. Prasad and Tampi (1953) — zoea I from laboratory hatched eggs. Yatsuzuka (1962) — zoeas I–IV, megalopa (not seen). Kurata and Midorikawa (1975) — zoea stages I–IV and megalopa reared in the laboratory. Shinkarenko (1979) — zoea stages I–IV and megalopa reared in the laboratory. Yatsuzuka and Sakai (1980) — zoea stages I–IV, megalopa, and first three juvenile crab stages reared in the laboratory.

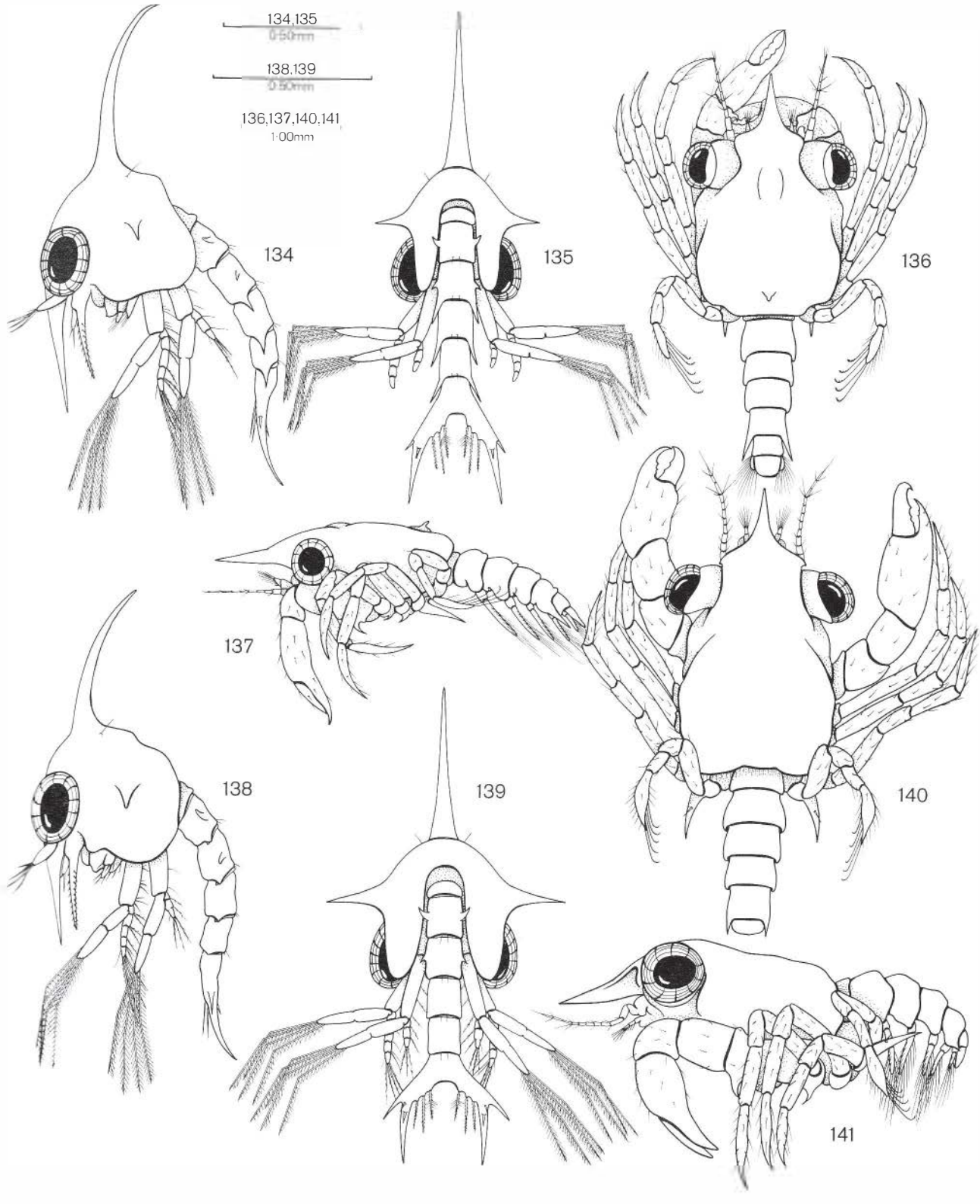
ZOEA LARVAL STAGES: Northern half of North Island, N.Z.; shallow water and pelagic. The species is a rare visitor to New Zealand waters and is occasionally cast ashore (*see*, for example, Dell 1964a). Indo-Pacific.

BREEDING AND EGGS: No knowledge of breeding in New Zealand waters.

ZOEA LARVAL STAGES: Four zoea stages; overall colour in life, not known; chromatophores black and red.

Zoea I (Figs 134, 135): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.6 mm; rostral spine 0.36 mm long, straight; dorsal carapace spine 0.48 mm long; spine to spine length 1.24 mm; lateral carapace spines 0.10 mm long; length of antenna 2 exopod 0.06 mm; ratio of antenna 2 spiniform process (0.24 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.66, 0.50, and 4.00* respectively; lateral protuberances on abdominal segments 2 and 3, those on segment 3 directed posteriorly; abdominal segments 3–5 with a well-developed posterolateral spine on each side; telson with one small lateral seta and one small dorsal seta at the base of the cornu on each side; the telson cornua lacking marginal setae.

Zoea II: Total length 2.0 mm; rostral spine 0.49 mm long; dorsal carapace spine 0.70 mm long; spine to



FIGS 134–141: Family PORTUNIDAE. *Portunus pelagicus* (Linnaeus, 1776). Zoea I: 134, lateral view; 135, posterior view. Megalopa: 136, dorsal view; 137, lateral view. *Scylla serrata* (Forskål, 1755). Zoea I: 138, lateral view; 139, posterior view. Megalopa: 140, dorsal view; 141, lateral view.

spine length 1.75 mm; lateral carapace spines 0.14 mm long; length of antenna 2 exopod 0.08 mm; ratio of antenna 2 spiniform process (0.28 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.57, 0.40, and 3.50* respectively; maxilliped 1 exopod with eight natatory setae (sometimes 7); maxilliped 2 exopod with eight setae; telson with 4+4 inner posterior setae.

Zoea III: Total length 2.8 mm; rostral spine 0.77 mm long; dorsal carapace spine 0.98 mm long; spine to spine length 2.48 mm; lateral carapace spines 0.14 mm long; length of antenna 2 exopod 0.16 mm, of endopod 0.21 mm; ratio of antenna 2 spiniform process (0.49 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.63, 0.50, and 3.06* respectively; maxillipeds 1 and 2 exopods each with 10 natatory setae; telson with 5+5 (or 5+4) inner posterior setae.

Zoea IV: Total length 3.3 mm; rostral spine 0.98 mm long; dorsal carapace spine 1.26 mm long; spine to spine length 3.20 mm; lateral carapace spines 0.14 mm long; length of antenna 2 exopod 0.18 mm, of endopod 0.32 mm; ratio of antenna 2 spiniform process (0.56 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.57, 0.44, and 3.11* respectively; maxillipeds 1 and 2 exopods each with 14 setae, two being very small; no lateral protuberance on abdominal segment 3; telson always with 5+5 inner posterior setae.

Later zoea stages reared in the laboratory vary considerably in size. This is apparently caused by spending an extra day per intermoult. The final moult can be about four days later than usual, thus producing an apparent fifth zoea stage (G. Campbell, pers. comm.). Brief measurements of these large stage IV larvae are as follows: Total length 4.0 mm; rostral spine 1.19 mm long; dorsal carapace spine 1.47 mm long; spine to spine length 4.0 mm; lateral carapace spines 0.15 mm long; length of antenna 2 exopod 0.21 mm, of endopod 0.42 mm; ratio of antenna 2 spiniform process (0.63 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.52, 0.42, and 3.00* respectively; maxilliped exopod and telson setation unchanged from usual stage IV.

MEGALOPA (Figs 136, 137): Carapace length (including rostrum) 2.40 mm; carapace width 1.40 mm; carapace smooth; rostrum 0.62 mm long, slender, tapering to a point and directed horizontally forward; anterior tubercle on carapace a rounded hump, posterior tubercle small but appearing as a prominent finger-like projection; pereiopod 1 with hook-like ischial spine and similar carpal spine; pereiopod 2 with basial spine; pereiopod 4 with large, straight, posteriorly directed coxal spine extending to about half the length of abdominal segment 2; pereiopod 5 with dactyl flattened and bearing five long, terminally hooked setae; abdominal segment 5 with a pair of strongly developed lateral spines directed posteriorly; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods; exopod of uropods with 11 plumose setae; telson rounded posteriorly and lacking setae.

NOTES: As there is no evidence of breeding in New Zealand waters it is unlikely that the larvae of *Portunus pelagicus* will be present in our plankton. However, the possibility of megalopa larvae or juvenile crabs drifting eastwards from Australia should not be ruled out.

There is some variation recorded in larval descriptions, especially concerning the overall size of larvae and the setation of the maxillipeds. Our zoea stages I–IV are similar to those of Shinkarenko (1979) with respect to overall size and the setation of the maxilliped exopods, except that the maxilliped 2 exopods in our zoea stage IV bear 12 natatory setae rather than the 14 noted by Shinkarenko in her specimens. Compared with Kurata and Midorikawa (1975), however, equivalent stage zoea larvae from Japan differ mainly in being between 10% and 20% larger than their New Zealand counterparts. The description of the megalopa by Kurata and Midorikawa compares well with our own except that the specimens from Japan are smaller (2.1 mm × 1.2 mm). Shinkarenko gives no measurements for her megalopa. It is probable, therefore, that conditions of environment and of available food strongly influence the length of intermoults and the size of larvae at each stage in the development of *P. pelagicus*. There appears to be general agreement that there are four rather than five zoea larval stages.

Scylla de Haan, 1833

Scylla serrata (Forskål, 1885)

SOURCE REFERENCES: This study — zoea stages I–V and megalopa reared from laboratory hatched eggs. Raja Bai Naidu (1955) — zoea I. Ong Kah Sin (1964) — zoea stages I–V, megalopa.

ADULT DISTRIBUTION AND HABITAT:Northern part of North Island, N.Z. The species is thought to establish itself in northern areas after periodic invasions of larvae, juveniles, or adults, the most recent of which occurred about 1964 (Dell 1964b; Manikiam 1967). We have little evidence to suggest that *Scylla serrata* is a permanent member of the New Zealand fauna, although once introduced, adults are clearly able to survive here in suitable habitats. Also Australia and throughout the Indo-Pacific in tropical and subtropical mangrove harbours and estuaries.

BREEDING AND EGGS: There is no evidence for breeding in New Zealand waters, as no ovigerous females have been found. Eggs, newly laid, yellow-orange or yellow-brown; becoming black when ready to hatch; very tiny and numerous but no measurements available.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, greenish black.

Zoea I (Figs 138, 139): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.5 mm; rostral spine 0.33 mm long, straight; dorsal carapace spine 0.54 mm long; spine to spine length 1.27 mm; lateral carapace spines 0.22 mm long; length of antenna 2 exopod 0.07 mm; ratio of antenna 2 spiniform process (0.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.75, 0.46, and 3.57* respectively; lateral protuberances on abdominal segments 2 and 3; abdominal segments 2–4 without lateral spines but with ventrolateral angles produced into two small teeth in an equivalent position; telson with a large lateral spine, a very tiny dorsolateral seta, and a small dorsal seta, at the base of the cornu on each side; the telson cornua lacking marginal setae.

Zoea II: Total length 2.0 mm; rostral spine 0.43 mm long; dorsal carapace spine 0.64 mm long; spine to spine length 1.50 mm; lateral carapace spines 0.22 mm long; length of antenna 2 exopod 0.09 mm; ratio of antenna spiniform process (0.34 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.79, 0.53, and 3.77* respectively; abdominal segments 3–5 with distinct but small ventrolateral spines; telson with 4+4 inner posterior setae.

Zoea III: Total length 2.5 mm; rostral spine 0.59 mm long; dorsal carapace spine 0.80 mm long; spine to spine length 1.97 mm; lateral carapace spines 0.23 mm long; length of antenna 2 exopod 0.12 mm; ratio of antenna 2 spiniform process (0.36 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.61, 0.45, and 3.00* respectively; maxilliped 2 exopod sometimes with nine natatory setae rather than the usual eight; abdominal segments 3–5 with long ventrolateral spines; tiny lateral telson setae now lost.

Zoea IV: Total length 3.45 mm; rostral spine 1.00 mm long; dorsal carapace spine 1.20 mm long; spine to spine length 3.06 mm; lateral carapace spines 0.29 mm long; length of antenna 2 exopod 0.17 mm, of endopod 0.15 mm; ratio of antenna 2 spiniform process (0.58 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.58, 0.48, and 3.41* respectively; maxilliped 2 exopod with 10 setae, but often one or two smaller setae in addition; telson with 5+5 inner posterior setae.

Zoea V: Total length 4.3 mm; rostral spine 1.14 mm long; dorsal carapace spine 1.33 mm long; spine to spine length 3.73 mm; lateral carapace spines 0.42 mm long; length of antenna 2 exopod 0.20 mm, of endopod 0.53 mm; ratio of antenna 2 spiniform process (0.64 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.56, 0.48, and 3.13* respectively; maxilliped 1 exopod with 11 long setae and one, two, or three short setae, maxilliped 2 exopod with 14 or 15 setae; ventrolateral spines of abdominal segments 3–5 now very long.

MEGALOPA (Figs 140, 141): Carapace length (including rostrum) 2.88 mm; carapace width 1.62 mm; carapace smooth but with fringe of posterior setae; rostrum 0.60 mm long, slender, tapering to a point and directed horizontally forward; anterior and posterior carapace tubercles indistinct; pereiopod 1 with a hook-like ischial spine but no carpal spine; pereiopod 2 with basial spine; pereiopod 4 with a very large, somewhat curved and posteriorly directed coxal spine extending to about half the length of abdominal segment 3; pereiopod 5 with slightly flattened dactyl bearing five long, terminally hooked setae; abdominal segment 5 with short lateral spines; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods; exopods of uropods with 11–14 plumose setae; telson rounded posteriorly and naked.

NOTES: Although there is no evidence of breeding by *Scylla serrata* in New Zealand waters it is possible that late stage zoea larvae, or megalopas, may occur from time to time in samples from the far north of the North Island. Comparison of our own larval series of *S. serrata* from Queensland, Australia, with those from the Philippines and from Malaysia as described by Ong Kah Sin (1964), reveals some variation in size and setation. This is not entirely unexpected between populations of a species with this wide geographic separation. The number of zoea larval stages, however, remains constant.

Macropipus Prestandrea, 1833

Macropipus corrugatus (Pennant, 1777)

SOURCE REFERENCES: This study — zoea stages II and IV from the plankton. Lebour (1928a) — zoea I from laboratory hatched eggs. Rice and Ingle (1975) — megalopa of *Macropipus holsatus* (Fabricius) as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; continental shelf; the species is the smallest of the New Zealand Portunidae and is infrequently captured. Indo-West Pacific and Atlantic.

BREEDING AND EGGS: No details of breeding in N.Z. In Europe, ovigerous females occur in April to June (spring) (Lebour 1928a). Eggs, newly laid, red-orange, 0.32 mm diameter; about to hatch, speckled brown, 0.40 mm diameter.

ZOEA LARVAL STAGES: Probably five zoea stages; colour in life, pinkish grey.

Zoea I (Figs 142, 143): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.6 mm; rostral spine 0.34 mm long, curved posteriorly; dorsal carapace spine 0.63 mm long, curved strongly posteriorly; spine to spine length 1.4 mm; lateral carapace spines 0.19 mm long; slightly declined but almost horizontal in some larvae; length of antenna 2 exopod 0.14 mm; ratio of antenna 2 spiniform process (0.28 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.82, 0.44, and 2.00* respectively; abdominal segments 2 and 3 with lateral protuber-

ances, those on segment 3 curved posteriorly; abdominal segments 3–5 with small ventrolateral spines; telson with a lateral spine, a small lateral (axillary) seta, and a dorsal spine, at the base of the cornu on each side.

Zoea II: Total length 2.25 mm; rostral spine 0.56 mm long; dorsal carapace spine 0.75 mm long; spine to spine length 2.00 mm; lateral carapace spines 0.21 mm long; length of antenna 2 exopod 0.15 mm; ratio of antenna 2 spiniform process (0.30 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.54, 0.4, and 2.0* respectively.

Zoea IV: Total length 3.6 mm; rostral spine 0.96 mm long; dorsal carapace spine 1.18 mm long; spine to spine length 3.15 mm; lateral carapace spines 0.23 mm long; length of antenna 2 exopod 0.28 mm; ratio of antenna 2 spiniform process (0.49 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.51, 0.42, and 1.75* respectively.

MEGALOPA: No knowledge. The megalopa of *Macropipus holsatus* (Figs 144, 145) is described and illustrated as an example of the genus.

Rostrum well-developed but declined at about 45°; carapace sparsely setose with a denser fringe of setae along posterior margins; pereiopod 1 with a prominent ischial spine but no carpal spine; pereiopods 2–4 with straight coxal spines, but that of the pereiopod 4 not greatly developed as in *Portunus pelagicus* and *Scylla serrata*; pereiopod 5 with slightly flattened dactyl bearing three long, terminally hooked setae; abdominal segment 5 with posterolateral angles rounded and not produced into a spine; abdominal segments 2–5 with pleopods, segment 6 with uropods; uropod exopod with nine or ten setae.

NOTES: Planktonic zoea larvae of *Macropipus corrugatus* from Leigh, near Auckland, and from Wellington Harbour, were identified by direct comparison with stage 1 larvae hatched by Lebour which are presently lodged in the biological collections of the Plymouth Laboratory, and examined there by R.G.W. in 1970. Larvae of *M. corrugatus* have been seen in New Zealand plankton samples only rarely. Lebour (1928a) was not successful in obtaining them from Plymouth, U.K.

FAMILY BELLIIDAE

The family consists of the genera *Bellia* H. Milne Edwards, *Corystoides* H. Milne Edwards & Lucas, *Acanthocyclus* H. Milne Edwards & Lucas, and the monotypic New Zealand genus *Heterozius* A. Milne Edwards, together comprising the subfamily Acanthocyclinae (Atelecyclidae) (Balss 1957), but separated from the Atelecyclidae and elevated to the level of superfamily (Bellioidea) by Guinot (1976, 1978). Zoea and megalopa larvae have been described from all genera except *Bellia*.

Rice (1980a) lists and discusses the zoea larval characters of *Corystoides* and *Heterozius* and treats them in the context of the Atelecyclinae following the earlier classification of Balss (1957), but takes no account of the larvae of *Acanthocyclus gayi* (Fagetti and Campodonico 1970) or those of *A. albatrossis* (Campodonico and Guzman 1973). Rice observed that although the zoea larvae of *Corystoides* and *Heterozius* clearly differ in several features such as the number of zoea stages (two in *Heterozius* compared with four in *Corystoides*), in the development of carapace spines, and in the armature of the abdominal segments, they share many characters including some which are so unusual elsewhere amongst the Brachyura that they surely indicate a close relationship between the genera. To this assemblage we should now add *Acanthocyclus*, with four zoea stages which conform with Rice's diagnosis of the Acanthocyclinae in almost all respects, but which show rather more affinity with *Corystoides* than with *Heterozius*.

Further evidence of a close relationship is seen in the megalopa larvae, which in all three genera have antenna 2 greatly reduced with the flagellum consisting of three very short segments only, pereiopod 5 dactyl lacking long terminally hooked setae, and abdominal segment 6 lacking any trace of uropods. This is a combination of characters unique among the Brachyura. Rice (1980a), while not generally covering megalopa larval features, is, however, clearly mistaken in his observation (p.335) that the megalopas of both *Corystoides* and *Heterozius* lack pleopods, as these are present on abdominal segments 2–5 in all belliid species described.

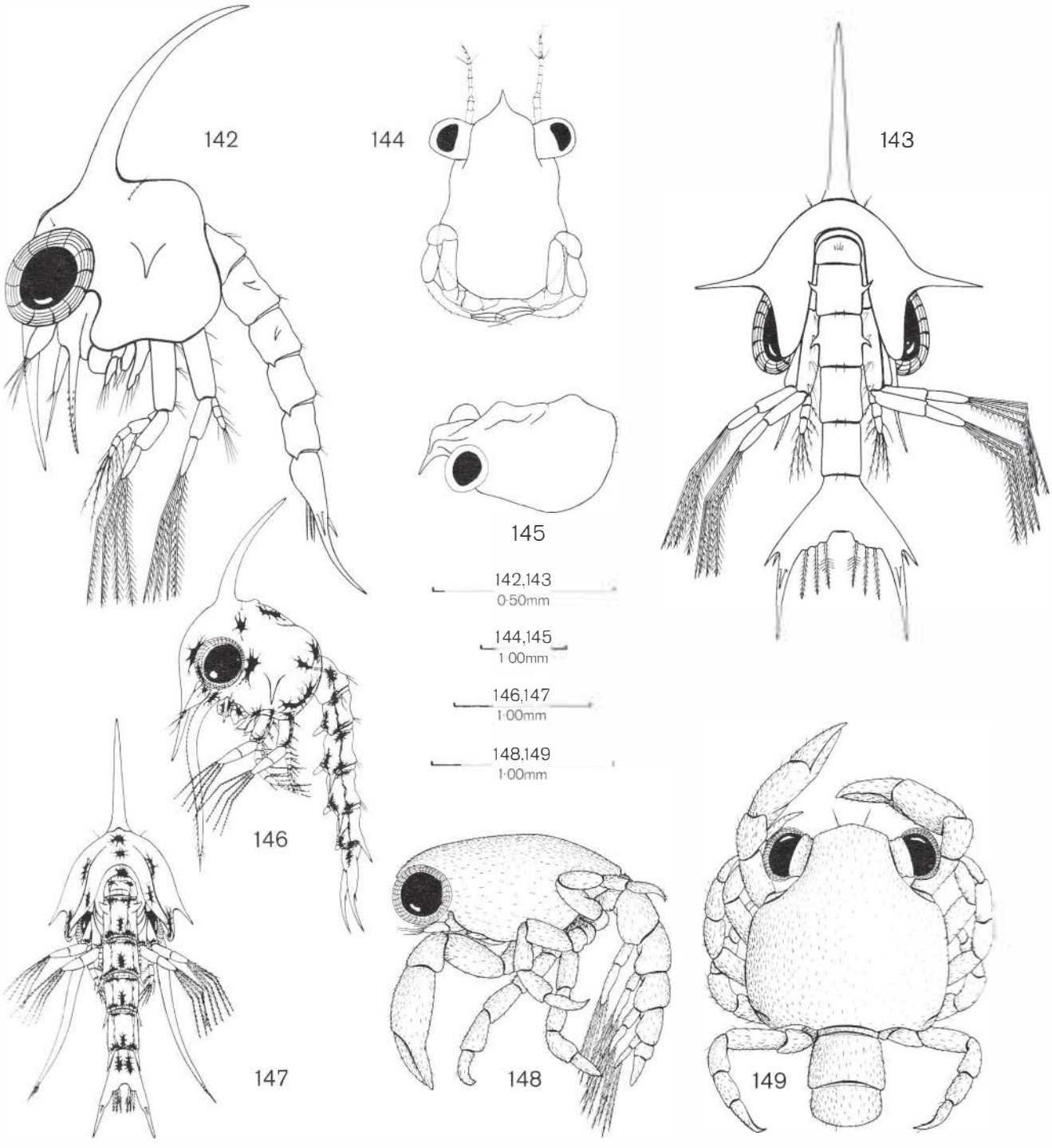
Zoea and megalopa larval characters generally support the separation of the genera *Corystoides, Acanthocyclus*, and *Heterozius*, and probably also the closely related genus *Bellia*, as a family separate from the Atelecyclidae, but without any clear phylogenetic sequence being implied within the four genera. Relationships of the larvae with those of other families are equally obscure, beyond indicating a fairly primitive evolutionary level as noted by Rice (1980a), who considers it necessary to postulate a distinct evolutionary history from an early brachyrhynchan ancestor since the zoea larvae possess a mixture of advanced and primitive characters.

Heterozius A. Milne Edwards, 1867

Heterozius rotundifrons A. Milne Edwards, 1867

SOURCE REFERENCES: Wear (1965) — zoea I from Wellington Harbour plankton. Wear (1968a) — zoea stages I and II, and megalopa reared from laboratory hatched eggs. Jones (1978) — breeding biology at Kaikoura.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal, very common on sheltered and moderately exposed rocky and stony shores. Endemic.



FIGS 142–149: Families PORTUNIDAE & BELLIIDAE. *Macropipus corrugatus* Pennant, 1777. Zoea I: 142, lateral view; 143, posterior view. *Macropipus holsatus* (Fabricius). Megalopa: 144, cephalothorax, dorsal view; 145, cephalothorax, lateral view. After Rice and Ingle (1975). Reproduced by permission of the Trustees of the British Museum (Natural History). *Heterozius rotundifrons* A. Milne Edwards, 1867. Zoea I: 146, lateral view; 147, posterior view. Megalopa: 148, lateral view; 149, dorsal view. Figs 146–149 after Wear (1968a).

BREEDING AND EGGS: Ovigerous females present at Kaikoura in all months of the year except February, with peaks in March-April and September-October; a relatively low level of breeding activity with fewer than 50% of mature females ovigerous in any month except June; most mating activity observed in January and February when few females were ovigerous; incubation period extended and probably occupying about three months over summer and five months over winter (Jones 1978). Eggs, newly laid, orange to bright red, 0.75 mm × 0.81 mm; about to hatch, faded yellow with dark larval chromatophores, 0.93 mm × 1.03 mm; eggs carried by females of equivalent size smaller and more numerous in the North Island than in the South Island.

ZOEA LARVAL STAGES: Two zoea stages; colour in life, olive green.

Zoea I (Figs 146, 147): Zoea with dorsal, rostral and lateral carapace spines. Total length 2.4 mm; rostral spine 0.56 mm long, straight or curved slightly forwards near tip; dorsal carapace spine 0.80 mm long, curved posteriorly; spine to spine length 2.09 mm; lateral carapace spines 0.19 mm long, directed markedly downwards (Fig. 147); carapace with small median dorsal tubercle; length of antenna 2 exopod 0.19 mm; ratio of antenna 2 spiniform process (1.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *2.23, 1.56, and 6.57* respectively; antenna 2 exopod lacks terminal setae, spiniform process very long, robust, with fine hairs along entire anterior margin and on posterior tip; dorsolateral protuberances on abdominal segment 2 only; abdominal segments 3 and 4 with a pair of ventrolateral spines, segment 5 with pair of long dorsolateral spines; short uniramous pleopod buds on abdominal segments 2–5; lateral telson cornua each armed with one small dorsal seta at base.

Zoea II: Total length 3.06 mm; rostral spine 0.69 mm long; dorsal carapace spine 1.00 mm long; spine to spine length 2.59 mm; lateral carapace spines 0.22 mm long; length of antenna 2 exopod 0.19 mm; ratio of antenna 2 spiniform process to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *1.90, 1.31, and 6.89* respectively; abdominal segment 6 now separate but uropod buds absent.

MEGALOPA (Figs 148, 149): Carapace length 1.12 mm; carapace width 1.12 mm; carapace broadly rounded, generally featureless, without ridges, spines or setae and sparingly covered with short fine pubescence; rostrum so poorly defined as to appear absent; antenna 2 flagellum reduced to three very short segments with one long terminal seta; pereiopods lacking spines, but generally hirsute; dactyl of pereiopod 5 without long, terminally hooked setae; abdominal segments 2–5 without lateral spines and with biramous natatory pleopods; uropods absent; telson triangular, without marginal setae.

NOTES: Larval development in *Heterozius rotundifrons* is abbreviated to two zoea stages. As such, the larvae hatch at a relatively late stage in development, and many of the characters normally associated with third to fourth or fifth stage zoeas of brachyrhynchous crabs such as pleopod buds, antenna 2 endopod, mandibular palp, and separation of the abdominal segment 6, occur in stage II. This is also the case in the Majidae (Oxyrhyncha). Zoea larvae of *H. rotundifrons* occur rarely in the plankton of the Wellington area (Wear 1965), and this is probably also true for other areas. Megalopa larvae have not been identified from plankton samples, and their laboratory behaviour and limited swimming ability suggests that they are crawling forms which live on the bottom until migrating shorewards, presumably as juvenile crabs.

FAMILY XANTHIDAE

Worldwide a very large family containing over 130 genera and almost 1000 species (Rice 1980a), but with only four species from New Zealand, two of which have abbreviated development. Major zoea larval characters of the family are: usually four zoea stages; rostral, dorsal and lateral carapace spines present; antenna 2 spiniform process always well-developed and usually equal to or longer than rostral spine; lateral protuberances on abdominal segment 2, usually also on segment 3 and sometimes on segments 4 and 5; mostly with ventrolateral spines on abdominal segments 3–5. Rice (1980a) lists in rather more detail the family larval characters, and has included mouthpart and maxilliped features hitherto unrecognised as significant.

Wear (1970a) divided zoea larvae of the family Xanthidae into two broad groups: those with a vestigial antenna 2 exopod (subfamily Xanthinae), and those with a well-developed antenna 2 exopod (subfamilies Menippinae, Pilumninae and Trapeziinae). Only the subfamilies Menippinae and Pilumninae are represented in New Zealand — by the genera *Ozius*, and *Pilumnus* and *Pilumnopeus* respectively.

With the benefit of larval descriptions published since 1970, Rice (1980a) recognised at least four zoea larval groups, one of which conforms with the "Xanthinae" group of Wear (1970a), but has fragmented the second group into at least three larval categories which do not correspond at all closely with the simple subfamily divisions of Balss (1957). According to Rice (1980a), his own analysis lends some support to the rather more complex adult taxonomic divisions proposed by Guinot (1978), and further, he suggests that the zoea larval evidence indicates that several distinct evolutionary lines are represented within the vast array of genera and species usually grouped together within the single family Xanthidae (*see* Rice 1980a for detailed discussion). For the megalopa larvae, no

characters have emerged which can be safely applied beyond the level of genus.

Pilumnus Leach, 1815

Pilumnus lumpinus Bennett, 1964

SOURCE REFERENCE: Wear (1967) — zoea I and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal in rock crevices and in shallow water among clusters of serpulid worm tubes, sponges and debris. Endemic.

BREEDING AND EGGS: Ovigerous females have been taken in October, December, and February. Eggs, newly laid, light pinkish brown, 1.10 mm × 1.25 mm; about to hatch, light pink to light brown, 1.45 mm × 1.35 mm. Females have been recorded carrying between 53 and 257 eggs.

ZOEA LARVAL STAGES: One zoea stage; colour in life, opaque or light brown; zoea short-lived (15–30 minutes in laboratory conditions) and not planktonic.

Zoea I (Wear 1967: fig. 118): Zoea without carapace spines. Total length 7.40–7.50 mm; carapace lacking hairs or setae; length of antenna 2 exopod 0.29 mm, with one terminal plumose seta; antenna 2 exopod up to 1.30 mm long, segmented, but often compressed within zoeal cuticle to less than this length; antenna 2 spiniform process 0.36 mm long, somewhat flattened, with three short terminal setae; maxilliped 1 and 2 exopods each with four rudimentary setae not used in swimming; pereiopod buds well-developed and segmented; living tissue in all thoracic and abdominal appendages, and in abdomen itself, usually withdrawn from extremities in immediate premoult condition; telson broadly V-shaped with 7+7 posterior setae, all plumose except the fourth pair, which are not significantly larger than the remainder and do not form a pronounced cornu on each side.

MEGALOPA (Figs 150, 151): Carapace length 1.36 mm; carapace width 1.38 mm; carapace regions poorly defined; rostrum short, triangular and depressed; frontal region with five or six stout plumose setae directed forwards and upwards; anterolateral margin of carapace with one strong spine arising from posterolateral corner of orbit; dorsal surface of carapace with sparse covering of fine hairs; pereiopod 1 well-developed and chelate, merus with a row of four small spines laterally, carpus with two spines on lateral face and one blunt spine on inner distal margin, propodus with six or seven small spines along medial and lateral faces; pereiopod 5 without long terminally hooked setae on dactyl; abdominal segments 2–5 each with one pair of biramous pleopods, segment 6 with a pair of uniramous uropods bearing six long, plumose setae and one short seta on exopod; telson almost rectangular and wider than long.

NOTES: Zoea larvae of *Pilumnus lumpinus* hatch at an advanced stage of development consistent with this phase being much abbreviated. Megalopa larvae obtained in the laboratory by moult from the zoea stage lived apart from the parent female, and did not shelter beneath its pleon at any time (Wear 1967). The megalopas are recluse, spend the greater part of the time hiding among coralline algae and in crevices in stones provided in laboratory aquaria, and do not swim unless strongly disturbed. Neither the zoea larvae nor the megalopa are likely to be found in plankton samples.

Pilumnus novaezelandiae Filhol, 1886

SOURCE REFERENCE: Wear (1967) — four embryonic zoea stages; megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; intertidal and shallow water, apparently more common in northern areas; often gregarious. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in August, October, and November. Eggs large and relatively few (usually less than 100 per female); newly laid, light mauve to purple, 1.50 mm × 1.40 mm; increasing to between 1.65 mm × 1.60 mm and 1.75 mm × 1.65 mm before hatching.

ZOEA LARVAL STAGES: No free-living zoea stages.

MEGALOPA (Figs 152, 153): Colour in life, translucent, light brown. Carapace length 1.66 mm; carapace width 1.88 mm; carapace broadly rounded, regions poorly defined; frontal region broad, depressed, and fringed on each side with six or seven stout plumose setae directed forwards and upwards; one pair of short forwardly directed spines lateral to these setae in anterior orbital position; anterolateral margin of carapace with three postorbital spines; posterior margin of carapace fringed with fine hairs; dorsal surface of carapace with paired groups of two to four stout plumose setae in each of protogastric, hepatic, branchial and cardiac regions; otherwise with sparse covering of fine hairs; anterolateral margin of eyestalk with two short plumose setae; pereiopod 1 well-developed, ischium, merus, and propodus each with two spines, fingers each with prominent teeth; pereiopod 5 without long terminally hooked setae on dactyl; abdominal segments 2–5 with biramous pleopods, segment 6 with uniramous uropods with two plumose setae on inner margin of protopod and eight, also plumose but longer, setae on exopod; telson rounded posteriorly, with a small median notch and with a variable number (usually four or six) of tiny posterior setae.

NOTES: Laboratory studies have shown that megalopa larvae of *Pilumnus novaezelandiae* spend the greater part of their lives enmeshed in the "brood pouch" formed by the large pleopods and lateral hairs of the female abdomen. They are able to swim, but such

migrations are of short duration and the young always return to the parent, either to take up a temporary position on the female's carapace or pereiopods, or to immediately crawl back beneath the abdomen (Wear 1967). Megalopa larvae thus remain in the vicinity of the parent, and since the juvenile crab stages lack natatory pleopods and cannot swim, this behaviour helps explain the gregariousness in the species noted by Bennett (1964).

Ozius Desmarest, 1825

Ozius truncatus H. Milne Edwards, 1834

SOURCE REFERENCE: Wear (1968a) — zoea stages I–IV and megalopa reared from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island south to Cook Strait; not recorded from South Island, Stewart Island, or the Chatham Islands; intertidal under rocks by day. Also Kermadec Islands and Australia.

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand in October and January. Eggs, newly laid, dark maroon, 0.50 mm × 0.45 mm; about to hatch, pale maroon, 0.70 mm × 0.65 mm.

ZOEA LARVAL STAGES: Four zoea stages; colour in life, greenish yellow. Larval chromatophores are fully described by Wear (1968a).

Zoea I (Figs 154, 155): Zoea with dorsal, rostral and lateral carapace spines. Total length 2.35–2.40 mm; rostral spine 0.50 mm long, straight; dorsal carapace spine 0.94 mm long, curved posteriorly; spine to spine length 1.83 mm; lateral carapace spines 0.40 mm long, at about 90° to carapace (Fig. 154); carapace with a frontal tubercle and prominent median dorsal tubercle; posteroventral border of carapace fringed with fine hairs; length of antenna 2 exopod 0.20 mm; ratio of antenna 2 spiniform process (0.30 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.66, 0.35, and 1.65* respectively; abdominal segment 1 with posterior dorsal spine, segments 2 and 3 with a pair of lateral protuberances, segments 3–5 with short ventrolateral spines; lateral telson cornua armed with a large, curved, dorsal spine and a small axillary seta located between dorsal spine and cornua itself.

Zoea II: Total length 3.0 mm; rostral spine 0.87 mm long; dorsal carapace spine 1.45 mm long; spine to spine length 3.17 mm; lateral carapace spines 0.45 mm long; length of antenna 2 exopod 0.25 mm; ratio of antenna 2 spiniform process (0.44 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.46, 0.27, and 1.32* respectively.

Zoea III: Total length 4.0 mm; rostral spine 1.10 mm long; dorsal carapace spine 2.00 mm long; spine to spine length 3.80 mm; lateral carapace spines 0.48 mm long; length of antenna 2 exopod 0.30 mm; ratio of antenna 2 spiniform process (0.50 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.45, 0.25, and 1.17* respectively; ventrolateral borders of abdominal segment 2 and dorsal borders of ventrolateral spines on abdominal segments 3–5 strongly toothed; pleopod buds on abdominal segments 2–5, segment 6 with uropod buds; telson with 5+5 posterior setae.

Zoea IV: Total length 4.75 mm; rostral spine 1.25 mm long; dorsal carapace spine 2.40 mm long, now only slightly curved; spine to spine length 4.81 mm; lateral carapace spines 0.50 mm long; length of antenna 2 exopod 0.36 mm; ratio of antenna 2 spiniform process (0.50 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.40, 0.21, and 1.4* respectively; axillary dorsal seta on telson cornua very small, often absent.

MEGALOPA (Figs 156, 157): Carapace length 2.00 mm; carapace width 1.95 mm; carapace sparingly pubescent and strongly ridged; lateral and posterior carapace margins fringed with fine hairs; frontal region longer than broad, with rostrum rounded but not depressed; posterior region with a pair of prominent tubercles; pereiopod 1 with a strong ischial spine; small ventral spine on propodus of each of pereiopods 2–5; pereiopod 5 dactyl bearing three long terminally hooked setae; abdominal segments 2–5 with pleura extended as rounded lobes, and with pleopods; uropods with reduced endopod present and exopod with 12 plumose setae; telson with posterior margin broadly rounded, almost straight, and with two or four very small posterior setae.

NOTES: In the plankton of the Wellington area, zoea larvae of *Ozius truncatus* are rare and the megalopa has not been seen to date. It is anticipated that these larvae may be more common in northern waters.

Pilumnopeus A. Milne Edwards, 1863

Pilumnopeus serratifrons (Kinahan, 1856)

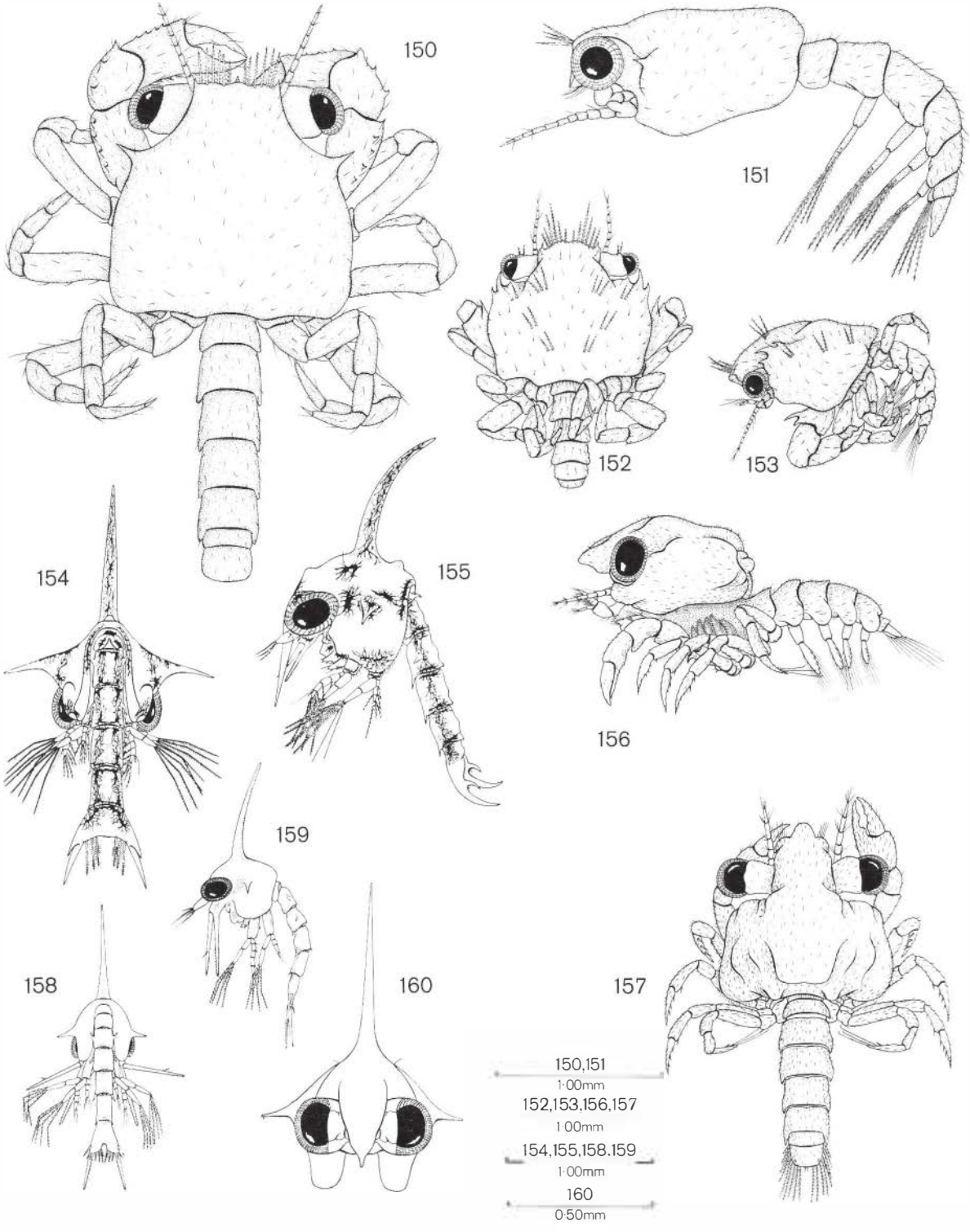
SOURCE REFERENCE: Wear (1968a) — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: Northern part of North Island, N.Z.; not recorded south of the Auckland area, or at the Chatham Islands; intertidal, occuring mainly on mudflats in harbours and estuaries. Also southern Australia.

BREEDING AND EGGS: Ovigerous females have been collected in November, December, January, and February. Eggs, newly laid, dark brownish green, about 0.40 mm diameter; about to hatch, light olive green, 0.45 mm × 0.40 mm.

ZOEA LARVAL STAGES: Probably four zoea stages; colour in life, almost transparent with chromatophores very small and lightly coloured (Wear 1968a).

Zoea I (Figs 158–160): Zoea with dorsal and lateral carapace spines, the rostral spine reduced to a very short process (Fig. 160) which cannot be seen in lateral view. Total length 1.75 mm; dorsal carapace spine 0.63 mm long, slightly curved posteriorly; lateral cara-



FIGS 150–160: Family XANTHIDAE. *Pilumnus lumpinus* Bennett, 1964. Megalopa: 150, dorsal view; 151, lateral view, pereiopods removed. After Wear (1967). *Pilumnus novaezelandiae* Filhol, 1886. Megalopa: 152, dorsal view; 153, lateral view. After Wear (1967). *Ozius truncatus* H. Milne Edwards, 1834. Zoea I: 154, posterior view; 155, lateral view. Megalopa: 156, lateral view; 157, dorsal view. Figs 154–157 after Wear (1968a). *Pilumnopeus serratifrons* (Kinahan, 1856). Zoea I: 158, posterior view; 159, lateral view; 160, cephalothorax, frontal view. After Wear (1968a).

pace spines 0.10 mm long, at 90° to carapace (Fig. 160); carapace smooth, without tubercles; length of antenna 2 exopod 0.44 mm; ratio of antenna 2 spiniform process (0.47 mm long) to dorsal carapace spine, and to antenna 2 exopod, *0.81 and 1.16* respectively; antenna 2 exopod with inner distal hairs and one strong lateral spine in its distal third; abdominal segments 2 and 3 with a pair of lateral protuberances, segments 3–5 each with a pair of short, unarmed, ventrolateral spines; lateral margins of telson and cornua aligned in a continuous straight line with inner margins of cornua bearing numerous stout setae; telson with a large seta located laterally, a second rather smaller seta posterior to the first, and a third seta lying dorsally, near the base of the cornu on each side.

MEGALOPA: No knowledge.

NOTES: Zoea larvae of *Pilumnopeus serratifrons* are likely to be common in the summer plankton in northern inshore waters and are readily identified by the reduced rostral process together with the presence of lateral carapace spines.

FAMILY GONEPLACIDAE

New Zealand zoea larvae of the family Goneplacidae are characterised as follows: four zoea larval stages with long and slender dorsal and rostral carapace spines, lateral spines present or absent; antenna 2 exopod, including its long terminal process, about as long as the spiniform process in all stages; abdomen with dorsolateral protuberances on segments 2–4 or 2–5 and with ventrolateral spines on segments 3–5 in later stages; telson with long and slender cornua bearing two or three accessory basal spines or setae. Rice (1980a) lists zoea larval characters of the family on a world scale and provides additional details concerning mouthparts and thoracic appendages. New Zealand larvae generally conform with this characterisation, with only *Ommatocarcinus huttoni* differing significantly in lacking lateral carapace spines. Megalopa larvae have the following characters: frontal region of carapace squarish with its anterolateral corners each produced into a sharp antorbital spine; rostrum a small blunt protuberance; carapace with a pair of protogastric spines; pereiopods 1–4, and sometimes also pereiopod 5, with coxal and ischial spines; pereiopod 5 usually with long terminally hooked setae on dactyl.

The systematic position of the family has always been somewhat controversial (*see* Rice 1980a), and Rice has attempted to assess the phylogenetic relationships of zoea larvae based on only two of the approximately 54 genera comprising the family. As would be anticipated, these, and the larvae of *Ommatocarcinus* described here, throw little light on the problem beyond giving the impression that they are generally primitive, with possible affinities with the Xanthidae, and rather more tenuous links with more advanced brachyrhynchous families such as the Grapsidae, Gecarcinidae, and Ocypodidae, based on the form of the antenna 2 exopod.

Carcinoplax H. Milne Edwards, 1852

Carcinoplax victoriensis Rathbun, 1923

SOURCE REFERENCE: Kurata (1968a) — zoea stages I–IV and megalopa of *Carcinoplax longimanus* (de Haan) reared in the laboratory, as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; offshore continental shelf and slope, mainly over soft bottoms with shell debris. Also southern Australia.

BREEDING AND EGGS: No knowledge of breeding in New Zealand waters.

ZOEA LARVAL STAGES: No knowledge. Zoea stages I (Figs 161, 162) and II–IV of *C. longimanus* are described and illustrated as an example of the genus.

Zoea I with dorsal, rostral, and lateral carapace spines; dorsal and rostral spines long and slender, the rostral spine smooth; ventrolateral carapace margins denticulate; antenna 2 exopod (including its long terminal spine) 0.7 times length of spiniform process, which is almost as long as the rostral spine; abdominal segments 3–5 with ventrolateral spines; lateral protuberances in the form of relatively sharp spines on abdominal segments 2–5 (in all zoea larval stages); abdominal segments 2–5 with minute denticles along posterodorsal margins; telson with small spine lateral to the cornu on each side, the cornua long and slender and each bearing one small spine dorsally near its base.

Zoeas II–IV in *C. longimanus* have ventrolateral spines on abdominal segments 3–5 which become exceptionally long and slender, those of segment 5 extending well beyond the level of segment 6.

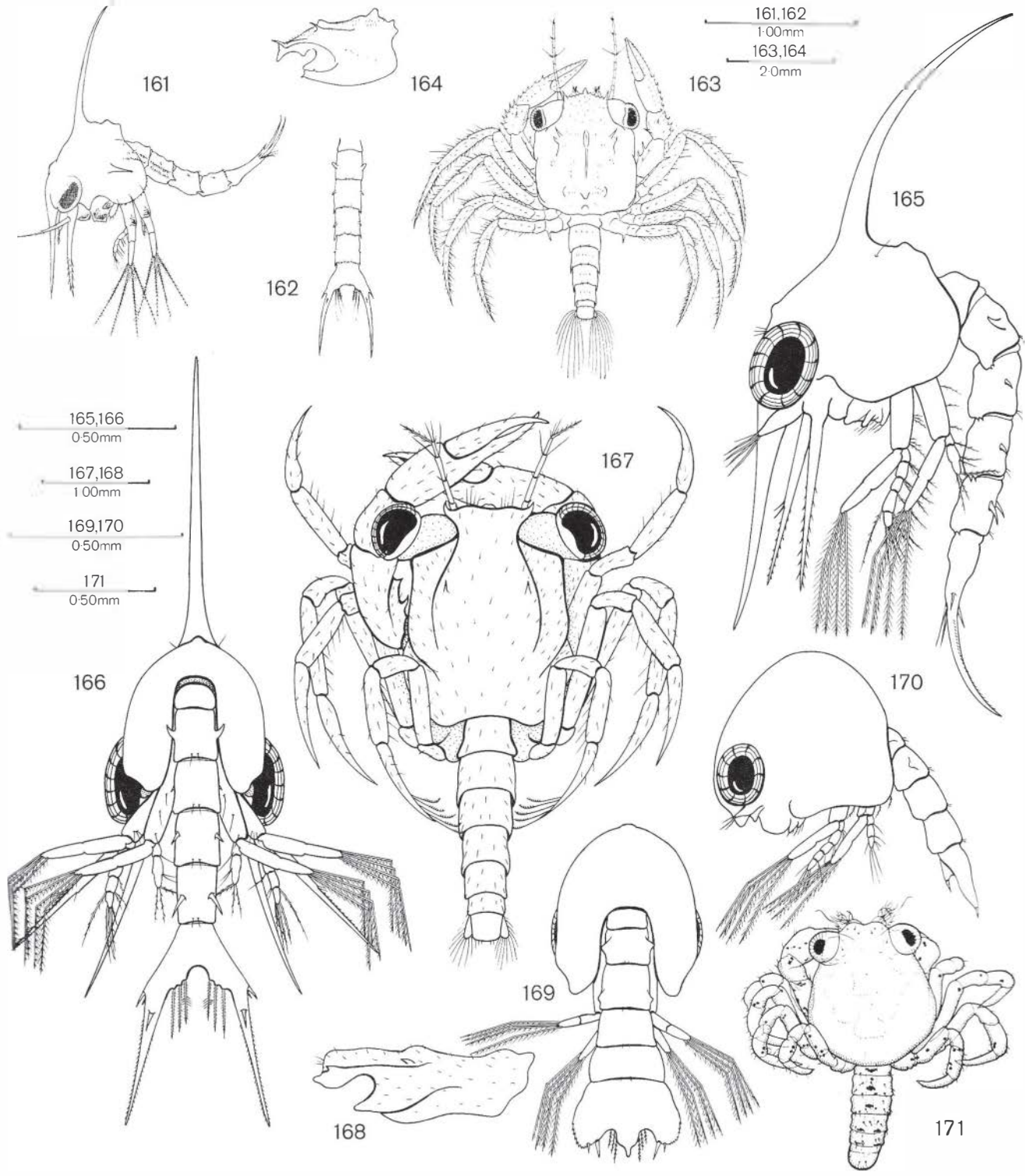
MEGALOPA: No knowledge. The megalopa of *C. longimanus* (Figs 163, 164) is described and illustrated as an example of the genus.

Frontal region of carapace broad with a small, depressed central rostral process and with anterolateral corners each produced into a sharp spine; carapace with well-defined anterior and posterior tubercles and a pair of protogastric spines; pereiopod 1 generally spinous; pereiopods 2–5 with hook-like spines on coxa, ischium and merus; pereiopod 5 lacking long terminally hooked setae on dactyl; abdominal segments 3–5 with short lateral spines, segments 2–5 with pleopods, segment 6 with uropods; uropods with eight or nine setae; telson rounded with posterior setae.

Ommatocarcinus White, 1852

Ommatocarcinus huttoni Filhol, 1886

SOURCE REFERENCES: This study — zoea stages I–IV and megalopa from plankton; megalopa reared in the laboratory from planktonic stage IV zoea larvae; identity of zoea larvae confirmed by rearing identifiable



FIGS 161–171: Families GONEPLACIDAE & PINNOTHERIDAE. *Carcinoplax longimanus* (de Haan). Zoea I: 161, lateral view; 162, abdomen and telson, dorsal view. Megalopa: 163, dorsal view; 164, carapace, lateral view. Figs 161–164 after Kurata (1968a). *Ommatocarcinus huttoni* Filhol, 1886. Zoea I: 165, lateral view; 166, posterior view. Megalopa: 167, dorsal view; 168, carapace, lateral view. *Pinnotheres novaezelandiae* Filhol, 1886. Zoea I: 169, posterior view, without appendages; 170, lateral view. *Pinnotheres ostreum* Say. Megalopa: 171, dorsal view. After Sandoz and Hopkins (1947).

juvenile crab stages from megalopa. Thomson and Anderton (1921) — zoea I hatched in the laboratory (description and illustration incomplete).

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, and Stewart Island, N.Z.; usually offshore continental shelf and slope, mainly over soft bottoms. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand during March (Bennett 1964). No knowledge of egg colour or dimensions.

ZOEA LARVAL STAGES: Four zoea stages; colour in life, pink or translucent light red.

Zoea I (Figs 165, 166): Zoea with dorsal and rostral carapace spines, lateral carapace spines absent. Total length 2.1 mm; rostral spine 0.70 mm long, straight; dorsal carapace spine 0.96 mm long, with strong posterior curve; spine to spine length 2.17 mm; length of antenna 2 exopod 0.28 mm or 0.56 mm*; ratio of antenna 2 spiniform process (0.56 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.8, 0.58, and 2.00 or 1.00* respectively; lateral protuberances on abdominal segments 2–5, those on segment 2 curved anteriorly, those on segments 3–5 as sharp posteriorly directed spines becoming progressively larger and more dorsolateral in position from third to fifth segments; ventrolateral angles of abdominal segments 3–5 without spines but with two or three small teeth; telson cornua long and slender, each cornu bearing two setae laterally and one seta dorsally near its base, the more posterior lateral seta tiny and difficult to see.

Zoea II: Total length 3.0 mm; rostral spine 1.19 mm long, curved slightly anteriorly in some larvae; dorsal carapace spine 1.40 mm long, now curved only gently; spine to spine length 3.40 mm; length of antenna 2 exopod 0.31 mm or 0.63 mm; ratio of antenna 2 spiniform process (0.63 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.53, 0.45, and 2.00 or 1.00* respectively; maxilliped 1 exopod with six natatory setae, maxilliped 2 exopod with six setae plus one smaller seta; abdominal segments 3–5 each with a pair of ventrolateral spines rather than several teeth; telson cornu with one lateral seta and one dorsal seta near its base; telson with 3+3 inner posterior setae as in zoea I.

Zoea III: Total length 3.7 mm; rostral spine 1.88 mm long; dorsal carapace spine 2.00 mm long, bearing several irregularly spaced fine setae projecting horizontally; spine to spine length 5.00 mm; length of antenna 2 exopod 0.70 mm or 0.93 mm, of endopod bud 0.21 mm; ratio of antenna 2 spiniform process (0.95 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.51, 0.48, and 1.34 or 1.02* respectively; maxilliped 1 exopod with eight natatory setae, maxilliped 2 exopod with nine setae; telson with 5+5 inner posterior setae.

Zoea IV: Total length 5.6 mm; rostral spine 2.44 mm long; dorsal carapace spine 2.60 mm long, bearing many setae projecting horizontally; spine to spine length 6.60 mm; length of antenna 2 exopod 0.98 mm or 1.19 mm, of endopod 0.56 mm; ratio of antenna 2 spiniform process (1.26 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.52, 0.48, and 1.29 or 1.06* respectively; maxilliped 1 exopod with 10 natatory setae, maxilliped 2 exopod with 12 setae; dorsolateral spine-like protuberance on abdominal segment 3 very tiny or absent in some larvae; telson with 6+6 inner posterior setae.

MEGALOPA (Figs 167, 168): Carapace length 2.00 mm; carapace width 1.50 mm; dorsal surface of carapace sparsely setose and with one protogastric spine on each side; frontal region broad, waisted, and expanded at anterolateral corners into a strong antorbital process curved forwards; rostrum reduced to an inconspicuous knob barely visible in dorsal view; pereiopods generally sparsely setose; pereiopods 1–5 each provided with a coxal and an ischial spine, the ischial spine on pereiopod 1 very large; pereiopod 1 also with two spines on medial margin of merus; pereiopod 5 with five long terminally hooked setae on dactyl; abdominal segments sparsely setose and without lateral spines, segments 2–5 with pleopods, segment 6 with uniramous uropods; exopods of uropods with 11 natatory setae; telson almost square, with a few very small posterior setae.

NOTES: In the Wellington Harbour plankton the larvae of *Ommatocarcinus huttoni* are common between the months of August and January inclusive, and a complete larval series was identified from this source. It is probable that the larvae are also common in samples from elsewhere, although none have been identified during this study.

FAMILY PINNOTHERIDAE

New Zealand pinnotherid zoea larvae are very small; the carapace is globose and smooth, lacking all spines other than an ill-defined rostral knob; the telson is trilobed and there are only five abdominal segments in the first three zoea stages, but if a fourth occurs, abdominal segment 6 may be separate. The megalopa has a broadly rounded carapace lacking spines or protuberances, and pereiopod 5 lacks long terminally hooked setae on the dactyl.

Zoea larvae described worldwide fall superficially into two broad groups: those with carapace spines, and

*The antenna 2 exopod consists of a long, robust spine bearing two small setae at the point of a slight constriction midway along its length. This is probably the level to which truly comparative measurements should be taken. However, since the major spinous seta is contiguous with the exopod itself from this point and is not jointed with it, i.e., the entire exopod appears as one long spine, both the shorter and the longer measurements are given here to avoid confusion.

those without (with which New Zealand larvae conform). Rice (1980a) has analysed the zoea larval characters of all species known, and discusses their affinities and broad relationships at length. He concludes that although the family shows considerable variability in carapace armature and in general body form, the ventral origin of the lateral carapace spines (when present) and detailed setation of the appendages reveals the pinnotherids to be a well-defined and homogeneous group. All have the unique combination of antenna 2 exopod vestigial or absent, unarmed basal segment of maxilla 1, maxilla 2 endopod with only three setae, and a two-segmented endopod on maxilliped 2, the proximal segment being unarmed (Rice 1980a). This combination of clearly advanced characters is seen elsewhere only in the Ocypodinae (Ocypodidae), Leucosiidae and Hymenosomatidae.

Rice (1980a) argues that the affinity of pinnotherid larvae with the leucosiids may well be the result of otherwise independently evolved larvae taking, to extreme lengths, the same evolutionary tendencies which seem to exist in all brachyuran phylogenetic lines. However, the scheme of classification proposed by Guinot (1978) contends that the adults are not closely related, with the leucosiids considered as highly specialised crabs occupying an isolated position in the Brachyura. Similarly, the strong resemblance between zoea larvae of the Pinnotheridae and Hymenosomatidae (Wear 1967, 1968b; Lucas 1971) is re-examined by Rice (1980a), who suggests on the basis of appendage setation, not fully considered by earlier authors, that the Hymenosomatidae are the more primitive and have evolved directly from one of the cyclometopous families of the Brachyrhyncha, and are not therefore on the line of ascent to the Pinnotheridae. Rice thus proposes that larval evidence points to origin of the Pinnotheridae from ancestral stock within, or close to, the Ocypodinae (Ocypodidae).

Pinnotheres Latreille, 1802

Pinnotheres novaezelandiae Filhol, 1886

SOURCE REFERENCES: This study — zoea I from laboratory hatched eggs, zoea stages II and III from plankton. Bennett (1964), Wear (1965) — zoea I hatched and described briefly. Sandoz and Hopkins (1947) — megalopa of *Pinnotheres ostreum* Say as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island, and Chatham Islands, N.Z.; shallow water and continental shelf; commensal in bivalve molluscs. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in January, February, March, April, August, October and November. The species probably breeds throughout the year. Eggs, newly laid, red-brown, 0.42 mm × 0.40 mm; about to hatch, brown-orange to yellow, 0.48 mm × 0.42 mm and up to 0.50 mm diameter; 1,600 to 5,000 eggs per parent female (Bennett 1964).

ZOEA LARVAL STAGES: Three, and possibly four, zoea stages; colour in life, blackish yellow. Larvae vary considerably in size, and mean measurements given in the text are subject to a range of ± 20%.

Zoea I (Figs 169, 170): Zoea with a very short rostral knob only, dorsal and lateral carapace spines absent. Carapace length 0.51 mm; carapace height 0.57 mm; carapace globose and smooth; rostrum a knob-like process, 0.06 mm long; antenna 2 reduced to a small unarmed stump; abdominal segments 2 and 3 with triangular dorsolateral protuberances; each abdominal segment broader than the one preceding; telson very broad and spatulate, trilobed with central lobe and median prominence longer than lateral lobes, posterolateral margins of lateral lobes serrate, posterior margin of each lateral lobe with two small spine-like setae, three short plumose setae located between each lateral lobe and the central lobe.

Zoea II: Carapace length 0.68 mm; carapace height 0.64 mm; abdomen of five segments only, the second to fifth with indistinct swellings representing pleopod primordia.

Zoea III: Carapace length 0.68 mm; carapace height 0.73 mm; pereiopods very well-developed and protruding beyond ventral carapace margins; abdomen remains with five segments; pleopod buds well-developed.

MEGALOPA: No knowledge. The megalopa of *Pinnotheres ostreum* (Fig. 171) is described and illustrated as an example of the genus.

Carapace broadly rounded, lacking spines or protuberances; pereiopod 5 without long terminally hooked setae on dactyl; abdominal segments unarmed, segments 2–5 with natatory pleopods, segment 6 not clearly divided from telson and apparently without uropods.

NOTES: Zoea larvae of *Pinnotheres novaezelandiae* hatched in the laboratory swim actively near the surface for their first few minutes of life, but very soon thereafter curl their abdomen beneath the cephalothorax and sink quickly to the bottom where they remain, swimming only spasmodically. This behaviour lends weight to our observation that larvae are not common in surface plankton samples but are often abundant at or near the bottom. It is also possible that our zoea stage III may in fact be the final stage, as suggested by the presence of very strongly developed, partly segmented pereiopods. Megalopa larvae have, however, not been obtained, and this stage may well be absent as is the case in some species described from beyond the New Zealand region and in the family Hymenosomatidae.

FAMILY GRAPSIDAE

Zoea larvae of the New Zealand representatives of the family Grapsidae fall into three groups following the grouping of adults into the subfamilies Grapsinae, Varuninae and Sesarminae together, and Plagusiinae. The characters of these groups, based on stage I zoea larvae from a survey of world literature, are summarised from Wear (1970b) as follows:

Subfamily Grapsinae: Carapace with short and stout rostral and dorsal spines about equal in length; lateral carapace spines absent; antenna 2 spiniform process robust, exopod a rudimentary seta, or less than one-third the length of spiniform process; abdominal segments 3–5 usually with lobed posterolateral ridges; telson more or less rectangular with short, straight cornua. Represented in New Zealand by *Leptograpsus variegatus* (Fabricius), *Planes cyaneus* Dana, and *P. marinus* Rathbun.

Subfamilies Varuninae and Sesarminae: Carapace with short rostrum and usually a relatively slender and curved dorsal spine; lateral carapace spines present, declined strongly downwards, directed posteriorly and without hairs, denticles or papillae; antenna 2 exopod about half the length of spiniform process; abdominal segments 3–5 usually lack lobed posterolateral ridges; telson widely forked with cornua usually curved slightly inwards in dorsal view. Represented in New Zealand by *Hemigrapsus crenulatus* (H. Milne Edwards) and *H. edwardsi* (Hilgendorf) (Varuninae); *Cyclograpsus lavauxi* (H. Milne Edwards), *C. insularum* Campbell & Griffin, and *Helice crassa* (Dana) (Sesarminae). Zoea larvae of the genera *Gaetice* (Varuninae) and *Metasesarma* and *Sesarma* (Sesarminae) lack lateral carapace spines, but otherwise conform with the above diagnosis (Wear 1970b). These three genera are not found in New Zealand.

Subfamily Plagusiinae: Carapace with long rostrum and slender, straight dorsal spine about equal in length; lateral carapace spines present, set at about 90° to carapace or only slightly depressed (in late zoea stages of *Plagusia chabrus* these become strongly declined and directed posteriorly); lateral spines armed dorsally with prominent hair-like setae and papillae; antenna 2 exopod about one-quarter the length of spiniform process; telson widely forked but with straight cornua. Represented in New Zealand by *Plagusia chabrus* (Linnaeus).

The above division into three groups, plus a further group comprising genera not represented in New Zealand (Wear 1970b), was based on consideration of the 34 species in 17 genera described up to that time. Since 1970, the larvae of a further 17 species representing at least six additional genera have been described, so that larvae from about one-sixth of the approximately 300 known species and more than 50% of the genera are now recorded in the literature.

Two of the primary groups, viz., those involving the subfamilies Grapsinae and Plagusiinae respectively, have been substantiated by recent work, except that in *Plagusia chabrus* described here, the antenna 2 exopod exceeds one-quarter the length of the spiniform process beyond zoea V and progressively increases to about four-fifths its length by zoea XII. This could perhaps be considered as abberant, due to the greatly extended larval development in this species. However, the two remaining groups, each comprising a cross-section of genera drawn from the subfamilies Varuninae and Sesarminae, have now lost their individual identity, but are together united and distinguished from the Grapsinae and Plagusiinae by having a well-developed antenna 2 exopod which is at least one-half as long as the spiniform process, and, as observed by Rice (1980a), at least ten (more than eight) setae on the basis of maxilliped 1.

Rice (1980a) discussed relationships among grapsid zoea larvae and pointed to the Grapsinae as being the most advanced, but was unable to arrange the remaining grapsids in any convincing phylogenetic order. He suggests that each group (the Grapsinae, Plagusiinae, and the remaining heterogeneous but larger assemblage respectively) evolved independently from a more primitive grapsid stock of which there is no larval evidence.

Leptograpsus H. Milne Edwards, 1853

Leptograpsus variegatus (Fabricius, 1793)

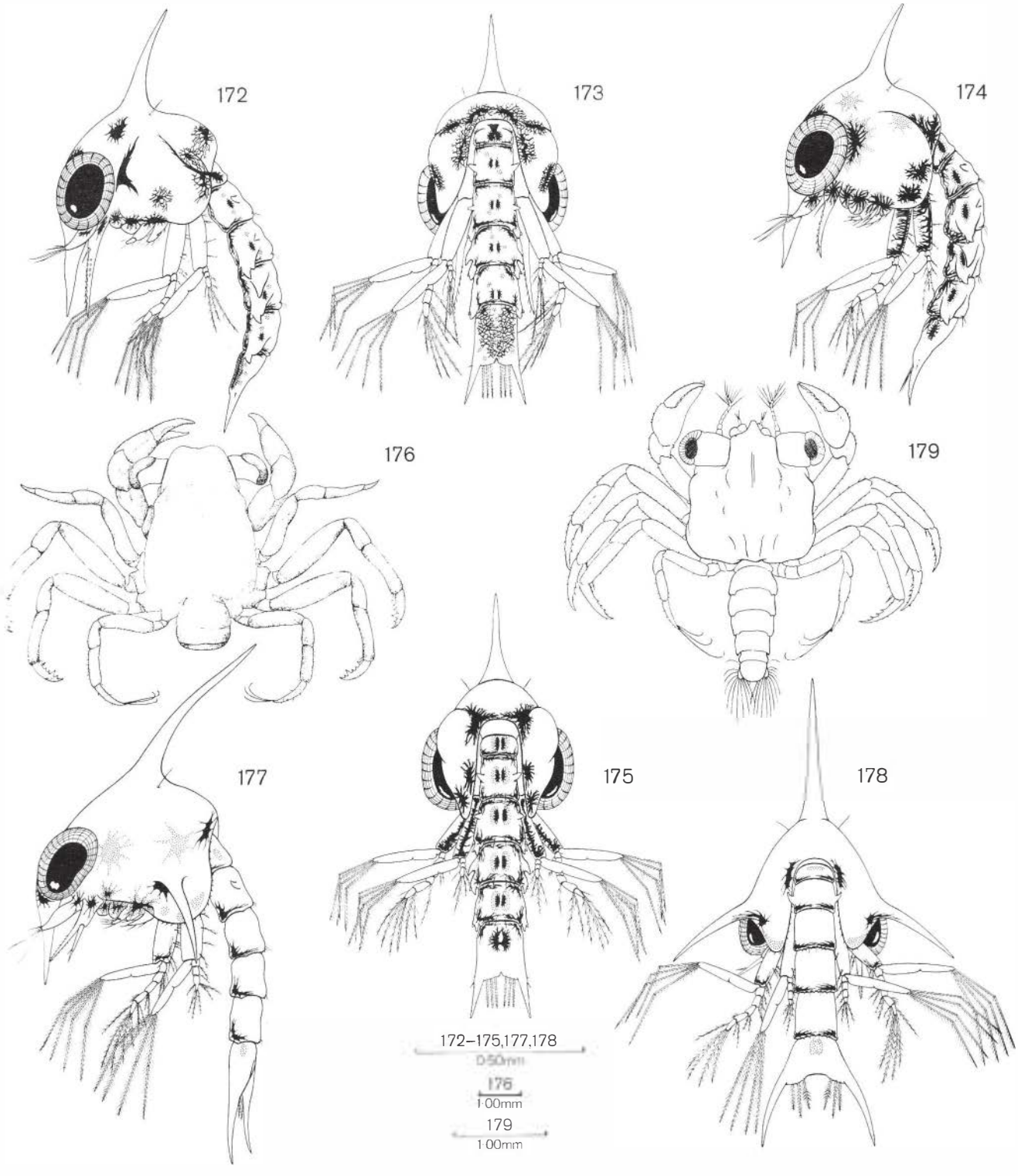
SOURCE REFERENCE: Wear (1970b) — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, but more common in the north of N.Z.; absent from Stewart Island and the Chatham Islands; intertidal under boulders, in rock crevices, in tidal pools, and on wharf piles in the north. Southern warm temperate Indian and Pacific Oceans from Western Australia through New Zealand to western South America (Griffin 1973).

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand in November, December, January, and March. Eggs, newly laid, dark brown to almost black, 0.37 mm × 0.35 mm; about to hatch, yolk light brown, 0.44 mm × 0.42 mm; egg mass irridescent green due to larval eyes and strongly developed black to greenish yellow chromatophores (Wear 1970b).

ZOEA LARVAL STAGES: Probably five zoea stages; colour in life, black or very dark green.

Zoea I (Figs 172, 173): Zoea with dorsal and rostral carapace spines, lateral carapace spines absent. Total length 1.3 mm; rostral spine 0.26 mm long, straight but slightly expanded midway; dorsal carapace spine 0.30 mm long, slightly curved posteriorly; spine to spine length 0.96 mm; carapace with posterolateral regions distinctly swollen, posterior margins fringed with short, fine hairs; antenna 2 exopod a vestigial seta, 0.05 mm long; ratio of antenna 2 spiniform pro-



FIGS 172–179: Family GRAPSIDAE. *Leptograpsus variegatus* (Fabricius, 1793). Zoea I: 172, lateral view; 173, posterior view. After Wear (1970b). *Planes marinus* Rathbun, 1915. Zoea I: 174, lateral view; 175, posterior view. After Wear (1970b). *Planes cyaneus* Dana, 1852. Megalopa: 176, dorsal view. After Muraoka (1973). *Hemigrapsus edwardsi* (Hilgendorf, 1882). Zoea I: 177, lateral view; 178, posterior view. After Wear (1970b). *Hemigrapsus sanguineus* (de Haan). Megalopa: 179, dorsal view. After Kurata (1968b).

cess (0.31 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.96, 0.83, and 6.20* respectively; antenna 2 spiniform process with four anterior rows of small basal spines decreasing to two rows of longer spines towards its tip, 11 or 12 spines in longitudinal series; abdominal segments 2 and 3 with a pair of dorsolateral protuberances appearing as triangular projections rather than curved or straight spines; abdominal segment 4 with a broad, mid-lateral projection curved posteriorly; posterolateral angles of abdominal segments 3–5 each expanded as a bilobed ridge bearing one short ventral spine; telson more or less rectangular, longer than wide; telson cornua straight in both dorsal and lateral views, with two dorsolateral rows of short hairs and with one tiny lateral seta only.

MEGALOPA: No knowledge.

NOTES: Later larval stages of *Leptograpsus variegatus* occur in the plankton, but specimens collected were unfortunately destroyed in a fire at the Victoria University Marine Laboratory during November 1979.

Planes Leach in Bowdich, 1825

Planes marinus Rathbun, 1915

SOURCE REFERENCE: Wear (1970b) — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: Indo-Pacific and South Atlantic oceanic drifting species associated with flotsam and often found among goose-necked barnacles (*Lepas* spp.); N.Z. records based on occasional strandings on the coasts of the North Island as far south as Cook Strait.

BREEDING AND EGGS: Ovigerous females have been recorded in New Zealand from February to May, but may breed in all months of the year. Eggs, newly laid, dark brownish purple, 0.30 mm × 0.29 mm; about to hatch, light brown, 0.42 mm × 0.39 mm.

ZOEA LARVAL STAGES: Possibly five zoea stages; colour in life, black or dark grey. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 174, 175): Zoea with dorsal and rostral carapace spines, lateral carapace spines absent. Generally very similar to larvae of *Leptograpsus variegatus*. Total length 1.25 mm; rostral spine 0.24 mm long, straight but slightly expanded midway; dorsal carapace spine 0.24 mm long, slightly curved posteriorly; spine to spine length 0.87 mm; carapace with posterolateral regions distinctly swollen, posterior margins fringed with short, fine hairs; antenna 2 exopod a vestigial seta 0.04 mm long; ratio of antenna 2 spiniform process (0.22 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.92, 0.92, and 5.50* respectively; antenna 2 spiniform process with four anterior rows of small basal spines decreasing to two rows of longer spines towards tip, spines number seven in longitudinal series; abdominal segments 2 and 3 with a pair of triangular dorsolateral protuberances; abdominal segment 4 with a broad, mid-lateral projection curved posteriorly; posterolateral angles of segments 3–5 each expanded as a bilobed ridge bearing one short ventral spine; telson cornua straight in dorsal view but curve upwards slightly, each cornu with two dorsolateral rows of short hairs and two tiny lateral setae.

MEGALOPA: No knowledge. The megalopa of this species is likely to compare closely with that of *P. cyaneus* (*see* p. 68 and Fig. 176).

NOTES: We have no knowledge of the later larval stages of *Planes marinus*, but it is likely that they occur in both inshore and offshore waters.

Planes cyaneus Dana, 1852

SOURCE REFERENCE: Muraoka (1973) — megalopa from *Sargassum* weed and floating timber in Sagami Bay, Japan.

ADULT DISTRIBUTION AND HABITAT: Indo-Pacific and South Atlantic oceanic drifting species; N.Z. records based on occasional strandings on northern coasts of the North Island.

BREEDING AND EGGS: Ovigerous females have been collected in January and February.

ZOEA LARVAL STAGES: No knowledge. Larvae are likely to be similar to those of *P. marinus* (*see* pp. 68 and Figs 174, 175).

MEGALOPA (Fig. 176): Carapace length 3.64 mm; carapace width 2.64 mm posteriorly, tapering to about 1.0 mm in the frontal region; surface of carapace smooth with no grooves or prominent tubercles; rostrum depressed, 0.88 mm long; pereiopods smooth and hairless; dactyls of pereiopods 2–4 armed with strong, tooth-like spines; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segments smooth and without armature, segments 2–5 with pleopods, segment 6 with uniramous uropods bearing three plumose setae on the protopod and between 20 and 23 setae on the exopod.

NOTES: We have no knowledge of the zoea larval stages of *Planus cyaneus*, but it is likely that they occur in oceanic waters. The strong tooth-like spines on the dactyl of pereiopods 2–4 of the megalopa may well be an adaptation for clinging to flotsam.

Hemigrapsus Dana, 1851

Hemigrapsus edwardsi (Hilgendorf, 1882)

SOURCE REFERENCES: This study — zoea stages III and V from plankton. Wear (1965) —zoea V from plankton; identity confirmed by rearing through to identifiable juvenile crab stages. Wear (1970b) — zoea I from laboratory hatched eggs. Kurata (1968b) — megalopa of *Hemigrapsus sanguineus* (de Haan) as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, and probably Stewart Island; absent from the Chatham Islands and the subantarctic islands; intertidal, in mud and gravel and among rocks, usually in sheltered places. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in the Wellington area from March through to August, but spring and summer breeding may occur in other localities. Eggs, newly laid, light brown, 0.37 mm × 0.33 mm; about to hatch, almost transparent with the little remaining yolk dark brown, 0.42 mm × 0.39 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, transparent, with greenish tinge. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 177, 178): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.5 mm; rostral spine 0.25 mm long, straight and smooth; dorsal carapace spine 0.50 mm long, curved posteriorly at base but straight or slightly recurved anteriorly over distal half; spine to spine length 1.20 mm; lateral carapace spines 0.25 mm long, curved downwards and inclined posteriorly (Fig. 177); carapace smooth and without tubercles, posterior and posteroventral margins fringed with short, stout setae; length of antenna 2 exopod 0.13 mm; ratio of antenna 2 spiniform process (0.20 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.80, 0.40, and 1.54* respectively; antenna 2 exopod with one strong seta and two very small setae arising about two-thirds the distance from its base; antenna 2 spiniform process with double row of small spines along its distal half; maxilliped 1 with endopod propodus bearing a tuft of fine hairs; abdomen with dorsolateral protuberances on segment 2 only; abdominal segments 3–5 without well-defined lateral spines and with fine dorsal denticles along posterior margins; telson very widely forked with long slender lateral cornua, the cornua only slightly curved dorsally and inwards and without accessory spines or setae.

Zoea III: Total length 2.1 mm; rostral spine 0.41 mm long; dorsal carapace spine 0.73 mm long; lateral carapace spines 0.42 mm long; spine to spine length 2.00 mm; length of antenna 2 exopod 0.20 mm, endopod a tiny bud; ratio of antenna 2 spiniform process (0.21 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.51, 0.29, and 1.05* respectively; pleopod buds barely developed; telson with 4+4 inner posterior setae.

Zoea V: Total length 3.6 mm; rostral spine 0.50 mm long; dorsal carapace spine 1.30 mm long; lateral carapace spines 0.60 mm long; spine to spine length 2.80 mm; length of antenna 2 exopod 0.25 mm, of endopod 0.30 mm; ratio of antenna 2 spiniform process (0.28 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.56, 0.22, and 1.12* respectively; maxilliped 1 exopod with 12 setae, maxilliped 2 exopod with 12 or 13 setae; pleopod buds 0.35 mm long (segment 2) to 0.25 mm long (segment 5); telson with 5+5 or 6+6 inner posterior setae.

MEGALOPA: No knowledge. The megalopa of *H. sanguineus* (Fig. 179) is described and illustrated as an example of the genus.

Carapace almost square with broad frontal region terminating in a small, depressed rostral process; carapace lacks spines or prominent tubercles; pereiopods sparsely setose; pereiopods 2–4 each with a sharp spine on the medial margin of the propodus distally, dactyls with several medial marginal teeth; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segment 5 with a pair of short, blunt and poorly developed lateral spines; abdominal segments 2–5 with pleopods, segment 6 with uniramous uropods; uropods with one seta on protopod and 10–12 setae on exopod; telson rounded posteriorly with a few marginal setae.

NOTES: Although zoea stages II and IV and the megalopa larvae of *Hemigrapsus edwardsi* had been held in the Victoria University Marine Laboratory collections since 1965, specimens were desiccated during the 1979 fire mentioned previously, thus making them useless for illustration or description. All larval stages occur in the Wellington Harbour and inshore plankton, especially during winter and early spring (June to September or October).

Hemigrapsus crenulatus (H. Milne Edwards, 1837)

SOURCE REFERENCES: This study — zoea stages II–V from plankton. Wear (1970b) —zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island; absent from the Chatham Islands and the subantarctic islands; intertidal or semiterrestrial in estuaries, on mud flats under rocks, occasionally in shallow burrows or depressions. Also Chile.

BREEDING AND EGGS: Ovigerous females have been collected in the Wellington area in October and November. Eggs, newly laid, light brownish yellow, 0.28 mm × 0.26 mm; about to hatch, almost transparent to light brown, 0.34 mm × 0.38 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, transparent, but may have a yellow tinge. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 180, 181): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.2 mm; rostral spine 0.29 mm long, straight and smooth; dorsal carapace spine 0.41 mm long, curved posteriorly; spine to spine length 1.05 mm; lateral carapace spines 0.19 mm long, directed posteroventrally (Fig. 180); carapace smooth and without tubercles, inner posterior margins fringed with short fine hairs; length of antenna 2 exopod 0.07 mm; ratio of antenna 2 spiniform process (0.12 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.34, 0.24, and 1.43*

respectively; antenna 2 exopod with one strong lateral seta and two smaller setae arising just below tip; antenna 2 spiniform process with double row of small spines along distal half; maxilliped 1 endopod propodus lacking a tuft of fine hairs; abdomen with dorsolateral protuberances on segment 2 only; abdominal segments 3–5 without well-defined lateral spines or dorsal denticles; telson widely forked with long slender lateral cornua curved slightly inwards and strongly curved dorsally, no lateral or dorsal basal setae present, but inner and outer margins of cornua lined with fine hairs.

Zoea II: Total length 1.3 mm; rostral spine 0.42 mm long; dorsal carapace spine 0.48 mm long; spine to spine length 1.26 mm; lateral carapace spines 0.20 mm long, markedly depressed; length of antenna 2 exopod 0.08 mm; ratio of antenna 2 spiniform process (0.14 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.33, 0.29, and 1.75* respectively; telson with 3+3 inner posterior setae as in zoea I.

Zoea III: Total length 1.8 mm; rostral spine 0.56 mm long; dorsal carapace spine 0.59 mm long; spine to spine length 1.75 mm; lateral carapace spines 0.20 mm long; length of antenna 2 exopod 0.14 mm; ratio of antenna 2 spiniform process (0.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.45, 0.42, and 1.79* respectively; pleopod buds scarcely defined; telson with 4+4 inner posterior setae, the inner pair being almost as long as its more lateral counterparts.

Zoea IV: Total length 2.2 mm; rostral spine 0.77 mm long; dorsal carapace spine 0.74 mm long; spine to spine length 2.40 mm; lateral carapace spines 0.20 mm long; length of antenna 2 exopod 0.18 mm, of endopod bud 0.14 mm; ratio of antenna 2 spiniform process (0.31 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.40, 0.42, and 1.72* respectively; telson with 4+4 inner posterior setae as in zoea III.

Zoea V: Total length 2.8 mm; rostral spine 0.98 mm long; dorsal carapace spine 0.84 mm long; spine to spine length 3.00 mm; lateral carapace spines 0.20 mm long; length of antenna 2 exopod 0.27 mm, of endopod bud 0.28 mm; ratio of antenna 2 spiniform process (0.42 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.43, 0.50, and 1.56* respectively; pleopod buds 0.35 mm long (segment 2) to 0.28 mm long (segment 5); uropod buds rudimentary; telson with 5+5 or 5+4 inner posterior setae, the fifth (inner) seta being much smaller.

MEGALOPA: No knowledge. The megalopa of this species is likely to closely resemble that of *Hemigrapsus sanguineus* described as a congeneric example (*see* p. 69 and Fig. 179).

NOTES: Zoea larvae of *Hemigrapsus crenulatus* are particularly abundant in summer plankton samples taken in shallow waters, especially in harbours and adjacent to estuaries and mangrove areas in northern New Zealand. Megalopa larvae, possibly belonging to this species, have also been isolated from the plankton, but since their identification is purely by association and therefore speculative at this stage, we have refrained from including a description in this work.

Helice de Haan, 1833

Helice crassa (Dana, 1851)

SOURCE REFERENCES: This study — zoea stages II–V and megalopa from plankton. (First 15 crab stages subsequently reared from planktonic megalopa larvae are deposited in the National Museum of N.Z., Cr.2504). Wear (1970b) — zoea I from laboratory hatched eggs. Jones (1980) — reproductive ecology including breeding cycle and brood biology. Jones and Simons (1983) — latitudinal variations in reproductive characteristics. Nye (1977) — breeding and incubation at Papanui Inlet, Otago Peninsula.

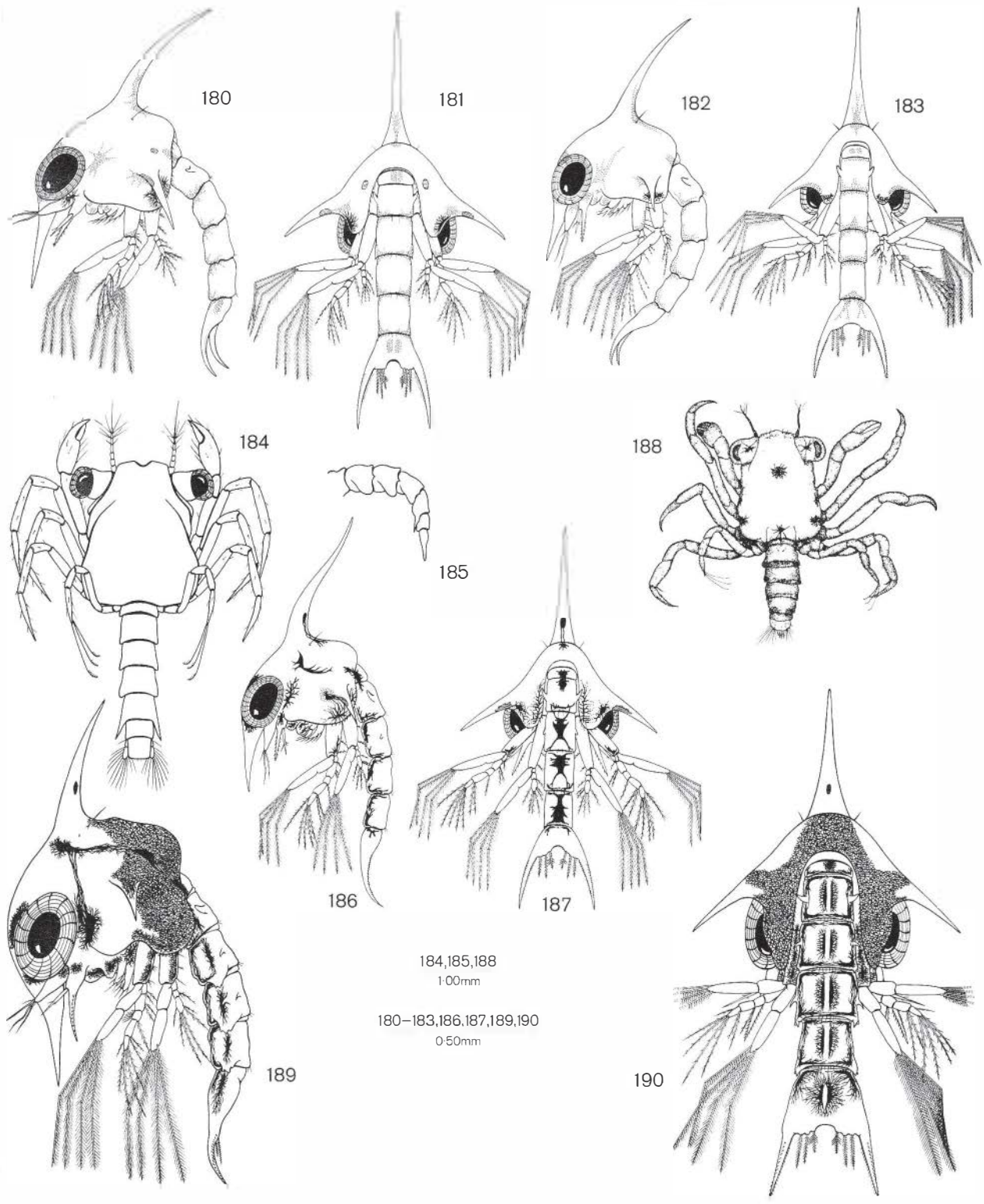
ADULT DISTRIBUTION AND HABITAT: North Island, South Island, Stewart Island; absent from the Chatham Islands and the subantarctic islands; intertidal, sometimes semi-terrestrial, normally occupying burrows dug in earth or mud on the fringes of estuaries or mangrove swamps. Endemic.

BREEDING AND EGGS: Ovigerous females have been found from August through to May. Eggs, newly laid, brownish yellow, 0.26 mm diameter; about to hatch, transparent or light grey-green, 0.32 mm × 0.31 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, transparent or light yellow-green. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 182, 183): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.1 mm; rostral spine 0.19 mm long, smooth; dorsal carapace spine 0.35 mm long, curved posteriorly; spine to spine length 0.90 mm; lateral carapace spines 0.15 mm long, directed only slightly posteriorly and declined; carapace smooth and without tubercles, inner posteroventral margins fringed with short, fine hairs; length of antenna 2 exopod 0.08 mm; ratio of antenna 2 spiniform process (0.10 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.56, 0.30, and 1.28* respectively; antenna 2 exopod with one strong lateral seta and two fine hair-like setae arising just below tip; antenna 2 spiniform process with double row of small spines along distal half; abdomen with dorsolateral protuberances on segment 2 only; abdominal segments 3–5 without well-defined lateral spines; telson widely forked with long slender lateral cornua curved slightly inwards and strongly curved dorsally, no lateral or dorsal basal setae present, but inner and outer margins of cornua lined with fine hairs.

Zoea II: Total length 1.25 mm; rostral spine 0.21 mm long; dorsal carapace spine 0.42 mm long; spine to



FIGS 180–190: Family GRAPSIDAE. *Hemigrapsus crenulatus* (H. Milne Edwards, 1837). Zoea I: 180, lateral view; 181, posterior view. After Wear (1970b). *Helice crassa* Dana, 1851. Zoea I: 182, lateral view; 183, posterior view. Megalopa: 184, dorsal view; 185, abdominal segments, lateral view. Figs 182, 183 after Wear (1970b). *Cyclograpsus lavauxi* H. Milne Edwards, 1853. Zoea I: 186, lateral view; 187, posterior view. After Wear (1970b). *Cyclograpsus cinereus* Dana. Megalopa: 188, dorsal view. After Costlow and Fagetti (1967). Reprinted from *Pacific Science* by permission of the University Press of Hawaii. *Cyclograpsus insularum* Campbell & Griffin, 1966. Zoea I: 189, lateral view; 190, posterior view. After Wear (1970b).

spine length 1.08 mm; lateral carapace spines 0.17 mm long; length of antenna 2 exopod 0.10 mm; ratio of antenna 2 spiniform process (0.12 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.57, 0.29, and 1.20* respectively; telson without additional inner posterior setae.

Zoea III: Total length 1.4 mm; rostral spine 0.25 mm long; dorsal carapace spine 0.53 mm long; spine to spine length 1.20 mm; lateral carapace spines 0.17 mm long; length of antenna 2 exopod 0.13 mm; ratio of antenna 2 spiniform process (0.15 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.60, 0.28, and 1.15* respectively; telson with 4+4 or 4+5 inner posterior setae.

Zoea IV: Total length 1.6 mm; rostral spine 0.33 mm long; dorsal carapace spine 0.70 mm long; spine to spine length 1.39 mm; lateral carapace spines 0.18 mm long; length of antenna 2 exopod 0.15 mm; ratio of antenna 2 spiniform process (0.18 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.55, 0.26, and 1.20* respectively; telson with 5+5 inner posterior setae.

Zoea V: Total length 1.9 mm; rostral spine 0.51 mm long; dorsal carapace spine 1.00 mm long; spine to spine length 1.75 mm; lateral carapace spines 0.20 mm long; length of antenna 2 exopod 0.19 mm, of endopod bud 0.12 mm; ratio of antenna 2 spiniform process (0.23 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.45, 0.23, and 1.21* respectively; telson with 5+5 inner posterior setae, sometimes 5+6 setae.

MEGALOPA (Figs 184, 185): Carapace length 2.0 mm; carapace width 1.4 mm, widest posteriorly, narrowing towards rostral region; carapace smooth and lacking spines or setae; rostrum short, depressed at 90° between two frontal lobes; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segments 2–4 with very short lateral spines appearing as little more than triangular projections (Fig. 185); abdominal segment 5 with posterolateral angles produced as a long spine extending posteriorly to the level of joint between abdominal segment 6 and the telson; abdominal segments 2–5 with pleopods, uropods uniramous, exopod with 11 setae, protopod with one seta arising laterally near its base; telson almost square with two short posterior setae, often difficult to see.

NOTES: Larvae of *Helice crassa* are often abundant in the spring and summer plankton of inshore waters adjacent to estuaries or harbour mudflats.

Cyclograpsus H. Milne Edwards, 1837

Cyclograpsus lavauxi H. Milne Edwards, 1853

SOURCE REFERENCES: This study — zoea stages II–V from plankton. Wear (1970b) —zoea I reared from laboratory hatched eggs. Costlow and Fagetti (1967) —megalopa of *Cyclograpsus cinereus* Dana as an example of the genus.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, but not recorded from Stewart Island, the Chatham Islands, or the N.Z. subantarctic islands (Bennett 1964); common in the littoral fringe among stones and pebbles. Also Juan Fernandez (Griffin 1968).

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand from September to January. Eggs, newly laid, dark purple, 0.32 mm × 0.31 mm; about to hatch, transparent, 0.38 mm × 0.35 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, transparent or tinged light green. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 186, 187): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.15 mm; rostral spine 0.20 mm long, sometimes curved slightly backwards at tip; dorsal carapace spine 0.40 mm long, curved posteriorly near base but recurved anteriorly near tip; spine to spine length 0.95 mm; lateral carapace spines 0.18 mm long, almost straight but depressed and directed posteriorly (Fig. 186); carapace smooth and without tubercles, posterior margins fringed with short setae; length of antenna 2 exopod 0.08 mm; ratio of antenna 2 spiniform process (0.11 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.55, 0.28, and 1.40* respectively; antenna 2 exopod with one strong lateral seta and two very small setae arising just below tip; antenna 2 spiniform process with double row of small spines along distal half; abdominal segments 2 and 3 each with a small pair of dorsolateral protuberances, those of segment 3 directed posteriorly; abdominal segments 3—5 without well-defined lateral spines; telson with long slender lateral cornua curved slightly inwards and dorsally, no lateral or dorsal basal setae present, but inner and outer margins of cornua lined with fine hairs.

Zoea II: Total length 1.5 mm; rostral spine 0.49 mm long; dorsal carapace spine 0.63 mm long; spine to spine length 1.61 mm; lateral carapace spines 0.42 mm long, swept strongly posteriorly; length of antenna 2 exopod (including its slender spine-like tip) 0.14 mm; ratio of antenna 2 spiniform process (0.17 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.35, 0.27, and 1.21* respectively; dorsolateral protuberances on abdominal segment 3 very small, but nevertheless well-defined; telson without additional inner posterior setae.

Zoea III: Total length 1.8 mm; rostral spine 0.77 mm long; dorsal carapace spine 0.98 mm long; spine to spine length 2.32 mm; lateral carapace spines 0.49 mm long, orientated as in zoea II; length of antenna 2 exopod 0.18 mm (measurement includes fine spine-like distal portion, which is not jointed and is contiguous with the exopod itself); ratio of antenna 2 spiniform

process (0.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.32, 0.26, and 1.39* respectively; abdominal segments 3–5 with short, blunt, ventrolateral spines, those on segment 4 being the longest; telson with 3+4 or 4+4 inner posterior setae.

Zoea IV: Total length 2.1 mm; rostral spine 1.00 mm long; dorsal carapace spine 1.12 mm long; spine to spine length 2.88 mm; lateral carapace spines 0.52 mm long; length of antenna 2 exopod (including spine-like tip) 0.25 mm, of endopod bud 0.06 mm; ratio of antenna 2 spiniform process (0.34 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.34, 0.30, and 1.36* respectively; telson with lateral cornua now practically straight in dorsal view, with 4+4 inner posterior setae, the innermost pair almost as long as the adjacent setae.

Zoea V: Total length 2.45 mm; rostral spine 1.40 mm long; dorsal carapace spine 1.50 mm long; spine to spine length 3.92 mm; lateral carapace spines 0.59 mm long; length of antenna 2 exopod 0.31 mm, of endopod 0.28 mm; ratio of antenna 2 spiniform process (0.39 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.28, 0.26, and 1.26* respectively; maxilliped 1 exopod with 12 natatory setae, maxilliped 2 exopod with 14 setae, the two most proximal setae being much the shortest; pleopod buds 0.31 mm long (segment 2) to 0.21 mm long (segment 5); uropod buds 0.11 mm long; telson with 4+4 inner posterior setae all of about equal length.

MEGALOPA: No knowledge. The megalopa of *Cyclograpsus cinereus* (Fig. 188) is described and illustrated as an example of the genus.

Carapace smooth, almost square in dorsal view, and with a few lateral marginal hairs; frontal region broad, bearing a few anterior marginal setae; rostrum, if present, not visible in dorsal view; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segments without lateral spines, segments 2–5 with pleopods, segment 6 with uropods; uropods uniramous, with one seta on protopod and 10 setae on exopod; telson armed with dorsal and posterior marginal setae.

NOTES: Larvae of *Cyclograpsus lavauxi* are common in inshore surface plankton samples taken during spring and summer, and early stage zoea larvae are at times particularly abundant off stony beaches in the Wellington area. They may be absent in waters off sandy beaches in the north-west and south-west of the North Island, and the east coast of the South Island, where adults are unlikely to occur.

Cyclograpsus insularum Campbell and Griffin, 1966

SOURCE REFERENCE: Wear (1970b) — zoea I from laboratory hatched eggs.

ADULT DISTRIBUTION AND HABITAT: Northern half of North Island, N.Z., but records from further south can be expected; absent from the Chatham Islands and the subantarctic islands; intertidal under rocks and boulders in restricted localities. Also Kermadec Islands, Lord Howe Island and Norfolk Island.

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand in August and September. Eggs, newly laid, dark purple, 0.45 mm × 0.40 mm; about to hatch, black, 0.50 mm × 0.48 mm.

ZOEA LARVAL STAGES: Probably five zoea stages; colour in life, black and heavily pigmented with small dendritic chromatophores covering the posterior carapace to the level of the dorsal carapace spine (Wear 1970b).

Zoea I (Figs 189, 190): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.6 mm; rostral spine 0.35 mm long; dorsal carapace spine 0.37 mm long, stout, and slightly curved posteriorly; spine to spine length 1.25 mm; lateral carapace spines 0.23 mm long, directed downwards and not posteriorly; posteroventral margin of carapace produced into a rather prominent lobe armed with small teeth; length of antenna 2 exopod 0.13 mm; ratio of antenna 2 spiniform process (0.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.54, 0.51, and 1.46* respectively; antenna 2 exopod terminating as slender spine bearing one subterminal seta laterally and two other fine hair-like setae; antenna 2 spiniform process with double row of small spines along distal half; abdominal segments 2–4 each with a pair of dorsolateral protuberances, those of segments 3 and 4 directed posteriorly, segments 3–5 with posterolateral margins produced into a trilobed ridge; lateral cornua of telson curved dorsally, but divergent and not curved inwards in dorsal view, without lateral or dorsal basal setae, but with two dorsolateral rows of coarse hairs. In Wear (1970), figure 42 omits the dorsolateral protuberances on abdominal segment 4, but they are here included (Fig. 189).

MEGALOPA: No knowledge.

NOTES: Later zoea stages and the megalopa larva of *Cyclograpsus insularum* have not been reared or found in the plankton up to the present time, although they may well occur in northern waters. Megalopa larvae are likely to be heavily pigmented in life as are the zoea larvae. It is probable that they are similar to those of *C. cinereus*, described as a congeneric example (*see* p. 73 and Fig. 188).

Plagusia Latreille, 1804

Plagusia chabrus (Linnaeus, 1764)

SOURCE REFERENCES: This study — zoea stages ?V and ?XII from the plankton; megalopas collected intertidally, by trawling, and from floating debris. Wear (1970b) — zoea I from laboratory hatched eggs. Rathbun (1918) — five megalopa larvae from surface off coast of Macquarie Island described and figured as *Marestia mawsoni* n.sp.

ADULT DISTRIBUTION AND HABITAT: North Island, and northern half of South Island, N.Z.; rare south of Banks Peninsula, and not recorded from Stewart Island, the Chatham Islands, or the subantarctic islands; intertidal and subtidal in deep crevices on exposed rocky coasts or wave-washed reefs. A partly circumpolar, southern hemisphere, cool temperate species confined to the Indo-Pacific from South Africa to Chile (Griffin 1973).

BREEDING AND EGGS: Ovigerous females have been collected in New Zealand from November to February. Eggs, newly laid, dull orange or brick red, 0.39 mm diameter; about to hatch, light green with blue iridescence in daylight, 0.47 mm × 0.45 mm.

ZOEA LARVAL STAGES: About 12 zoea stages; colour in life, black or very dark green. A table of chromatophores is given by Wear (1970b).

Zoea I (Figs 191, 192): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.6 mm; rostral spine 0.55–0.60 mm long, straight but often curved slightly forwards through its distal half, bearing a variable number of denticles; dorsal carapace spine smooth, straight or slightly curved, usually 0.60 mm long, but may be as short as 0.35 mm (when relatively short it is often malformed with multispinous tip); spine to spine length 1.60 mm; lateral carapace spines 0.22–0.25 mm long, slightly depressed, dorsal surface with a few basal hairs and a number of small denticles or tubercles irregularly arranged; posterolateral regions of carapace extended ventrally as a conspicuous lobe on each side; length of antenna 2 exopod 0.06 mm; ratio of antenna 2 spiniform process (0.37 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.64, 0.62, and 6.17* respectively; tip of antenna 2 exopod with a slender, articulating spine about one-half the length of the spiniform process and two very small setae; antenna 2 spiniform process with two rows of 10 or 11 small spines; abdominal segments 3–5 each with a pair of small posteriorly directed dorsolateral protuberances, one large forwardly directed pair of dorsolateral protuberances on segment 2, segments 2–5 with short lateral spines, those on segments 2 and 3 usually bilobed, those on segments 4 and 5 trilobed; telson cornua slender, straight and only slightly curved dorsally, each with one tiny lateral seta near its base.

Zoea ?V: The following single zoea, collected from the plankton off East Cape in February 1969, has been designated stage V on the basis of its overall size and the degree of development of the pereiopod buds and pleopod buds. Maxilliped setation alone suggests a much later zoea, but this has been discounted by comparison with reared stage V zoeas of *Ovalipes catharus*, which also has extended larval development.

Total length 4.5 mm; rostral spine 1.45 mm long, straight; dorsal carapace spine 2.38 mm long, straight; spine to spine length 5.00 mm; lateral carapace spines 0.56 mm long; length of antenna 2 exopod (excluding long seta) 0.11 mm, endopod absent; ratio of antenna 2 spiniform process (0.45 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.31, 0.19, and 4.09* respectively; maxillipeds 1 and 2 each with 18 setae on exopod; abdominal segment 1 with one strong dorsal seta; abdominal segments 2–5 with ventrolateral spines, those on segment 2 very short; pleopod buds 0.15 mm long (segment 2) to 0.12 mm long (segment 5); telson with 4+4 inner posterior setae.

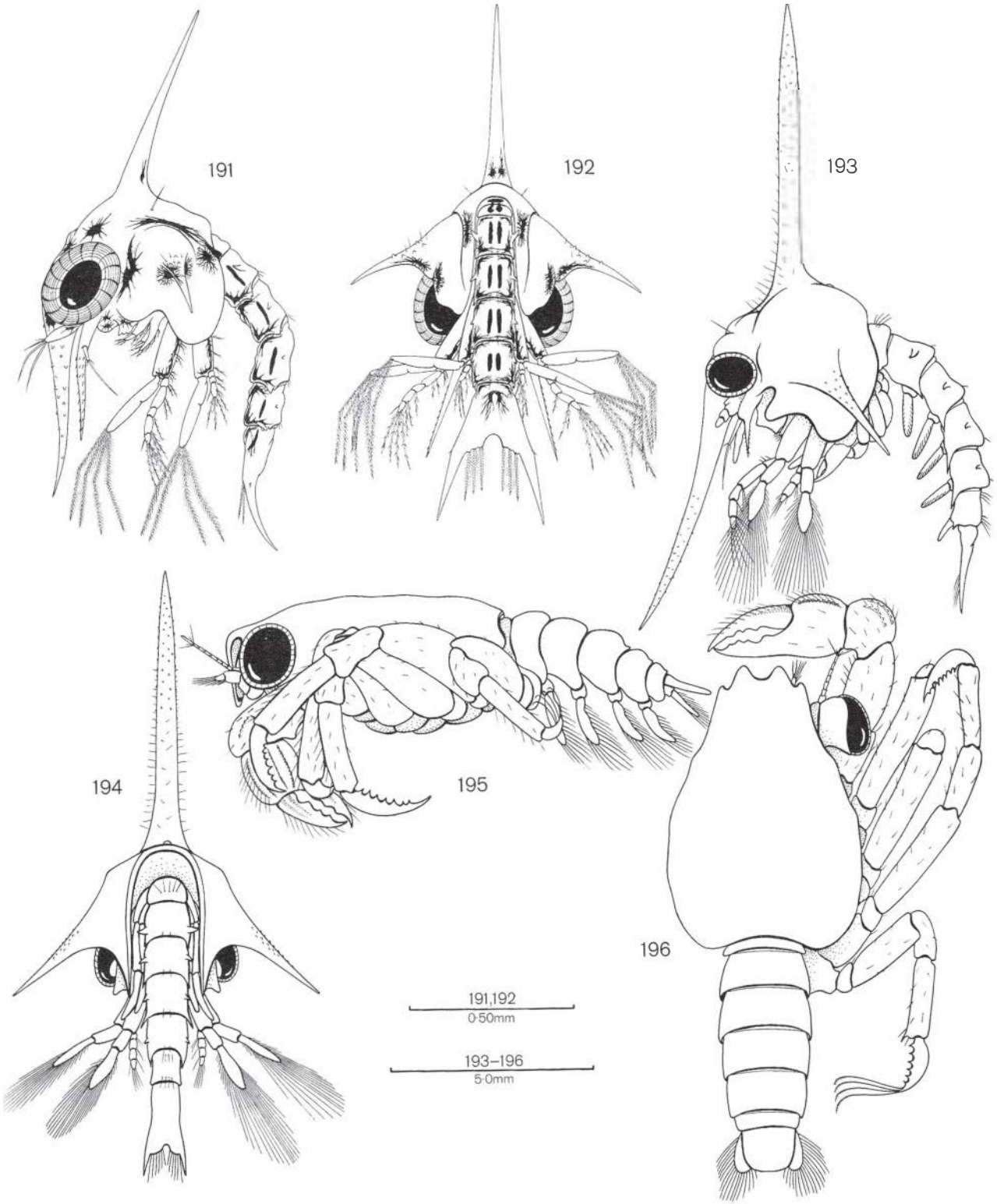
Zoea ?XII (Figs 193, 194): A single specimen collected from the plankton off East Cape in February 1969. The precise designation of this instar is uncertain since it is based solely on a calculation using a total length increment of about 1.00 mm per stage from ?stage V described above.

Total length 11.8 mm; rostral spine 6.00 mm long; dorsal carapace spine 6.75 mm long; spine to spine length 15.25 mm; lateral carapace spines 2.55 mm long, swept strongly posteriorly and depressed; length of antenna 2 exopod 0.64 mm, of endopod 0.85 mm; ratio of antenna 2 spiniform process (0.80 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.13, 0.12, and 1.25* respectively; maxilliped exopods somewhat flattened and bearing 38 plumose setae; pereiopod buds large, extending below ventral carapace margins and partly segmented; abdominal segment 1 with four or five central dorsal setae; pleopod buds 1.25 mm long (segment 2) to 1.00 mm long (segment 5); uropod buds 0.60 mm long; telson plate about twice as long as broad, posterior margins with 6+6 inner setae, lateral telson seta now absent.

MEGALOPA ?II (Figs 195, 196): Identification of the specimens examined is based on consideration of their very large size and comparison with the megalopa of *P. dentipes* described by Aikawa (1937).

Colour in life, dark olive green. Carapace length 8.0 mm; carapace width 4.9 mm; carapace generally pyriform in dorsal view, smooth, and without prominent tubercles or ridges; relatively narrow frontal region developed into two prominent anterior lobes and two smaller anterolateral lobes as viewed dorsally, with rostrum depressed at an angle of 90° between the anterior lobes; pereiopod 1 heavy, with a small ischial spine and with well-defined longitudinal ridges on outer face of propodus as in the adult; dactyls of pereiopods 2–4 bearing seven strong teeth and terminating as a strong, slightly curved spine; pereiopod 5 dactyl with six teeth and four long terminally hooked setae; abdominal segments wider than long and without prominent lateral spines, segments 2–5 with pleopods, segment 6 with uniramous uropods with about 40 setae on exopod; telson broadly rounded and lacking posterior setae.

NOTES: Our knowledge of the larval development of



FIGS 191–196: Family GRAPSIDAE. *Plagusia chabrus* (Linnaeus, 1764). Zoea I: 191, lateral view; 192, posterior view. Zoea ?XII: 193, lateral view; 194, posterior view. Megalopa ?II: 195, lateral view; 196, dorsal view, left appendages not figured. Figs 191, 192 after Wear (1970b).

Plagusia chabrus is still incomplete. That the zoea larva described above as stage ?XII is probably the final stage is suggested by the pleopod setae being visible beneath the cuticle, tissue withdrawal from the telson cornua, and the degree of development and segmentation of the pereiopods. However, this zoea, although very large, is of insufficient size to imply a direct transition to the bulky megalopa. Aikawa (1937) described two megalopa stages in *P. dentipes* — stage I having a carapace 5.1 mm × 3.5 mm, with a forwardly directed rostrum; stage II much larger and without this central process, but having a lobed frontal region as described here. *P. chabrus* may follow a similar course of development although a first stage megalopa has not yet been identified.

Zoea larval stages of *P. chabrus* may well be most abundant in offshore waters, although we have little evidence to support this claim. Aikawa (1937) notes that the stage I megalopas of *P. dentipes* usually form swarms in the open seas from late winter to spring, and those of stage II live in great abundance on floating weeds and timbers from spring to early summer and are carried to the coast on such flotsam. The megalopa stage(s) of *P. chabrus* may be similarly distributed.

FAMILY OCYPODIDAE

Wear (1968b) reviewed larval affinities of the 14 species and seven genera available at the time. In the analysis, primary significance was given to the presence or absence of lateral carapace spines, and secondary significance to lateral expansion of abdominal segments 4 and 5 and to the degree of development of the exopod of antenna 2. On this basis, two principal conclusions were then reached: first, that there was no significant character common to all ocypodid zoea larvae, and that a definitive list of characters pertaining to the whole family could not be therefore framed; and second, that no grouping of the zoea larvae conformed with the arrangement of genera into the three subfamilies —Macrophthalminae, Ocypodinae, and Dotillinae (= Scopimerinae).

Rice (1975) re-examined available information on ocypodid zoea larvae, and later (1980a) reiterated his earlier conclusions and published the most recent analysis taking account of all literature concerning larvae of the group. Using only the setation pattern of the endopods of maxilla 1, maxilla 2, and maxilliped 2 (characters not taken into consideration by most previous authors), he found variations to be rather more conservative, and that clear and consistent distinctions were apparent between larvae of the three subfamilies as defined by adult characters (Balss 1957). Zoea larval characters of each of the three subfamilies are listed by Rice (1980a) and need not be repeated here. Rice, however, specifically excludes the single New Zealand ocypodid species, *Hemiplax hirtipes* (Jacquinot), from his definition of the subfamily Macrophthalminae, and bases his subfamilial characters entirely on accounts of zoea larvae belonging to the genus *Macrophthalmus*. There seems little logic in such an exclusion, since the monotypic genus *Hemiplax* Heller is a genuine member of the subfamily. Moreover, Rice (1980a) overlooked the fact that Barnes (1967: 236) regarded *Hemiplax hirtipes* (Jacquinot) as belonging more appropriately to the genus *Macrophthalmus* subgenus *Hemiplax*, and this change has been adopted in all subsequently published references to adults of the species. Rice's characters applying to zoea larvae of the subfamily Macrophthalminae thus become rather less convincing and must now be confined to details of selected appendage setation relating to one genus only.

Phylogenetic relationships of the family as a whole are obscure among the larvae (Wear 1968b; Rice 1980a). At the level of subfamily, however, zoea larvae of the Ocypodinae are clearly the most advanced, with setation of maxilla 1, maxilla 2, and maxilliped 2 very similar to that in the Pinnotheridae (Rice 1980a). Rice suggests that these characters of the Ocypodinae could be derived from either of the other two subfamilies, but proposed an independent phylogeny for the more primitive Macrophthalminae and Dotillinae which are difficult to derive from each other.

Macrophthalmus Desmarest, 1823

Macrophthalmus hirtipes (Jacquinot, 1853)

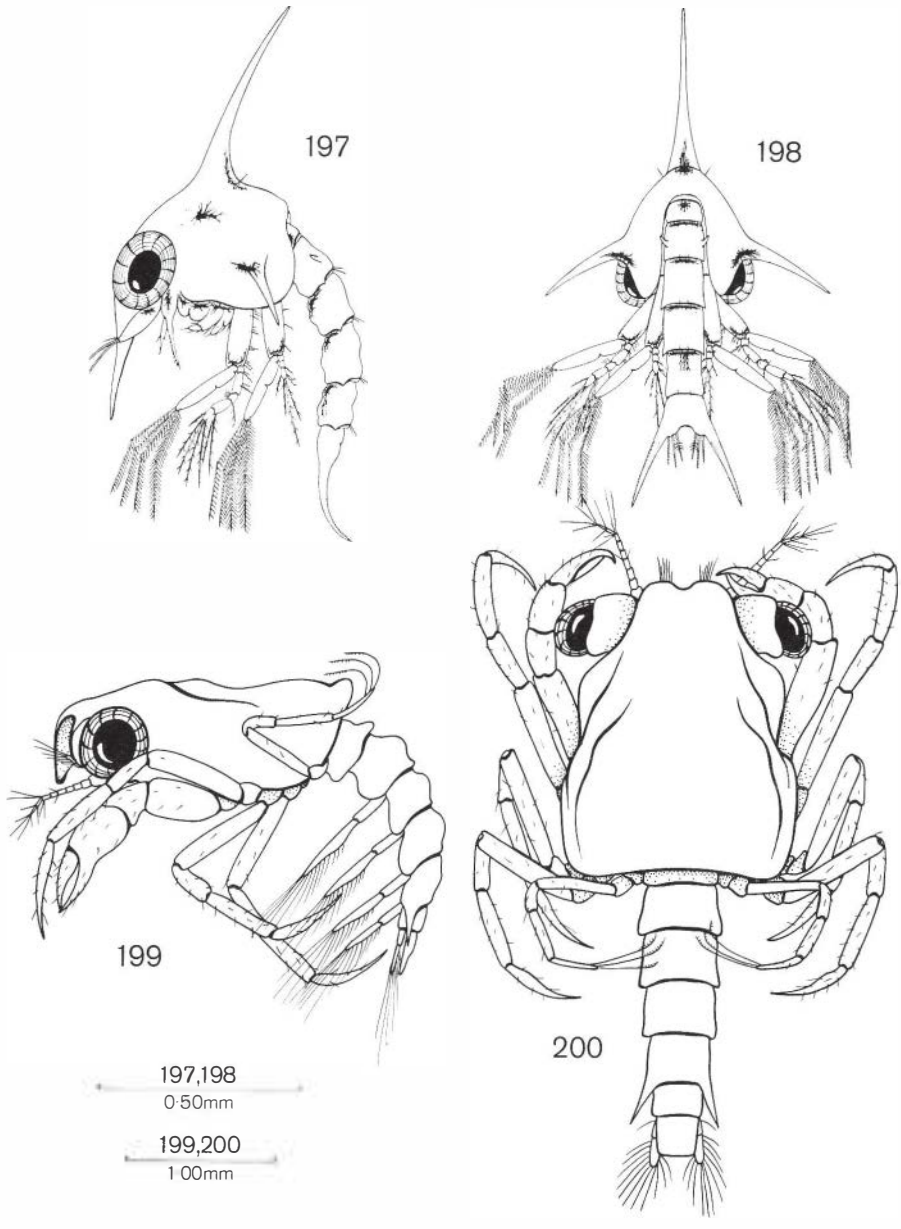
SOURCE REFERENCES: This study — zoea stages II–V from plankton; megalopa reared from planktonic stage V zoea larvae. Wear (1968b) — zoea I from laboratory hatched eggs. Simons and Jones (1981) — population and reproductive biology. Jones and Simons (1982) — responses of embryonic stages to salinity.

ADULT DISTRIBUTION AND HABITAT: North Island, South Island, and probably Stewart Island, N.Z.; absent from the Chatham Islands and the subantarctic islands; burrowing in mudflats in tidal estuaries. Endemic.

BREEDING AND EGGS: Ovigerous females have been collected in January, March, and June through to November; the species probably breeds throughout the year. Eggs, newly laid, dark brown, 0.25 mm × 0.24 mm; about to hatch, light brown, 0.28 mm × 0.26 mm.

ZOEA LARVAL STAGES: Five zoea stages; colour in life, transparent, or faint red. A table of chromatophores is given by Wear (1968b).

Zoea I (Figs 197, 198): Zoea with dorsal, rostral and lateral carapace spines. Total length 1.25 mm; rostral spine 0.29 mm long, straight and smooth; dorsal carapace spine 0.46 mm long, slightly curved posteriorly; spine to spine length 1.22 mm; lateral carapace spines 0.25 mm long, slightly depressed and directed posteriorly; carapace smooth, posterior margins fringed with very short fine hairs; length of antenna 2 exopod



FIGS 197–200: Family OCYPODIDAE. *Macrophthalmus hirtipes* (Jacquinot, 1853). Zoea I: 197, lateral view; 198, posterior view. Megalopa: 199, lateral view; 200, dorsal view. Figs 197, 198 after Wear (1968b).

0.09 mm; ratio of antenna 2 spiniform process (0.16 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.55, 0.35, and 1.80* respectively; antenna 2 exopod terminating as slender acicular process and bearing one strong subterminal seta laterally and one other fine hair-like seta; antenna 2 spiniform process with a single anterolateral row of small spines along distal half; maxilliped 1 endopod with tuft of fine hairs on carpus; abdominal segments with poorly defined ventrolateral spines, and dorsolateral protuberances on segment 2 only; telson cornua slender with almost straight sides viewed dorsally, curved upwards, without basodorsal or lateral spines or setae, but each with two dorsolateral rows of tiny setae.

Zoea II: Total length 1.5 mm; rostral spine 0.38 mm long; dorsal carapace spine 0.55 mm long; spine to spine length 1.48 mm; lateral carapace spines 0.28 mm long; length of antenna 2 exopod 0.11 mm; ratio of antenna 2 spiniform process (0.20 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.53, 0.36, and 1.80* respectively; telson with 3+3 inner posterior setae as in zoea I.

Zoea III: Total length 1.8 mm; rostral spine 0.63 mm long; dorsal carapace spine 0.70 mm long; spine to spine length 1.96 mm; lateral carapace spines 0.28 mm long; length of antenna 2 exopod 0.14 mm; ratio of antenna 2 spiniform process (0.25 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exo-

pod, *0.40, 0.36, and 1.79* respectively; maxilliped 1 exopod with eight setae, maxilliped 2 exopod with seven setae; abdominal segments 3–5 with short but well-defined ventrolateral spines; telson bearing 4+4 inner posterior setae.

Zoea IV: Total length 2.8 mm; rostral spine 1.05 mm long; dorsal carapace spine 1.05 mm long; spine to spine length 2.80 mm; lateral carapace spines 0.28 mm long; length of antenna 2 exopod 0.24 mm, of endopod bud 0.15 mm; ratio of antenna 2 spiniform process (0.38 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.36, 0.36, and 1.58* respectively; maxilliped 1 exopod with 10 setae, maxilliped 2 exopod with nine setae; telson bearing 4+4 inner posterior setae, with the fourth (inner) pair almost as long as the third pair.

Zoea V: Total length 3.8 mm; rostral spine 1.40 mm long; dorsal carapace spine 1.20 mm long; spine to spine length 4.00 mm; lateral carapace spines 0.36 mm long; length of antenna 2 exopod 0.29 mm, of endopod bud 0.43 mm; ratio of antenna 2 spiniform process (0.50 mm long) to rostral spine, to dorsal carapace spine, and to antenna 2 exopod, *0.36, 0.42, and 1.72* respectively; maxilliped 1 exopod with 11 or 12 setae, maxilliped 2 exopod with 12 setae; pleopod buds 0.49 mm long (segment 2) to 0.35 mm long (segment 5); uropod buds 0.17 mm long; telson with 4+4 inner posterior setae as in zoea IV.

MEGALOPA (Figs 199, 200): Carapace length 2.00 mm; carapace width 1.60 mm; carapace smooth but with well-defined branchial ridges, almost square in dorsal view with a broad frontal region; rostrum not visible dorsally, but depressed from a shallow frontal depression at an angle of about 90°; pereiopods without prominent spines and with a sparse armature of setae on distal segments; coxae of pereiopods 2–4 each produced into a blunt ventral protuberance; pereiopod 5 with three long terminally hooked setae on dactyl; abdominal segments 2–4 lacking lateral spines, segment 5 produced posterolaterally into a long spine on each side reaching beyond the posterior margin of segment 6; abdominal segments 2–5 with pleopods; uropods uniramous, with one lateral seta on protopod and 11 setae on exopod; telson almost square in outline and lacking marginal setae.

NOTES: Larvae of *Macrophthalmus hirtipes* are often abundant between July and December in inshore waters, especially in plankton obtained adjacent to estuary or harbour mudflats.

KEYS TO THE LARVAE OF THE BRACHYURA FROM THE NEW ZEALAND REGION

The following section is intended to assist workers faced with the problem of identifying brachyuran larvae contained in plankton collections. In samples taken in coastal or inshore waters, these larvae often comprise the bulk of the catch.

In the tabular guide (Table 1), zoea larvae are grouped according to the number and arrangement of carapace spines. In the keys, we have attempted to use the minimum of obvious characters to separate species, so that in all cases a dissecting microscope should be sufficient for rapid identification. When the identity of an unknown larva has been established provisionally, we would suggest that this be verified by reference to the previous section, in which a more comprehensive list of characters is given, and also by reference to the relevant illustrations. This is especially important for those species asterisked in the key, as these represent genera in which other species exist in the New Zealand fauna for which larvae are as yet unknown. Larval characters used in the keys are those common to all zoea stages of a given species unless otherwise indicated, but for the designation of particular zoea larval instars it will be necessary to refer to the main systematic and descriptive part of this work.

In a number of cases, the larvae of species from beyond the New Zealand region have been postulated as congeneric larval types representing New Zealand species from which the larvae are as yet unknown. Details are contained in the descriptive section, and probable diagnoses are here confined to the level of genus. It should be emphasised that the following arrangement of species is one of convenience only, and there has been no serious attempt to follow established groupings of adult genera or families.

Key to the Zoea Larvae

1. Zoea "anomuran", with rostrum directed anteriorly in the same horizontal plane as dorsum of carapace; antenna 2 exopod broad, flattened, and fringed with many setae; telson triangular or spatuliform rather than forked 2

— Zoea "brachyuran", with rostrum usually present and directed ventrally at about 90° to dorsum of carapace; antenna 2 exopod usually tubular or reduced to a seta, but in a few cases slender, flattened, and fringed with a few setae; telson usually forked, with a deep central notch and prominent lateral cornua 5

TABLE 1: Guide to the zoea larvae of the New Zealand Brachyura based on the position of carapace spines.

FAMILY	NONE	DORSAL ONLY	ROSTRAL ONLY	DORSAL/ROSTRAL	DORSAL/ROSTRAL/LATERAL	DORSAL/LATERAL	ROSTRAL/LATERAL
HOMOLIDAE			*Latreillia australis*		*Homola orientalis** *Paromola*		
DROMIIDAE					*Petalomera wilsoni*		
TYMOLIDAE					*Cymonomus bathamae*†		
RANINIDAE					*Lyreidus tridentatus*		
LEUCOSIIDAE	*Ebalia laevis*						
MAJIDAE		*Achaeus fissifrons* *Pyromaia tuberculata*		*Eurynolambrus australis* *Eurynome* *Jacquinotia edwardsii* *Leptomithrax longimanus* *L. tuberculatus mortenseni* *Notomithrax minor* *Notomithrax peronii* *Notomithrax ursus*	*Cyrtomaia hispida* *Leptomithrax longipes* *Rochinia*		
HYMENOSOMATIDAE			*Elamena longirostris* *Elamena momona* *Elamena producta* *Halicarcinus cookii* *Halicarcinus innominatus* *Halicarcinus planatus* *Halicarcinus varius* *Halicarcinus whitei*		*Neohymenicus pubescens*		*Hymenosoma depressum*
ATELECYCLIDAE					*Trichopeltarion fantasticum*		
CANCRIDAE					*Cancer novaezelandiae*		
PORTUNIDAE					*Macropipus corrugatus* *Nectocarcinus antarcticus* *Ovalipes catharus* *Portunus pelagicus* *Scylla serrata*		
BELLIIDAE					*Heterozius rotundifrons*		
XANTHIDAE	*Pilumnus lumpinus*				*Ozius truncatus*	*Pilumnopeus serratifrons*	
GONEPLACIDAE				*Ommatocarcinus huttoni*	*Carcinoplax*		
PINNOTHERIDAE	*Pinnotheres novaezelandiae*						
GRAPSIDAE				*Leptograpsus variegatus* *Planes marinus*	*Cyclograpsus insularum* *Cyclograpsus lavauxi* *Helice crassa* *Hemigrapsus crenulatus* *Hemigrapsus edwardsi* *Plagusia chabrus*		
OCYPODIDAE					*Macrophthalmus hirtipes*		

*adrostral spine and paired antorbital and postorbital spines also present
†two pairs of lateral spines are present

2. Carapace with a rostral spine only..... *Latreillia australiensis*

— Carapace with a rostral spine and with additional carapace spines.....3

3. Carapace armature includes a rostral spine, dorsal spine, 1 pair of lateral spines, and accessory spines or processes ..... *Homola orientalis*

— Carapace armature restricted to a rostral spine, dorsal spine, and 1 pair of lateral spines 4

4. Carapace spines not broadly based; posterior carapace margins with many close-set teeth; abdominal segment 1 with several large plumose setae dorsally ..... *Paromola*

— Carapace spines broadly based; posterior carapace margins lacking teeth; abdominal segment 1 lacking large dorsal setae.....*Petalomera wilsoni*

5. Antenna 2 exopod flattened, scale-like, and bearing a setal fringe 6

— Antenna 2 exopod tubular or reduced to a small seta.....7

6. Carapace with dorsal, rostral, and 2 pairs of lateral spines; all carapace spines shorter than carapace length; abdominal spines long, slender, and strongly spinulated; 4th posterior spines of telson no longer or more strongly developed than 1st to 3rd spines.....*Cymonomus bathamae**

— Carapace with dorsal, rostral, and 1 pair of lateral spines; all carapace spines much longer than carapace length; abdominal spines short and smooth; 4th posterior spines of telson much longer and more strongly developed than 1st to 3rd spines ..... *Lyreidus tridentatus*

7. Carapace with dorsal, rostral, and 1 pair of lateral spines (GROUP A).....8

— Carapace armature not as above, i.e., any or all of the major carapace spines are absent and no additional large spines are present (GROUPS B–G).....27

GROUP A

8. Lateral carapace spines inclined anteriorly and strongly upwards; telson with 2 large spines lateral to cornua ..... *Trichopeltarion fantasticum*

— Lateral carapace spines set at 90° to carapace, or declined; telson with only 1 large spine lateral to cornua, or lacking such a process 9

9. Antenna 2 spiniform process longer than dorsal carapace spine, rostral spine, or carapace ..... *Heterozius rotundifrons*

— Antenna 2 spiniform process shorter than dorsal carapace spine, rostral spine, or carapace 10

10. Abdominal segment 5 inflated in dorsal view, with its lateral wings overlapping joint with telson; antenna 2 exopod reduced to a small seta ..... *Neohymenicus pubescens*

— Abdominal segment 5 not inflated in dorsal view; antenna 2 exopod not reduced to a small seta, but 0.16–1.0 times the length of spiniform process.....11

11. Telson with 1 robust spine lateral to base of cornu on each side; cornua lacking a basal dorsal spine or seta.....12

— Telson lacking a large spine lateral to base of cornu on each side, or, if present, then only in association with a small dorsal spine or seta, or a stout, curved dorsal spine 13

12. Abdomen with dorsolateral protuberances on segments 2 and 3; telson with 2 well-developed spines in axilla between base of cornu and lateral spine on each side..... *Leptomithrax longipes**

— Abdomen with dorsolateral protuberances on segment 2 only; telson lacking axillary spines between base of cornu and lateral spine on each side.....*Rochinia*

13. Telson cornua each with a large, curved spine arising dorsally from near its base..... *Ozius truncatus*

— Telson cornua lacking a large, curved dorsal spine.....14

14. Lateral or dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segment 2 only, or on segments 2 and 3 — absent from the 4th and 5th segments...15

— Lateral or dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segments 2–4 or 2–5.....25

15. Dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segment 2 only.....16

— Lateral or dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segments 2 and 3 21

16. Abdominal segment 5 with a large pair of dorsolateral spines; rostral spine with small teeth or denticles distally, and with setae in later stages..... *Nectocarcinus antarcticus**

— Abdominal segment 5 lacking dorsolateral spines; rostral spine smooth 17

17. Zoea almost cruciform in posterior view with lateral carapace spines projecting horizontally; rostral spine > carapace length; telson with 2 or 3 small, spine-like setae near base of cornu on each side..... *Cancer novaezelandiae*

— Zoea with lateral carapace spines depressed; rostral spine < carapace length; telson lacking spines or small setae near base of cornu on each side.....18

18. Telson cornua smooth, with margins lacking a dense double row of short setae; propodus of maxilliped 1 endopod with a tuft of fine hairs .....*Hemigrapsus edwardsi*

— Telson cornua margins lined with a dense, double row of short setae; propodus of maxilliped 1 endopod lacking a tuft of fine hairs.....19

19. Antenna 2 exopod > 0.75 times the length of spiniform process.....*Helice crassa*

— Antenna 2 exopod < 0.75 times the length of spiniform process.....20

20. Maxilliped 1 endopod with a tuft of fine hairs on carpus..... *Macrophthalmus hirtipes*

— Maxilliped 1 endopod lacking a tuft of fine hairs on carpus ..... *Hemigrapsus crenulatus*

21. Telson lacking lateral or dorsal spines or setae near base of cornua ..... *Cyclograpsus lavauxi*

— Telson with lateral or dorsal spines or setae near base of cornua 22

22. Antenna 2 exopod almost as long as spiniform process; larvae < 5.0 mm total length .....*Cyrtomaia hispida*

— Antenna 2 exopod about 0.5 times or < 0.5 times as long as spiniform process unless larva is > 5.0 mm total length.....23

23. Rostral spine curved posteriorly..... *Macropipus corrugatus*

— Rostral spine straight or almost straight.....24

24. Antenna 2 exopod about 0.4 times the length of spiniform process, increasing to about equal its length in later stages ..... *Ovalipes catharus**

— Antenna 2 exopod not more than 0.35 times the length of spiniform process in any zoea stage..... *Portunus pelagicus*
Scylla serrata†

25. Lateral or dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segments 2–4.....
..... *Cyclograpsus insularum*

— Lateral or dorsolateral knob-like, hook-like, or spine-like protuberances present on abdominal segments 2–5.....26

26. Antenna 2 spiniform process much shorter than rostral spine; rostral spine denticulate ..... *Plagusia chabrus*

— Antenna 2 spiniform process almost as long as rostral spine; rostral spine smooth ..... *Carcinoplax*

27. Dorsal and rostral carapace spines present; *lateral carapace spines absent* (GROUP B) 28

— Dorsal and lateral carapace spines present; *rostral spine absent* (GROUP C) 38

— Dorsal carapace spine present; *rostral and lateral carapace spines absent* (GROUP D).....39

— Rostral and lateral carapace spines present; *dorsal carapace spine absent* (GROUP E).....40

— Rostral spine present; *dorsal and lateral carapace spines absent* (GROUP F).....41

— Carapace lacking all spines (GROUP G).....48

GROUP B

28. Telson with 1 robust spine or two small spines lateral to base of cornu on each side 29

— Telson lacking spines lateral to base of cornua, but 1 or 2 very small setae may be present laterally on each side.....36

29. Dorsal carapace spine and antenna 2 spiniform process both longer than carapace length.....*Notomithrax minor*

— Dorsal carapace spine and antenna 2 spiniform process both shorter than carapace length 30

30. Antenna 2 exopod no more than 0.5 times the length of spiniform process ..... *Eurynome*

— Antenna 2 exopod > 0.5 times the length of spiniform process.....31

31. Antenna 2 exopod < 0.66 times the length of spiniform process; total length of larva > 4.0 mm..... *Jacquinotia edwardsii*

— Antenna 2 exopod equal to or > 0.66 times the length of spiniform process; total length of larva < 4.0 mm.....32

32. Telson with 1 large spine and 2 small spines lateral to base of cornu on each side, the small spines about 0.5 times the length of the large spine..... *Leptomithrax tuberculatus mortenseni**

— Telson with 1 large spine and 2 small spines lateral to base of cornu on each side, the small spines very much less than 0.5 times the length of the large spine 33

33. Rostral spine < 0.66 times the length of dorsal carapace spine; antenna 2 spiniform process armed with a double row of spinules numbering > 25 per 0.50 mm in each row.....
..... *Notomithrax peronii*

— Rostral spine 0.66 or > 0.66 times the length of dorsal carapace spine; antenna 2 spiniform process armed with a double row of spinules numbering 25 or fewer per 0.05 mm in each row 34

34. Rostral spine > 0.66 times the length of dorsal carapace spine; antenna 2 spiniform process armed with a double row of spinules numbering > 15 per 0.05 mm in each row, and accessory spinules present..... *Eurynolambrus australis*

— Rostral spine about 0.66 times the length of dorsal carapace spine; antenna 2 spiniform process armed with a double row of spinules numbering < 15 per 0.05 mm in each row, accessory spinules absent.....35

35. Antenna 2 spiniform process with 7–11 spinules per 0.05 mm; maxilliped 2 endopod of 2 segments in zoea I; telson notch with a stout median posterior seta in zoea II.....
..... *Notomithrax ursus*

— Antenna 2 spiniform process with 7 spinules per 0.05 mm; maxilliped 2 endopod of 1 segment in zoea I; telson notch probably without a median posterior seta in zoea II.....
..... *Leptomithrax longimanus**

36. Dorsal carapace spine and rostral spine both longer than carapace length; both antenna 2 exopod and spiniform process at least as long as carapace length; lateral spine-like protuberances on abdominal segments 2–5... *Ommatocarcinus huttoni*

— Dorsal carapace spine, rostral spine, and antenna 2 spiniform process all shorter than carapace length; antenna 2 exopod reduced to a vestigial seta; dorsolateral protuberances on abdominal segments 2–4, the protuberances on segment 4 much the largest.....37

37. Dorsal carapace spine and rostral spine both longer than antenna 2 spiniform process; spiniform process with 4 rows of spines proximally, reducing to 2 rows distally, and numbering < 10 in longitudinal series.....*Planes marinus**

— Dorsal carapace spine and rostral spine both about as long as antenna 2 spiniform process; spiniform process with 4 rows of spines proximally, reducing to 2 rows distally, and numbering > 10 in longitudinal series.....*Leptograpsus variegatus*

GROUP C

38. Antenna 2 spiniform process about 0.66 times the length of dorsal carapace spine, and only a little longer than antenna 2 exopod; dorsolateral protuberances on abdominal segments 2 and 3 .....*Pilumnopeus serratifrons*

GROUP D

39. Abdominal segment 5 with a pair of large lateral spines considerably overlapping telson; antenna 2 exopod about as long as spiniform process; eyestalks without an anterior papilla .....*Achaeus fissifrons*

— Abdominal segment 5 lacking lateral spines; antenna 2 exopod about 0.75 times the length of spiniform process; eyestalks with a small anterior papilla ..... *Pyromaia tuberculata*

†There is no evidence that either of these species breeds in New Zealand waters. Sufficient details are provided in the main descriptive part of this work to separate their zoea larvae should this prove necessary.

GROUP E

40. Lateral carapace spines tending dorsolateral in origin and angled upwards; antenna 2 exopod reduced to a very small seta; abdomen and telson very narrow; 5 abdominal segments, and no pleopod buds in all zoea stages ..... *Hymenosoma depressum*

GROUP F

41. Abdominal segments 4 and 5 greatly inflated laterally, with lateral wings of segment 5 overlapping telson by about one-third 42

— Abdominal segments all very narrow, with segments 4 and 5 no wider than the first three 44

42. Carapace considerably higher than long (rostrum with an indistinct anterior hump; colour yellowish black) ..... *Elamena momona*

— Carapace only a little higher than long 43

43. Rostral spine with anterior and posterior humps; colour yellow ..... *Elamena producta*

— Rostral spine with anterior hump, but no posterior hump; colour dark red or black ..... *Elamena longirostris*

44. Rostral spine with a distinct anterior hump; telson with a pair of prominent anal spines ..... *Halicarcinus planatus**

— Rostral spine lacking an anterior hump; telson with a pair of weakly developed anal spines 45

45. Rostral spine > 1.25 times the vertical eye diameter 46

— Rostral spine < 1.25 times the vertical eye diameter 47

46. Rostral spine robust, straight but angled slightly anteriorly; colour black ..... *Halicarcinus varius**

— Rostral spine slender and curved anteriorly; colour blackish yellow ..... *Halicarcinus whitei**

47. Rostral spine straight and angled slightly forward; colour orange to transparent ..... *Halicarcinus cookii**

— Rostral spine straight and not angled forward; colour black to olive green ..... *Halicarcinus innominatus**

GROUP G

48. Development abbreviated; zoea stages absent, or confined to 1 non-planktonic zoea > 7.0 mm total length 49

— Development not abbreviated; zoea stages planktonic and all much smaller than 7.0 mm total length 51

49. 1 zoea stage ..... *Pilumnus lumpinus*

— No zoea stages 50

50. Confined to freshwater in northern N.Z. ..... *Amarinus lacustris*

— Confined to intertidal and shallow water marine habitats throughout N.Z. ..... *Pilumnus novaezelandiae*

51. Telson broad and spatulate, trilobed ..... *Pinnotheres novaezelandiae*

— Telson broad and spatulate, with no central lobe ..... *Ebalia laevis**

Key to the Megalopa Larvae

1. Setose natatory pleopods present on abdominal segments 2

— Setose natatory pleopods absent on abdominal sgments (GROUP A) 3

2. Setose uropods present on last abdominal segment (GROUP B) 9

— Setose uropods absent on last abdominal segment (GROUP C) 37

GROUP A

3. Exclusively freshwater ..... *Amarinus lacustris*

— Exclusively marine, or sometimes estuarine 4

4. Carapace almost perfectly circular in dorsal outline; distal segments of pereiopods 2–5 armed with long, evenly-spaced plumose setae along lateral margins; dactyl of pereiopods 2–5 lacking subterminal spines ..... *Hymenosoma depressum*

— Carapace not circular in dorsal outline; distal segments of pereiopods 2–5 lacking a fringe of long, evenly-spaced plumose setae; dactyl of pereiopods 2–5 with 1 or 2 subterminal spines 5

5. Rostrum with trilobed ventral keel ..... *Elamena longirostris**

— Rostrum lacking a ventral keel 6

6. Carapace with defined lateral postorbital and branchial angles; rostrum not trilobed 7

— Carapace lacking defined postorbital and branchial angles; rostrum trilobed 8

7. Rostrum tapering but terminally rounded and without well-defined antorbital angles; rostrum provided with long setae distally; dactyl of pereiopods 2–5 with a large subterminal spine but lacking an associated row of smaller spines ..... *Neohymenicus pubescens*

— Rostrum tapering to a point and with well-defined antorbital angles; rostrum lacking distal setae; dactyl of pereiopods 2–5 with a large subterminal spine and with an associated row of smaller spines along its distal half ..... *Elamena producta**

8. Rostrum with an apical tuft of curved setae; dactyl of pereiopods 2–5 with 2 subterminal spines ..... *Halicarcinus cookii**

— Rostrum without an apical tuft of curved setae; dactyl of pereiopods 2–5 with 1 subterminal spine ..... *Halicarcinus planatus**

GROUP B

9. Megalopa with a prominent rostrum and major accessory carapace spines 10

— Megalopa with or without a prominent rostrum and lacking major accessory carapace spines 13

10. One pair of supraorbital carapace spines present and longer than carapace 11

— Supraorbital carapace spines absent 12

11. Supraorbital carapace spines parallel and projecting forwards: carapace with long lateral spines ..... *Paromola petterdi**

— Supraorbital carapace spines widely divergent; carapace without lateral spines ..... *Latreillia australiensis*

12. Dorsal carapace spine located posteriorly, inclined upwards almost at right angles to forwardly directed rostrum ..... *Rochinia*

— Dorsal carapace spine located posteriorly, directed posteriorly in same plane as rostrum ..... *Cancer novaezelandiae*

13. Pereiopod 5 dactyl bearing long, terminally hooked setae ..14

— Pereiopod 5 dactyl without long, terminally hooked setae ..29

14. Uropods biramous, with setose exopod and large setose endopod ..... *Homola*

— Uropods uniramous, with setose exopod; endopod absent, or reduced to a tiny unarmed rudiment 15

15. Rostrum prominent in dorsal view, directed forwards and not depressed 16

— Rostrum not prominent in dorsal view, depressed or virtually absent 19

16. Rostrum broadly rounded rather than pointed; carapace strongly ridged and with a pair of posterior tubercles — 1 on each side of posterior midline; abdominal segment 5 lacking lateral spines ..... *Ozius truncatus*

— Rostrum tapered or pointed; carapace relatively smooth and not strongly ridged; paired posterior tubercles absent, but a single median posterior tubercle may be present; abdominal segment 5 with lateral spines 17

17. Pereiopod 1 with propodus swollen and broader than long; pereiopod 4 dactyl flattened; pereiopod 5 dactyl not flattened; uropods with endopod rudiment present ..... *Lyreidus tridentatus*

— Pereiopod 1 with propodus not swollen and longer than broad; pereiopod 4 dactyl not flattened; pereiopod 5 dactyl flattened into a slender paddle; uropods with no endopod rudiment 18

18. Carapace with a small, finger-like, median posterior tubercle; pereiopod 1 with an ischial spine and a carpal spine; pereiopod 4 with a straight coxal spine extending posteriorly to about halfway down abdominal segment 2 ..... *Portunus pelagicus*

— Carapace lacking a finger-like, median posterior tubercle; pereiopod 1 with an ischial spine but lacking a carpal spine; pereiopod 4 with a long, inwardly curved coxal spine extending posteriorly to about halfway down abdominal segment 3 ..... *Scylla serrata*

19. Carapace markedly pubescent and granular; pereiopod 5 superficially chelate; uropods with endopod rudiment ..... *Petalomera wilsoni*

— Carapace relatively smooth or with a few spines and setae; pereiopod 5 simple; uropods uniramous, with no endopod rudiment 20

20. Frontal regions of carapace waisted laterally and with anterolateral corners developed into a sharp, curved process ..... *Ommatocarcinus huttoni*

— Frontal region of carapace with relatively straight lateral margins and lacking curved anterolateral processes 21

21. Abdominal segment 5 with well-developed lateral spines ...22

— Abdominal segment 5 lacking prominent lateral spines 25

22. Pereiopod 5 dactyl flattened into a slender paddle 23

— Pereiopod 5 dactyl not flattened 24

23. Rostrum depressed by about 90°; pereiopods 2 and 3 with coxal spines but lacking a basial spine; pereiopod 5 dactyl bearing 3 long terminally hooked setae; uropod exopods with 12 setae; carapace length little more than 2 mm ..... *Nectocarcinus antarcticus**

— Rostrum depressed by about 45°; pereiopods 2 and 3 lacking coxal spines but with a basial spine; pereiopod 5 dactyl bearing 6 or 7 long terminally hooked setae; uropod exopods with 22–24 setae; carapace length 4.4 mm to almost 5 mm ..... *Ovalipes catharus**

24. Lateral spines on abdominal segment 5 not reaching beyond posterior margin of segment 6; abdominal segments 2–4 with short, triangular lateral spines; telson with 2 very small posterior setae ..... *Helice crassa*

— Lateral spines on abdominal segment 5 reaching beyond posterior margin of segment 6; abdominal segments 2–4 lacking lateral spines; telson without posterior setae ..... *Macrophthalmus hirtipes*

25. Pereiopod 5 dactyl flattened into a slender paddle ..... *Macropipus*

— Pereiopod 5 dactyl not flattened 26

26. Carapace length > 7 mm; frontal region of carapace with 2 large anterior lobes and 2 smaller anterolateral lobes; propodus of pereiopod 1 strongly ridged; dactyl of pereiopod 5 with 4 long, terminally hooked setae; uropod exopods with about 40 plumose setae ..... *Plagusia chabrus* (megalopa II)

— Carapace length < 7 mm; frontal region of carapace not lobed; propodus of pereiopod 1 smooth and not ridged; dactyl of pereiopod 5 with 3 long, terminally hooked setae; uropod exopods bearing < 30 plumose setae 27

27. Uropod exopods bearing > 15 plumose setae ..... *Planes cyaneus**

— Uropod exopods bearing < 15 plumose setae 28

28. Pereiopods 2–4 with a sharp distal spine on propodus and with several medial marginal teeth on dactyl; abdominal segment 5 with a pair of blunt, poorly developed lateral spines ..... *Hemigrapsus*

— Pereiopods 2–4 lacking a distal spine on propodus or medial marginal teeth on dactyl; abdominal segment 5 without lateral spines ..... *Cyclograpsus*

29. Carapace with a pair of short but prominent protogastric spines ..... *Carcinoplax*

— Carapace lacking protogastric spines 30

30. Carapace broader than long, with stout plumose setae in frontal region; dorsal surface of carapace hirsute, but lacking short spines or tubercles 31

— Carapace longer than broad, lacking stout plumose setae in frontal region; dorsal surface of carapace with few or no setae, but 1 or more short spines or tubercles present in most species 32

31. Carapace with a single postorbital spine on each side; uropod exopod with 7 setae ..... *Pilumnus lumpinus*

— Carapace with 3 postorbital spines on each side (1 large spine flanked by 2 smaller spines); uropod exopod with 8 setae ..... *Pilumnus novaezelandiae*

32. Rostrum depressed by much more than 45° 33

— Rostrum depressed by about 45° or less 34

33. Carapace with 1 or no prominent tubercles; uropod exopod probably with 4 or more setae ..... *Ebalia*

— Carapace with numerous prominent tubercles; uropod exopod probably with < 4 setae ..... *Eurynome*

34. Carapace dorsal tubercles very prominent; telson with a small median posterior prominence ..... *Notomithrax minor*

— Carapace dorsal tubercles not prominent; telson margin smooth and gently rounded, lacking a median posterior prominence 35

35. Uropod exopod with 5 plumose setae; pereiopod 1 lacking an ischial spine ..... *Eurynolambrus australis*

— Uropod exopod with 4 plumose setae; pereiopod 1 with an ischial spine 36

36. Pereiopod 3 with an ischial spine ..... *Notomithrax peronii*

— Pereiopod 3 lacking an ischial spine ..... *Notomithrax ursus*

GROUP C

37. Carapace with pronounced spines and tubercles ..... *Achaeus fissifrons*

— Carapace lacking spines or tubercles 38

38. Abdomen with 3 pairs of pleopods ... *Cymonomus bathamae**

— Abdomen with 4 pairs of pleopods 39

39. Carapace length > 1 mm; antenna 2 flagellum of 3 segments only ..... *Heterozius rotundifrons*

— Carapace length < 1 mm; antenna 2 flagellum of more than 3 segments ..... *Pinnotheres*

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APPENDIX: REARING OF CRAB LARVAE

A satisfactory way of rearing crab larvae is to hatch them from ovigerous female crabs, place a very few larvae in a small container of fresh sea water changed daily, and feed them with newly hatched *Artemia* (brine shrimp) nauplii. Brachyuran larvae captured along with other zooplankton will remain alive for

only an hour or two unless removed soon after capture and treated as described for larvae hatched in the laboratory.

Although the larvae of New Zealand Brachyura can be reared at temperatures anywhere between 12°C and 20°C, the most satisfactory results are obtained between 16°C and 18°C and with minimal temperature fluctuation. It is often helpful to rear the larvae in conical containers gently aerated from the narrower bottom so as to keep the larvae in constant, slow circulation.

Hatching larvae from ovigerous females taken from water deeper than 100 m presents some difficulty, since eggs with larval eyespots developed (usually within about two weeks of hatching) tend to hatch spontaneously after reaching the surface, presumably due to abruptly decreased pressure or increased temperature, or both. The larvae are not fully formed and quickly die. Similarly, newly spawned eggs often fail to develop. Best results with deep-water crabs are achieved either by being fortunate enough to obtain a female with eggs on the point of hatching, or by keeping females carrying eggs about mid-way through development in the laboratory for several weeks at below about 12°C, thus allowing the eggs to acclimatise and continue normal development. Generally, larval survival is low, but eggs from ovigerous females of both *Achaeus fissifrons* and *Cyrtomaia hispida* (Majidae), captured in water deeper than 200 m, were hatched and the larvae subsequently reared using this second method.

INDEX

Bold numerals indicate major references; italic numerals indicate a text-figure.

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