ISSN 2538-1016; 34

NEW ZEALAND
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

New Zealand Oceanographic Institute Memoir No. 34

The Marine Fauna of New Zealand: Family Hymenosomatidae (Crustacea, Decapoda, Brachyura)

MARY J. MELROSE

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New Zealand Oceanographic Institute Memoir No. 34, 1975. 123 pp., 58 figs, 2 pl., refs, index.
ISSN 0083–7903

ABSTRACT

Approximately 1,800 specimens of hymenosomatids from 14 species belonging to 4 genera, have been examined. A new genus intermediate in character between the genera *Halicarcinus* and *Elamena* has been established. The classification used follows that of Balss (1957). Literature on the New Zealand species is relatively sparse: the original descriptions and figures of the type specimens collected by Filhol, Dana, and Jacquinot in the early nineteenth century are extremely sketchy, but species discovered more recently, for example *Halicarcinus lacustris* (Chilton), have been more adequately described. The types of the earlier recorded species are lodged in Paris and London. Unequivocal identification of two New Zealand species, here referred to as *Halicarcinus cookii* and *Halicarcinus varius*, must wait a thorough examination of the types.

Garth (1958) and Gordon (1940) indicated the value of the form of the first male pleopod in classification at the specific level, and this appendage has been figured wherever possible.

With the exception of the freshwater crab *Halicarcinus lacustris*, the subantarctic species *Halicarcinus planatus*, and *Halicarcinus ovatus*, all the species are endemic to New Zealand. *Halicarcinus ovatus* is an Australian species which has been ascribed to New Zealand as well (Heller 1868) although none were found in any New Zealand collection; however, it is included as an aid to future identification. *Halicarcinus planatus*, a widespread subantarctic species, is amply represented by specimens from Auckland and Campbell Islands, in Dominion Museum collections. The only authenticated occurrence of *Halicarcinus planatus* in New Zealand coastal waters is noted by Richardson (*in* Garth 1957, p. 33) who collected specimens from Cook Strait. The whereabouts of these specimens is unknown.

All the specimens described are found intertidally, with the exception of *Halicarcinus lacustris* (from fresh water), *Elamena longirostris* (from continental shelf) and two new species both from subtidal depths. Preliminary investigations were made of the ecology of *Halicarcinus cookii*, *Halicarcinus varius*, *Halicarcinus innominatus*, *Halicarcinus whitei*, *Halicarcinus pubescens*, and *Elamena producta*. The substrate and food preferences, salinity tolerances and the behaviour and colour patterns of these species have been described.

Differences in substrate preferences, tolerance to salinity changes, and possibly resistance to desiccation, appear to be most important in determining the distribution of species. All marine species from mainland shores are distributed throughout New Zealand. (On the other hand, the freshwater *Halicarcinus lacustris* is restricted to northern New Zealand.) It appears that the common marine hymenosomatid species are tolerant of regional temperature variations. Local conditions at certain levels on the shore and competition are more important limiting factors.

There is an apparent absence of overlap between New Zealand and Australian littoral species of Hymenosomatidae. However, the only New Zealand freshwater species, *Halicarcinus lacustris*, is shared with Australia. Specimens of this species from the two countries differ remarkably little and divergence has not reached even subspecific level.

Inset 1*

INTRODUCTION

The position of the family Hymenosomatidae within the Brachyura according to Balss (1957) is:

Phylum Arthropoda
Class Crustacea
Subclass Malacostraca
Division Eucarida
Order Decapoda
Suborder Reptantia
Tribe Brachyura
Subtribe Brachygnatha
Superfamily Oxyrhyncha
Family Hymenosomatidae

Members of the Brachygnatha have a square mouth-frame, the last pair of legs is rarely reduced in size or carried up on the carapace, and in the female the oviducts open on the sternum and there is no trace of appendages on the first abdominal somite.

Most shore crabs belong to Superfamily Brachyrhyncha. They possess an oval, round, or square carapace, rounded or square-cut in front with hardly any rostrum and usually with enclosed orbits. The Oxyrhyncha are distinguished by their semitriangular or, rarely, subcircular carapace with a rostrum and relatively incomplete orbits. The nearest relatives of the Oxyrhyncha within the Brachyrhyncha have been suggested to be the cancroid or cyclometopous, and not the grapsoid or catometopous crabs.

Three families, the Majidae (Maiidae) (Griffin 1966), Hymenosomatidae, and Parthenopidae comprise the Oxyrhyncha. Species of Majidae are the most numerous. The Parthenopidae are not represented in New Zealand.

Borradaile (1907) gives the following key to the families of the Oxyrhyncha:

1 Carapace thin and flat. First legs (chelipeds) not long or especially mobile or with fingers bent at angle to the hand. Male opening sternal. No orbits. Second joint of antennal stalk slender. Fused with epistome but not with front. No hooked hairs. . . . . Hymenosomatidae

2 Carapace not thin and flat. First legs either mobile or powerful, with bent fingers. Male opening coxal.
(a) Chelipeds especially mobile, rarely much greater than other legs, or with fingers bent at angle on hand. Second joint of antenna well developed, generally fused with epistome and often with front. Orbits generally more or less complete. Hooked hairs almost always present. . . . . Majidae
(b) Chelipeds not especially mobile, usually much longer and heavier than other legs, and with fingers bent on hand at angle towards the side on which fixed finger is set. Second joint of antenna small, short and not fused with epistome or front. Orbits well made. Hooked hairs almost always wanting. . . . . Parthenopidae

The Hymenosomatidae are found almost exclusively in the Indo-Pacific. The majority of species inhabit Australia (Montgomery 1929) and New Zealand. However, the family is represented in China and Japan, across the Indian Ocean in India and Africa, in New Caledonia and on the west coast of America where *Halicarcinus planatus*, characteristic of subantarctic regions, is the only species found. New Zealand shares the genera *Halicarcinus* and *Elamena* with Australia. The monotypic genus *Cyclohombronia* (previously known as *Hombronia*) is endemic to New Zealand, although it is closely related to the monotypic African genus *Hymenosoma*. *Halimena* gen. nov. is also monotypic and endemic to New Zealand. *Rhynchoplax* and *Neorhynchoplax* are tropical genera which replace *Halicarcinus* north of Australia. *Hymenicoides* and *Elamenopsis* are both monotypic tropical genera.

At the specific level, there is a high percentage of endemism, 10 of the 12 species represented in New Zealand collections being restricted to the mainland shores of this country. One is shared with Australia, and it is of subantarctic distribution and rarely found near the mainland of New Zealand. The New Zealand Majidae are also typically Indo-West Pacific; at the generic level there is an overwhelming Australian element, and 13 of the 18 New Zealand species are endemic (Griffin 1962).

The majority of Hymenosomatidae are marine. Most Indian species inhabit estuaries or lagoons where the water is of low or variable salinity (Kemp 1917). *Halicarcinus australis* is a common euryhaline Australian species, and *Halicarcinus whitei* and *Halicarcinus varius* are New Zealand species which inhabit sea water of normal and lowered salinity. At least two species inhabit pure fresh water permanently: the Indian *Rhynchoplax introversus* and the Australian and New Zealand species *Halicarcinus lacustris*, which has been taken from lakes 1,000 m above sea level. (Six species of Hymenosomatidae now are recorded from fresh water, *see* Holthuis 1968.)

In New Zealand, hymenosomatid species are typically littoral or sublittoral, although *Halicarcinus planatus* has been taken at a depth of 500 m at Tierra del Fuego (Garth 1958, p. 34). Four New Zealand species, *Halicarcinus cookii*, *Halicarcinus varius*, *Halicarcinus pubescens*, and *Halicarcinus innominatus*, can colonise hard shores as high as the lower mid-littoral zone. The first two extend to the top of this zone, as both inhabit the band of *Hormosira* present there on sheltered shores. *Halicarcinus pubescens* may be found in *Corallina* below the *Hormosira* band and under rocks or on the open reef in the barnacle zone on exposed shores. *Halicarcinus innominatus* is commonly associated with *Perna canaliculus*, which grows in the lower mid-littoral. *Elamena producta* is found in rock pools in the *Corallina* zone. On soft shores, *Halicarcinus whitei* may be found at the top of the lower mid-littoral sometimes with *Halicarcinus varius*.

New Zealand hymenosomatids are not very resistant to desiccation, possibly because they are small and have

a thin carapace. The two soft-shore species burrow just below the surface and remain there while the tide is low, and seaweed inhabiting species crawl under water-retaining algae such as *Hormosira*.

Some species are excluded from all but clean, constantly agitated water. Even those that live on soft shores are found only where there is an abundance of fine sand, with some shell but relatively little silt which would clog the gills. It is possible that the absence of podobranchs on the maxillipeds makes respiration more easily disrupted in this family than in the Majidae.

At least one species of hymenosomatid may be found on almost any beach, reef, or wharf pile in New Zealand, but their small size, cryptic coloration and behavioural reactions to any disturbance make them difficult to detect. Although small, they play an important role in many shore zone communities, eating debris or catching live prey, and providing an important food source for many fish (Graham 1938).

The Majidae rely for camouflage on their masking behaviour. They take algae, sponges, and anemones from their immediate environment and place these on the carapace, where thickly scattered curved hairs hold this material. Sponge crabs (Tribe Dromiacea) hold pieces of sponge with their back legs which are bent up over the carapace. The Hymenosomatidae rely on the cryptic colour patterns formed by chromatophores in the exoskeleton. Disruptive banding and paired pseudo "eyes" on the posterior border of the carapace are common. However, on the carapace of some species there are well developed hairs that are sometimes curved like those of the Majidae. Most of these hairs have secondary feathering which helps to retain particles of sand. Although hymenosomatids do not select and place material on the carapace, the hairy nature of the carapace in some species, for example *Halicarcinus pubescens*, encourages the growth of bryozoans and sponges. Other species with sparse hair still provide settling space for sessile animals (*Elminius*, *Perna*, *Spirorbis*, and *Pomatoceros* species), and even the anemone *Actinothoe* rests temporarily on their carapaces. Algal sporelings growing on these crabs rarely develop past the four-cell stage, Hymenosomatids living in algae frequently burrow backwards under scraps of seaweed and occasionally they may be observed carrying a tuft of *Corallina* over the hind carapace. This is held in place by the hind legs which bend upwards and over just like those of the sponge crabs. The hind legs may also be bent up in this manner when the crab clings to growing fronds of algae, or grasps the inside of the gaping valve of a dead mussel.

Chilton (1907) considered that the elongated, hair-fringed legs of *Cyclohombronia depressa* indicated that the animal could swim. This species was not obtained alive in the present study, but Dr R. G. Wear (pers. comm.) has observed vigorous and prolonged swimming activity in this species. Burrowing occurs in *Halicarcinus whitei* and *Halicarcinus varius*. The posterior carapace is levered backwards and downwards into the sand as the crab shifts back and forth on its splayed walking legs. No permanent burrows are constructed and *Halicarcinus varius*, the only species which penetrates as far as 5 to 8 cm below the surface, relies on its own respiratory current to clear a space between the sand grains, rather than maintaining a permanent burrow entrance.

The highly developed patterns of courting and territorial behaviour displayed by grapsid crabs (Beer 1959) were not observed in the Hymenosomatidae. The larger males of some species adopted aggressive display postures in response to disturbance or to the presence of other males. In most species, the claws of the chelae were usually banded at their base with orange or red and always tipped with white, so that they were more conspicuous than the darker palm. When the males reared up aggressively on the dactyls of their walking legs, with their chelipeds extended and the ventral surface of the body off the ground they appeared larger than before. This reaction is similar to the *aufbaumreflex* described by Beer. Often the *aufbaumreflex* was followed by retreat or by defensive responses. Each species possessed a typical defensive pattern of behaviour. In some, a series of stereotyped reactions was produced and any one of the postures adopted might be held.

Autotomy is developed to a considerable degree. Rough treatment or the introduction of a noxious chemical will cause the shedding of most of the walking legs. The chelipeds, which are more robust and more essential for feeding, are not as readily shed.

Young stages of Hymenosomatidae occur in the plankton, and adults have been collected from storage tanks where their only mode of access would be as larvae. Previous work on the life history of overseas species includes that of Gurney (1938) and Aikawa (1929). The zoea of *Halicarcinus cookii* figured here, agrees in the form of the telson and the first and second maxillipeds, and in the absence of a rostral spine, with Gurney's figures (1938) of *Elamena mathaei*.

Food and substrate preferences, salinity tolerance, resistance to desiccation, and behavioural reactions of six common species, *Halicarcinus cookii*, *Halicarcinus varius*, *Halicarcinus innominatus*, *Halicarcinus pubescens*, *Halicarcinus whitei*, and *Elamena producta*, were briefly studied, and notes are included on the freshwater species *Halicarcinus lacustris*.

Diagnosis of the Hymenosomatidae
(adapted from Garth 1958)

Carapace thin, flat, triangular or subcircular, poorly calcified, usually produced to form a horizontal rostrum. Antennular fossae shallow and ill-defined. Antennal peduncle slender. Buccal cavern square; epistome sometimes nearly as long as broad. Ischium of the external maxillipeds well developed; palp articulating near the antero-external angle of the merus; exognath slender and partly or entirely concealed. Male openings sternal (Alcock 1900).

Inset 2

Chelipeds not long or especially mobile or with fingers bent at an angle to the hand. No orbits; eyes exposed and a little contractile. Second segment of antennal stalk slender, fused with epistome but not with front (Borradaile 1907).

Pleopod 1 varying, especially in the apex. Pleopod 2 short (Stephenson 1920).

Position of the Family Hymenosomatidae

The Oxyrhyncha were established as a subdivision of the Brachyura by Latrielle in 1803, and at this time included Maioids, Oxystomes, and some Anomura. Not until 1839 did de Haan refer the species *Ocypode* (*Elamene*) *unguiformis* to the "Majacea", thus recognising the affinity between the Majidae and the Hymenosomatidae, although the Hymenosomatidae were still not recognised as a separate family.

Before 1839 hymenosomatid species were always regarded as catometopous, not cyclometopous crabs. The controversy over their position has continued to the present day.

In 1834 H. Milne Edwards placed *Hymenosoma* in the Tribe Pinnotheriens among the Catometopa. Subsequently Dana (1851, 1852) and Haswell (1882b) amended this classification to Family Pinnotheridae, Subfamily Hymenicinae. Miers (1876b) gave the classification of *Halicarcinus* as F. Pinnotheridae, Subfamily Hymenosominae. By 1853 Milne Edwards had recognised *Hymenosoma* as separate from the Pinnotheridae and placed it in the Tribe Hymenosominae. Hodgson (1902), Hutton (1904), and Baker (1906) all retained hymenosomatid species in the family Pinnotheridae or Pinnoteridae without any mention of a Subfamily.

White (1846) placed his new genus *Halicarcinus* in the Family Mictyridae of the Catometopa. Alcock (1900) regarded the Hymenosomatidae as an aberrent family of Catometopous crabs more closely related to the Mictyridae than to the Pinnoteridae (in this he agreed with White), and having "a superficial resemblance to some of the Oxyrhynch crabs of the Inachine subfamily".

Carcinologists other than Alcock, who have regarded the Hymenosomatidae as a separate family of Catometopes, include Stimpson (1858), Stebbing (1900, 1914), and Fulton and Grant (1902). The main reason for this view is the sternal position of the male genital apertures in the Hymenosomatidae. In addition, the branchiae are fewer than nine on each side, as they are in most Catometopes.

However, the Hymenosomatidae differ from catometopous crabs in having a round or triangular carapace, a conspicuous rostrum, longitudinally folding antennules and an obvious epistome in all genera but one, also in lacking orbits; the antennae too are different. Therefore most taxonomists who have recently worked with this family, e.g. Borradaile (1907), Kemp (1917), Tesch (1918), Rathbun (1925), Hale (1927b), Montgomery (1931), Balss (1930), Gurney (1938), Richardson (1949a), Garth (1957), and Bennett (1964), follow de Haan in placing the Hymenosomatidae in the Oxyrhyncha near the Majidae.

However, Gurney (1938) pointed out that the zoeae of Hymenosomatidae are similar to those of the Pinnotheridae, and even similar to those of the family Leucosiidae in the Oxystomata. They have nothing in common with the larvae of the Oxyrhyncha.

Validity of the Family name Hymenosomatidae

The following family names have been used in the literature: Hymenosomidae, Hymenosomatidae, Pinnotheridae, and Pinnoteridae.* It is now recognised that the family is separate from the Pinnotheridae so that only the first two names need concern us.

"Hymenosomidae" was first used in 1838 by MacLeay, and subsequently by Stimpson (1858), Ortmann (1894), Alcock (1900), Baker (1906), Fulton and Grant (1902, 1906), Rathbun (1925), Balss (1929, 1930), Tesch (1918), Richardson (1949a), Garth (1958), Dell (1963), and others.

Ortmann in 1894 recorded the family as Hymenosomidae nov. fam. and made no reference to Stimpson's 1858 paper, so it is possible that the two authors came to independent and strangely coincidental decisions on nomenclature. Although some authors, e.g., Alcock, have written of the family Hymenosomidae Ortmann, most use the appellation Hymenosomidae Stimpson.

A few writers have consistently used "Hymenosomatidae" as the family name. They include Hale (1929 1931), Montgomery (1929), and Kemp (1917). Several workers have used both forms in different articles. Stimpson himself began the confusion, but his 1858 "Hymenosomidae" predates his use of "Hymenosomatidae" in 1908. Stebbing used "Hymenosomidae" in 1900 and "Hymenosomatidae" in 1914. Borradaile switched from "Hymenosomidae" (1907) to Hymenosomatidae" (1916). Balss used "Hymenosomidae" in 1929 and 1930, but "Hymenosomatidae" in 1957. Stephenson compromised by employing brackets—"Hymenosom(at)idae in 1927.

It is clear from the 1961 edition of the International Code of Zoological Nomenclature (Appendix D, 129) that family names formed from Greek word "soma" are to be latinised as "-somatidae". (*See also* Holthuis (1968) for a discussion of the correct form of this family name.)

*Milne Edward's use of Hymenosominae in 1853 must be considered a valid introduction of the family Hymenosomatidae even though he did use it for a Tribe of the family "Ocypodiens", which also included the Pinnotheridae. Miers (1876b) also used Hymenosominae, but as a name of a subfamily.

Genera of Hymenosomatidae

Balss (1957) provided the following list of genera, which has been chronologically arranged and somewhat modified:

Hymenosoma Desmarest, 1825. 1 species from southern Africa.
Elamena H. Milne Edwards, 1837. Approximately 8 species. Indo-pacific and West Africa.
Halicarcinus White, 1846 (=*Hymenicus* Dana, 1852). Approximately 16 species, chiefly from the shores of Australia, New Zealand, Japan, and South America. Isolated species in fresh water in New Zealand, New Caledonia, New Guinea, and the Philippines.
Trigonoplax H. Milne Edwards, 1853. About 8 species. Indo-pacific and West Africa.
Rhynchoplax Stimpson, 1858. Approximately 4 species. South Africa to Japan and China.
Elamenopsis A. Milne Edwards, 1873. 1 species. Celebes, New Caledonia, from a coral reef.
Hymenicoides Kemp, 1917. 1 species, at Calcutta in brackish and fresh water.
Neorhynchoplax Sakai, 1938. (=*Rhynchoplax autorum*). About 13 species, chiefly coastal.

Three main reviews of the Hymenosomatidae have been written by Kemp (1917), Tesch (1918), and Sakai (1938). I was unable to obtain Sakai's paper, but Kemp and Tesch described all the genera, with the exception of *Neorhynchoplax*, which Sakai established to include most of the species previously placed under *Rhynchoplax* by Kemp and Tesch. New Zealand species are variously referred to the genera *Halicarcinus*, *Hymenicus*, *Elamena*, and *Hymenosoma* by Tesch and Kemp.

Kemp followed Alcock (1900) in regarding *Trigonoplax* as merely a subgenus of *Elamena*. Tesch preferred to leave them separate, as did Balss. Gordon (1940) agreed with Kemp.

Balss, however, followed Kemp in uniting *Halicarcinus* and *Hymenicus*, which Tesch regarded as separate entities.

Graham (1938) used the generic name *Hombronia* for the New Zealand species which had previously been referred to as either *Hymenosoma depressum* or *Halicarcinus depressus*. Since *Hombronia* Lucas, 1853, cannot be used for this species a new generic name must be chosen, and I am proposing *Cyclohombronia*. Finally, material found during the present study required a second new genus so that the following genera should be added to Balss's list:

Cyclohombronia gen. nov. 1 species from New Zealand
Halimena gen. nov. 1 species from New Zealand

Previous work on New Zealand material

In this account the spellings of species names vary, depending on the spelling used by the author under discussion.

The first specimens of Hymenosomatidae from New Zealand were collected on D'Urville's 1837–1840 cruise of the *Astrolabe* and *Zelee*, Hombron and Jacquinot were zoologists on the cruise but their paintings and Lucas's manuscript were not published until 1853. Two species, *Hymenosoma depressum* and *Hymenosoma*? *tridentatum* were described by Lucas, Jacquinot's plate of the first species being labelled *Hymenosoma depressa*.

Meanwhile Dana (1851, 1852) had already published his account of the species collected by Wilkes's U.S. Exploring Expedition of 1840. Dana described *Halicarcinus pubescens*, *Hymenicus varius*, *Hymenicus pubescens*, and *Hymenicus Novi-Zealandiae* (which he regarded as a probable synonym of *Hymenicus varius*) from New Zealand.

H. Milne Edwards (1853) redescribed several of these species. He referred Jacquinot and Lucas's *Hymenosoma tridentata* to *Halicarcinus planatus* (Fabricius), and mentioned *Halicarcinus depressus* and *Elamena quoyi* as coming from New Zealand.

Heller (1868) reported *Halicarcinus planatus*, *Hymenicus varius*, and *Hymenicus pubescens* from Auckland, in his "Crustaceen" of the *Novara* Expedition of 1857–1859.

The publication in 1876 of a "Catalogue of the Stalk- and Sessile-eyed Crustacea of New Zealand" by Miers marked the first attempt to list all known New Zealand species. Miers listed *Halicarcinus planatus* (with the synonyms *Hymenosoma*? *tridentatum* and *Halicarcinus ovatus* Stimpson), *Hymenicus varius* (with which *Hymenicus Novi-Zealandiae* was synonymised), *Hymenicus pubescens*, *Hymenicus depressus*?, *Elamena quoyi*, and *Elamena whitei* (which Miers himself had described earlier the same year). He realised that *Halicarcinus depressus* White was a different species from *Hymenosoma depressum* Jacquinot and Lucas.

In 1878 Kirk described *Elamena producta*. Hutton (1882) compiled "The Stalk-eyed Crustacea of New Zealand", including a discussion which became known as the "Black List", where Hutton reprimanded Miers for including species in his catalogue that were not represented in collections in this country. Hymenosomatidae in this category were *Elamena quoyi* and *Elamena whitei*.

Elamena ? *lacustris* and *Hymenicus marmoratus* were described by Chilton in 1882. In 1883 he assigned *Elamena* ? *lacustris* to the genus *Hymenosoma* and expanded the description.

Filhol published very brief descriptions of three new species, *Hymenicus edwardsii*, *Hymenicus cookii*, and *Hymenicus haasti* in 1885a. In "Mission de l'Ile Campbell" he redescribed these (1886) and added *Halicarcinus huttoni*, *Elamena longirostris*, and *Elamena kirki*. He also listed and redescribed the previously recorded species *Halicarcinus planatus* and *Halicarcinus tridentatus*.

Ortmann (1894) incorrectly listed Heller's Auckland record of *Hymenicus pubescens* Dana under *Halicarcinus planatus* var. *pubescens*, having apparently confused Dana's separate species *Halicarcinus pubescens* (from Patagonia) and *Hymenicus pubescens* from New Zealand. Only *Halicarcinus pubescens* has been regarded by later systematists as a synonym of *Halicarcinus planatus*.

Fulton and Grant (1902, 1906) reported the presence of *Hymenosoma lacustris* Chilton in Australian lakes

and rivers. Chilton, who has been the principal New Zealand worker on the Hymenosomatidae this century, made this species the subject of papers in 1906a, 1911b, 1914 and 1919. In his list of Crustacea from the Chatham Islands (1906), he noted *Halicarcinus planatus*, *Hymenicus marmoratus*, and *Elamena producta*. In 1907 he described and figured the male of *Hymenosoma depressum*, as only the female had previously been known. He briefly discussed the position of *Halicarcinus planatus*, *Halicarcinus tridentatus*, and *Halicarcinus ovatus* in 1909. He reported *Halicarcinus planatus* var. *tridentatus* from the Chathams and from 65 m near Cape Palliser, and *Elamena producta* from Stewart Island in 1911. He considered *Elamena kirki* to be a synonym for *Elamena producta*, which Lenz (1901) had regarded as a variable species.

In 1904 Hutton produced the "Index Faunae Novae Zealandiae", which listed all previously discovered species: *Halicarcinus planatus*, *Halicarcinus tridentatus*, *Halicarcinus huttoni*, *Hymenicus varius*, *Hymenicus pubescens*, *Hymenicus haasti*, *Hymenicus depressus*, *Hymenicus edwardsii*, *Hymenicus marmoratus*, *Hymenosoma lacustris*, *Elamena quoyi*, *Elamena whitei*, *Elamena longirostris*, *Elamena kirki*, and *Elamena producta*.

Thompson (1912) reported *Halicarcinus planatus*, *Hymenicus varius*, *Hymenicus pubescens*, *Hymenosoma depressum*, and *Elamena producta* from Otago Harbour, and recorded some species from fish stomachs. He regarded the zoea as a source of fish food. Graham (1938), after finding Hymenosomatidae in the stomachs of 26 fish species, concluded that adults were a very important food source for many fish.

Borradaile (1916) reported a damaged specimen, possibly *Elamena longirostris*, in plankton near New Zealand taken by the Terra Nova Expedition.

Kemp (1917) included most New Zealand species in the genus *Halicarcinus* as he regarded *Hymenicus* as a synonym of White's genus, and also thought that *Hymenosoma depressa* Jacquinot and Lucas probably belonged to *Halicarcinus*. He placed *Halicarcinus lacustris* in this genus also. Kemp stated that Lucas's "*Hombronia*" had been suggested as a generic name for Jacquinot's *Hymenosoma depressa*. However, Lucas originally proposed this name for a new genus to which he thought *Hymenosoma* ? *tridentatum* probably belonged, for he was ignorant of White's genus *Halicarcinus*.

Tesch (1918) separated *Halicarcinus* from *Hymenicus*, to which he assigned most of the New Zealand species. He allowed *Hymenosoma depressum* to remain in the original genus and synonymised *Elamena quoyi* with *Hymenicus pubescens* without reference to actual specimens.

Chilton and Bennett (1929) attempted to disperse some of the confusion by listing the New Zealand Hymenosomatidae. They listed *Halicarcinus planatus* and *Halicarcinus tridentatus* separately, united *Elamena producta* and *Elamena kirki*, and left *Hymenosoma depressum* and *Hymenosoma lacustris* in the original genus.

Young (1929) included *Halicarcinus planatus*, *Halicarcinus planatus* var. *tridentatus*, *Hymenicus marmoratus*, and *Elamena producta* in his survey of the marine fauna of the Chatham Islands.

Bennett (1930) briefly mentioned the family in his notes on New Zealand Brachyura. He stated that the synonymy of *Halicarcinus planatus* given by him in 1929 was incorrect, and that "*Hymenosoma*" *depressum* required a new genus. His full account of these changes has never been published. In "The Marine Fauna of New Zealand: Crustacea Brachyura", published in 1964, Bennett merely listed all the known species of Hymenosomatidae, included two photographs, and provided a comprehensive bibliography of New Zealand Brachyura.

Gordon (1940), who described and figured the species of *Elamena* in the British Museum, included a description of *Halicarcinus whitei* which she transferred from *Elamena*.

Powell (1936) discussed animal communities of the Manukau and Auckland Harbours in which *Halicarcinus planatus* occurred.

Richardson (1949a, b) gave a key to the New Zealand Hymenosomatidae. The taxonomic difficulties of the family were made obvious in his "Additions and Corrections for the Guides to the Brachyura", where he stated that "*Halicarcinus ovatus* in the key is actually *Halicarcinus planatus*, and as I had suspected, the species listed as *Halicarcinus planatus* in the key is a new species for which I propose the name of *Halicarcinus innominata*."

Ralph and Yaldwyn (1956) reported *Halicarcinus cooki* as a member of the *Maoricolpus* association in Otago Harbour.

Dell (1960) recorded *Elamena producta*, *Halicarcinus innominatus*, and *Halicarcinus cooki* from the 1954 Chatham Islands Expedition.

In a survey of Howick Beach, Wood (1962) found *Halicarcinus cooki* on the main beach, sheltered beach, and *Zostera* flat.

In a popular work, Dell (1963) figured *Halicarcinus innominatus*, *Halicarcinus planatus*, *Halicarcinus lacustris*, *Elamena producta*, and *Hombronia depressa*.

In addition to the above literature there are numerous papers on *Halicarcinus planatus*, which is found in the subantarctic islands of New Zealand, but rarely occurs in the coastal waters of the main islands. *Halicarcinus huttoni* from New Zealand has been synonymised with *Halicarcinus ovatus* by Heller, and several Australian and European writers have discussed the latter. The most relevant references to these two species are White (1846), Targionni-Tozetti (1877), Lenz (1901), Stebbing (1900, 1914), Hodgson (1902), Rathbun (1918, 1925), Stephensen (1927), Hale (1927, 1929–30), and Garth (1957, 1958).

Specimens of *Halicarcinus ovatus* sent by Dr J. S. Lucas from University of Western Australia are quite different from any New Zealand specimens I have seen, but as previous descriptions of *Halicarcinus ovatus* are insufficient, the species is redescribed here.

New Zealand species mentioned in the Literature

The original spellings are given here, although many species have been transferred subsequently to other genera.

x marks species which have been synonymised with previously discovered ones.

? marks species which are rare on the New Zealand mainland, if they occur here at all, but common elsewhere.

?*Halicarcinus planatus* Fabricius, 1775
Hymenicus varius Dana, 1851
Hymenicus pubescens Dana, 1851
x*Hymenicus Novi-Zealandiae* Dana, 1851
Hymenosoma depressum Jacquinot, 1853
x*Hymenosoma* ? *tridentatum* Jacquinot and Lucas, 1853
x*Elamena quoyi* H. Milne Edwards, 1853
?*Halicarcinus ovatus* Stimpson, 1858
Elamena whitei Miers, 1876
Elamena producta Kirk, 1878
Elamena ? *lacustris* Chilton, 1882
x*Hymenicus marmoratus* Chilton, 1882
x*Hymenicus Edwardsii* Filhol, 1885
Hymenicus Cookii Filhol, 1885
x*Hymenicus Haasti* Filhol, 1885
x*Halicarcinus huttoni* Filhol, 1886
Elamena longirostris Filhol, 1886
x*Elamena kirki* Filhol, 1886
Halicarcinus innominata Richardson, 1949

Materials and methods

Apart from material collected by hand and from seaweed washings, collections at the Dominion (now National) and Auckland Museums, Auckland University, Victoria University of Wellington, and Kaikoura Research Stations were examined. Specimens were also sent from Canterbury University and Australia.

Specimens were preserved in 80 percent isopropyl alcohol. Weaker solutions allowed slow decomposition, and absolute alcohol made the specimens too brittle.

The appendages were removed with jeweller's tweezers and tungsten needles, sharpened by dipping their tips in molten nitrite.

Figures of whole crabs were drawn to scale, using a grid eyepiece in a binocular microscope and graph paper. A camera lucida and monocular microscope were used for drawing the mouthparts and male pleopods. These appendages were mounted in lactophenol (Salmon 1947), with a purple stain added.

Measurements were made either with a linear scale eyepiece in a binocular microscope or with calipers and a steel ruler marked in half millimetres. Both methods gave comparable good results.

Measurement standards followed those of Garth (1958, p. 27), except for the length of the rostrum which was defined by Rathbun (1925, p. 1).

The length of the carapace was measured along the median line from the posterior margin to the tip of the rostrum. The width of the carapace was measured in its widest part, usually across the branchial region, behind the second lateral teeth, but excluding the teeth from the measurement.

The length of the rostrum was measured from the "posterior line of the upper margins of the orbits" (Rathbun), i.e. from the centre of a line, often imaginary, crossing the carapace behind the eyestalks, to the extreme central tip of the rostrum. The width of the rostrum was measured at its base, along this line, to the carapace rim.

The lengths of individual segments of the legs were taken along their upper margins. The length of the propodus or palm of the cheliped was measured along the dorsal edge between the points of articulation with the carpus and the movable finger. This measurement differs from that of Garth, who included the immovable finger. The height of the palm was measured at its maximum. Garth stated that the length of the entire cheliped or walking leg should be measured along the lower margin, from the base of the coxa to the tip of the dactyl. However, it proved very difficult to consistently stretch the legs of Hymenosomatids out straight enough to make this measurement without causing the legs to be shed. Instead the lengths of the upper edges of the ischium, merus, carpus, propodus, and dactylus were added together to give the leg length. The upper edges of the leg segments are longer than the lower so that as the short coxa is left out, the measurements given here should compare quite well with those of Garth. The height of the leg segments was measured where it reached a maximum on the posterior face of the leg, at right angles to the longitudinal axis. This was usually at the distal end of a segment, except for the dactylus which tapered to a point distally.

The length of segments of the palp of the external maxilliped was taken along the posterior edge, adjacent to the merus. The length of the ischium and merus of the endopod was measured between the median extremity of the articulation of each segment with the two adjacent to it, parallel with the median edge.

The width of the epistome was measured anteriorly, between the inner free edges of the bases of the antennae. The length was taken along the median line, from the base of the interantennular septum (or from the point where the antennular bases meet if there was no septum) to the centre of the ridge bordering the mouthfield anteriorly.

Wherever possible measurements were taken from at least five male and five female specimens of each species.

Where the overall size of a crab was required, the measurement used was the maximum width of the upper carapace.

Allometric growth occurs in this family, so that the relative size of parts of the body depends often on the overall size of the specimen, Male specimens show mature characteristics when the carapace reaches a width of approximately 4 mm. The chelipeds enlarge and become more inflated, and a basal tooth appears on

the movable finger in most species. The walking legs become relatively slightly shorter in comparison with the carapace width. The eyes and rostrum grow little in length, so that they are relatively smaller in large specimens. Appendages, especially the mouthparts, become hairier with more rows of setae. In the females the abdomen is expanded laterally in mature specimens, and the pleopods change profoundly in shape and become pubescent at the moult which precedes egg-laying. Coloration also varies with age. Therefore, the following taxonomic descriptions are based on mature specimens.

For the study of live specimens, Hymenosomatidae from hard shores were kept in aquaria stocked with algae and under constant aeration. The algae were replaced fortnightly and the sea water renewed weekly. The level of sea water in the tanks was marked and distilled water was used to top up the level every 2 days. The normal algal populations of small crustacea, polychaetes, and molluscs were also introduced to the tanks, so that special feeding of the hymenosomatids was not necessary. The aquaria were kept on a work bench beside a window.

Species which inhabited soft substrates were kept in narrow glass aquaria with 15–23 cm of sand on the bottom and approximately 23 cm of water above. This sand was taken unsieved from a local beach, stored overnight, and all larger molluscs removed. Water renewal and the adding of distilled water followed the same schedule as for the other aquaria.

Chromatophore expansion and contraction was investigated. Specimens which were required in a dark-adapted state were kept overnight in an aerated bowl swathed with black paper. They were transferred in the dark to a small glass cell in the same bowl, which was then uncovered and placed on a sheet of white paper in bright light, and examined at intervals. Light-adapted individuals were transferred to a similar cell in a bowl which was also completely covered with black paper. The paper on top of the bowl was removed briefly at intervals so that the state of the chromatophores could be recorded.

Paintings of colour patterns of the species were executed in water colours while the live crab was observed in artificial bright light under a binocular microscope. Artificial light did not affect the colour of the chromatophores to any marked extent. In all specimens the colour patterns were the same for both legs of each pair.

Abbreviations used in the illustrations

aa.	antenna
a.c.	antero-external corner of mouthfield
a.f.	antennular fossa
a.l.	anterior lobe on basal segment of antennule
a.l.a.	anterior lateral angle of tooth of carapace
a.s.	antennal spine
a.t.	apical tuft of hairs on rostrum
au.	antennule
b.	basis
b.f.	basal fold between fingers of chela
b.l.	basal lobe of epipod
b.p.	branchiostegite projection between leg bases
c.	carpus
cl.	claw
co.	coxa
d.	dactylus
de.	dentation
1°d.	primary dentation
2°d.	secondary dentation
e.	eye
e.cl.	cleft in centre of ridge between epistome and mouthfield
e.s.	eyestalk
g.	cover of "green" gland
i.	ischium
k.	keel on rostrum
l′, l″	pterygostomian lobes
la.	lamella of epipod
m.	merus
ma.	maxilla
mp′, mp″, mp‴	1st, 2nd and 3rd maxillipeds
m.t.	tooth or merus
o.c.	ocular lobe
p.	propodus
p.cl.	pterygostomian cleft
p.f.	fringe on posterior face of leg segment
p.l.a.	posterior lateral angle of tooth of carapace
p.o.	postocular lobe
r.	ridge
ra′, ra″	small and large ramus on antennule
ri.	rim around carapace on pterygostomian region
rm.	rostrum
r.p.	rostral peak
r.r.	ventral ridge on rostrum
s.	antennular septum
t.	chela tooth
t.b.	terminal bulb on 2nd ramus of antennule
t.l.	terminal lips of aperture of vas deferens
tn.	telson
v.d.	aperture of vas deferens
v.f.	ventral fringe of hairs
v.t.	ventral tuft of hairs

EXTERNAL MORPHOLOGY

Figs. 1–7

The body of a hymenosomatid, like that of all Brachyura, is divided into a cephalothorax, or carapace, and an abdomen. The former is expanded laterally and depressed, and the latter is reduced, flattened and folded beneath the cephalothorax.

The lateral downward-sloping regions of the carapace, or branchiostegites, enclose two branchial chambers within which lie the gills (arthrobranchs, podobranchs, and pleurobranchs), and epipods of the legs and maxillipeds. Short projections of the branchiostegites lie between the leg bases.

Milne Edward's opening, the main entrance of the gill stream, lies ventrally in front of the sternum and coxa of the cheliped. This paired aperture is protected by three fringes of hairs; on the anterior edge of the cheliped, on the edge of the branchiostegite adjacent to the base of the cheliped, and on the anterior edge of the epipod of the third maxilliped. These fringes curve into the mid-line of the opening and interlock, providing a most effective filter for the inflowing water. The rapid beating of the scaphognathite on the maxilla drives the exhalent current to meet that from the opposite side in the middle of the anterior edge of the mouthfield. These currents deflect from each other and flow outwards and forwards under the antennules. Flicking movements of the antennules and antennae turn the currents back to form miniature whirlpools. Often only one exhalent current is maintained, and the water flows from under the labrum, obliquely across the epistome to swirl under the opposite antennule.

The carapace is commonly encircled by a raised rim, and anteriorly a ridge may continue across the base of the rostrum. The rostrum may be a simple single projection or trilobed, short or long, wide or narrow. Because a basal suture is absent in some species, the rostrum is regarded as beginning at the base of the eyestalks, in front of the postocular lobe which lies below the rim of the carapace. In most species the suture between carapace and rostrum tapers off at this point, but curves upward in the centre.

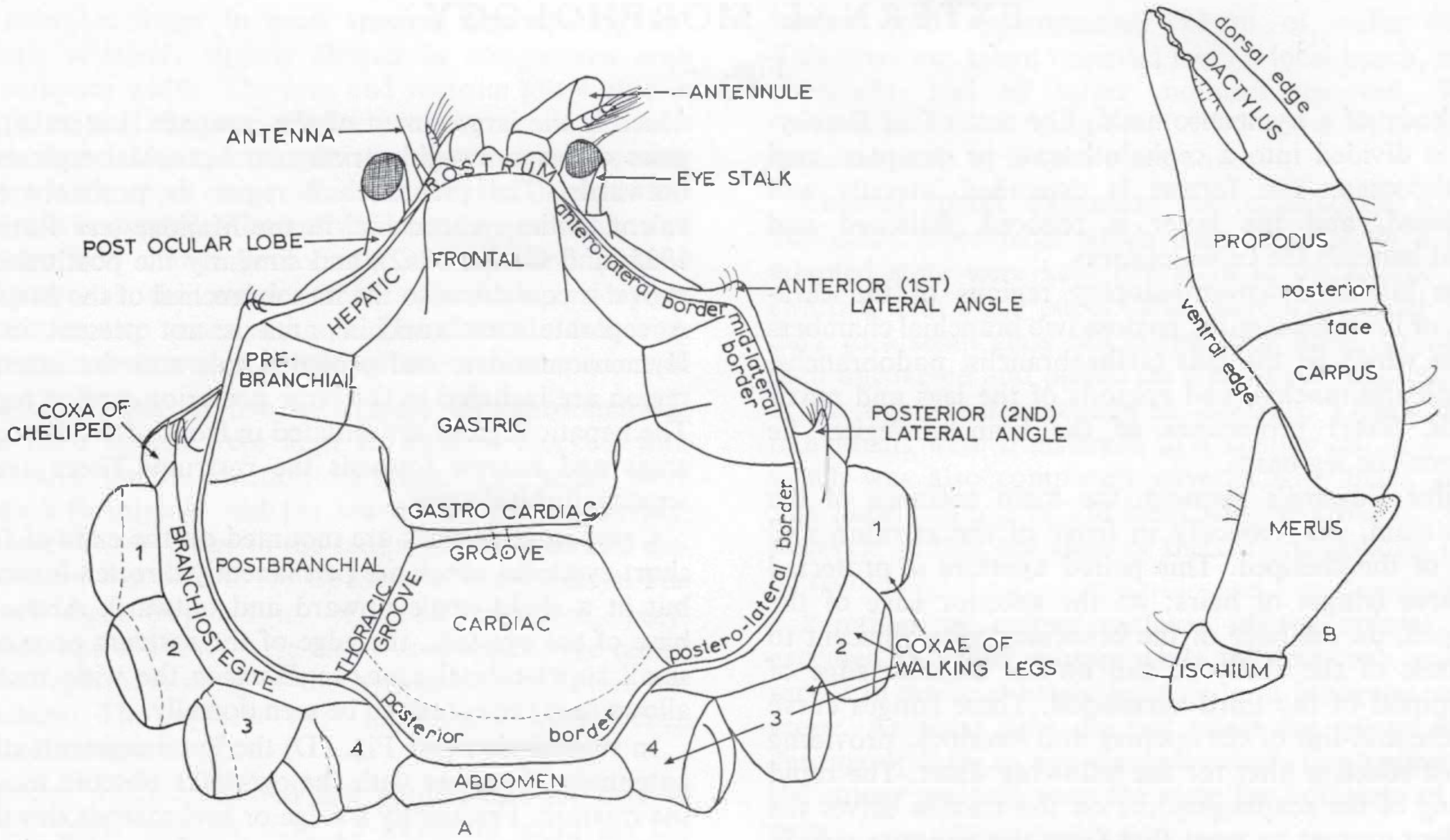
Two lateral teeth are frequently present on the carapace, although they may be reduced to obtuse angles or be absent altogether. The first lateral tooth or angle projects from the rim itself. If a second tooth is present, the anterior upper edge of the base of this tooth is adjacent to the rim, but it slopes posteriorly on to the branchiostegite. Sometimes only a posterior angle is present, on the rim itself.

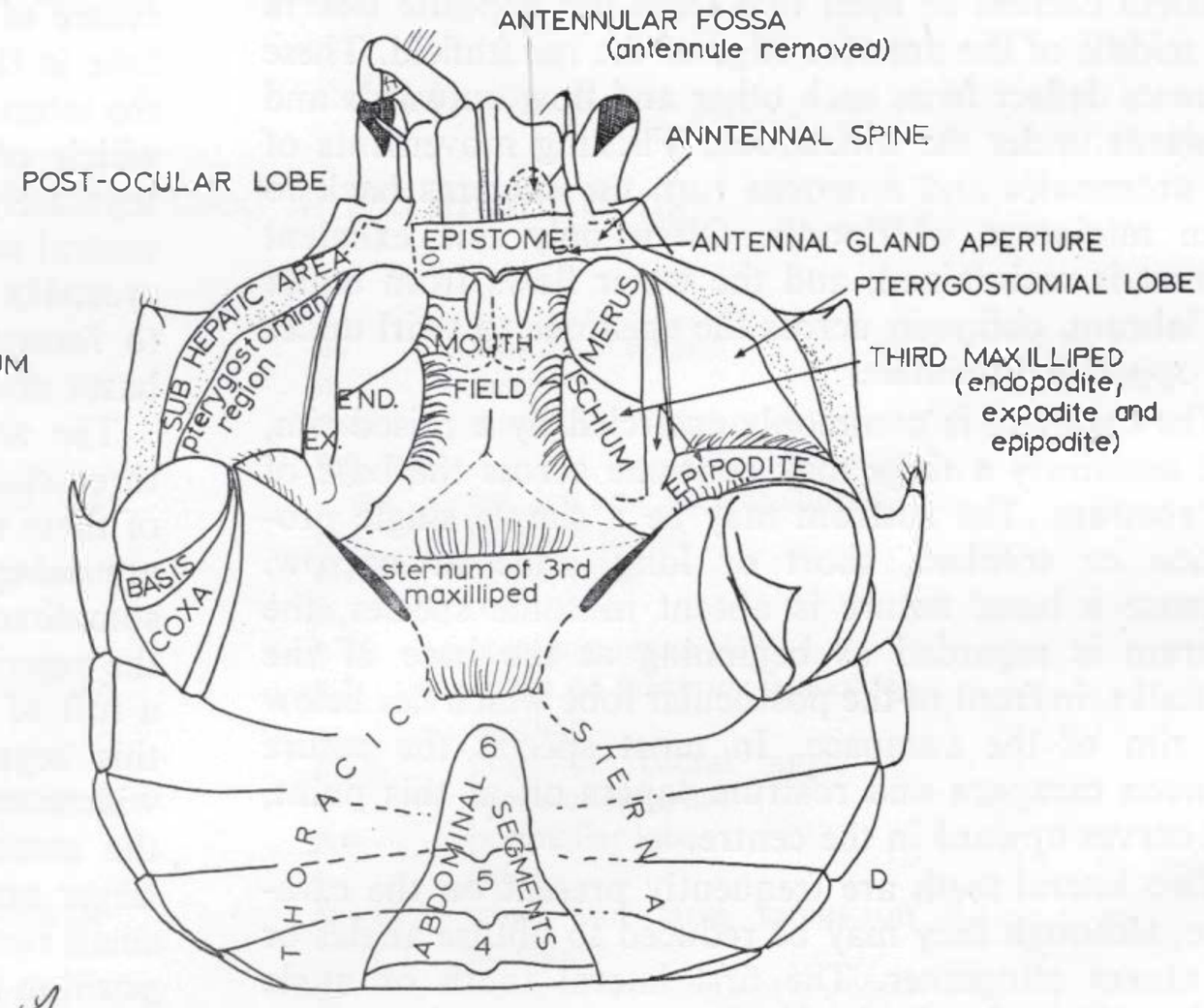
Surface grooves on the carapace are most distinct in some species of *Halicarcinus* (*see* Fig. 1A). Almost always a horizontal gastrocardiac groove is present, through which the heart may be seen beating, approximately two-thirds of the way from the tip of the rostrum to the rear of the carapace. Lateral arms of this groove reach forward, forming the cervical grooves. There is a frontal region behind the rostrum, but there is usually no distinct groove between this and the gastric region, which is the largest area of the carapace. Laterally, two pairs of large, roughly triangular branchial regions fan outwards. The prebranchial region is probably equivalent to the epibranchial in the Majidae (*see* Rathbun 1925, and Griffin 1962), and similarly the postbranchial region is equivalent to the mesobranchial of the Majidae. A separate metabranchial area is not present in the Hymensomatidae, and probably this and the intestinal region are included in the large posterior cardiac region. The hepatic regions are situated in front of the branchial areas and narrow towards the rostrum. There are no separate orbital areas.

Compound corneas are mounted on the ends of fairly short eyestalks which are permanently directed forwards, but at a slight angle upward and outward. Above the base of the eyestalk, the edge of the rostrum provides a small supra-orbital eave. In *Elamena* the wide rostrum allows only the cornea to be seen dorsally.

In ventral view (*see* Fig. 1D) the basal segments of the antennules, together with the eyestalks obscure most of the rostrum. Frequently a ridge or keel extends down the centre of the rostrum. and there is a forward-projecting lobe in the centre of the anterior edge of the epistome—the interantennular septum. These are separate structures which often meet but never fuse, and are developed separately to varying degrees in different species. The ventral surface of the rostrum, the interior margin of the eyestalks and the anterior edge of the epistome combine to form the shallow antennular fossae into which the bases of the antennules fit.

The antennules (first antennae) have a peduncle of three stout segments. The relative length and thickness of these three segments varies with the species. All three are subcylindrical in cross section. The basal segment sometimes has a prominent lobe projecting forward from the anterior portion of its outer edge, and there is usually a tuft of feathery hairs at the outer edge of the base of this segment. The third peduncular segment usually widens markedly distally and bears two rami. At rest, the antennule is folded so that the third segment and larger ramus lie above the other two segments, and the small ramus juts outward laterally (*see* Fig. 2A). In this position the small ramus is set on the outer corner of the upper face of the peduncle, and it consists of a small basal segment and a longer one which is adorned with setae. The second ramus has a variable number (which depends on the species and the size of the specimen) of very short, very broad, subcircular segments stacked on top of a larger basal one. The diameter of these small segments decreases sharply towards the tip of the ramus. Almost at the distal edge of each segment, except the basal one, a line of strong setae extends dorsally across a third of the diameter. The last segment in the diminishing series often has no distinct line of setae, and is invariably surmounted by a long, thin, tapering segment with setae on its dorsal edge. This terminates in a tiny, waisted bulb, and a very long, strong seta. The bulbar segment may





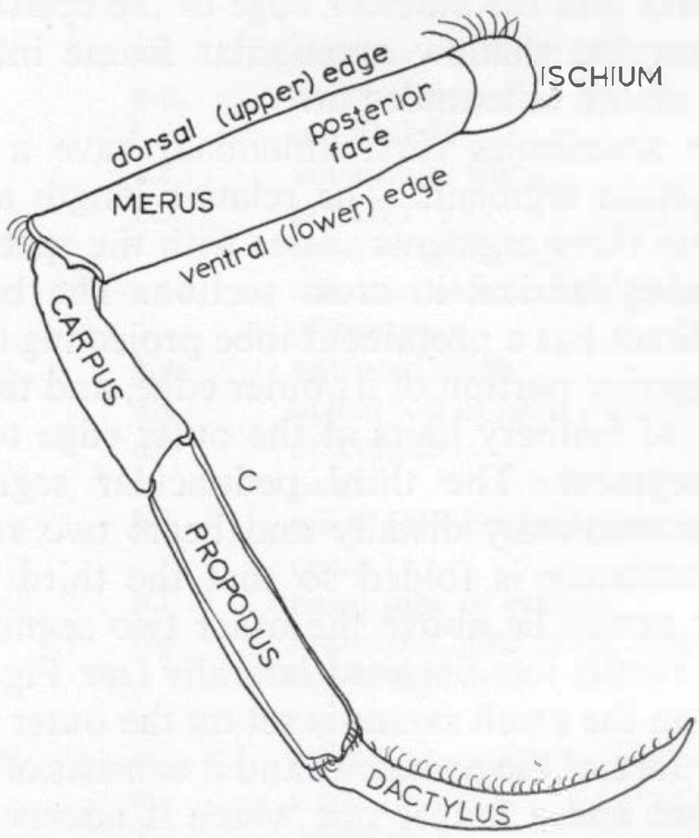
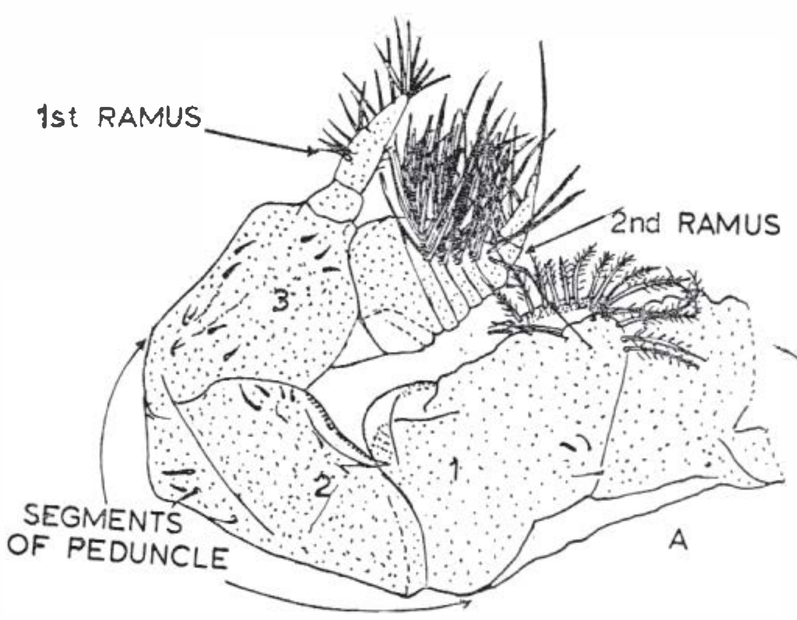
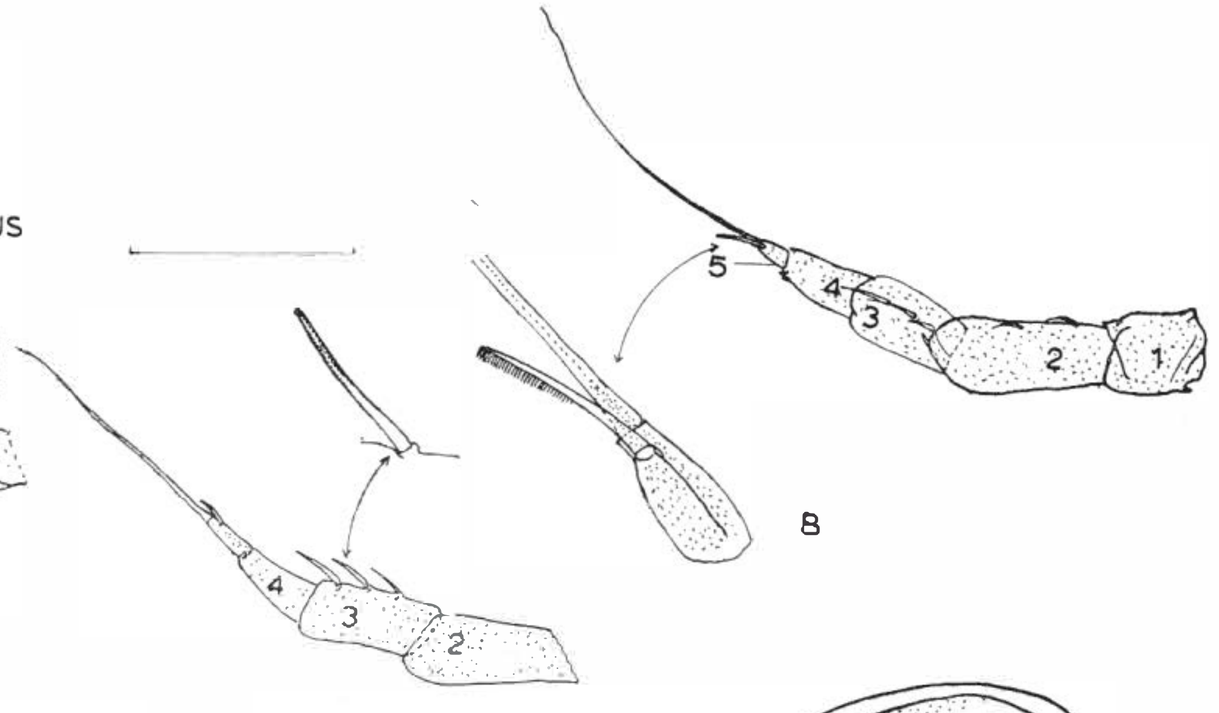


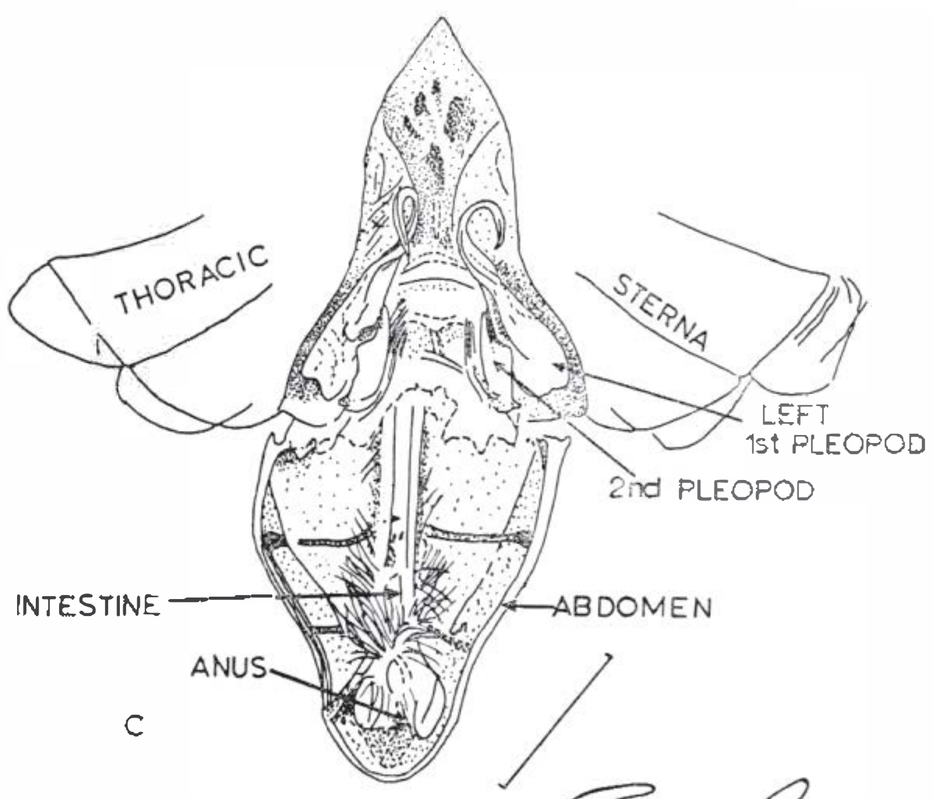
Fig. 1 General hymenosomatid *(Halicarcinus cookii)*: A—Dorsal view of carapace and leg bases; B—Posterior view of male cheliped; C—Posterior view of 3rd walking leg; D—Ventral view of carapace and leg bases

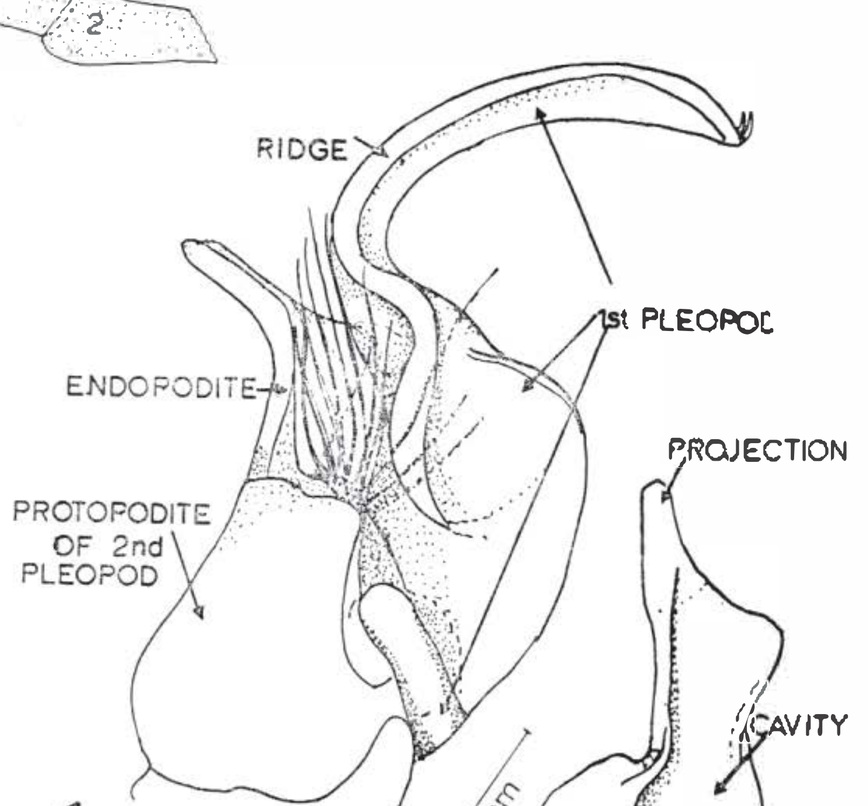
be elongated. The long penultimate segment may have a line of setae a short distance from its base, which presumably indicates how the other ramal segments have been formed during growth.

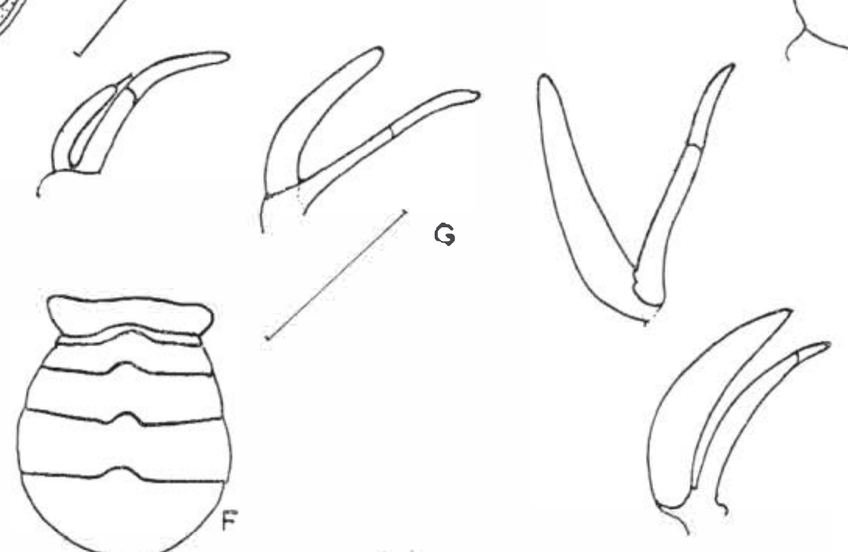
In front of the mouth the antennal sternites have fused to form the epistome, a plate which varies greatly in shape and size depending on the genus, and which is perforated by paired openings of the excretory antennal ("green") glands. The small antenna, which lies outside the antennules, is fused with epistome at its base where an antennal spine, sometimes reduced to a tiny hump, is situated. The top of the basal segment is free (*see* Fig. 2B). The remaining four segments diminish in size, the ultimate tiny segment bearing one long seta and one or

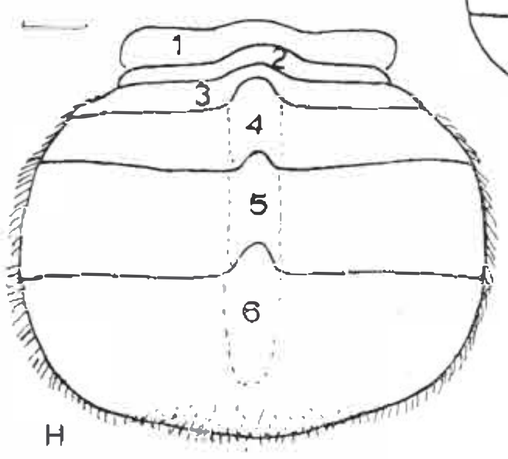












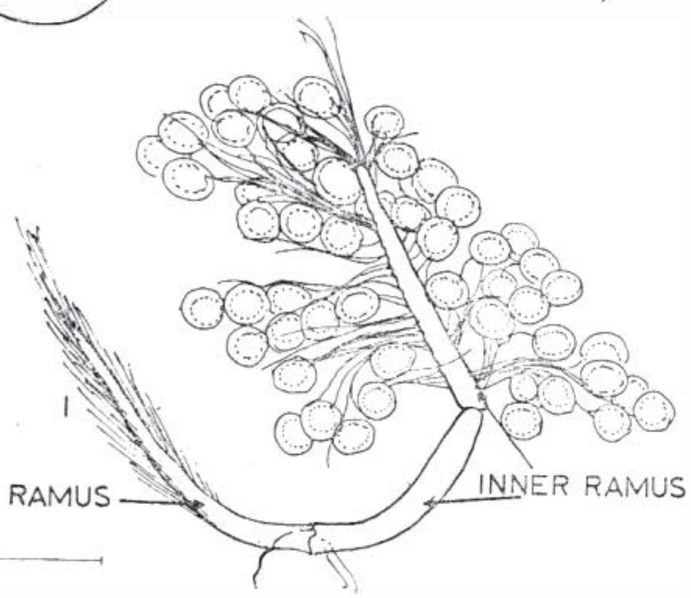


Fig. 2 General hymenosomatid *(Halicarcinus cookii)*: A—Ventral view of antennule; B—Antenna from two angles in lateral view; C—Male abdomen raised and folded back to expose 1st and 2nd pleopod in ventral view; D*—1st and 2nd left pleopod in situ, exposed as in C; E*—2nd male pleopod detached from 1st; F—Abdomen of immature female; G—Pleopods 1–4 of immature female; H—Abdomen of gravid female; I—2nd pleopod of gravid female, with attached eggs; J—3rd and 4th pleopod of gravid female, with embryos attached. (scales represent 1 mm except where otherwise stated)

*The scale between D and E should read 0.4 mm

Inset—3

two short ones. The three larger, free antennal segments all bear sparse, short hairs.

The epistome, united with the carapace on each side, frames the mouthparts. A wavy ridge with a central cleft separates the anterior epistome from the posterior endostome or palate which roofs the mouthfield. Beside the buccal cavity the carapace is raised up into triangular pterygostomian regions, and halfway down the longest side of each triangle is a pterygostomial lobe. A second pterygostomial lobe may occur near the edge of the carapace in front of the cheliped. The subhepatic regions of the carapace may have a prominent longitudinal hump in line with the antennal spine, and sometimes further rounded ridges are present parallel to this.

Behind the mouthfield, the sternum of the second maxilliped forms a triangle in the mid-line, and the sternum of the third maxilliped lies behind this. On the anterior edge of both, there is sometimes a fringe of hairs. The thoracic sterna radiate outward to the coxae of the chelipeds and ambulatory legs. In the male, a groove runs up the centre of these sterna to receive the abdomen. The tip of the male abdomen usually lies anterior to the posterior edge of the sternum of the second walking leg, but the abdomen length and shape varies with the species. The abdomen in both sexes usually consists of six distinct segments, although coalescence of segments is common in overseas species. In the male, only two pairs of pleopods are present, on the first and second segments, and these are visible when the abdomen is lifted (*see* Fig. 2C). During copulation the first pleopod protrudes between the thorax and abdomen. The first male pleopod is expanded at the base, with a long, slender, curved tip. A groove lies at the bottom of a prominent ridge which curves up the pleopod to the subterminal or terminal aperture of the vas deferens. The first pleopod has a sternal lobe fringed with long hairs, just above a short basal segment. The second pleopod is much shorter, with a large basal protopod and a distal endopod. The endopod comprises a small lobe adorned with hairs and a chitinous distal portion which is hollowed to fit the curved side of the first pleopod. The end of the second pleopod is prolonged into a blunt narrow process that projects for a short distance under the ridge of the first pleopod (*see* Figs. 2D, E).

Garth (1958, p. 14) discussed the terminology of the male first pleopod, referring to the position *in situ*. "The concave surface that lies against the thoracic sternal surface is called the sternal surface . . . and the opposite side, lying against the abdomen, is referred to as the abdominal surface." Also, an outer and an inner abdominal facet can be recognised, "the former lying against the inner surface of the abdominal segments, the latter against the hinder part of the alimentary canal". The presence or absence of setae at the tip of the first male pleopod and their length and arrangement, varies with the species.

The female abdomen is larger, and in gravid females is almost circular, extending laterally to the bases of the ambulatory legs, and anteriorly almost to the posterior margin of the mouthfield. Four pairs of biramous pleopods, on segments 2–5 inclusive, are present, even in very small females with a carapace of 2–3 mm in diameter. In these tiny specimens, segments 3, 4, and 5 are equally wide and convex sided and the last segment is rounded at the tip. The abdomen of small males, in contrast, has the ultimate and penultimate segments narrower than the others, and the other segments parallel sided. Figs 2E and 2G shows the abdomen and the four pleopods of a small female, (carapace width = 5.5 mm). Each pleopod consists of an unsegmented curved outer ramus and a bisegmented inner ramus. The relative length and breadth of the outer ramus compared with the inner one increases as the pleopods increase in size, and the second segment of the inner ramus decreases in size compared with the first segrnent. Figs. 2H and 2I show the abdomen and first pleopod of a more mature female (carapace width = 8 mm). The width of the abdomen has increased relative to its length, although the basal segments remain comparatively narrow. The outer ramus, which follows the line of the edge of the abdomen, now bears hairs on the lateral edges, but the second segment of the inner ramus has even longer hairs which stick together and on which the eggs are deposited. In approximately a month the embryos develop to the stage where the eyes and chromatophores are present (*see* Fig. 2J).

Five pairs of legs, including the chelipeds, are formed from the enlarged endopods of the thoracic segments. The chelipeds (*see* Fig. 1B) are shorter, stouter, and chelate, but they follow the same basic construction as the ambulatory legs. There are seven segments to each walking leg (*see* Fig. 1C): a very stout, short, basal coxa, a subsquare ischium which is shortest on its upper edge, a very long merus, a shorter carpus, a propodus of intermediate length, and a dactylus subequal with the propodus, usually curved in contrast with the preceding segments, and terminating in a delicate claw. The ischium, merus, carpus, and propodus are all sometimes partially flattened from side to side (the ischium less so than the others), and the upper edge of the first three of these is sharper than the rounded lower edge. The dactylus is always flattened.

When the legs are used in walking, they may occupy two separate positions. When they are straightened sideways, the knife-edge of the segments which is uppermost is termed the dorsal or upper edge, and the opposite edge is the ventral one. The flattened face that is nearest to the eyes is the anterior face, and on the other side is the posterior face. When the legs are bent, the ventral edge is turned backward, and the posterior face becomes dorsally situated. Similarly the upper edge of the leg segments is now anterior. Thus some writers refer to "the upper or anterior edge."

The joints of these segments differ in their articulation. The ischium-merus joint is virtually unembellished, but anteriorly the ischium extends as a small peak over the merus. This peak may be very shallow. There is a ridge along the ischium corresponding to this peak, so that this segment is almost triangular in cross section.

On the anterior and posterior faces at the tip of the merus is a pair of small, central projections, between which the carpus pivots in a vertical plane. The anterior edge of the merus projects above the carpus, and this tooth frequently bears a tuft of hairs. On both edges of the distal end of the carpus are narrow rounded projections which fit into corresponding cavities on the propodus. This method of articulation allows a little movement in the dorsoventral plane, and also permits some circular twisting of the propodus on the carpus. The anterior and posterior faces of the propodus each end in a hair-fringed V, and between these the dactylus pivots vertically. During locomotion the greatest bending of the legs takes place at the merus-carpus and propodus-dactylus joints. Any of these leg segments (*see* Fig. 1C) may be fringed with hairs on the edges, and the dactylus is always armed with a row of setae or recurved teeth.

The cheliped, especially in the male, has a massive inflated propodus. The lower portion extends as a process, the fixed finger, against which fits the dactylus or movable finger, which frequently has a basal tooth in the male. These two fingers form the pincers. Often there is a large gape between the basal half to one-third of the fingers, but in females and young males and in the adult male of one species (*see* Fig. 1B) there is only a "linear gape": this term was coined by Bennett (1964) for the state when "the fingers of the chela neither gape widely nor meet along the inner margins when closed, but leave a narrow slit through about half the length or more, narrowing distally and uninterrupted by a distinct basal excavation or tubercle". The tips of the fingers are often slightly spooned and curve across each other.

The functional morphology of the mouthparts of *Carcinus* was described by Borradaile (1922), and the present observations of the Hymenosomatidae agree with his account. The following description is based on *Halicarcinus cookii* (Figs. 3, 4) and *Halicarcinus innominatus* (Figs. 5–7) but there is little variation in the mouthparts of different species. The central edge of the mandibles may be toothed or heavily ridged or plain. The scaphognathite may have squared or wavy edges. The size and shape of the ischium and merus of the third maxilliped vary most, and this appendage has therefore been figured for each species. Both the first and second maxillae are very much reduced in comparison with the Majidae. Also the epipods of the second and third maxillipeds are not equipped with a podobranch as in the Majidae. The basal segment, or coxa, of each mouthpart is not detached with the rest of the appendage.

The third maxillipeds (*see* Figs. 3A, 5) are the largest and most heavily chitinised and pigmented mouthparts. They form the outer cover to the buccal cavity; in some species they almost meet in the mid line, in others there is a larger gap. The coxa is elongate laterally and narrow lengthwise, except in the centre where it widens in a subtriangular projection between the bases of the endopod and the epipod. Strong muscles radiate downward into the coxa from the three main parts of the maxilliped: the anteriorly pointing endopod and exopod and the lateral, backwardly curving epipod, all of which are flattened dorsoventrally. The endopod is made up of the same six segments as the legs, but the basis, a small triangular segment, is fused with the ischium and very indistinct. The ischium is subrectangular, with the median anterior margin prolonged into a lobe which fits against the posterior median edge of the merus. The ischium is fringed with several rows of setae of variable lengths on its median edge. This fringe peters out towards the top of the anterior lobe. The merus, which may be slightly longer, subequal with, or much shorter than the ischium, articulates flush with the outer edge of the ischium, which may have a small tuft of strong setae at this point. Equipped on its median edge with a fringe of sparser hairs of a more uniform length than those on the ischium, the merus is typically subchordate, subrectangular or subquadrangular.

The remaining three segments lie at right angles to the first two, but this palp may be extended upward during feeding. The carpus is set slightly off centre, usually nearer to the outer edge of the end of the merus. The rounded outer corner of the merus has curved setae. A few scattered setae are present on the ventral surface of the carpus, propodus, and dactylus, which are all stout, semicylindrical segments. The carpus is more massive than the other two segments, of which the dactylus is the longer, tapering to a bluntly rounded tip from which setae sprout.

Dorsally, i.e. next to the second maxillipeds, the distal ends of all three palp segments are covered with long setae, but the anterior part of the dorsal face of each segment, is relatively free of setae. The proximal portion of the segments is also naked. Along the anterior edge of the carpus is a row of setae, with one or two also present on the anterior edge of the remaining segments. The carpus is especially strongly muscled, and a band of muscle runs back through the thickened anterior central portion of the merus from the merus-carpus joint. The outer half of the ischium, which is also muscled, is thicker than the rest.

The exopod is long, narrow, and flattened. The basal segment, banded longitudinally with regular muscle bands, is fringed on its inner edge with very long feathery hairs, and a denser tuft of these is usually present at the point before this segment begins to narrow anteriorly. A horizontal line of three or more shorter hairs is often present distally. Sometimes a fringe of setae or hairs is present along the outer edge of this segment as well. The flagellum, which is present on this expod in the Majidae, is reduced in the Hymenosomatidae to a single, elongate, flat segment, with up to six, long, feathered and segmented hairs present distally, plus one or two short ones. The exopod normally lies alongside the endopod with the medial edge of the basal segment obscured, and the terminal segment folded and concealed beneath the merus. However, this terminal segment can be straightened so that the apical tuft of hairs reaches across the epistome.

Inset 3*

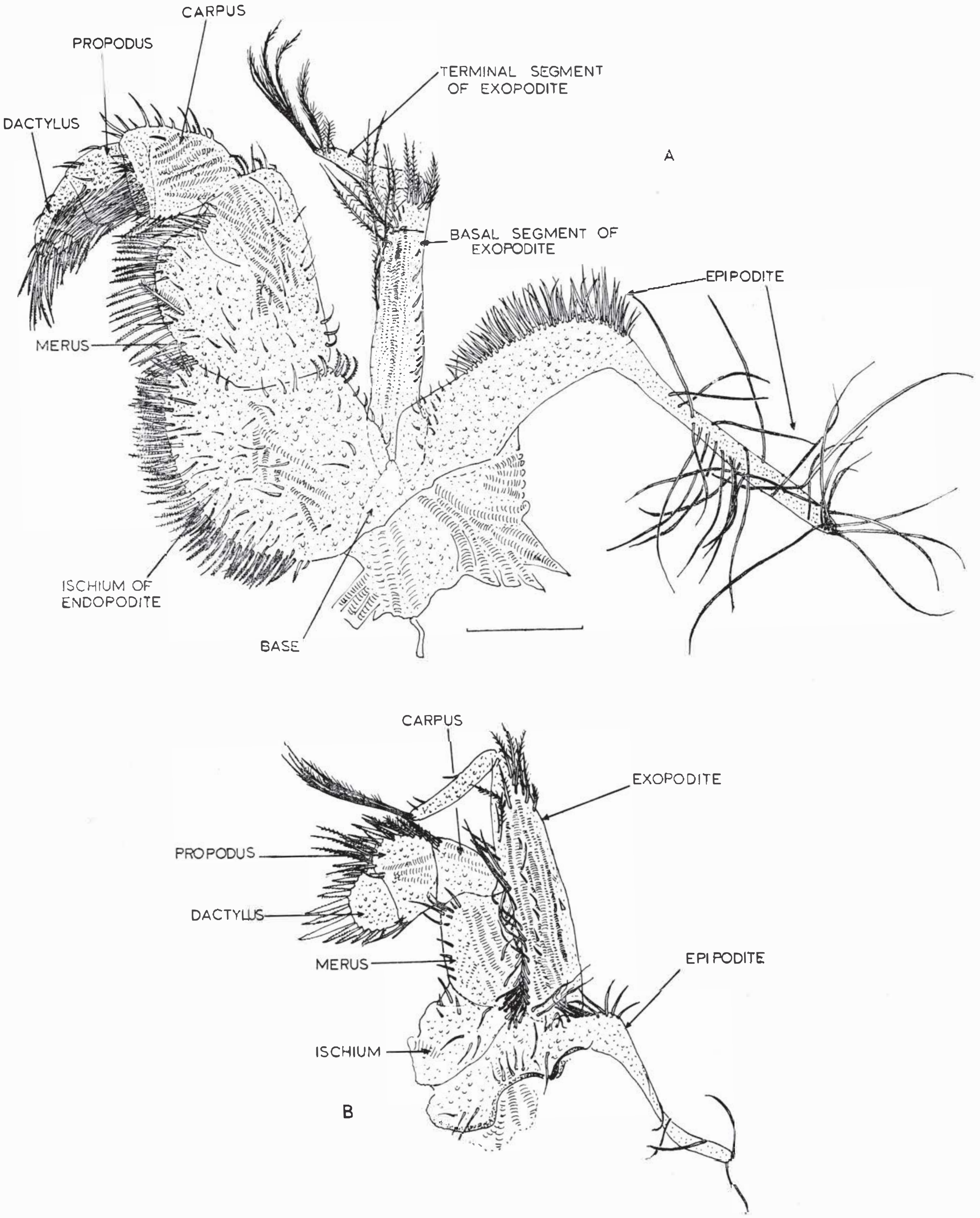


Fig. 3 General hymenosomatid *(Halicarcinus cookii)*: A—Left 3rd maxilliped; B—Left 2nd maxilliped. (scale represents 1 mm).

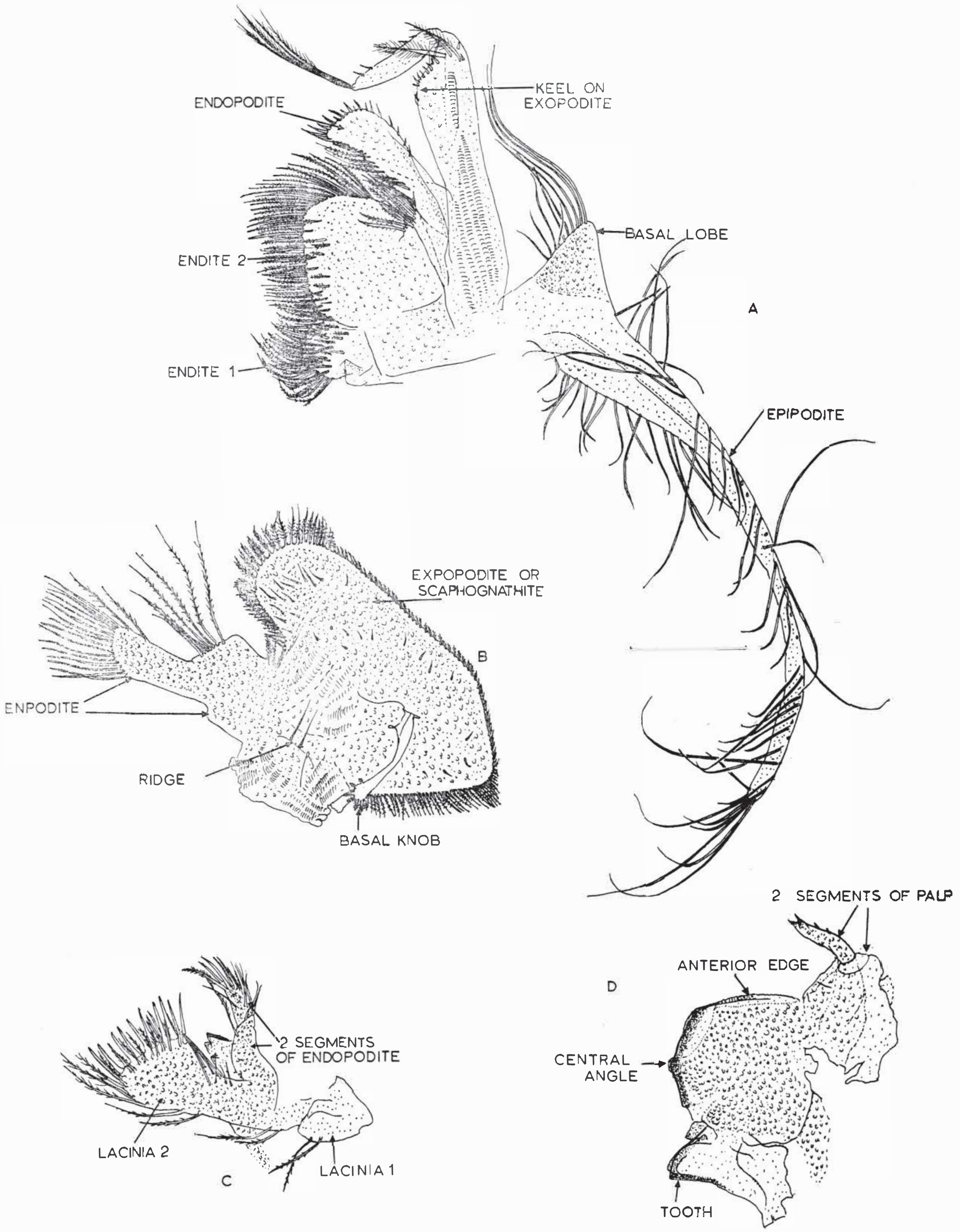


Fig. 4 General hymenosomatid *(Halicarcinus cookii)*: A—Left 1st maxilliped; B—Left 2nd maxilla (maxilla); C—Left 1st maxilla (maxillule); D—Left mandible. (scale represents 1 mm)

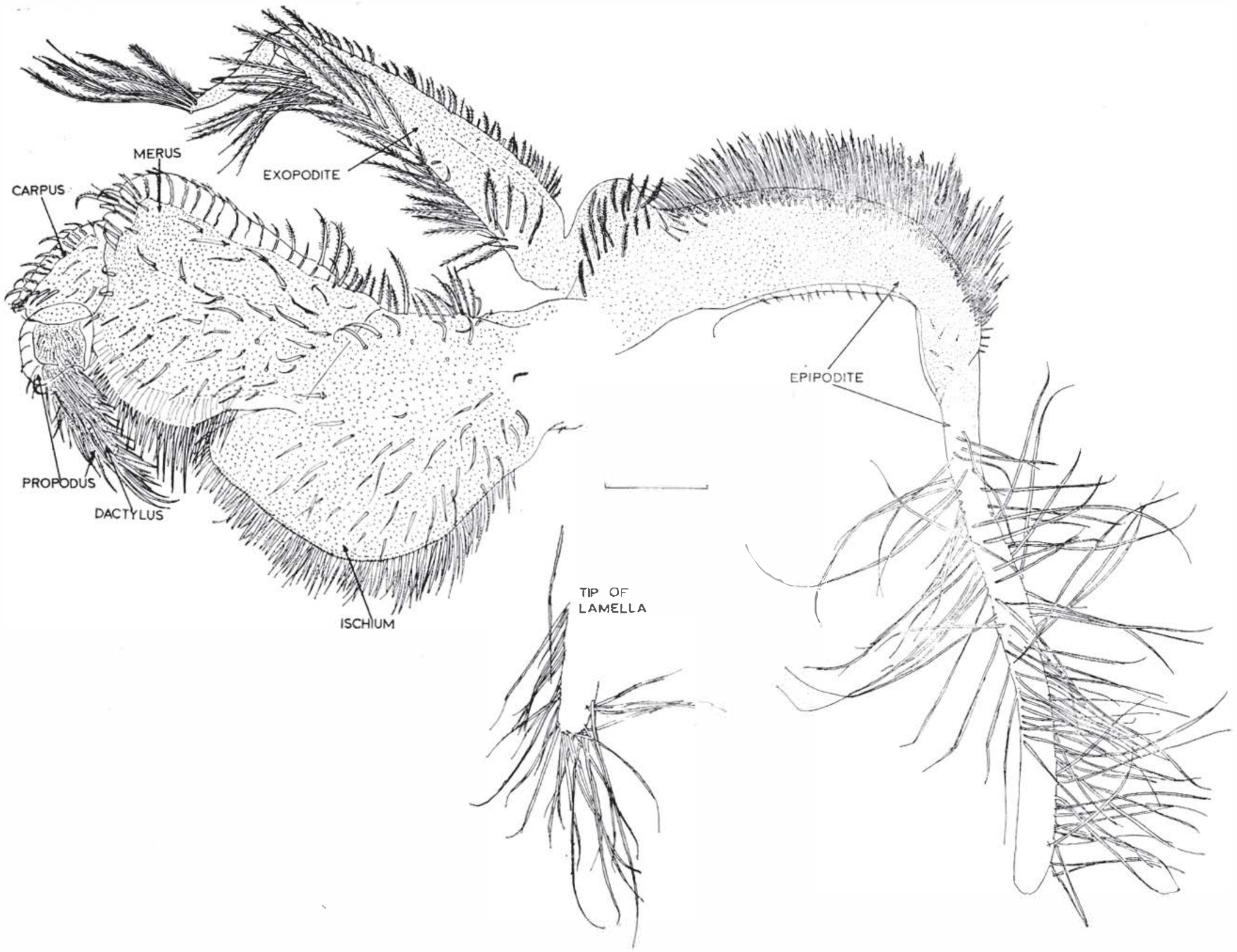


Fig. 5 General hymenosomatid *(Halicarcinus innominatus)*: Left 3rd maxilliped. (scale represents 1 mm)

The very fragile epipod is fused to the bases of the endopod and exopod and consists of two distinct parts. There is a more robust basal portion, which tapers outward from a basal setiferous lobe and has one or many rows of thick setae on its anterior edge. There is sometimes a distinct joint between this portion and the elongated membranous lamella which is fringed with very long secondarily feathered hairs on both edges. The end is narrowly rounded and the two rows of hairs are continuous there.

The second maxilliped (*see* Figs. 3B, 6A) is much smaller than the third, but the three parts are constructed similarly. The endopod is shorter than the basal segment of the exopod. The basis is indistinguishable, and the ischium is reduced to an indistinct subtriangular segment, with its longest median edge scattered with hairs. A scattered row of setae is seen near both lateral edges of the merus, the longest and stoutest segment. The carpus is subtriangular and narrow basally with a few hairs on the distal anterior corner. The propodus widens from its base; the anterior edge being much more curved than the posterior and fringed with strong setae. The dactylus is semicircular and its circumference is completely ringed with setae which increase in length and basal diameter towards the end of the dactylus. The basal segment of the exopod is relatively stouter and shorter than that of the third maxilliped. There is a fringe of hairs on the median edge and a tuft apically. The second segment has fewer terminal hairs than in the third maxilliped. The epipod is very reduced, smaller than in the other two maxillipeds. Again there is no podobranch on the short basal portion, which is fringed anteriorly with a single row of setae. The lamella has a few hairs.

The first maxillipeds (*see* Figs. 4A, 6B) are membranous and consist of a large, flattened exopod of the same construction as before, a single, jointed, flattened endopod bearing two endites medially and a very long epipod. The endopod is almost as long as the basal segment of the exopod, and on its outer edge is a ridge which tapers off distally. The endopod is narrowest near its centre, and the anterior part is expanded with a truncate end. The inner edge has a dense row of hairs, and the flattened top bears another row which disappears down the outer edge. The distal endite (endite 2) is very

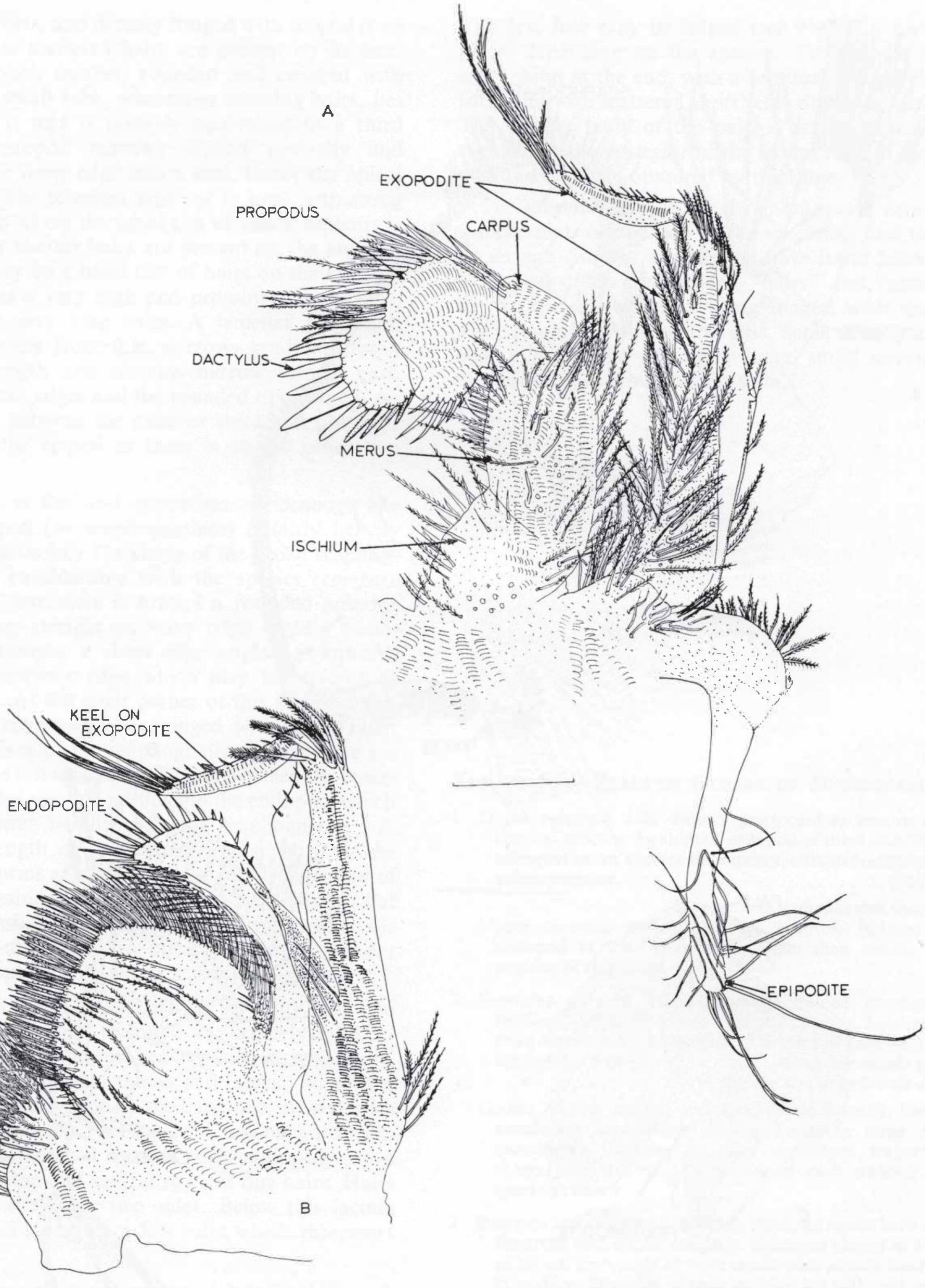


Fig. 6 General hymenosomatid *(Halicarcinus innominatus)*: A—Left 2nd maxilliped; B—Left 1st maxilliped (epipod detached). (scale represents 1 mm)

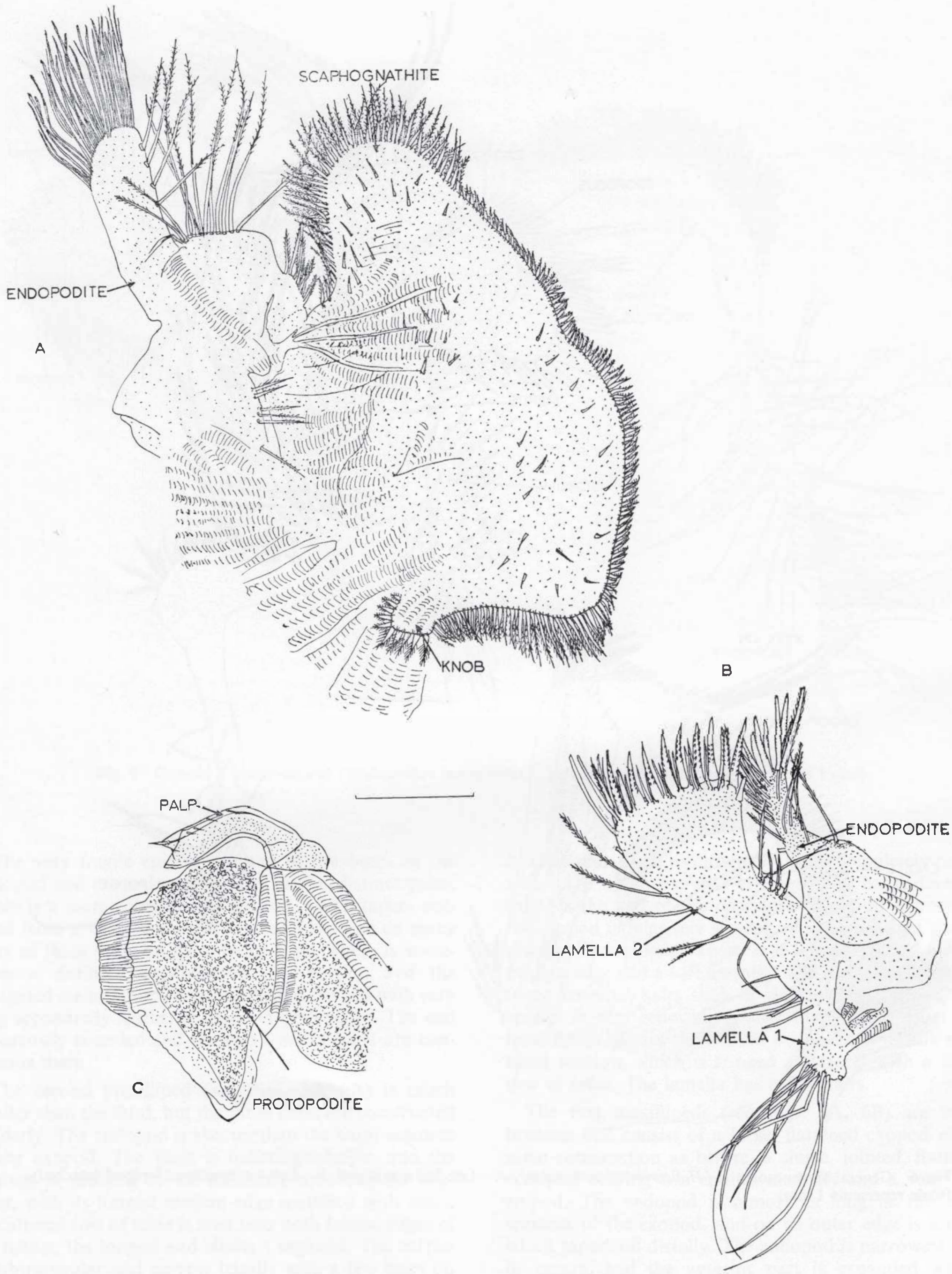


Fig. 7 General hymenosomatid *(Halicarcinus innominatus)*: A—Left 2nd maxilla (maxilla); B—Left 1st maxilla (maxillule); C—Left mandible. (scale represents 1 mm)

broad, subcircular, and densely fringed with several rows of hairs. A few scattered hairs are present on its face. Endite 1 is much smaller, rounded and covered with hairs. A very small lobe, sometimes sporting hairs, lies below endite 1, and is possibly equivalent to a third endite. The exopod narrows slightly centrally and expands on the inner edge into a keel, below the apical tuft of hairs. The terminal segment is long, narrowing towards the tip where the usual tuft of very long hairs is present. A few shorter hairs are present on the anterior edge. There may be a basal tuft of hairs on the exopod. The epipod has a very high and prominent basal lobe, equipped with very long hairs. A lamellar projection arises immediately from this, narrows gradually for a third of its length and remains narrow for the rest. Hairs fringe both edges and the rounded tip. There is no "neck" region between the anterior third and posterior two-thirds of the epipod as there is on the other two maxillipeds.

The maxilla is flat and membranous, although the expanded exopod (= scaphognathite) is fairly heavily chitinised and muscled. The shape of the broad scaphognathite varies considerably with the species (*compare* Figs. 4B, 7A), but there is always a rounded anterior portion, a long, straight or wavy edge sloping posteriorly and outwards, a short edge angled downward, and a short posterior edge which may be straight or slightly curved. At the inner corner of this last edge is a small subcircular prominence, ringed with stout, short setae. On the face of the scaphognathite short setae are scattered. There is a small tuft of hairs between the anterior portion of the scaphognathite and the endopod, which is much narrower basally than the scaphognathite. A third of the length of the endopod is wide; then the anterior edge forms a sharp, straight ledge, with a row of hairs. The remainder of the endopod is a narrow, flat lobe, widening slightly distally where a fringe of hairs is situated. There are no endites, but a faint ridge is present below the endopod, from which a few hairs sprout.

The maxillule (*see* Figs. 4C, 7B) is very tiny. The two segments of the narrow endopod are scarcely differentiated. The terminal one is heavily fringed with hairs. Between the endopod and the second lacinia, which are of similar length, is a small median lobe, tipped with hairs. The second lacinia is large, widened outward from the base with a flattened median edge equipped with a row of sturdy setae and several rows of fine hairs. Hairs also ornament the other two sides. Below this lacinia is a very tiny lobe bearing a few hairs which represents the first lacinia.

The mandible consists of a protopod, heavily chitinised, and concave on its outer surface and hollowed below, and a palp. The whole mandible is easily detached from the apophysis and tendon which extend backwards below the mouthfield. The anterior edge of the mandible is slightly rounded; medially the cutting edge is divided by a very small angle into two straight faces. In Fig. 4D the mandible has been squashed to show the strong tooth which lies below the posterior end of the second face. The first face may be ridged (*see* Fig. 7C), toothed or plain, depending on the species. The palp is delicate, short, bifid at the end, with a terminal seta on the other fork, and with scattered short setae down the outer edge. The slender body of the palp is set on a small basal segment at the posterior of the lateral edge of the protopod and is partly obscured by this edge.

The amount of hair on the mouthparts depends, to some extent, on the size of the specimen, and therefore on its age. Smaller mouthparts have fewer hairs. There is no real difference between "hairs" and "setae", but the former are taken as being longer, with secondary hairs coming off the central axis. Setae usually have the beginnings of the secondary hairs, small serrations or tiny projections from a stout stem.

Key to New Zealand Genera of Hymenosomatidae

1 Upper carapace with distinct gastrocardiac groove and cervical grooves. Ischium of endopod of third maxilliped subequal to, or shorter than merus, subquadrangular or subrectangular. ..... *Halicarcinus*
(8 authenticated species)

Upper carapace without distinct grooves. Ischium of endopod of third maxilliped longer than merus, triangular or trapezoid. 2

2 Eyestalks entirely visible dorsally, folded antennules similarly visible. Epistome tiny, semicircular. Ischium of third maxilliped subtriangular. Dactylus of each walking leg devoid of teeth ..... *Cyclohombronia* gen. nov.
(1 species, *Cyclohombronia depressa*)

Cornea of eye, but not eyestalks, visible dorsally, folded antennules completely hidden. Epistome large and rectangular. Ischium of third maxilliped trapezoid, shaped like axe-blade. Dactylus of each walking leg sparsely dentate 3

3 Rostrum and carapace completely fused, no suture between. Rostrum with a keel ventrally. Epistome almost as long as broad. Endopods of third maxillipeds almost meeting in midline. Dactylus of each walking leg with two large teeth adjacent to claw, lacking other dentation.
..... *Elamena* s.s.
(2 species)

Distinct suture between carapace and rostrum. Rostrum without keel or ridge ventrally. Epistome only half as long as broad. Endopods of third maxillipeds gaping in midline. Dactylus of each walking leg with a single large tooth adjacent to claw, lacking other dentation.
..... *Halimena* gen. nov.
(1 species, *Halimena aotearoa*)

Inset 4

SYSTEMATICS

Genus **Halicarcinus** White

Halicarcinus White 1846, p. 178. Dana 1852, p. 379. H. Milne Edwards 1853, p. 222. Stimpson 1858, p. 107. Miers 1876b, p. 49; 1886, p. 280. Targionni-Tozzetti 1877, p. 172. Stebbing 1900, pp. 520–26; 1914, p. 271. Alcock 1900, p. 291. Stimpson 1907, p. 146. Kemp 1917, pp. 246–50. Tesch 1918, p. 9. Rathbun 1925, p. 261. Richardson 1949a, p. 67. Balss 1957, p. 1632. Garth 1957, p. 32; 1958, p. 30.

Liriopea Nicolet 1849, p. 158.

Hymenicus Dana 1851, p. 253; 1852, p. 387. Filhol 1885a, pp. 43–4; 1886, pp. 401, 402. Stebbing 1914, p. 271. Tesch 1918, pp. 11–12. Chilton and Bennett 1929, p. 776.

Hombronia Jacquinot and Lucas 1853, p. 60.

Hymenosoma Haswell 1882, p. 114. Chilton 1882, p. 172.

Hymeniscus Filhol 1885, pp. 399-400

TYPE-SPECIES: *Halicarcinus planatus* (Fabricius)

RANGE: Indo-Pacific (subantarctic islands, New Zealand, Australia, South America, and Japan).

DESCRIPTION: Carapace subcircular, suboctagonal, or longitudinally elongate, always broadest across the branchial region. Lateral angles may be pronounced or absent. Second lateral tooth, if present, well below the carapace rim; rim itself never angled at this point, although sometimes angled adjacent to the first lateral tooth. A distinct suture or rim invariably present between carapace and rostrum; gastrocardiac groove and cervical grooves obvious on upper carapace. Rostrum very variable in length and shape, of two types, with transitional examples: either tridentate (trilobular) or simple. Where the lobules of the rostrum have fused basally, a longitudinal central ridge is developed ventrally, but this never assumes the proportions of a keel, and may sometimes be altogether absent. Interantennular septum forming a longitudinal ridge, variable in its degree of development. Antennular fossae deeper than in other genera. Antennules folding longitudinally beneath the rostrum, but still, with one exception, visible dorsally. No pronounced lobe on the anterior outer corner of the basal segment of the peduncle of the antennule. Eyestalks short, fully exposed in dorsal view. Eyes set well apart, angled to some extent outward as well as forward. Epistome at least approximately twice as wide as long; of equal breadth throughout or tapering a little laterally. Endopod of external maxillipeds not especially broad, gaping in the mid line. Ischium and merus of endopod subequal, or ischium shorter than the merus. Ischium subquadrangular, antero-median lobe short and broad. Merus subrectangular or subquadrangular, median anterior corner oblique. Basal and lamellar portions of epipod subequal in length. Chelipeds of male stout, length up to twice the carapace width, palm commonly inflated. Length of first pair of walking legs also nearly twice the width of the carapace. Dactylus of the walking legs armed with rows of teeth, and/or hairs. Other segments of the walking legs hardly flattened and subcircular in cross-section. Abdomen in both sexes of six segments. Male first pleopod twisted and curved to a variable extent. Aperture of vas deferens terminal and elongate.

REMARKS: White's original description of *Halicarcinus* did not include any characteristics which truly separate his genus from any other. He distinguished *Halicarcinus* "by the great size of the thickened forefeet, by the carapace being generally wider than long, and having the edge of the strongly depressed upper surface with two teeth or angles on each side. The last pairs of legs are cylindrical and free from hairs, while the claws are considerably curved and compressed. The tail of the mail is six-jointed and deeply notched on each side about the middle. The outer pedipalps, as in *Hymenosoma*, are covered on the outside with short hairs." Although most of these characters are valid, they may apply equally well to other genera. The degree of hairiness and the amount of curvature of the dactylus or "claw" of the walking legs, and the development of lateral angles on the carapace are very variable in the genus, and even in some single species within the genus. The abdomen, as Miers (1876b) has observed, though frequently concave on either side, cannot be described as "deeply notched", and Stebbing (1900) considers that White's description of this part may have been based on a figure in Guerin's "Iconographie" of 1829–44 rather than on actual material.

White included in his genus, as well as *Halicarcinus planatus*, the species known previously as *Hymenosoma depressum* Jacquinot and Lucas. However, Miers (1876b) pointed out that the specimens referred by White to Jacquinot's species were distinct from it, and Miers named them *Elamena whitei*. Gordon (1940) correctly transferred this species to *Halicarcinus*, so that White's original description was indeed based on two species which do belong to his genus.

The two most recent descriptions of *Halicarcinus* are:

"Epistome well-defined. Antennules not concealed by front. No septum between antennules. Merus and ischium of outer maxillipeds of sub-equal size." (Rathbun 1925.)

"Epistome of considerable length. Antennules unconcealed by front. No interantennular septum. Merus and ischium of outer maxillipeds sub-equal." (Garth 1958).

Although these descriptions are in such complete agreement, they are not entirely adequate.

The epistome is "well-defined" in all the New Zealand genera of Hymenosomatidae, though not in the overseas *Hymenosoma*. It is not "of considerable length" in *Halicarcinus*, when this genus is compared with *Elamena*, but it is relatively *wider* than in other genera. The antennules are unconcealed by the rostrum when folded in all the New Zealand species except *Halicarcinus lacustris*, where they are somewhat smaller than usual. As this species resembles other members

of the genus in other important respects, its separation would appear unwarranted, so that the visibility of the antennules in dorsal view does not seem to be a valid characteristic of the genus.

Halicarcinus White and *Hymenicus* Dana were regarded as synonyms by Kemp (1918, p. 59), Richardson (1949a, p. 59), and Balss (1957, p. 1632). These two genera were previously separated by Dana who described *Hymenicus* thus: "In this genus the front has not the three teeth of *Halicarcinus* (between which the flexed first antennae are seen), but a simple rounded or trilobate prominence forms the front, and the first antennae are covered. The feet are much longer and more slender than in any of the species of *Halicarcinus* seen by the author. As in *Halicarcinus*, the eyes are more distant than in *Hymenosoma* and there is no prominent extra-orbital tooth, or but a short one." (Dana 1852, p. 387.)

The apparently greater length of the walking legs in some species of *Halicarcinus*, to which Dana referred, is illusory. The length of the walking legs is approximately 1½–2 times as great as the width of the carapace in all species, but the slenderness of the segments makes them seem longer in some. The slender, spidery appearance of the legs in such species is of adaptive rather than taxonomic significance at a generic level; thin legs are found in those species which frequent soft bottoms, and have the evolutionary advantage of making progression over mud and sand easier, possibly by decreasing the body weight, and by lessening resistance to forward progression or burrowing. A slight lengthening of the segments may sometimes occur, and this would aid distribution of the body weight over a greater radius of the unstable substrate. Long, slender, hairy legs are also useful in swimming, and the dispersive young stages of *Halicarcinus* species often have comparatively longer legs than the adults.

Intermediate stages exist between the two extremes of rostrum contrasted by Dana; a series that illustrates this transition is *H. innominatus*, *H. planatus*, *H. ovatus*, *H. cookii*, *H. varius*, *H. whitei*, and *H. pubescens*. The three rostral lobes become fused basally and elevated until the rostrum forms a horizontal platform at the same level as the upper carapace, fusion continuing until only the tip is minutely tridentate, then finally simple. In this same series, the lateral teeth below the carapace enlarge to a maximum in *H. cookii*, and the anterolateral border of the carapace becomes concave, the rim forming an angle at the level of the anterior lateral tooth. From this point in the series, the lateral angles decrease again in prominence. The series is an artificial one and does not necessarily indicate sequential evolution. It is most likely that the simple rostrum came first, and a trilobate, depressed rostrum and sharp, lateral angles were later developed, probably more than once.

Where the rostrum takes this form the antennules are always visible dorsally between the three lobes or teeth, and they are also visible in all the species referred by Dana to his new genus, although he apparently could not see these antennules. *H. lacustris*, which was unknown to Dana, is the only New Zealand species where the antennules are completely hidden in dorsal view.

Stimpson (1907), Rathbun (1925), and Garth (1958) all maintained that a characteristic of *Halicarcinus* was the absence of an interantennular septum. Yet Gordon (1940, p. 75, fig. 9a) says of *Halicarcinus whitei* "a long, low, rostral keel extends backwards from the median lobe to touch the anterior end of the interantennular septum." Gordon's "keel" is best described as a rostral ridge, as it never reaches the proportions of the keel in *Elamena* s.s. In all the species of *Halicarcinus* examined here, an interantennular septum was invariably present, although it may be so reduced that it is difficult to detect, e.g. in *H. planatus*, the species encountered by Rathbun and Garth. Although the septum is a low ridge rather than a fleshy lobe as in *Elamena* s.s., it is never absent in *Halicarcinus*.

The grooves on the carapace, the suture or rim at the base of the rostrum, the broad, shallow shape of the epistome, the subequality of the ischium and merus of the endopod of the external maxillipeds, and the ridged nature of the interantennular septum are the most reliable indications of the genus.

Key to New Zealand Species of *Halicarcinus* (after Melrose 1968)

1 Rostrum trilobate or tridentate, arising below level of carapace, carapace rim being continuous above rostrum and concavities between lobules extending below this rim. 2

Rostrum simple or, if trilobate, lobes arising from level of carapace, separated from it only by a suture. 4

2 Three rostral lobes arising considerable distance below carapace rim, with lateral lobes at same level as median one and not set at angle to it. Anterolateral border of carapace convex. Dactylus of each walking leg with single row of teeth or tubercles. . . . . *Halicarcinus innominatus* (mainland, littoral)

Three rostral lobes arising just below rim of carapace, with lateral lobes set at an oblique angle to median lobe. Anterolateral border of carapace straight or concave. Dactylus of each walking leg with double row of teeth. 3

3 Rostral lobes widely separated, median rostral tooth shortest, lateral lobes sloping downward and outward. Neither of the two lateral angles of carapace marked above by angles in carapace rim. Dactylus of each walking leg armed with two irregular but distinctly separate rows of short, pointed teeth. . . . . *Halicarcinus planatus* (subantarctic, littoral and deep water)

Rostral lobes close together; median lobe a little longer than laterals, all lobes projecting straight forward. First of the two lateral angles of the carapace marked above by angle in carapace rim. Dactylus of each walking leg with two irregular and very closely approximated rows of teeth which therefore appear to form a single row. . . . . *Halicarcinus ovatus* (probably confined to Australia)

4 Rostrum distinctly trilobate or tridentate, concavities between lobes reaching almost to suture between carapace and rostrum. 5

Rostrum simple or, trilobate only distally, any concavities between lobes not reaching near suture between rostrum and carapace. 6

5 Rostrum extending past eyes. Rostral lobes acute, subequal. Carapace longer than wide, narrowing anteriorly. Anterolateral border of carapace straight or alightly convex. Two pairs of angles below carapace rim, which is itself uninterrupted by the angles. Postocular lobe large. Dactylus of each walking leg with single row of recurved basal large teeth. Chela of male equipped with typical basal tooth on moveable finger.

. . . . . *Halicarcinus tongi*
(deep water)

Rostrum not projecting past eyes. Rostral lobes rounded apically, median one fraction longer than laterals. Anterlateral border of carapace markedly concave. Two pairs of lateral teeth marked by angle in carapace rim. Postocular lobe very small. Dactylus of each walking leg with two irregular rows of recurved narrow teeth. Chela of male without usual basal tooth on moveable finger. . . . . *Halicarcinus cookii*
(littoral)

6 Rostrum not projecting past eyes, and forming flat almost horizontal platform . . . . . *Halicarcinus varius*
(littoral and deep water)

Rostrum projecting past eyes, and downwardly deflexed anteriorly. 7

7 Rostrum always distinctly trilobate on tip, projecting well past eyes. Chela of male inflated laterally. Dactylus of each walking leg with single row of sharp recurved teeth. Male abdomen and first pleopod of normal length and form. . . . . *Halicarcinus whitei*
(littoral)

Rostrum simple, just projecting past eyes. Chela of male of normal width. Dactylus of each walking leg lacking teeth or sparcely dentate. Male abdomen short, abnormal in narrowing evenly to ultimate segment; male pleopod of unusual form. 8

8 Rostrum deflexed only a little downwardly, convex from side to side above, narrowing to a blunt point anteriorly. Male first pleopod with longitudinal row of long, sturdy setae subterminally, as in *Elamena*, tip forming tiny knob. Dactylus of each walking leg curved, with single blunt tooth adjacent to claw. Whole body surface covered with long feathery hairs. . . . . *Halicarcinus pubescens*
(marine, littoral and deep water)

Rostrum strongly deflexed downward, concave from side to side above, narrowing only slightly anteriorly to somewhat truncate but curved tip, sometimes with scarcely visible trilobation on tip. Male first pleopod very stout, with long slender setae in tufts subterminally, tip tapering normally. Dactylus of each walking leg straight, without teeth. Whole body surface covered with short fine setae. . . . . *Halicarcinus lacustris*
(fresh water)

Halicarcinus innominatus Richardson

Figs. 5–11, Plate 1

?1775 *Cancer orbiculus* Fabricius, p. 402
?1853 *Elamena quoyi* H. Milne Edwards, p. 223, pl. 11, fig. 3
?1858 *Halicarcinus planatus* Heller, p. 66
1886 *Halicarcinus tridentatus* Filhol, pp. 396–8, pl. 1, fig. 3
?1886 *Halicarcinus huttoni* Filhol, pp. 398, 399, pl. 47, fig. 4
?1906b *Halicarcinus planatus*, Chilton, p. 270
?1911 *Halicarcinus planatus* var *tridentatus*, Chilton, p. 293
1912 *Halicarcinus planatus*, Thompson, p. 238
?1929 *Halicarcinus planatus*, Chilton and Bennett, p. 776
?1929 *Halicarcinus planatus*, Young, p. 152
?1930 *Halicarcinus planatus*, Balss, pp. 195–210
1949a *Halicarcinus planatus*, Richardson, p. 68, fig. 48
1949b *Halicarcinus innominata* Richardson, p. 130
1957 *Halicarcinus innominata*, Garth, p. 33
1958 *Halicarcinus innominata*, Garth, p. 35
1960 *Halicarcinus innominatus*, Dell, p. 4
1963 *Halicarcinus innominatus*, Dell, p. 37

NOT

1853 *Hymenosoma ? tridentatum* Jacquinot and Lucas, p. 60, pl. 5, fig. 27
1958 *Halicarcinus planatus*, Garth, pp. 30–5, fig. 1A, B

TYPE LOCALITY: No type locality was specified by Richardson (1949b) although this species was recorded from "Among weeds on piles, ships, etc., and in shallow sheltered water" in his 1949a reference. I take this opportunity to restrict the type locality of *Halicarcinus innominatus* to Wellington Harbour. No type material appears to have been designated and no specimens identified by Richardson are available in the Dominion Museum or Victoria University of Wellington Zoology Department Collections.

SUMMARY OF LOCALITIES: Northland: Cape Maria van Diemen. Auckland: Muriwai; Devonport; Piha; Kaipara. South Auckland: Waiuku. Wellington: Kau Point, Seatoun; Days Bay; Lyall Bay; Evans Bay; Breaker Bay. Nelson: Cape Foulwind. Marlborough: Kaikoura (Seal Reef, Armers Beach, Wairepo Flat). Christchurch: Taylors Mistake; Redcliffs. Otago: Potato Point; Blueskin Bay; Shag Point; Otago Harbour; Little Papanui Beach, Portobello; St. Clair, Dunedin. Chatham Islands: Kaingaroa; Owenga; Port Hutt; Waitangi. Stewart Island.

DISTRIBUTION: New Zealand mainland, endemic.

DIAGNOSIS: Carapace suboval, broader than long, with a wide rim; upper surface convex with the regions of the carapace obvious. Rostrum short, not reaching to the limit of the eyes, trilobular, the lobules arising close together well below the level of carapace rim, which is gently convex frontally, following the same shallow curvature as the anterolateral border which is also convex. Frontal region therefore not produced. Two pairs of lateral teeth absent or both obtuse; carapace rim never interrupted by angles. Lobules of the rostrum small, subequal, rounded apically, flattened dorsally. Lateral lobes arising at the same level as the median lobe, not set at an angle to it, and all three similar in shape and projecting straight forward. Ventral edge of rostrum with a central rounded protruberance adjacent to the interantennular septum. Postocular lobe present but reduced; antennal spine large, just obtuse. Chela of male greatly inflated, dentation reduced, basal gape large. Segments of walking legs stout, moderately curved dactylus armed with blunt teeth in a single row. Ischium of the third maxilliped a little broader than the merus; merus not much expanded anteriorly. Male abdomen long, separated by a deep vertical ledge from the carapace. First segment expanded laterally, wider than any other segment; second subequal with first centrally, shortening

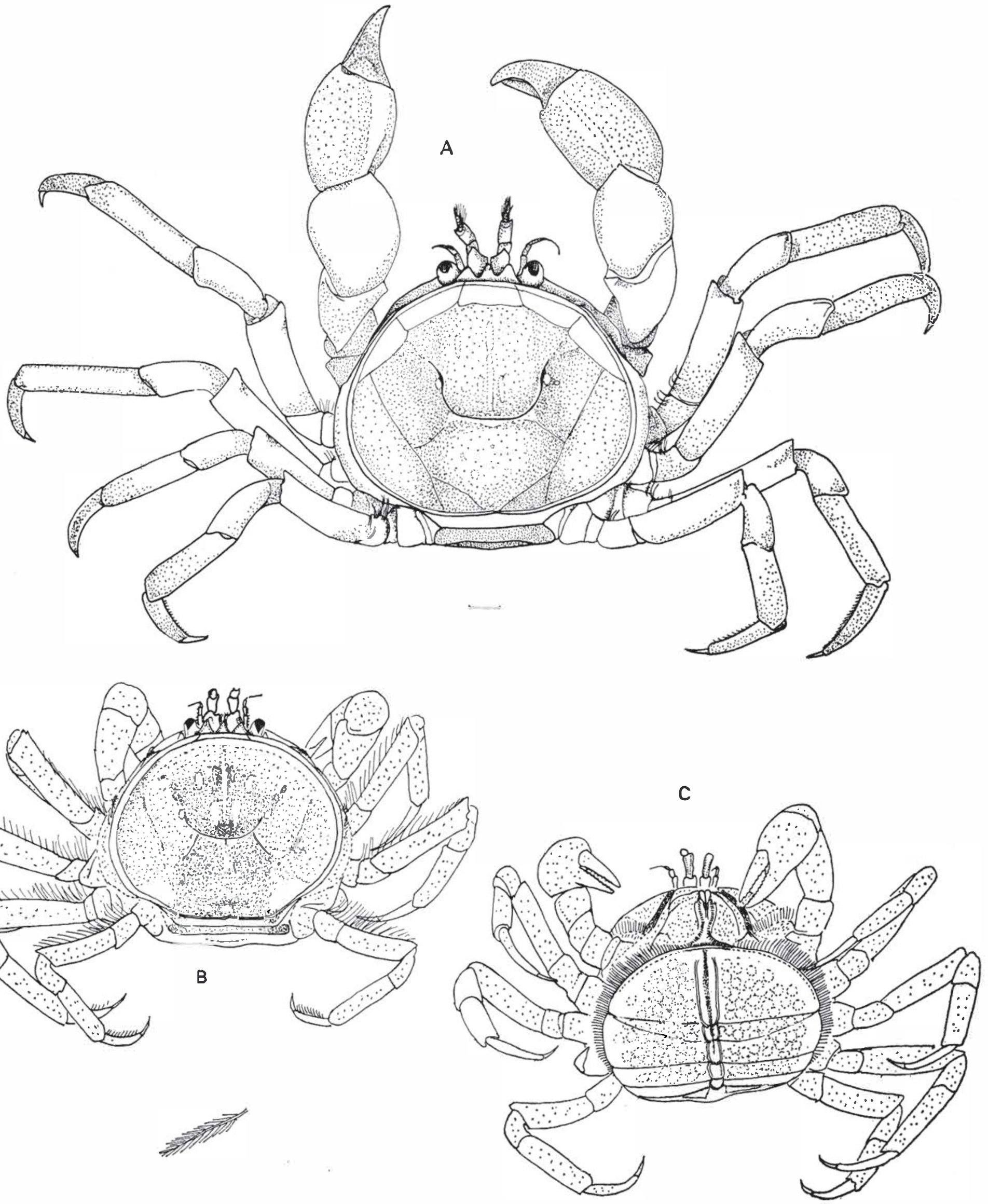
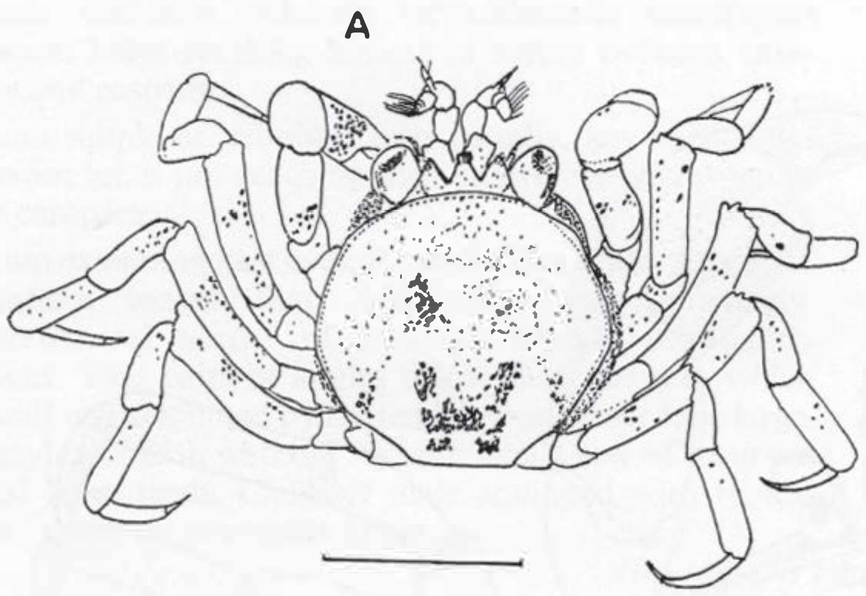
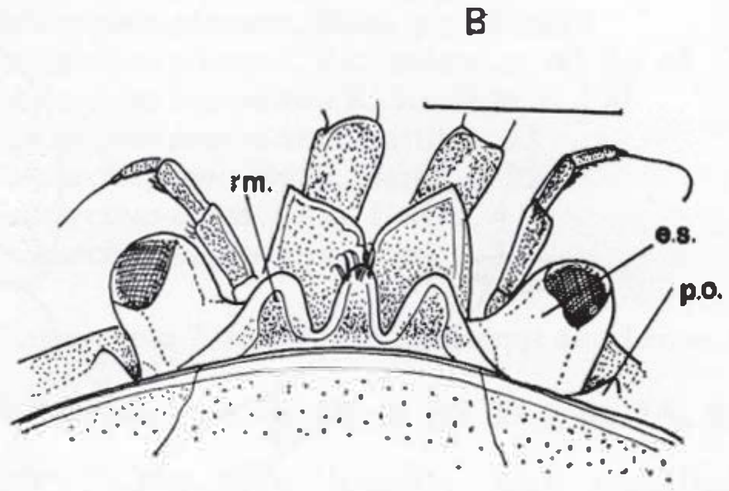
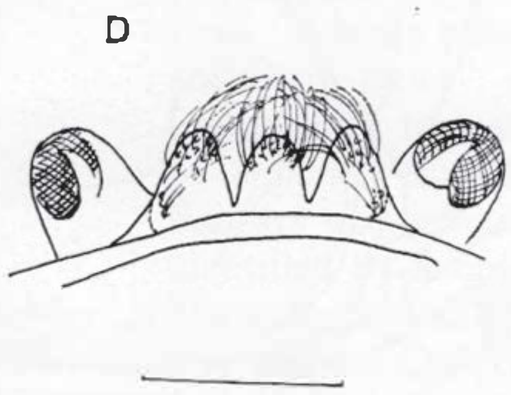
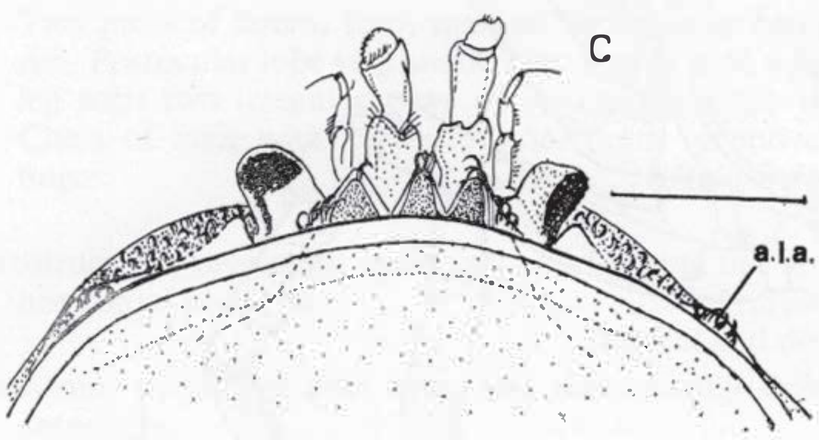


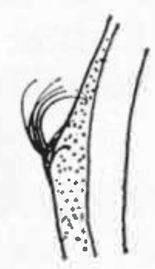
Fig. 8 *Halicarcinus innominatus*: A—Male, dorsal view; B—Female, dorsal view; C—Female, ventral view. (scale represents 1 mm)

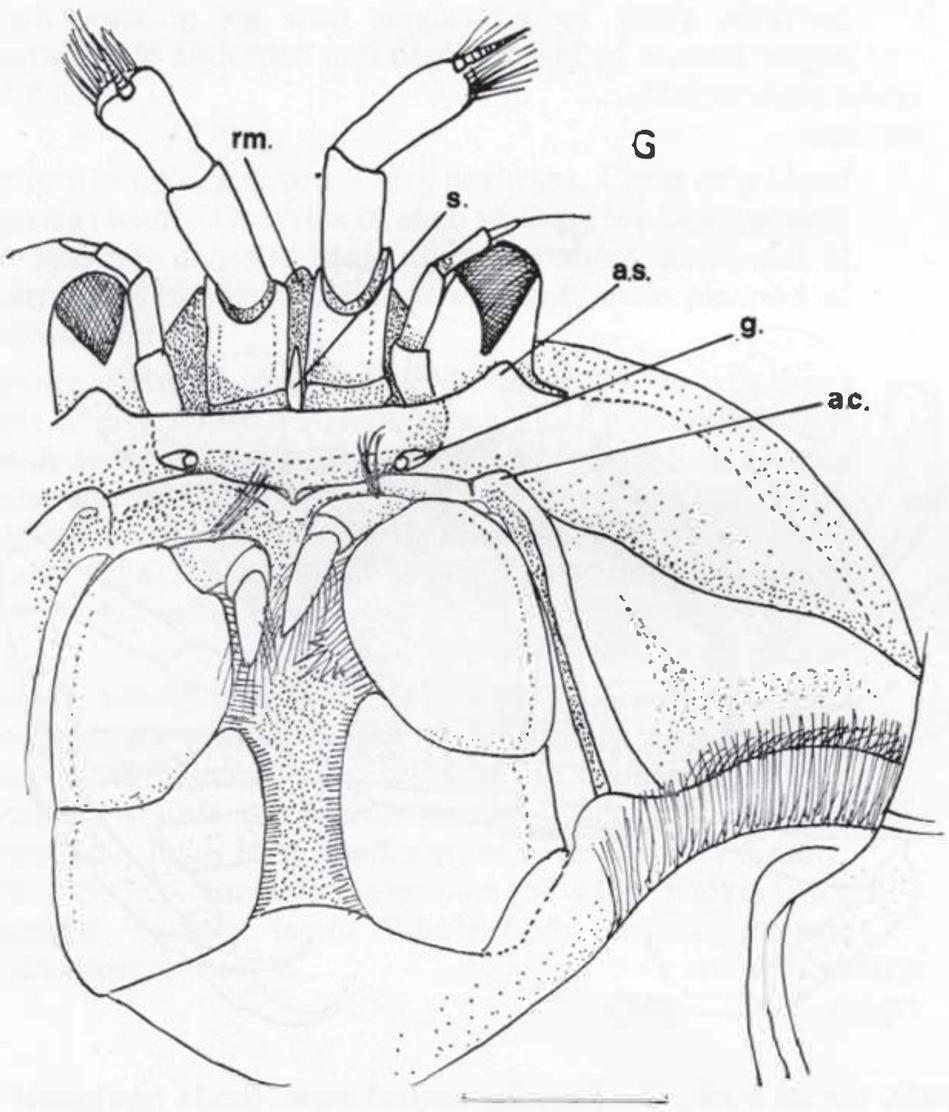


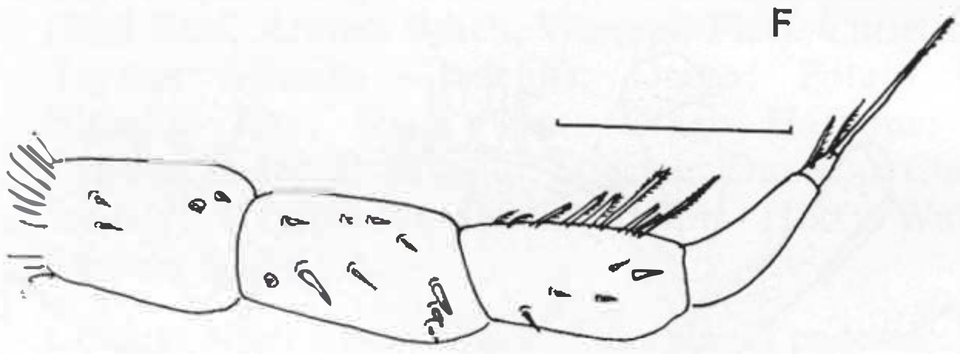












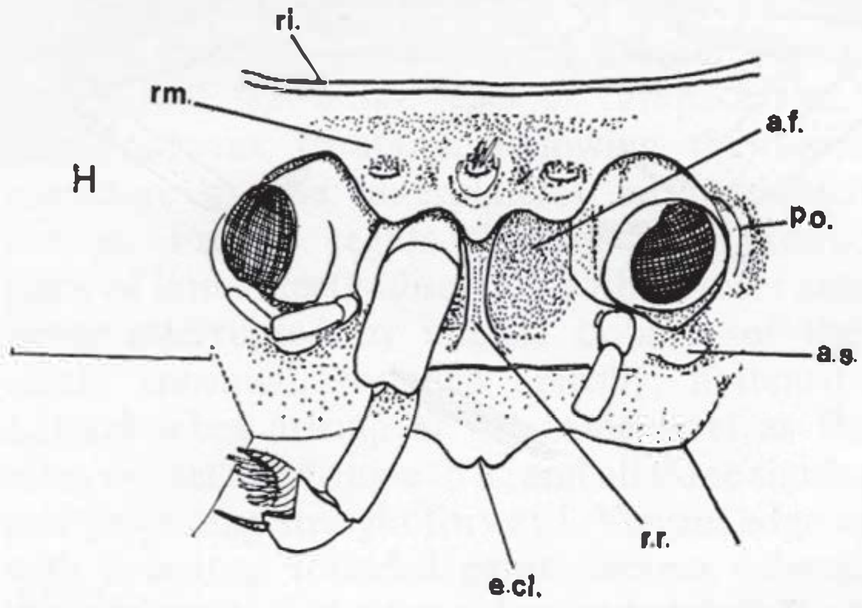


Fig. 9 *Halicarcinus innominatus:* A—Juvenile male, dorsal view; B—Rostrum of male in Fig. 8A; C—Rostrum of female in Fig. 8B; D—Rostrum of female, more hairy than usual; E—Posterior lateral angle of the same female as D; F—Left antenna, inner lateral view; G—Ventral view of mouthfield and epistome of male in Fig. 8A; H—Frontal view of male in Fig. 8A at right angles to the plane of vision, left antennule removed. (scales represent 1 mm except for A, which represents 0.4 mm)

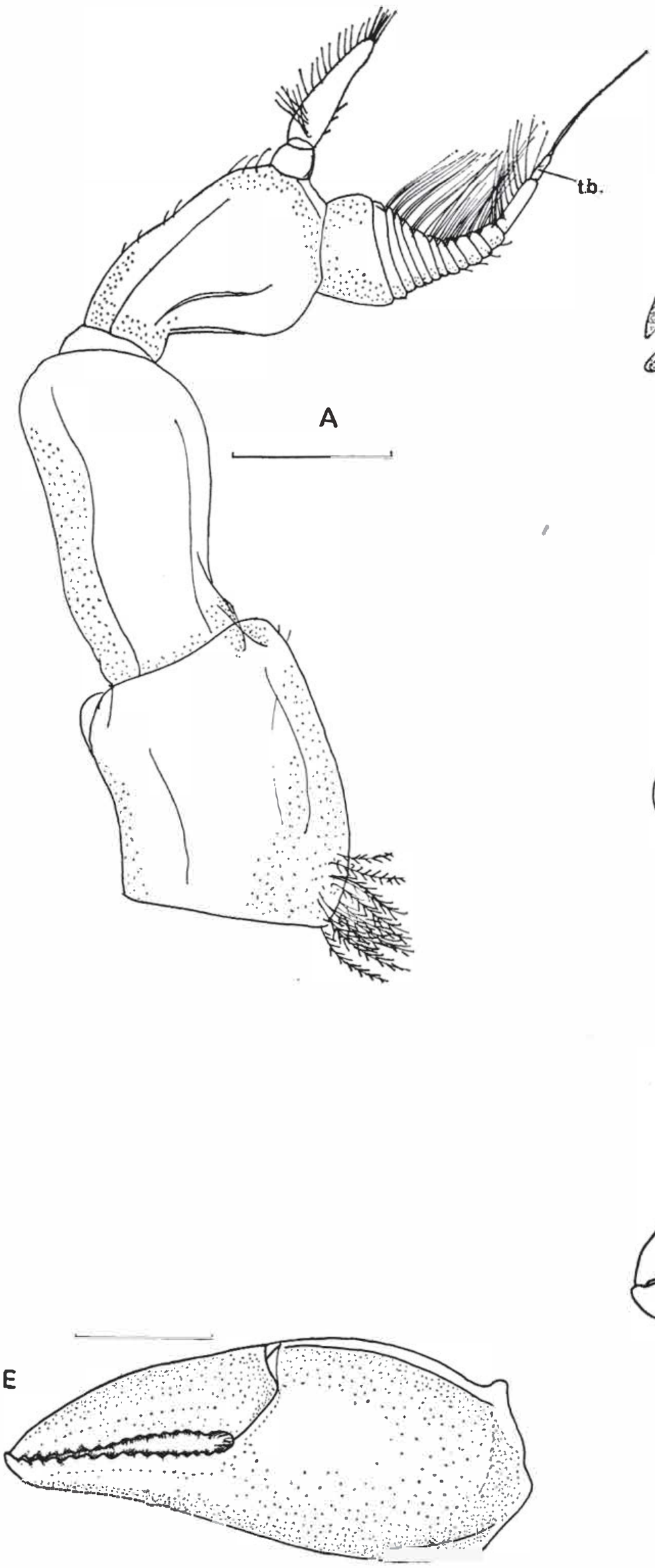


Fig. 10 *Halicarcinus immominatus:* A—Left antenna in lateral ventral view; B—Left cheliped of male, posterior view; C—Left cheliped of male, anterior view; D—Fingers of left chela of male, posterior view; E—Left chela of female, posterior view (scales represent 1 mm)

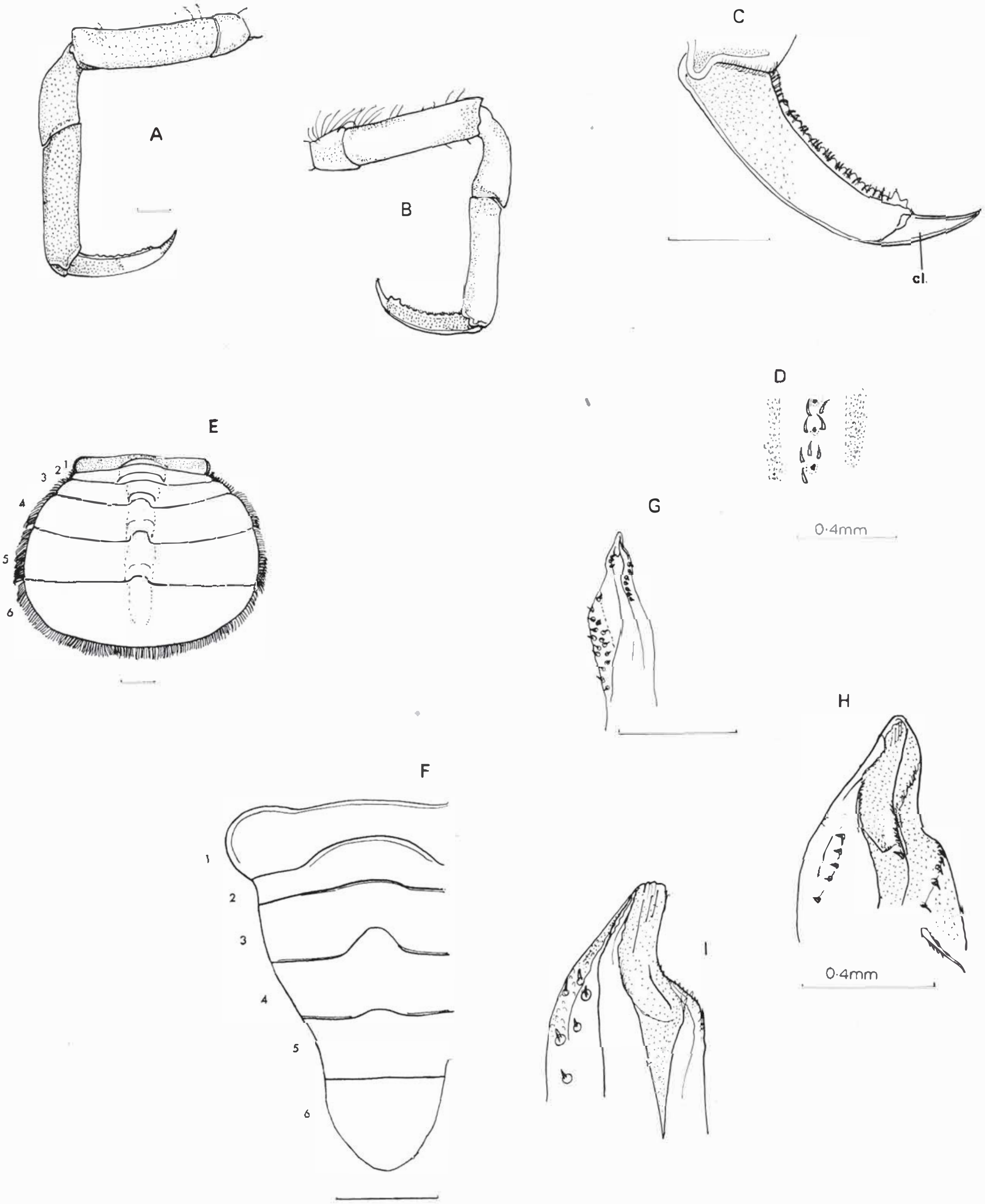


Fig. 11 *Halicarcinus innominatus:* A—Left 3rd walking leg of male, posterior view; B—Left 3rd walking leg of male, anterior view; C—Dactylus of left 3rd walking leg of male, posterior view; D—Dactylus of left 3rd walking leg of male, ventral edge; E—Abdomen of female extended, dorsal view; F—Abdomen of male extended, dorsal view, left side; G—Extremity of 1st male pleopod, sternal view; H—Tip of 1st male pleopod; I—Tip of 1st male pleopod from second specimen. (scales represent 1 mm except where otherwise stated)

a little laterally; 3, 4, 5 subequal in length, longer than first; edges of third almost straight; fourth and fifth narrowing distally; sixth an elongate semicircle. Male first pleopod long, slender, sparsely setiferous; sternal edge slightly expanded into a shelf subterminally, eave vertical.

SIZE RANGE: ♂♂ 1.25 mm* (Piha, rock pool) – 19 mm (Wellington, floating dock). ♀♀ 3.5 mm (Piha, rock pool) – 15.5 mm (hull of dredge *Porituta*).

DESCRIPTION: Carapace suboval, shorter than broad (ratio w.:l. = 1.04–1.22), entirely surrounded by a wide, raised rim. Rim narrows posteriorly, shallowly curved though not concave above the last pair of legs, but indented in the centre of the posterior border. Carapace usually naked, deep grooves delimitating regions. Frontal region completely separated from the gastric region, not produced anteriorly where the rim is gently convex like the short anterolateral border. Gastrocardiac and cervical grooves forming a continuous curve, undeflected centrally. Hepatic and prebranchial regions small, postbranchial obliquely divided by a ridge passing forward from the end of the thoracic groove to the prebranchial region. Cardiac region subdivided by a groove which cuts off a subtriangular area equivalent to the metabranchial region of the Majidae. Sides of the carapace almost vertical posteriorly, not inflated, sometimes with short curved hairs. Branchiostegite projections between the legs reduced. Two rudimentary lateral teeth sometimes present, usually reduced; first just below the rim, equivalent to a slight expansion of the carapace side, with longer hairs than usual; second like the first, obtuse, never projecting up as far as the carapace rim. Rim itself never angled.

Trilobular rostrum of average breadth (a quarter to one-sixth as wide basally as the carapace), very short (a third to one-sixth as long as broad), not longer than 0.5 mm even when the basal breadth is large, never reaching as far as the extremity of the eyes. Lobules arising close together, well below the carapace rim, subequal in length, the free portions being flattened dorsally and a little rounded ventrally, all projecting straight forward from the same level, the laterals not set at an angle to the median lobe. Median lobe narrower basally than the others, with upwardly curved hairs on its tip; remnants of hairs sometimes present on the laterals, or strong tufts curving inward towards the median lobe. Raised ridge passes dorsally from the base of each outer lobule to the carapace rim, broadening as it reaches the rim, frequently with hairs on its inner side. Ventral posterior margin of the rostrum with three rounded projections below the lobules; central one largest, adjacent to the interantennular septum. Postocular lobe adjacent to the expanded edges of each lateral lobule and close to the eyestalk, but reduced to a small ridge. Eyes directed almost straight forward; eyestalks very short and fairly stout.

*Sizes of specimens were recorded by noting the width of the carapace.

Antennules short, basal segment very stout, tufted proximally with short, feathery hairs. Second segment of peduncle almost as stout as basal; third narrow basally, expanded distally as wide as second but slightly shorter. Small ramus with large setiferous terminal segment, ending in a tuft of 6 hairs; large ramus elongate, with up to 12 short subcircular segments. Terminal bulb of average length, unwaisted, terminal seta long. Antennal spine large, barely obtuse. Interantennular septum well developed with a deep ridge. Epistome small, short (width almost three times length), deeply sunken, a faint suture laterally separating it from the swollen subhepatic regions which obliterate the carapace from ventral view. Posterior ridge of epistome very deep, central cleft reduced to a small indentation. Pterygostomian regions large, smooth, the long edge of the triangular area somewhat concave medianly. Long fringes of hairs guarding the narrow Milne Edward's opening. No hairs on the sterna of the third maxillipeds.

Endopods of the third maxillipeds gaping in the mid line; ischium and merus both laterally expanded; ischium wider than long, curvature of median edge reduced, armed medianly with one or two rows of short setae. Short setae sparsely scattered over the ventral face of ischium and merus; longer setae on the posterior portion of the median edge and on the external edge of the ischium. Anteromedian lobe short and broad; articulation with the merus wide. Merus as long as ischium, maximum width equal to length, median edge deeply curved, with a row of setae of medium length; straight outer edge has scattered setae; proximal carpus articulating near this edge. Carpus small, anterior edge almost straight and setiferous. Propodus subquadrangular and as long as carpus. Dactylus half as long again as propodus, more slender, bluntly pointed. Dorsal hairs on carpus and propodus sparse, dactylus has setae of median length.

Basal segment of exopod broad, lateral edges tapering gradually to the apex, fringed with feathery hairs, hairs on the median edge being much longer, forming a double row along the anterior half, a single row posteriorly; a basal median oblique row and a tuft on the median edge below the apex. Terminal segment short and slender with six long apical hairs.

Basal lobe of the epipod large, semicircular, with scattered feathery hairs; basal portion of median curvature has two to four rows of long setae anteriorly, a few short setae on the posterior edge. No distinct suture between basal portion and lamella; lamella slightly longer than the base, densely hairy on both edges and the broadly rounded tip.

Chelipeds massive in adult males (length 1.5–1.8 times width of carapace), slighter in females (length 1.2–1.3 times width of carapace). Ischium short, subtriangular. Merus only slightly narrower than long, expanded centrally along the ventral edge, distal ventral projection reduced to a small knob; other distal projections rounded, virtually absent. Carpus a little longer then merus, almost as broad distally as long, a pronounced distal projection ventrally over the propodus.

Palm somewhat shorter than carpus, expanded laterally so that maximum depth is equal to length, greatly inflated, the posterior surface deeply convex, the anterior face a little flattened, palm and fingers together arching greatly. Fingers longer than palm in both sexes (1.2–1.5 times as long). Cheliped segments typically naked in both sexes, except sometimes on the inner edges of the fingers. Fingers with a deep linear gape in the female, a pronounced basal gape in the male; dentation reduced in the male, especially on the movable finger which has a square tooth basally, tips of the fingers barely occluding at all. Female, palm also as deep as long, but not as inflated as in male so that the palm is not wide in edge-wise view, fingers and palm not much arched; finger occluding distally where dentation is most marked, short tufts of hairs between the teeth and at base of sinus between fingers.

First and second walking legs both slightly longer than chelipeds (ratio l. of first leg: w. of carapace = 1.6–1.8); third and fourth walking legs a little shorter and subequal, fourth usually a fraction shorter than third (ratio l. of fourth leg: w. of carapace=1.4–1.7). Ischium, merus, carpus, and propodus all broad, subcylindrical in cross section. Ischium very short, subquadrangular, no anterior process extending over the merus. Merus longest, breadth a quarter to a third of its length, sparsely fringed dorsally with hairs; tooth reduced to obtuse prominence. Carpus about two-thirds as long as merus, as broad distally, anterodorsal projection pronounced but blunt. Propodus a little shorter and narrower than the merus, ending in a shallow V, the sides of which are almost perpendicular with the edges of the segment, and sparsely hairy. Stout dactylus shorter than the propodus, flattened, broad, tapering a little to a strong and distinctly separate claw; ventral edge has a central single row of blunt tubercles, tipped with dark chitin, the two teeth nearest the claw enlarged, the penultimate largest and slightly recurved; very short setae between and on either side of the tubercules.

Female abdomen subcircular, a long fringe of hairs on all segments except first, last segment broad, evenly rounded distally. Proximal central projections subequal, small but most marked on the last three segments.

Male abdomen separated from the carapace by a wide vertical ledge, long, reaching to level of suture between sterna of cheliped and first walking legs. First segment widest, short centrally, expanded somewhat laterally into rounded lobes; second subequal with the first centrally, shortening laterally where the edges are straight; edges of third almost straight, over twice as long as edges of segment two; fourth subequal with third, but with a much more pronounced narrowing distally; fifth segment as long as each of preceding two, narrowing distally; sixth segment semicircular, slightly elongated, broadly rounded terminally. Whole abdomen narrowing to half way down the fifth segment, the sixth segment tapering from this width half way down its length; sides of fifth segment therefore a little concave. Convex projections of the proximal edges on segments two to five; that of segment two broad and deep; of three slightly narrower and very shallow; of four even narrower but very deep; of five shallow and equal in width with that of the fourth segment.

Long first pleopod of male twisted through more than 90°; distally very slender, no long setae but several short longitudinal rows of short setae near the tip, the sternal edge expanded into a small keel below the tip. Opening of vas deferens very long; the tip therefore prolonged into a narrow, vertical, internally ridged, hollow eave, so that in outline the end of the pleopod is sharply constricted.

MATERIAL EXAMINED:

Personal Collection: Piha, Auckland, 16/3/1965, 4 ♂ ♂ 1.75–3.5 mm, 2 s. ♀ ♀* 7.25–7.5 mm (rock pools); 13/4/1965, 8 ♂ ♂ 1.4–6.26 mm, 1 g. ♀* 7 mm, 3 ♀ ♀ 3.5–4 mm (rock pools); 13/4/1965, 17 ♂ ♂ 1.25–13 mm, 8 g. ♀ ♀ 7–10 mm, 5 s. ♀ ♀ 6–9 mm, 2 ♀ ♀ 6–10.5 mm (mussel beds on Lion Rock, Piha); –/9/1965, 1 ♂ 9 mm. Devonport, Auckland, 10/9/1965, 1 ♂ 12.5 mm (paint raft at Naval Base).

Victoria University of Wellington, Zoology Department Collection: Wainui Bay, Wellington, 22/10/1964, 1 ♀ 7 mm (under rocks in sand, labelled *H. ovatus*). Breaker Bay, Wellington, 20/11/1964, 1 ♂ 9.5 mm (labelled *H. planatus*).

Edward Percival Marine Laboratory Collection: From s.s. *Waipaki* on floating dock, Wellington, 13/5/1955, 15 ♂ ♂ 7–19 mm, 4 g. ♀ ♀ 7–12 mm, 1 ♀ 7 mm. Taylors Mistake, Christchurch, 15/4/1961, 2 ♂ ♂ 5–12 mm, 1 g. ♀ 14.5 mm, 1 ♀ 5.5 mm (inter-tidal). Kaikoura, –/8/1965, 2 ♀ ♀ 4.5–7.5 mm. Wairepo Flats, Kaikoura, 21/8/1963, 1 ♂ 5 mm (from *Zostera* beds, K 339A). Seal Reef, Kaikoura, 3/9/1964, 1 ♂ 7 mm (from *Carpophyllum* fronds, K 410A), 1 ♂ 3.5 mm (from holdfast of *Durvillea antarctica*, K 420N). Armers Beach, Kaikoura, 9/5/1962, 1 ♂ 2 mm (plankton net in shallows, incoming tide, K 085A). Redcliffs, Christchurch, 22/10/1965, 2 ♂ ♂ 3.5 mm (from a group of boulders spanning the intertidal region of the estuary beside the road, C 022K).

Dominion Museum Collection: Little Papanui Beach, Otago Peninsula, 27/12/1920, 1 g. ♀ 11.5 mm (coll. W. R. B. Oliver). Lyall Bay, Wellington, 27/12/1947, 1 ♂ 12.5 mm, 1 g. ♀ 11.5 mm (under stones resting on mud, coll. R. K. Dell). Muriwai, Auckland, 17/1/1961, 8 ♂ ♂ 3–11 mm, 3 g. ♀ ♀ 7.5–8.5 mm, 2 ♀ ♀ 3–8 mm (underneath mussels, coll. R. K. Dell). Waitangi, Chatham Is., 1 ♂ 12 mm, 1 g. ♀ 10 mm (Chatham Islands Expedition, St.26, Cr.920). Kaingaroa, Chatham Is., 1 ♂ 9.5 mm, 2 g. ♀ ♀ 15.5 mm (Chatham Is. Expedition, St.16, Cr.920). From hull of the New Plymouth dredge *Porituta*, arrived in Wellington 5/5/1954, slipped Evans Bay, 9 ♂ ♂ 2.5–11 mm, 6 ♀ ♀ 4.5–9 mm (with a small majid, coll. J. H. Sorenson). Lyall Bay, Wellington, –/9/1947, 1 ♂ 12 mm, 2 g. ♀ ♀ 7.5–10.5 mm (coll. R. K. Dell). Evans Bay, Wellington, 13/10/1954, 1 ♂ 9 mm, 1 s. ♀ 12 mm (powerhouse intake, coll. R. K. Dell). St Clair, Dunedin, 24/12/1920, 2 g. ♀ ♀ 14.5–15 mm (under base of *Durvillea*, with *Cyclograpsus lavauxi*, coll. W. R. B. Oliver). Kau Point, Seatoun, Wellington Harbour, 14/10/1945, 7 ♂ ♂ 3–8 mm, 2 g. ♀ ♀ 6.5–8.5 mm, 6 ♀ ♀ 4–7.5 mm (on algae, coll. R. K. Dell). Shag Point, Otago, 1 ♂ 10 mm (Cr.387). Days Bay, Wellington, –/1/1953, 1 ♂ 15.5 mm (coll. H. Kirk).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: October, December, January, March, April, May.

COLORATION (Plate 1, facing this page): Brown, with green or black tints, banding on legs rare in mature males.

In young specimens the pale yellow carapace is flecked with black, orange, and white chromatophores, but these collectively cover only a small percentage of the carapace so that pale yellow areas predominate.

* g. ♀ = gravid female, s. ♀ = spent female.

A

B

C

D

E

F

Plate 1 A—*Halicarcinus whitei*, male, 6 mm; B—*Elamena producta*, female, 6 mm; C—*Halicarcinus innominatus*, female, 3.5 mm; D—*H. innominatus*, male, 7.5 mm; E—*H. innominatus*, female, 8.75 mm; F—*H. innominatus*, male, 7 mm.

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[facing page 32]

The cuticle darkens later to a pale yellow-brown overlaid with darker brown chromatophores. Large males are almost entirely dark brown usually with several lighter patches on the upper carapace.

In mature crabs the two convex areas in front of and behind the gastrocardiac groove are typically darker than the rest of the carapace, brown tinged with blue-grey, green, or red.

Females frequently have disruptive coloration and yellow, white, and brown splotches are common on their carapaces.

REMARKS: Richardson (1949b) realised that the species he had termed "*H. ovatus*" (Richardson 1949a) was in fact *H. planatus*, and his "*H. planatus*" was a new species, which he called *H. innominata*. Although superficially similar, the two species are easily separated on close examination, (*see* Key, pp. 25–6). Their colour is also different, *H. planatus* being "slaty-blue to reddish-brown with banded legs", or "greyish-brown with spots of a different colour" (Garth 1958, p. 34), whereas *H. innominatus* is usually brown, with green and black tints, and in adult males the legs are rarely banded.

The lack of lateral angles at the side of the carapace in Jacquinot's figure of *Hymenosoma tridentatum* (1853, plate 5, fig. 27), indicates *H. innominatus* rather than *H. planatus*, but the legs are more slender, the carapace is relatively broader, and the rostral lobes further apart than in *H. innominatus*. Moreover, the locality of Jacquinot's specimen, the Auckland Islands, points strongly to *H. planatus*.

Filhol's "*Halicarcinus tridentatus*", on the other hand, is almost certainly synonymous with *H. innominatus*. Although his figure is poor, he correctly differentiates between his specimens from Cook Strait and specimens of *H. planatus* which he collected from Campbell Island. He accurately recorded *H. planatus* as not extending as far north as Stewart Island. He noted the absence of marginal "spines" on the carapace of "*H. tridentatus*" and their presence in *H. planatus*: the fact that the rostral teeth in "*H. tridentatus*" are directed straight forward and all on the same level, whereas the laterals are angled outward below the median tooth in *H. planatus*; and that there is a "small projection" on the lower edge of the rostrum below the "middle spine" corresponding to a concavity in the same position in *H. planatus*. However, Filhol mistakenly referred his specimens to the species previously described by Lucas, although he transferred it to the genus *Halicarcinus* not realising that he had discovered a new species. Later taxonomists have recognised the almost certain synonymy between *Hymenosoma tridentatus* Jacquinot and Lucas and *Halicarcinus planatus* without understanding that Filhol's description refers to another species. Filhol also said that Hombron and Jacquinot had reported *H. planatus* from the Auckland Islands, when in fact only *Hymenosoma ? tridentatum* and *Hymenosoma depressum* were recorded in Lucas's script. Perhaps Filhol was hinting that Lucas's *Hymenosoma ? tridentatum* was equivalent to *H. planatus* but he did not adjust his nomenclature accordingly. It is therefore necessary to retain Richardson's *Halicarcinus innominatus* as the specific name.

Garth (1958, p. 31) lists *Cancer orbiculus* Fabricius as a probably synonym of *Halicarcinus planatus*, but Miers (1876a) writes: "The type specimen of the *C. orbiculus* Fabricius is in the collection of the British Museum. It is very much injured, but I think it can be nothing but a specimen of *H. planatus* with the marginal teeth obsolete." If Miers's description of the marginal teeth is accurate, the specimen must be *H. innominatus* rather than *H. planatus*. (*See also* Garth 1958, p. 34–5.)

Chilton has left specimens of *H. innominatus* labelled as *Hymenicus varius*, yet he also identified specimens of *H. varius* correctly. Bennett labelled some specimens of *Halicarcinus innominatus* as *H. tridentatus*, and others as *H. huttoni*. (Bennett also determined specimens of *H. tongi* as *H. huttoni*.)

OCCURRENCE: *H. innominatus* was found associated with the mussel *Perna canaliculus* on hard substrates, and has been collected from the keels of ships.

H. innominatus formed an important part of the community in the lower mid-littoral zone at Piha. This open shore has a striking fringe of bull kelp, *Durvillea antarctica*, which lies stranded on the sand at the base of Lion Rock at low spring tides. *Perna canaliculus* occupies a zone up to 0.6 m above *Durvillea*. No hymenosomatids were ever found in the brown or red seaweeds below average low tide level at Piha. *H. innominatus* was always found in the *Perna* zone and in pools higher on the shore in which were *Perna*, *Ulva*, and *Laurencia thircifera*. On the more sheltered parts of the rock platform where *Perna* specimens were scattered and small, *H. innominatus* were also small and infrequent, occurring only where shallow depressions allowed sea water to collect. In larger pools, up to 1.5 m above extreme low water springs, *H. innominatus* occurred in densities of 3–4 per 0.1 m^2, but remained under 7 mm in width.

Beneath large clumps of adhering mussels on Lion Rock at Piha *H. innominatus* occurred with a density of 10–15 per 0.1 m^2, with a size range of 1.25–13 mm.

BEHAVIOURAL NOTES: When dropped into water, *H. innominatus* floated with legs folded tightly under the carapace, the merus-carpus joints jutting sharply out from the spherical line of the body. Specimens often remained on their back with legs all tightly folded for several minutes before scrambling upright and scuttling off. Crabs that died in fresh water always assumed this folded posture before death and almost always stayed upside down until they died. Sometimes a specimen which had continually been prodded and flipped on to its upper carapace would "play dead" in this pose.

A needle brandished a short distance in front of *H. innominatus* frequently stimulated the crab to rush forward, chelae high and swinging from side to side, pincers opening and shutting. This was the most aggressive species studied.

Placed in an aquarium with mussel shells, *H. innominatus* hides beneath the valves with its back legs hooked

Inset 5*

under the edge of the valve. The crabs often climbed between the shell and mantle of paua in the same aquarium gripping the mantle edge with the last pair of legs and searching for food with the chelipeds. At times only the rostrum, eyes, and chelae could be seen protruding from under the shell. In the field, *H. innominatus* was often found inside the partially open valves of a dead mussel, or walking between or over the valves.

Display between males was not seen. Occasionally, when a pair of males met and their chelae happened to touch, they would briefly lock the chelae together.

Feeding: H. innominatus assumed a feeding posture, with the carapace sloping upwards anteriorly braced on the bent fourth pair of walking legs, the other legs radiating outwards and the chelipeds half bent with the fingers open.

Food preferences: H. innominatus would eat pieces of mussel and paua and was seen entering the valves of recently dead mussels—this crab is probably important in scavenging decaying mussel flesh. Apparently it does not prey on live *Perna*, nor attack live *Perinereis* in the aquarium. It did eat pieces of dead polychaetes and would catch worms as they floated past but usually lost interest if the prey were still alive.

Epifauna: One specimen had an anemone, *Actinothoe albocincta*, on the carapace but when it was dislodged the crab made no attempt to retrieve it. Small, settled *Perna* (0.5–2 mm in length) were sometimes seen on the leg bases and the carapace sides of larger crabs, never more than three mussels on any one crab. One male carried a large barnacle, *Elminius modestus*, on its carapace.

Halicarcinus planatus (Fabricius)

Figs. 12 and 13

(Shortened synonomy; *see also* Garth 1958, p. 31)

1775 *Cancer planatus* Fabricius, p. 403
1798 *Leucosia planata*, Fabricius, p. 350
?1829 *Hymenosoma leachii* Guerin, pl. 10, fig. 1
?1830 *Hymenosoma leachii* Guerin, p. 22
1843 *Leucosia orbiculus* White, p. 266
1846 *Halicarcinus planatus*, White, p. 178, pl. 2, fig. 1
1849 *Liriopea leachii*, Nicolet, p. 160, Atlas, pl. 1, figs. 1–1f
1849 *Liriopea lucasii*, Nicolet, p. 161
?1851 *Halicarcinus pubescens* Dana, p. 253
?1852 *Halicarcinus pubescens* Dana, p. 386, 1855 Atlas, pl. 24, fig. 6
1852 *Halicarcinus planatus*, Dana, p. 385, 1855 Atlas, pl. 24, figs. 7a, 7b
?1853 *Halicarcinus planatus*, *Halicarcinus leachii* and *Halicarcinus pubescens*, H. Milne Edwards, p. 223
?1853 *Hymenosoma* ? *tridentatum* Jacquinot and Lucas, p. 60, Atlas, figs. 27–33
1876a *Halicarcinus planatus*, Miers, p. 281
1877 *Halicarcinus planatus*, Targioni-Tozzette, p. 176, pl. 10, figs 4, 4a–f
?1881 *Halicarcinus planatus*, Miers, p. 70
1882b *Hymenosoma planatum*, Haswell, p. 114
?1886 *Halicarcinus ovatus* Cano, pp. 164, 177 (Not *Halicarcinus ovatus* Stimpson, 1858)
1888 *Halicarcinus planatus*, Cano, pp. 164, 177
1893 *Halicarcinus planatus*, Ortmann, p. 31
?1893 *Halicarcinus planatus* var *pubescens*, Ortmann, p. 32
1900 *Halicarcinus planatus*, Stebbing, p. 524, pl. 36B
1902 *Halicarcinus planatus*, Hodgson, p. 231
1902 *Halicarcinus planatus*, Lenz, p. 755
1904 *Halicarcinus planatus*, Hutton, p. 250
1909 *Halicarcinus planatus*, Chilton, pp. 609, 610
1914 *Halicarcinus planatus*, Stebbing, p. 270
1918 *Halicarcinus planatus*, Tesch, pp. 9–11
1925 *Halicarcinus planatus*, Rathbun, p. 563, pls. 202, fig. 5, pl. 283
1927 *Halicarcinus planatus*, Stephenson, pp. 289–390
?1929 *Halicarcinus planatus*, Chilton and Bennett, pp. 735, 776
1930 *Halicarcinus planatus*, Balss, pp. 195, 210
1930 *Halicarcinus planatus*, Bennett, pp. 259–60
1941 *Halicarcinus planatus*, Hale, p. 284
1949a *Halicarcinus ovatus*, Richardson, pp. 59, 68, fig. 49
1949b *Halicarcinus planatus*, Richardson, p. 130
1957 *Halicarcinus planatus*, Garth, p. 32
1958 *Halicarcinus planatus*, Garth, pp. 31–5
1963 *Halicarcinus planatus*, Dell, p. 38
1964 *Halicarcinus planatus*, Bennett, p. 109, fig. 128

TYPE LOCALITY: New Zealand? (*see* Garth 1958, and Miers 1876b).

SUMMARY OF LOCALITIES: For overseas localities (Chile, Strait of Magellan, Tierra del Fuego, etc.) see Garth (1958, p. 32). Localities near New Zealand include Kerguelen Island, Macquarie Islands, Auckland Islands, Campbell Island, off Gannet Island, and Cook Strait.

DISTRIBUTION: South Pacific from Tatal, Chile, through the Strait of Magellan to the Falkland Islands, thence eastward via the antarctic islands of South Orkney, Prince Edward, Kerguelen, Macquarie, Campbell, and Auckland, to New Zealand.

DIAGNOSIS: Carapace suboval, broader than long; convex, with regions of the carapace not usually obvious. Short tridentate rostrum just reaching to the limits of the small eyes; teeth arising far apart, immediately below the frontal rim of the carapace which is more strongly convex than the rim on either side; frontal region therefore produced anteriorly. Anterolateral border short, straight. Median rostral tooth shortest, projecting straight forward. Lateral teeth sloping outward and downward, at an angle to the median one; all three sometimes setiferous, median one almost always. Lower edge of rostrum indented centrally. Two pairs of lateral teeth present well below the carapace rim; the first obtuse and sometimes marked by a faint angle interrupting the rim itself, the second always acute though small. Postocular lobe very reduced, set unusually far from the eyestalk. Antennal spine absent. Chela of male moderately inflated, basal gape narrow with a tiny tooth on the movable finger, dentation well developed on the distal third of the fingers. Segments of walking legs stout, dactylus moderately curved, short, armed with two irregular rows of short, pointed teeth. Ischium of third maxilliped broader and shorter than the merus. Male abdomen separated by a wide vertical ledge from the carapace. First segment small, little expanded laterally; second segment subequal with first centrally, shortening greatly laterally; third, fourth, and fifth

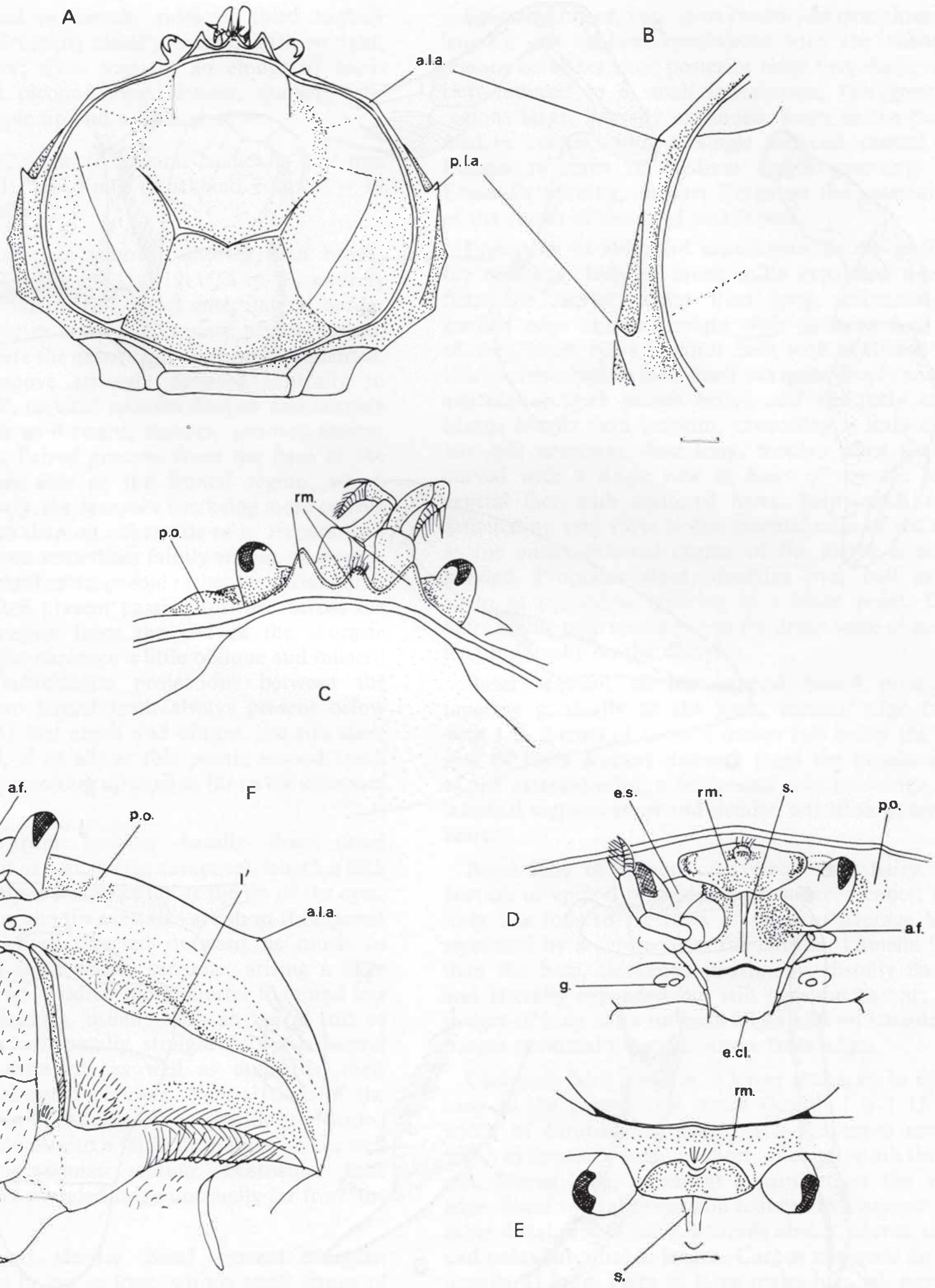


Fig. 12 *Halicarcinus planatus:* A—Male, dorsal view; B—Enlargement of lateral angles; C—Rostrum of different male from A; D—Frontal view of male in C, upper carapace almost perpendicular to the plane of vision, left antennule removed; E—Second view of front shown in C, angled downward a little to show the sloping lateral lobes and the straight median lobe; F—Ventral view of left side of epistome and mouthfield of same male as C. (scale, below B, represents 1 mm for A, C, D, E, and F. B is an enlargement.)

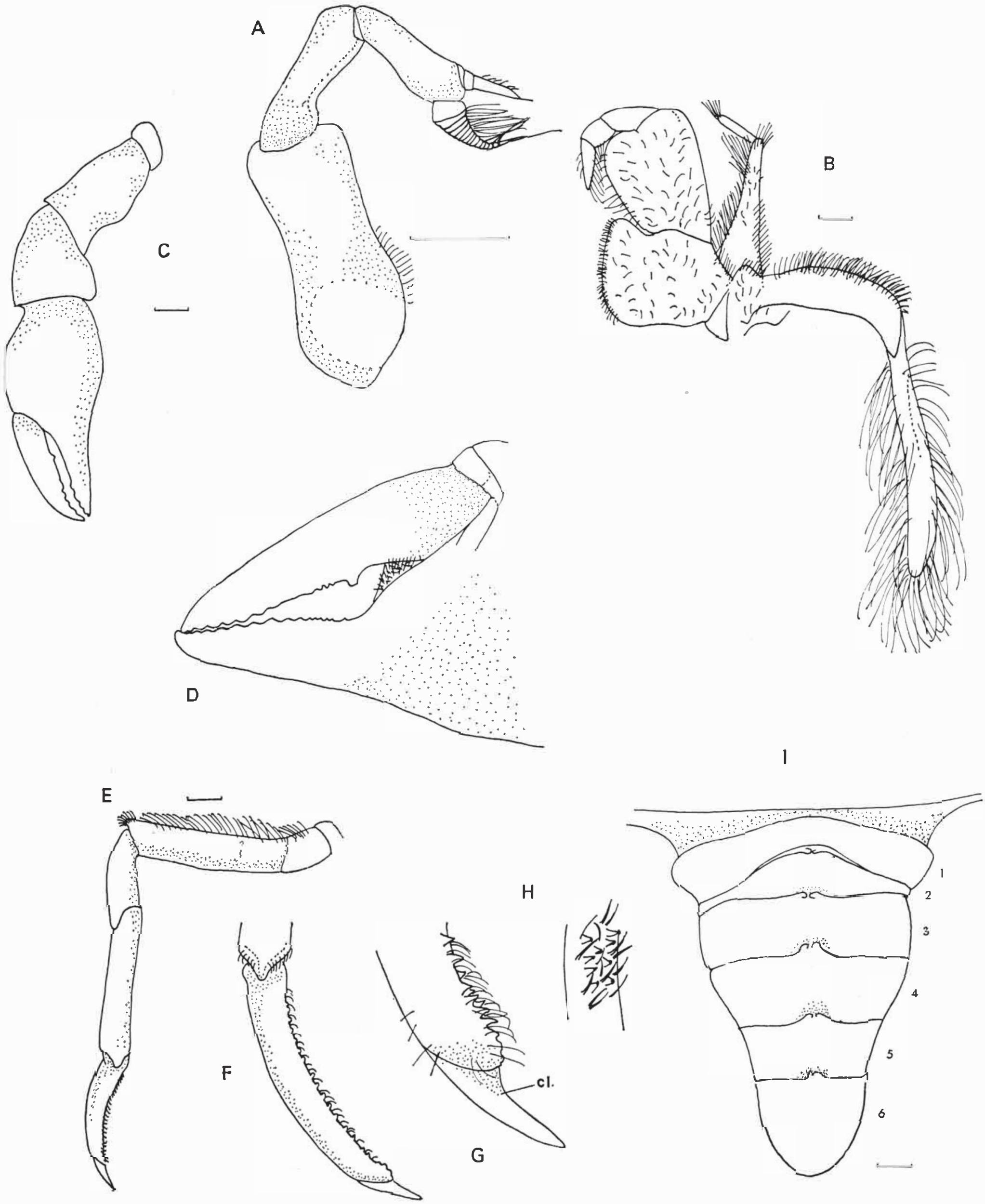


Fig. 13 *Halicarcinus planatus:* A—Left antennule in lateral-ventral view; B—Left 3rd maxilliped of male; C—Left male cheliped, posterior view; D—Fingers of left male chela, posterior view; E—Left 3rd walking leg of male, posterior view; F—Dactylus of left 3rd walking leg of male; G—Tip of dactylus of left 3rd walking leg of male; H—Ventral edge of dactylus of left 3rd walking leg of male; I—Abdomen of male extended, dorsal view. (scales represent 1 mm)

segments subequal in length; sides of third slightly convex, fourth narrowing distally, sides of fifth straight, narrowing distally; sixth segment an elongated semicircle. Male first pleopod long, slender, sparsely setiferous with a simple tip and a vertical eave.

SIZE RANGE: ♂♂2.5 mm (Auckland Islands) – 23.5 mm (Campbell Island). ♀♀3.5 mm (Auckland Islands) – 19 mm (Campbell Island).

DESCRIPTION: Carapace suboval, shorter than broad, (ratio w.: l.=1.07–1.21 in ♂; 1.19–1.35 in ♀), entirely surrounded by a narrow rim. Short anterolateral border almost straight, never convex. Carapace usually naked, convex except where the gastrocardiac groove is indented. Gastrocardiac groove strongly deflexed centrally to form a shallow V, cervical grooves distinct and curving outward as much as forward, thoracic grooves shorter but also distinct. Paired grooves from the base of the rostrum on either side of the frontal region, which protrudes anteriorly, the carapace rim being more convex above the rostrum than on either side of it. Hepatic and prebranchial regions sometimes faintly visible, of average size, the prebranchial subtrapezoid rather than triangular. Oblique ridge often present passing forward across the post branchial region from the end of the thoracic groove. Sides of the carapace a little oblique and inflated posteriorly, branchiostegite projections between the legs reduced. Two lateral teeth always present below the carapace rim; first small and obtuse, the rim itself shallowly angled, if at all, at this point; second small but acute, never projecting upward as far as the carapace rim.

Tridentate rostrum broader basally than usual (quarter to a third as wide as the carapace), length a fifth breadth, frequently reaching as far as the tip of the eyes, as the eyes are tiny and the eyestalks are short though not especially stout. Eyes directed outward as much as forward. Rostral teeth widely separate, arising a little below carapace rim; median tooth shorter than and less sharp than the laterals, usually with an apical tuft of hairs, projecting horizontally straight forward; lateral teeth sloping downwards as well as outwards, their median edges somewhat concave. Ventral edge of the rostrum convex on either side of the shallowly indented centre which is adjacent to a fairly deep ridge on the well developed interantennular septum. Postocular lobe reduced to a small rounded ridge unusually far from the eyestalk.

Antennules short, slender. Basal segment elongate, only one-third as broad as long, with a small fringe of short hairs on the external edge; second and third peduncular segments subequal (second a fraction shorter than third), much shorter, more slender than the first; third segment hardly expanded distally; the small ramus has a single terminal hair; the large ramus reduced so that it is scarcely longer than the small ramus, narrow, with up to 15 small, subcircular segments and a long, thin, non-waisted terminal bulb surmounted by a long hair.

Epistome broad, very short (width just over three times length), not sunken, continuous with the subhepatic regions on either side; posterior ridge very deep, central cleft reduced to a small indentation. Pterygostomian regions large, laterally expanded, hairy in the posteromedian corner, with a single reduced central lobe. Fringes of hairs of medium length guarding Milne Edward's opening, another fringe on the anterior edge of the sterna of the third maxillipeds.

Endopods of the third maxillipeds hardly gaping in the mid line. Ischium much more expanded medianly than the merus, wider than long, subrectangular, median edge almost straight with three to four rows of very short hairs, ventral face with scattered short hairs, anteromedian lobe small but quite deeply rounded, articulation with merus broad and obliquely curved. Merus longer than ischium, expanding a little distally but still narrower than long, median edge shallowly curved with a single row of hairs of average length, ventral face with scattered hairs. Palp small, carpus articulating very close to the external edge of the merus as the antero-external corner of the merus is not expanded. Propodus stout; dactylus over half as long again as propodus, tapering to a blunt point. Dorsal hairs on the palp sparse except for dense setae of medium length dorsally on the dactylus.

Basal segment of the exopod broad proximally, tapering gradually to the apex, median edge fringed with 1 to 2 rows of hairs, a denser tuft below the apex; row of hairs a short distance from the proximal half of the external edge, a horizontal row below the apex; terminal segment short and slender, has 10 short terminal hairs.

Basal lobe of epipod of average size, hairy. Basal portion of epipod of medium curvature, slender, anteriorly has four to six rows of setae of average length, separated by a suture from the lamella. Lamella longer than the base, thickened proximally, distally flattened and laterally expanded but still not transparent; dense fringes of long hairs on both edges and on rounded tip, fringes proximally some distance from edges.

Chelipeds fairly massive in larger males, up to twice as long as the carapace is broad (length 1.6–2.15 times width of carapace in males; 1.2–1.3 times carapace width in females). Ischium short, of equal width throughout. Merus long, a central expansion on the ventral edge, distal ventral projection reduced to a narrow knob, other distal projections practically absent. Merus, carpus, and palm subequal in length. Carpus not quite as broad distally as long. Palm of large males inflated, especially on the posterior face, expanded laterally so that it is deeper than long; in smaller males and females depth less than length. Fingers and palm together somewhat arched. Fingers slim, longer than the palm (1.25–1.4 as long) occluding over the distal third to two-thirds as dentation is well developed; linear gape between the basal third of the female fingers, small basal gape with a small square tooth on the movable finger of the male. First three pairs of walking legs subequal, decreasing in

size posteriorly, but first two pairs sometimes equal. First pair twice as long as carapace is wide, as long as, or a little longer than the chelipeds. Fourth walking leg shorter (1.5–1.7 times width of carapace). Ischium, merus, carpus, and propodus all broad, subcylindrical in cross section. Ischium short, subquadrangular, extending a little over the merus anteriorly. Merus longest, breadth quarter to a third of its length, fringed dorsally with hairs; tooth reduced to an obtuse, hairy prominence. Carpus half to two-thirds as long as merus, with a bluntly pointed distal projection. Propodus five-sixths as long as the merus, ending in a pronounced V. Stout dactylus as long as propodus, flattened, of average curvature, tapering only slightly towards the tip, ending in a large, separate claw. Ventral edge of the dactylus has two irregular but distinct rows of small, sharp teeth (tipped with dark chitin), curved hairs between and beside these teeth. Teeth nearest the claw reduced.

Female abdomen subcircular, hair-fringed. End segment broad, semicircular, the edge expanded slightly on each side below the joint with penultimate segment.

Male abdomen long, separated from the carapace by a wide, vertical ledge. First segment quite small, not much expanded laterally; second as long as first centrally, shortening greatly outwards, lateral edges tiny and straight; edges of third segment convex; fourth and fifth narrowing distally; fifth less markedly, its edges almost straight. Third and fifth segments subequal in length, fourth a fraction longer, all much longer than the first; sixth segment an elongate semicircle. Proximal edges of segments two to six have convex projections which are depressed centrally forming twin peaks. Projection of segment two evenly and deeply curved; of three, almost straight; of four small; of five, wider but shallower than that of four; of six, tiny.

Long first pleopod of male bent through more than 90°. Distal portion very slender, without long setae but with a few longitudinal rows of short setae well below the tip (*see* Garth 1958, p. 33, fig. 1A, B). Longitudinal ridge reduced on distal portion, tip prolonged as a narrow vertical eave, so that in outline the end of the pleopod shows a sharp constriction. No small subterminal expansion of the sternal edge into a keel.

MATERIAL EXAMINED:

Dominion Museum Collection: Waterfall Inlet, Auckland Islands 1 ♂ 18 mm, 1 ♀ 7.5 mm (among rocks, coll. E. M. and W. D. Cape Expedition, No. 196). Perseverance Harbour, Campbell Island, 18/5/1944, 2 ♂ ♂ 17.4–22 mm (Cape Expedition). Smoothwater Bay, Campbell Island, 16/11/1945, 4 ♂ ♂ 16–22.5 mm (rock pool, coll. J. H. Sorenson, Cape Expedition). Tucker Cove, Campbell Island, 24/5/1960, 5 ♂ ♂ 19–23 mm (after tidal wave, coll. Clague and Poppleton, 0400Z). Ranui Cove, Auckland Islands, 9/11/1964, 21 ♂ ♂ 2.5–16 mm, 9 ♀ ♀ 3.5–11.5 mm, 1 g. ♀ 14 mm (coll. E. S. Gourley, Cr. 505). Crozier Point, Auckland Islands, 8/8/1943, 39 ♂ ♂ 3.5–15.5 mm, 36 g. ♀ ♀ 8–15.5 mm, 12 ♀ ♀ 6–9.5 mm (under boulders at low tide, coll. W. H. Dawbin, No. 311, Cape Expedition, Cr.513). Camp and Garden Coves, Campbell Island, 24/5/1960, 1 ♂ 19.5 mm, 1 ♀ 10.5 mm (after tidal wave, coll. Rae and Poppleton, 0400Z). Penguin Harbour, Campbell Island, 3/4/1946, 1 ♂ 23.5 mm (cast ashore, coll. J. H. Sorenson, Cape Expedition, 475). Port Ross, Enderby Island, Auckland Islands, 19/3/1954, 1 ♂ 12 mm, 2 ♀ ♀ 13.5–10 mm (in intertidal pools and under stones, coll. R. K. Dell). Perseverance Harbour, Campbell Island, 1 ♀ 19 mm, 1 g. ♀ 14 mm, 1 ♂ 8 mm (3–4 fathoms (5.5–7 m), coll. R. L. Oliver). Port Ross, Auckland Islands, 1 ♂ 7.5 mm (coll. G. Jones, Cape Expedition, 474). Perseverance Harbour, Campbell Island, –/1/1952, 5 ♂ ♂ 11.5–18 mm, 2 ♀ ♀ 13.5–14.5 mm, 1 s. ♀ 17.5 mm (coll. J. Moreland). Tucker Cove, Campbell Island, 11/3/1957, 4 ♂ ♂ 9.5–18.5 mm (rocky shore), Penguin Harbour, Campbell Island, 1/4/1944, 1 ♂ 15.5 mm, 1 ♀ 14.5 mm (Cape Expedition). Musgrave Peninsula, Carnley Harbour, Auckland Islands, 8 ♂ ♂ 10.5–19 mm (eating an unidentified polychaete), 4 g. ♀ ♀ 15–19 m (Cape Expedition, 487). Rose Island, Port Ross, Auckland Islands, 19/3/1954, 1 ♀ 9.5 mm (under stones, coll. R. K. Dell). Ranui Cove, Auckland Islands, 19/5/1954, 13 ♂ ♂ 11.5 mm, 5 ♀ ♀ 6–11 mm (Cape Expedition, coll. E. G. Turbott, 469). Beeman Wharf, Campbell Island, 16/1/1958, 1 ♀ 13 mm (ring pot, coll. D. J. Street, Cr.778). Perseverance Harbour, Campbell Island, 21/1/1961, 1 ♀ 4.5 mm, 1 s. ♀ 8 mm (otter trawl, 4–5 fm (14–18 m), between wharf, Lookout Bay, coll. J. Moreland). Tucker Cove, Campbell Island, 20/2/1960, 2 ♀ ♀ 15–15.5 mm (taken from under rocks, coll. R. G. Rae). Tucker Cove jetty, Campbell Island, 3/1/1963, 1 g. ♀ 16 mm (coll. A. Wright). Emergency Bay, Carnley Harbour, Auckland Islands, 1 ♂ 7 mm, 1 ♀ 10.5 mm (dredged in 6 fm (11 m) Cape Expedition). Campbell Island, 1958–59, 6 ♂ ♂ 6–12 mm (coll. P. G. Poppleton). Venus Bay, Campbell Island, 23/8/1943, 3 ♂ ♂ 9.5–15 mm, 1 g. ♀ 15.5 mm (coll. J. H. Sorenson, Cape Expedition). Ranui Cove, Auckland Islands, 8/11/1954, 1 ♂ 14.5 mm (rocks and *Durvillea*, coll. E. S. Gourlay, Cr.507). Perseverance Harbour, Campbell Island, 29/9/1944, 1 ♂ 14.5 mm, 1 ♀ 13 mm (under stones between tide marks, coll. R. L. Oliver). Carnley Harbour, Auckland Islands, 15/2/1943, 2 ♂ ♂ 4.5–14 mm, 1 ♀ 4 mm (dredged in 8 fm (14.5 m), coll. W. H. Dawbin, No. 83, Cape Expedition, Cr.525). Laurie Harbour, Auckland Islands, 16/2/1943, 1 ♂ 9 mm, 2 ♀ ♀ 4, 8.5 mm (near top 10 fm (18 m), coll. W. H. Dawbin, No. 95, Cape Expedition). Ewing Island, Auckland Islands, 28/2/1943, 5 ♂ ♂ 6–13 mm (in rock pools, coll. W. H. Dawbin, No. 37, Cape Expedition); 1 ♂ 19 mm, 1 ♀ 11.5 mm (labelled *Halicarcinus* species, N.Z. Cr.384).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: January, February, March, April, May, August, November.

COLORATION: Slaty-blue, greyish-brown, or reddish-brown, with banded legs (Garth 1958, p. 34). Not seen in life.

REMARKS: The early misidentification of specimens of *H. planatus* and *H. innominatus* can be understood if their descriptions are compared. However, they differ in many important respects, e.g. the arrangement of the rostral teeth, the shape of the male abdomen and the third maxilliped, and in the teeth of the dactylus of the walking legs. Quite probably their similarity reflects descent from a common ancestral stock, and the Australian *H. ovatus* may well be closely related to both *H. planatus* and *H. innominatus*.

Specimens of *H. planatus* from the Auckland and Campbell Islands agree with the descriptions given by Stebbing, Tesch, Rathbun, and Garth. The walking legs have been described as slender (Garth 1958, p. 33; Rathbun 1925, p. 563); they are really quite stout compared with other species in the genus, though not when compared with Brachyura in general. Stebbing mentions the interantennular septum, whose presence is denied by Tesch (1918, p. 10), Rathbun (1925 p. 561), and Garth (1958, p. 31), probably because it is not as obvious as in

Elamena; the interantennular septum in all *Halicarcinus* species can best be seen if one of the antennules is removed.

That the species represents a classic example of polar emergence was pointed out by Garth (1958, p. 34). Most specimens from the Auckland and Campbell Islands have been shore collected although several have been dredged from as deep as 8 fathoms (15 m). Garth's statement therefore holds true.

Invertebrate species are less likely than warm-blooded species to show a cline of increasing body size with decreasing mean temperature of their habitat. Such species often have an environmental optimum where they attain their maximum size (Huxley 1942, p. 212).

Table 1 summarises Garth's findings and data from the present study.

Table 1 Size range of carapace width of *Halicarcinus planatus* from different localities

	Concepcion, Chile 36.5°S	Auckland Islands 50.45°S	Campbell Island 51.3°S	Strait of Magellan 53°S
	mm	mm	mm	mm
Males	4.5–5.1	2.5–19	6–23.5	8.3–14.1
Non-ovigerous females	3.9–6.8	3.5–13.5	4.5–19	5.3–11.6
Ovigerous females	3.5–5.8	8–19	8–17.5	7.6–11.4

Although the Strait of Magellan is further south than the Auckland Islands or Campbell Island, the maximum size reached on the American mainland is less than on the islands. However, *H. planatus* does show a general increase in size with decreasing temperature, so this species obviously thrives in cold latitudes. It does not extend as far north in the New Zealand region as the Chatham Islands (44°S), where *Halicarcinus innominatus* is common.

Halicarcinus ovatus (Stimpson)

Figs. 14 and 15

?1851 *Halicarcinus pubescens* Dana, p. 253
?1852 *Halicarcinus pubescens*, Dana, p. 386, pl. 24, fig. 8
1858 *Halicarcinus ovatus* Stimpson, p. 107
?1868 *Halicarcinus ovatus*, Heller, p. 66
?1876 *Halicarcinus planatus*, Miers, p. 49
1877 *Halicarcinus ovatus*, Targioni-Tozetti, p. 173, pl. X, fig. 5a–d, pl. XI, fig. 3, 3a
1882b *Hymenosoma planatum*, Haswell, p. 114
?1885c *Halicarcinus huttoni* Filhol, p. 46
?1886 *Halicarcinus huttoni* Filhol, pp. 398, 399, pl. 47, fig. 4
?1886 *Halicarcinus planatus*, Miers, p. 49
1886 *Halicarcinus ovatus*, Miers, p. 282
1900 *Halicarcinus ovatus*, Stebbing, p. 255, pl. 36A
1906 *Halicarcinus ovatus*, Fulton and Grant, pp. 16–20
1907 *Halicarcinus ovatus*, Stimpson, p. 146
?1909 *Halicarcinus ovatus*, Chilton, p. 609
?1911a *Halicarcinus ovatus*, Chilton p. 294
?1911a *Halicarcinus huttoni*, Chilton, p. 294
1917 *Halicarcinus ovatus*, Kemp, p. 247
1918 *Halicarcinus ovatus*, Tesch, pp. 9, 11
1927a *Halicarcinus ovatus*, Hale, p. 310
1927b *Halicarcinus ovatus*, Hale, pp. 116, 117, fig. 113
?1929 *Halicarcinus ovatus*, Chilton and Bennett, p. 776
?1930 *Halicarcinus ovatus*, Balss, pp. 195–210

NOT
1888 *Halicarcinus ovatus*, Cano, pp. 164, 177
1949a *Halicarcinus ovatus*, Richardson, pp. 59, 68, fig. 49

TYPE LOCALITY: Port Jackson, Australia.

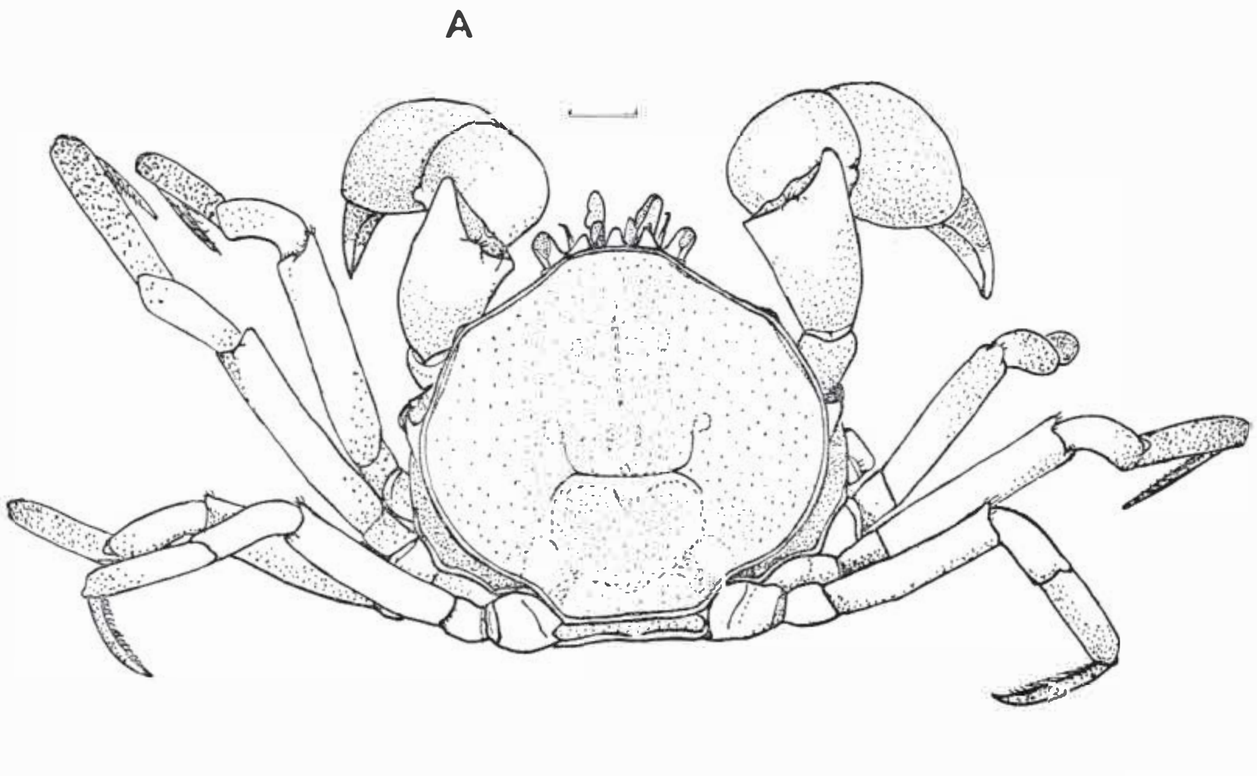
SUMMARY OF LOCALITIES:
Australia. Victoria: Port Phillip; Western Port; Port Fairy; Lake Tyers. New South Wales: Jervis Bay; Collaroy. Western Australia: King George Sound; Cockburn Sound. Southern Australia: Kangaroo Island. Tasmania: Oyster Bay.
New Zealand. Port Chalmers, Otago.

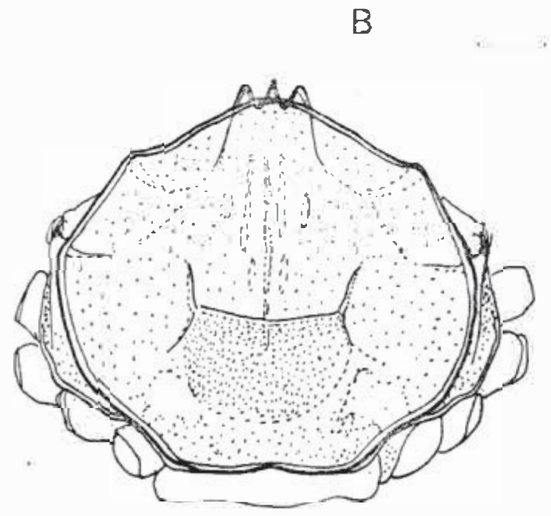
DISTRIBUTION: Australian endemic?

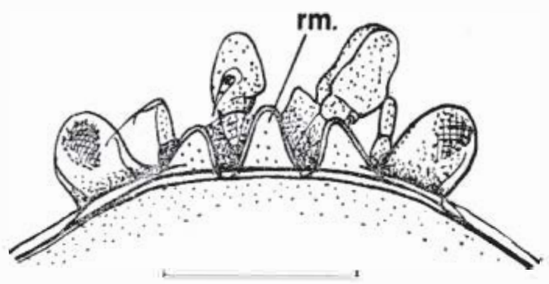
DIAGNOSIS: Carapace suboval, broader than long, with an octagonally angled rim. Trilobular rostrum arising just below the carapace rim, concavities between the lobules continuing under the rim. Lobules small, close together, median lobe a little longer than the laterals, all directed straight forwards, but the bases of the laterals obliquely set at an angle to the base of the median lobe. Lower edge of rostrum with a central peak, adjacent to the inter antennular septum. Anterolateral border concave or straight; rim above rostrum straight, frontal region not produced. Two pairs of lateral teeth always present; first small, obtuse, marked by an angle in the carapace rim; second medium in size, acute, projecting upward to the carapace rim. Postocular lobe and antennal spine both reduced until almost absent. Chelae of male greatly arched, inflated and deep, dentation reduced, basal gape shallow. Segments of walking legs of average breadth. Ischium and merus of third maxilliped subequal, the ischium slightly broader. Male abdomen long, base adjacent to the carapace without an intervening ledge. First segment expanded laterally, wider than any other segment; second very short throughout its width; segments three, four, and five subequal in length, longer than the first; edges of third almost straight, fourth and fifth narrowing distally, sixth an elongate semicircle. Male first pleopod of average length and slenderness, sparsely setiferous, the sternal edge expanded a little below the tip to form a small shelf, the eave slightly recurved.

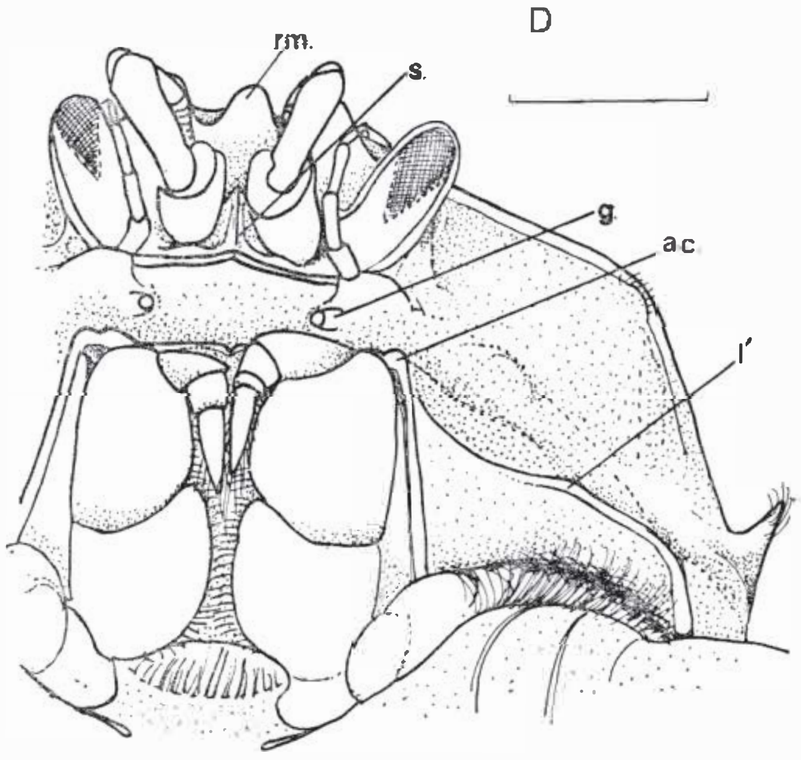
SIZE RANGE: ♂♂6.5–7 mm (Cockburn Sound, W. Australia). ♀♀ 6–6.5 mm (Collaroy, Sydney, N.S.W.).

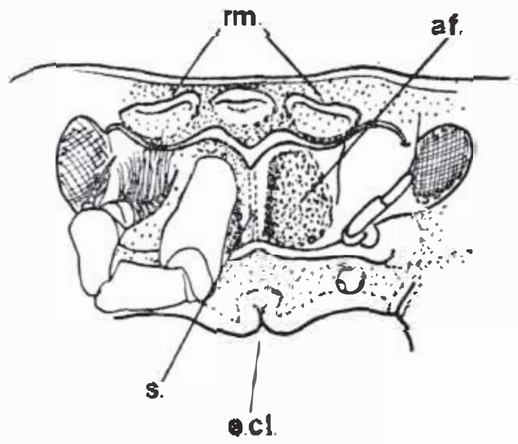
DESCRIPTION: Carapace suboval, shorter than broad (ratio w.: l. = 1.05–1.1), only a little narrower at the first lateral angles than across the postbranchial region. Upper carapace slightly convex, naked or with a few short hairs, semi-octagonal. Carapace rim of average width, straight frontally above the rostrum; frontal region therefore not projecting. Anterolateral border straight or concave, mid-lateral border straight, posterolateral border convex, a pair of obvious concavities over the bases of the last legs, posterior border straight.

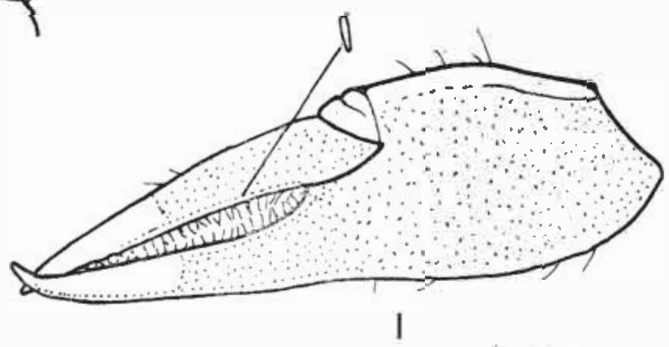


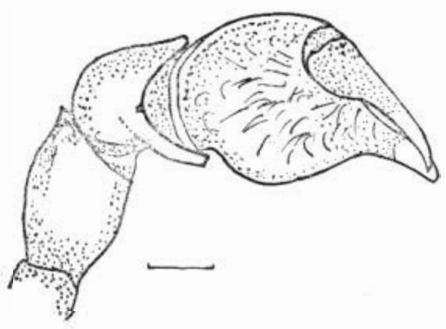


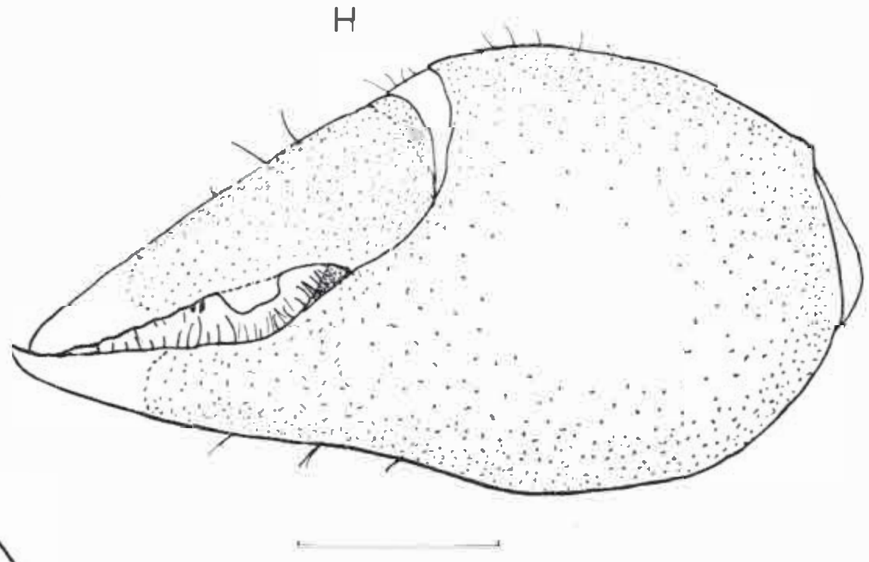


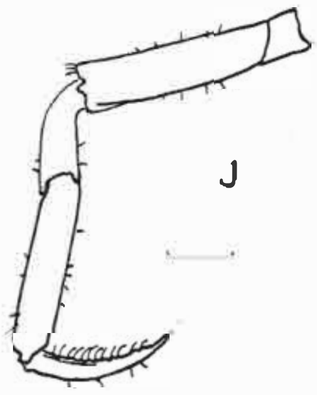












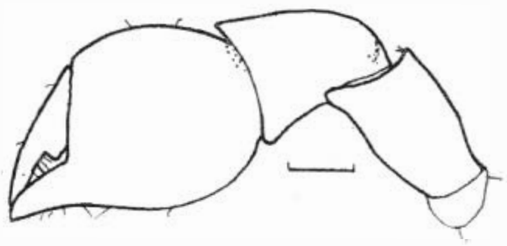


Fig. 14 *Halicarcinus ovatus:* A—Male, dorsal view; B—Female, dorsal view; C—Rostrum of male in A; D—Ventral view of left side of mouthfield and epistome; E—Frontal view of male in A, carapace perpendicular to the plane of vision; F—Left cheliped of male, anterior view; G—Left cheliped of male, posterior view; H—Left chela of male, posterior view; I—Left chela of female, posterior view; J—Left 3rd walking leg of male, posterior view. (scales represent 1 mm)

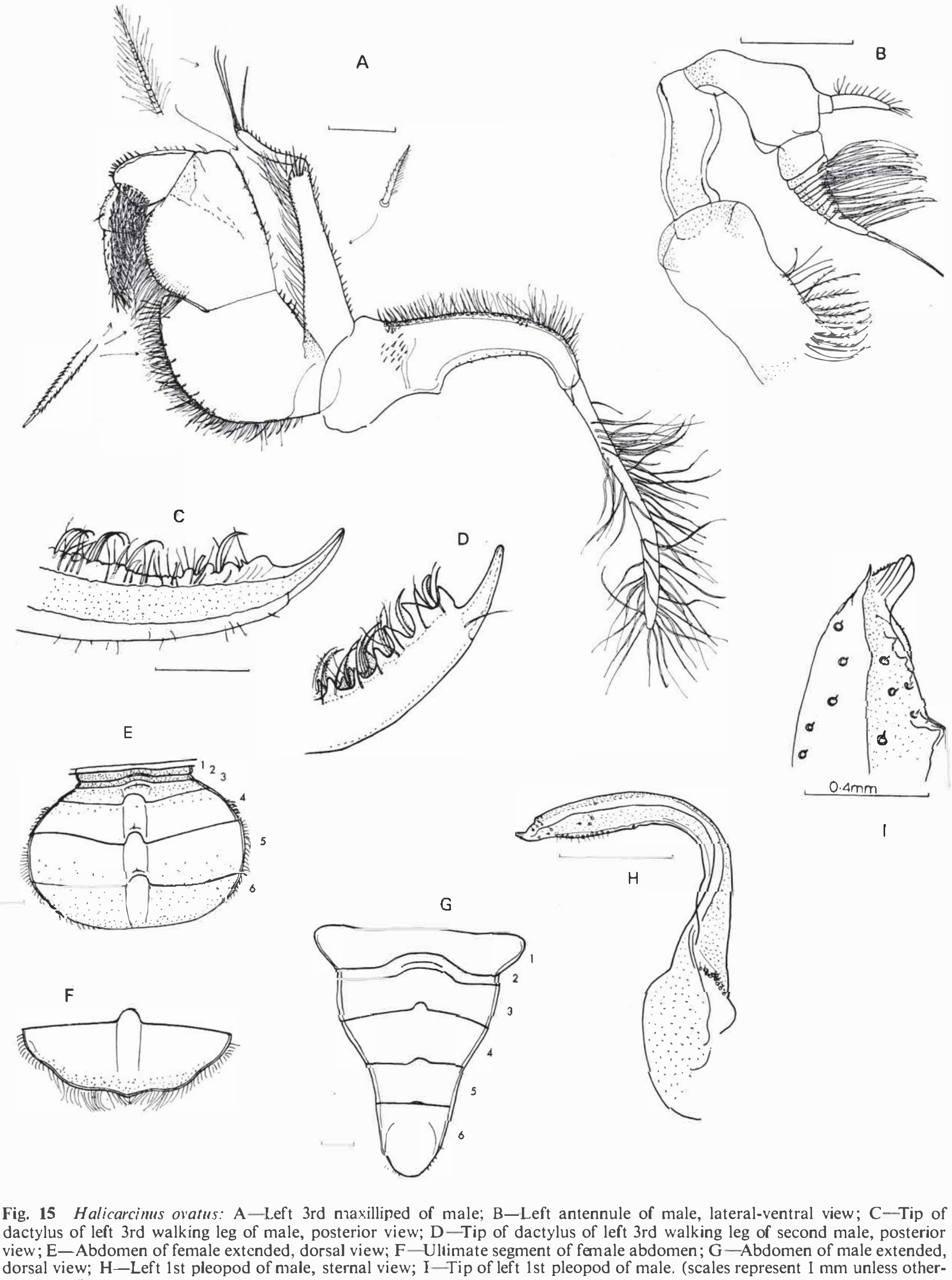


Fig. 15 *Halicarcinus ovatus:* A—Left 3rd maxilliped of male; B—Left antennule of male, lateral-ventral view; C—Tip of dactylus of left 3rd walking leg of male, posterior view; D—Tip of dactylus of left 3rd walking leg of second male, posterior view; E—Abdomen of female extended, dorsal view; F—Ultimate segment of female abdomen; G—Abdomen of male extended, dorsal view; H—Left 1st pleopod of male, sternal view; I—Tip of left 1st pleopod of male. (scales represent 1 mm unless otherwise stated)

Inset 6*

Carapace rim noticeably angled at the level of the first lateral tooth, less noticeably above the second lateral tooth. Raised ridges commonly occur on the carapace, one passing inward from the level of each lateral tooth. Pair of grooves sometimes present, passing from the base of the rostrum on either side of the frontal region. Gastrocardiac groove almost straight, deflected backward centrally to a small extent. Cervical and thoracic grooves equally short. Sides of the carapace oblique posteriorly but not inflated, branchiostegite projections between the legs with marked marginal rim in dorsal view. Two pairs of lateral angles always present on the carapace rim; first pair small, obtuse, sparsely hairy, at the same level at the carapace rim; second pair acute, short, a tuft of hair subterminally, originating well below the carapace rim, projecting upwards to the same level as rim.

Trilobular rostrum of average breadth, short, (one-fifth to one-sixth as long as broad), not projecting past the end of the eyes; lobules originating close together just below the carapace rim, with the narrow concavities between extending under this rim. Median lobe longer than laterals, flat above, rounded from side to side below. Bases of the lateral lobes angled obliquely, the short inner edge and narrowly rounded tip of each lateral lobe at the same level as median lobe, outer elongate edge sloping downward next to the eyesocket. Rounded tips of all three lobes point directly forward in dorsal view, all slope gently upward distally from carapace rim. Rostral ventral posterior margin has two rounded expansions below the lateral lobes; a central large, sharp peak below the median lobe, adjacent to the short, interantennular septum. Postocular lobe adjacent to the eyestalk, but so reduced as to be virtually absent. Eyestalks very short and slender; eyes small, directed outward as much as forward.

Antennules small. Basal segment of peduncle longer than wide, proximally very hairy on the external edge; second segment short, a little slimmer than basal; third narrow basally, greatly expanded distally, as long as second. Small ramus with four short terminal hairs; large ramus slender, elongate, up to eight small subcircular segments, terminal bulb long, slender, without a waist. Antennal spine absent.

Interantennular septum short, ridge deepest adjacent to the epistome. Epistome of average size (breadth twice length), not sunken, posterior rim deep with a deep, narrow, central cleft. Antero-external corner of mouthfield more sharply projecting than usual, a deep concavity adjacent to it on the longest edge of the pterygostomian region. Pterygostomian region very short, extended laterally; faint remnant of a central lobe present, the edge forming a strong ridge from this point to base of cheliped. Subhepatic regions not inflated; carapace rim and teeth visible in ventral view. Milne Edwards's opening narrow, with fringes of long, curved hairs. Rows of hairs of average length on the sterna of third maxillipeds.

Endopods of the third maxillipeds narrowly gaping in the mid line, little expanded laterally. Ischium subquadrangular, median edge considerably curved, two to three rows of short marginal setae, anteromedian lobe small and short, merus articulation at right angles to the axis; merus as wide as long, slightly smaller than ischium, median edge gently curved with a single row of long setae, outer edge almost straight, fringed with short setae as is outer edge of ischium, antero-external corner almost square. Carpus large, articulating centrally on oblique end of merus, some distance from external edge; anterior edge scarcely curved and setiferous. Subsquare propodus also stout, dactylus twice as long, narrowing to a blunt point. Ventral hairs on the palp of average length.

Basal segment of exopod basally broad, tapering sharply so that distal half is narrow, both edges fringed with single row of hairs, those on internal edge much longer, another row a short distance below apex where there is also a horizontal row of hairs. Terminal segment long and slender with four long distal hairs.

Basal lobe of epipod small, narrow, naked. Basal part of epipod elongate, little curved for most of length, three or four rows of long setae on anterior edge, a few short setae proximally on posterior edge separated by suture from lamella. Lamella a little longer than base, slender, narrowly rounded at tip, fringed densely with long hairs.

Chelipeds very massive in adult males. (Length cheliped: width carapace=1.75 in ♂; 1.2 in ♀). Ischium very short, subtriangular.

Merus long, two-thirds as broad as long, has three distal rounded protuberances; carpus slightly expanded distally, a little longer than merus in adult males, a little shorter in females. Palm as long as merus in males, as carpus in females; deeper than broad, very inflated in male; fingers longer than palm in both sexes, broad basally, tapering sharply, without definite denticulation except for short, wide tuberculate tooth at base of movable finger. Basal gape shallow but extending to spooned tips of fingers; internal edges with short, blunt hairs. Palm inner surface sparsely hairy; palm in female narrower than long, fingers very slender, tapering, spooned distally with reduced dentation, fringe of short, blunt hairs on inner edges.

First pair of walking legs longest, others successively shorter, fourth much the shortest. First pair longer than chelae, nearly twice as long as the carapace is wide in adult males, shorter in females. Ischium short, subquadrangular; merus longer and broader than other segments, about a fifth as broad as long, merus tooth short but acute and hairy; carpus not two-thirds merus length, distal processes long and acutely rounded; propodus seven-eighths merus length, distal V pronounced. Segments all subcylindrical, of average breadth; except for ischium, with sparse, short hairs on ventral and lateral edges. Dactylus shorter than propodus, flattened, slender, curved, almost equally wide throughout, ending in long, strong claw, which is completely fused with rest of dactylus. Sparse hairs on dorsal edge of dactylus; ventral edge with short, curved hairs either side between two very closely approximated rows of short teeth, sometimes reduced to blunt tubercles; the

three distal teeth enlarged, sometimes recurved, in single row.

Female abdomen deeply convex, broad, short, first wot segments very reduced, edge of terminal segment expanded and constricted in turn to form a pair of convex projections either side of central terminal shallow peak, a longer fringe of hairs than on preceding segments. Central convex projection on proximal edges of abdominal segments deep on last three segments only.

Male abdomen adjacent to the carapace, without intervening ledge. First segment of average length centrally, moderately expanded laterally into two bluntly pointed lobes; second tiny, of equal length throughout; third longer than first, sides almost straight, barely narrowing distally; fourth slightly longer than third, much narrower distally, sides almost straight; sixth an elongate semicircle, broadly rounded terminally. Proximal central projections on segments two to six, shallow on segments two and three; that of four narrow and short; that of five, wider but shallower, minute on segment six.

First pleopod of male of average length, sturdy, bent through 90°. Keel at base of longitudinal ridge has several rows of small setae, single row of setae on abdominal edge below the tip. Sternal edge constricted subterminally to form a small shelf, then gently sloping to internally ridged eave, which is somewhat recurved over aperture of vas deferens. A few scattered setae subterminally.

MATERIAL EXAMINED:

University of Western Australia Zoology Department Collection: Cockburn Sound, W. Australia, 1/7/1965, 2 ♂ ♂ 6.5, 7 mm, 2 g. ♀ ♀ 6, 6.5 mm (coll. J. S. Lucas, from among *Mytilus*). Long Reef, Collaroy, Sydney, N.S.W., 8/2/1965, 2 ♂ ♂ 6.5, 7.5 mm, 3 g. ♀ ♀ 5–6.5 mm (under rocks in weed, coll. J. S. Lucas).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: February, June.

COLORATION: Very variable. Brown, red, orange, green, yellow, white, and black splotches and mottling, pure white, brown, red-brown, or black. Females more often having speckled coloration than the males (J. Lucas, pers. comm.)

REMARKS: Although most recent authors, e.g. Garth (1958), regard Dana's "*Halicarcinus pubescens*" from Chile as a probable synonym of *Halicarcinus planatus*, Tesch (1918, p. 9), thought it might belong to either *Halicarcinus planatus* or *H. ovatus*. According to Garth, the type of Dana's species is no longer extant, so that Tesch's remark cannot be challenged.

Stimpson, who established the species, did not describe it adequately enough in 1858 or 1907 to permit its distinction from the closely allied *H. planatus* and *H. cookii*.

Haswell (1882b), Miers (1876b), and others have united *H. planatus* and *H. ovatus*, but after Tozetti (1877) separated them, some authors, including Miers (1886) and Stebbing (1900), followed his lead. Stebbing (1900) and Tesch (1918) separated the two species almost solely according to the type of dentation on the dactylus of the walking legs. Stebbing (1900) wrote that, in *H. planatus*, the dactyl is "broader in comparison with its length, less curved, with the teeth of the inner margin not reverted and implanted, some on one side and some on another, whereas in *H. ovatus* they are in single file and provide the joint with a slightly backwardly directed serrature". Stebbing's figures agree well with mine, and even his own drawing of the dactylus of *H. ovatus* shows a tooth partially hidden behind the foremost row and therefore in a different plane. Dr Lucas (pers. comm.) working with *H. ovatus* in Australia, also queries Stebbing's description of the dactylus. Stebbing correctly shows the rostral lobes of *H. ovatus* closer together than those of *H. planatus*, and projecting straight forward, not radiating outward as in the latter species. As Stebbing's specimens came from the type locality Port Jackson, Sydney, it is likely that he was dealing with the same species as Stimpson. The specimens figured here came from Collaroy, Sydney, and agree well with Stebbing's description and figures, and with Hale's figures (1927b, fig. 113). Hale's figure is of a female, with abnormally thin legs, but this is a common mistake in early drawings.

Richardson (1949a, p. 59) stated that Balss (1930) had shown *Halicarcinus huttoni* to be a synonym of *H. ovatus*. In the publication in question, Balss merely listed the previous records of *H. ovatus*, and added Filhol's (1885c) and Chilton's (1911a) references to *H. huttoni* to the list. Balss then stated that he had examined examples from Port Chalmers (N.Z.), the type locality of Filhol's species, and of *H. ovatus* from Port Jackson (Australia), and added, "it seems to me (that) our animals from the same place agree and thus belong in the synonymy of *ovatus*". Balss did not give any description or figures himself; he did note that Targioni-Tozetti's 1877 figure of *H. ovatus* marked in the text is false, and that Filhol's 1885 and Hale's 1927 figures were both bad. Filhol's figure is certainly "bad", because the figure that Balss cites, although the one listed as *Halicarcinus huttoni* by Filhol, was also referred to as *Hymenicus haasti*, and Filhol's description of *Hymenicus haasti* corresponds with this figure (pl. 47, fig. 4) whereas his description of *Halicarcinus huttoni* does not. As Tesch (1918, p. 9) and Chilton (1909, p. 293) realised, the figure belonging to Filhol's description of *Halicarcinus huttoni* is fig. 1, pl. 47. Tesch was of the opinion that *H. huttoni* was a synonym of *H. planatus*. though not of *H. ovatus*. In his original description, Filhol mentioned only one pair of obtuse marginal spines, which does not correspond with either species.

Filhol's fig. 3 of pl. 50, although listed by him under *Hymenicus cookii*, does not agree with his description of *H. cookii* and is now regarded as belonging to his description of *Halicarcinus tridentatus* (Stebbing 1900). Chilton (1910) appeared to regard Filhol's *Halicarcinus tridentatus*, or as Chilton termed it in later publications, *H. planatus* var. *tridentatus*, as synonymous with *H. planatus*. Other authors equate *H. tridentatus* Jacquinot and Lucas (which is not the same as Filhol's species of

the same name, *see* p. 33) quite definitely with *Halicarcinus planatus* (White 1846, Milne Edwards 1853, Heller 1868, and Tozetti 1877, all of whom quote the species accurately from Jacquinot's (1853) plate as *Hymenosoma tridentata*). A concise account of the references to *H. tridentatus* was given by Stebbing (1900), but he reached no conclusion as to its synonymy.

Without a thorough examination of the types of *Halicarcinus huttoni*, *H. tridentatus*, *H. planatus*, and *H. ovatus* (most of which are not extant) the synonymy cannot be resolved.

Probably *H. ovatus* Stimpson does not occur in New Zealand, as no specimens like the Australian ones were found in any New Zealand collection examined during this study.

Halicarcinus cookii (Filhol)

Figs. 1–4, 16–24, Plate 2

?1882 *Hymenicus marmoratus*, Chilton, p. 172
1885a *Hymenicus cookii*, Filhol, p. 44
1886 *Hymenicus cookii*, Filhol, pp. 401, 402
1904 *Hymenicus cookii*, Hutton, p. 250
?1906b *Hymenicus marmoratus*, Chilton, p. 270
1918 *Hymenicus cookii*, Tesch, pp. 12, 16
?1929 *Hymenicus marmoratus*, Young, p. 152
?1929 *Hymenicus marmoratus*, Chilton and Bennett, p. 776
1949a *Halicarcinus cooki*, Richardson, pp. 66, 68, fig. 46
?1956 *Halicarcinus cooki*, Ralph and Yaldwyn, p. 74, pl. 6, fig. 40
1960 *Halicarcinus cooki*, Dell, p. 4

TYPE LOCALITY: Cook Strait.

SUMMARY OF LOCALITIES: Northland: Cavalli Island; Cable Bay; Doubtless Bay; Great Barrier Island; Tauranga Bay, Whangaroa; Leigh. Coromandel: Whangamata; Onemana Beach. Auckland: Brampton Shoal; Long Bay; Auckland Harbour. Gisborne: Lottin Point; Tolaga Bay. New Plymouth. Wellington: Castlepoint; Lyall Bay. Marlborough: Kaikoura; Seal Reef, Kaikoura. Canterbury: Akaroa, Banks Peninsula. Southland: Waipapa Point. Stewart Island: Lee Bay. Chatham Islands: Owenga; Kaingaroa; Waitangi; Te Whanga Lagoon; Port Hutt.

DISTRIBUTION: New Zealand endemic.

DIAGNOSIS: Carapace suboctagonal, as long as broad, convex with the regions of the carapace obvious only in the largest specimens, rim narrow. Rostrum a trilobular horizontal shelf, at the same level as the upper carapace, the lobules completely fused basally but the concavities between reaching almost to the suture between carapace and rostrum. Lobules subequal, median lobule a fraction longer than, and frequently narrower basally, than laterals. Rostrum short, not reaching past the tip of the eyes. Anterolateral border markedly concave, suture at base of rostrum convex anteriorly; frontal region therefore projecting a little. Ventral edge of rostrum with three pointed peaks below the lobules, central one most pronounced. Two pairs of lateral teeth always present below carapace rim; the first obtuse, marked by a distinct angle in the rim itself; the second large, acute, with finely pointed tip. Postocular lobe reduced, almost absent; antennal spine reduced to a small obtuse protruberance. Chelae of male not much inflated, general dentation well developed but the enlarged tooth usually found on the base of the movable finger always absent, narrow linear gape in both sexes. Palm of male with a few long hairs anteriorly, not much inflated. Segments of walking legs of average breadth; curved, slender dactylus has recurved narrow teeth in two irregular rows. Ischium of third maxilliped considerably broader than merus. Male abdomen long, slender, separated from carapace by tiny, vertical ledge; first segment very large, expanded laterally into lobes; second very small, almost linear; third, fourth, and fifth subequal in length, shorter than first; third segment with straight sides, not narrowing distally; fourth narrowing markedly; fifth with barely concave sides, little narrowed distally; sixth segment elongate, semi-elliptical, tip rounded or slightly truncate. Ischium considerably broader than the merus. Male first pleopod of average length, stout, the tip simple, sparsely setiferous, the eave a little curved.

SIZE RANGE: ♂♂ 1.5 (Leigh) – 13 mm (Seal Reef, Kaikoura). ♀♀ 3.0 mm (Leigh) – 8.5 mm (Stewart Island).

DESCRIPTION: Carapace octagonal, narrowing anteriorly, of equal total length and breadth (ratio w. : l. = 1.08–0.93). Carapace convex or flat, with narrow rim. Wide gastrocardiac groove always obvious, deflexed backwards a little centrally. Cervical and thoracic grooves also present, thoracic grooves shortest, cervical grooves sometimes dividing anteriorly to delimit the hepatic and prebranchial regions. Upper carapace typically naked, sometimes with a few setae especially on the frontal region. Anterolateral border markedly concave, suture between carapace and rostrum convex anteriorly, frontal region therefore somewhat produced. Short groove on either side of the frontal region passing backward from base of rostrum. Mid-lateral border straight. Posterolateral border convex, posterior border straight. Small, shallow concavity above base of each last walking leg. Carapace sides almost vertical, and not inflated posteriorly; branchiostegite projections between the legs small. Two lateral teeth always on carapace; carapace rim barely deflected at second tooth, angled next to first tooth. First tooth small, obtuse, jutting upward above carapace rim, setiferous, second large, acute, jutting upward above level of carapace rim, with a needle point and subterminal ring of curved setae.

Trilobular rostrum short, never projecting past the eyes, of average breadth (about one-fifth as broad as carapace), forming a horizontal platform at the same level as the carapace. Subequal lobes, especially fractionally longer median lobe, crowned by upwardly curved hairs or their remnants; all three narrowly rounded apically, sloping slightly upward anteriorly; inner edges of lobes shorter than outer edges, leading into deep concavities between the lobes, which approach close to but

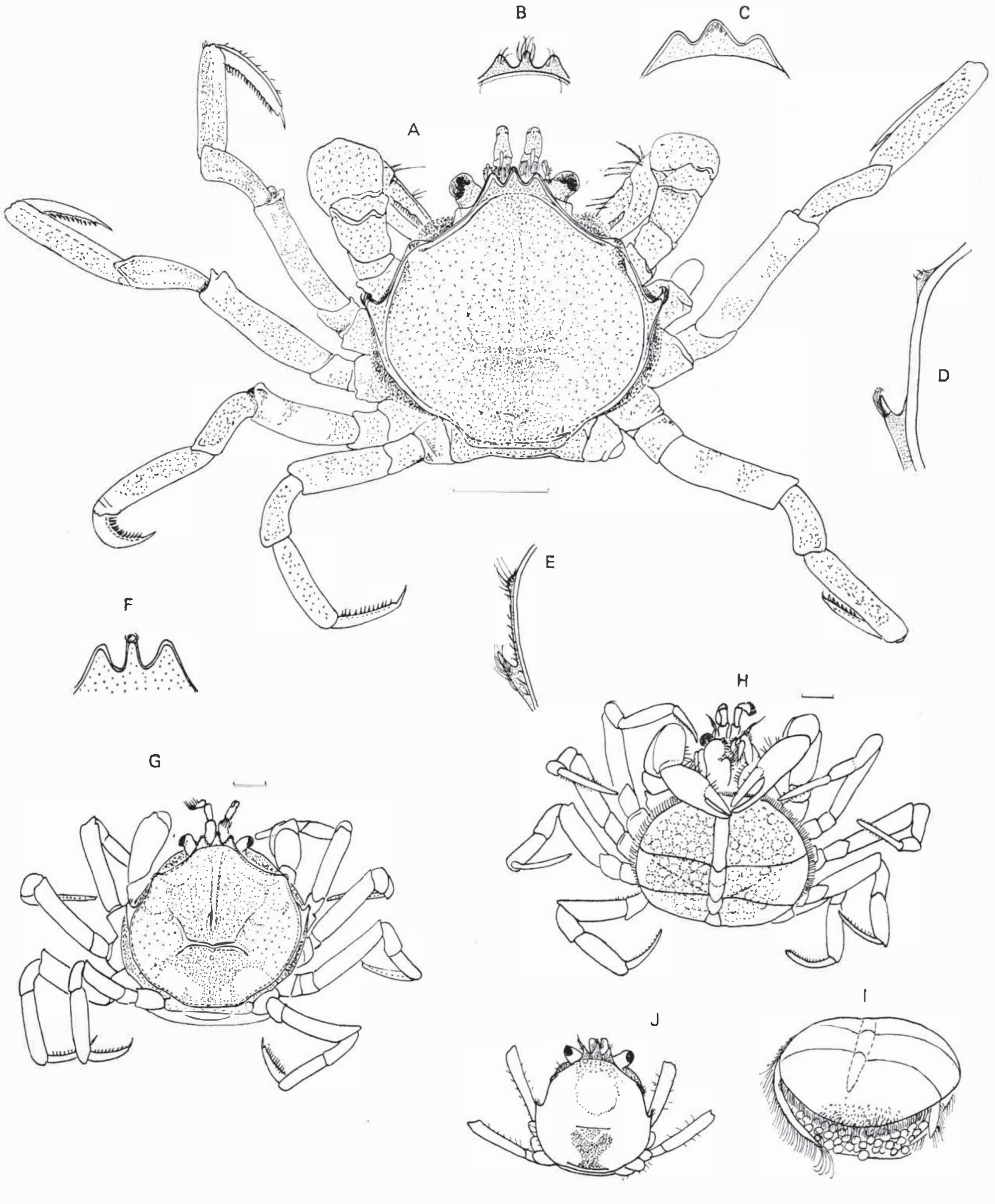


Fig. 16 *Halicarcinus cookii:* A—Male dorsal view; B—Rostrum of second male; C—Rostrum of third male; D—Lateral angles on carapace of third male; E—Lateral angles on carapace of second male; F—Rostrum of fourth male; G—Female, dorsal view; H—Female ventral view; I—Female abdomen, slightly lifted to show eggs; J—Immature male, dorsal view. (scales represent 1 mm)

do not meet the suture between carapace and rostrum. Sides of central lobe commonly more steeply sloping than those of the laterals so it is usually narrower across its base than the laterals at the same level, more narrowly rounded, and more often setiferous. Rostrum edge a little expanded next to the very reduced postocular lobe; ventral edge expanded into three narrow peaks, sharpest and largest peak centrally below median lobe and next to the shallow interantennular septum. Eyes directed outward as much as forward; eyestalks short and very stout.

Antennules short, stout. Peduncle segments subequal, first with a dense tuft of hairs basally, second and third both narrow basally, expanded distally. Small ramus has apical tuft of six to eight setae; large ramus short, as long as small ramus, stout, with about six small subcircular segments, minute terminal bulb, apical seta of average length. Shallow ridge along the whole length of rostrum ventrally, deepest beside the interantennular septum. Antennal spine reduced, obtuse.

Interantennular septum short, deeply ridged only near epistome, the ridge very shallow anteriorly. Epistome of average size, twice as broad as long, sunken a little centrally but laterally completely fused with the subhepatic regions. Subhepatic regions not inflated, rim and teeth of carapace visible in ventral view. Subtriangular pterygostomian regions small, the long edge sloping steeply backwards and slightly concave anterior to a very shallow central lobe, posterior lobe even more reduced. Pterygostomian region shallowly ridged from central lobe to posterior lateral corner of the mouthfield. Milne Edward's opening large, with flanking fringes of long hairs especially on cheliped. Line of short hairs on anterior edge of sterna of third maxillipeds.

Endopods of third maxillipeds gaping widely in mid line, not expanded laterally. Ischium wider than long, median edge strongly curved with one or two rows of short setae, ventral face sparsely setiferous, anteromedian lobe short and broad, articulating edge of median extent; subrectangular merus as long as ischium, narrower than long, median edge of average curvature, has single row of setae a little longer than those on the ischium, ventral surface and straight outer edge sparsely setiferous, antero-external corner square. Carpus articulating near merus outer edge, very large, anterior edge curved, distally expanded so wider than long. Propodus half carpus length, stout; dactylus barely longer than propodus, stout, tip rounded.

Basal segment of exopod slender, parallel sides tapering immediately below apex, median edge bordered by long, feathery hairs which also form a horizontal row below apex. Terminal segment long, slender, ending in four long and two short hairs.

Basal lobe of epipod very shallow, meagrely provided with tiny setae. Basal portion of epipod subequal with the lamella, has a double row of setae on its anterior edge, not cut off from the lamella by a distinct suture. Lamella widening slightly distally, end rounded, slender, fringed with two interrupted rows of setae near the lateral edges.

Chelipeds not very massive even in adult males, length nearly twice carapace width. Ischium subquadrangular, shortest on dorsal edge, sparsely hairy; merus long, expanded distally so width three-quarters length, all three distal peaks well developed, ventral peak blunt. Carpus three-eighths longer than merus, expanded distally, anterior face sparsely hairy. Palm long as merus, as deep as long, not inflated, anterior face has sparse, long hairs, longest towards dorsal and ventral edges. Fingers longer than palm, slender, with simple dentation along entire inner edges in both sexes, the teeth enlarged distally, sometimes with hairs between. Male movable finger lacks usual large basal tooth. Narrow linear gape commonly present in both sexes over the distal half of fingers; more rarely the finger tips curve over each other to allow complete occlusion. Fingers relatively longer in female than male, over twice palmar length.

First and second walking legs subequal in length, length approximately twice carapace width, as long as chelipeds. Third and fourth walking legs progressively shorter (length of fourth 1.5–1.7 times the carapace width). Segments subcylindrical in cross section, of moderate width. Ischium very short, subquadrangular, fringed with short hairs on dorsal edge, small blunt anterior process extending over merus. Merus longest, breadth about one-fifth length; tooth prominent, apically rounded with tuft of hairs. Carpus just over half as long as merus, distal projections on dorsal and ventral edges equally developed, of average size. Propodus a little longer than carpus, a pronounced V fringed with short hairs distally. Dactylus as long as propodus, curved, slender, tapering to a separate elongate claw. Although flattened, the ventral edge is not knife thin, is broad enough to bear two irregularly arranged rows of sharply pointed narrow teeth, increasing in size towards claw, and slightly recurved; short, fine setae, curving towards the claw, between and beside these teeth. Female abdomen laterally expanded, terminal segment broadly rounded distally, fringed by long hairs.

Male abdomen long, reaching suture behind sterna of cheliped, separated from carapace by very thin, vertical ledge. First segment larger than usual, has large, shallow, lateral lobes, exceeded in length only by the penultimate and ultimate segments; second segment tiny, almost linear throughout; third and fourth segments of equal length, third slightly expanded distally with faintly convex sides, fourth narrowing considerably distally, fifth segment narrowing distally, edges almost straight; sixth segment semi-elliptical, twice as long as first, rounded or truncate distally. Central convexities of proximal edge on segments 2 to 6 are deep and moderately wide on segments 4 and 5 and small and flanked by a smaller expansion of the edge on either side on segment 6.

Male first pleopod of average length, sturdy, bent through 90°, longitudinal ridge reduced, sides of distal portion tapering fairly evenly to tip; eave extending above vas deferens aperture, a little recurved and strongly longitudinally ridged inside, tip sparsely setiferous. Basal lobe adjacent to first pleopod with long, feathery hairs.

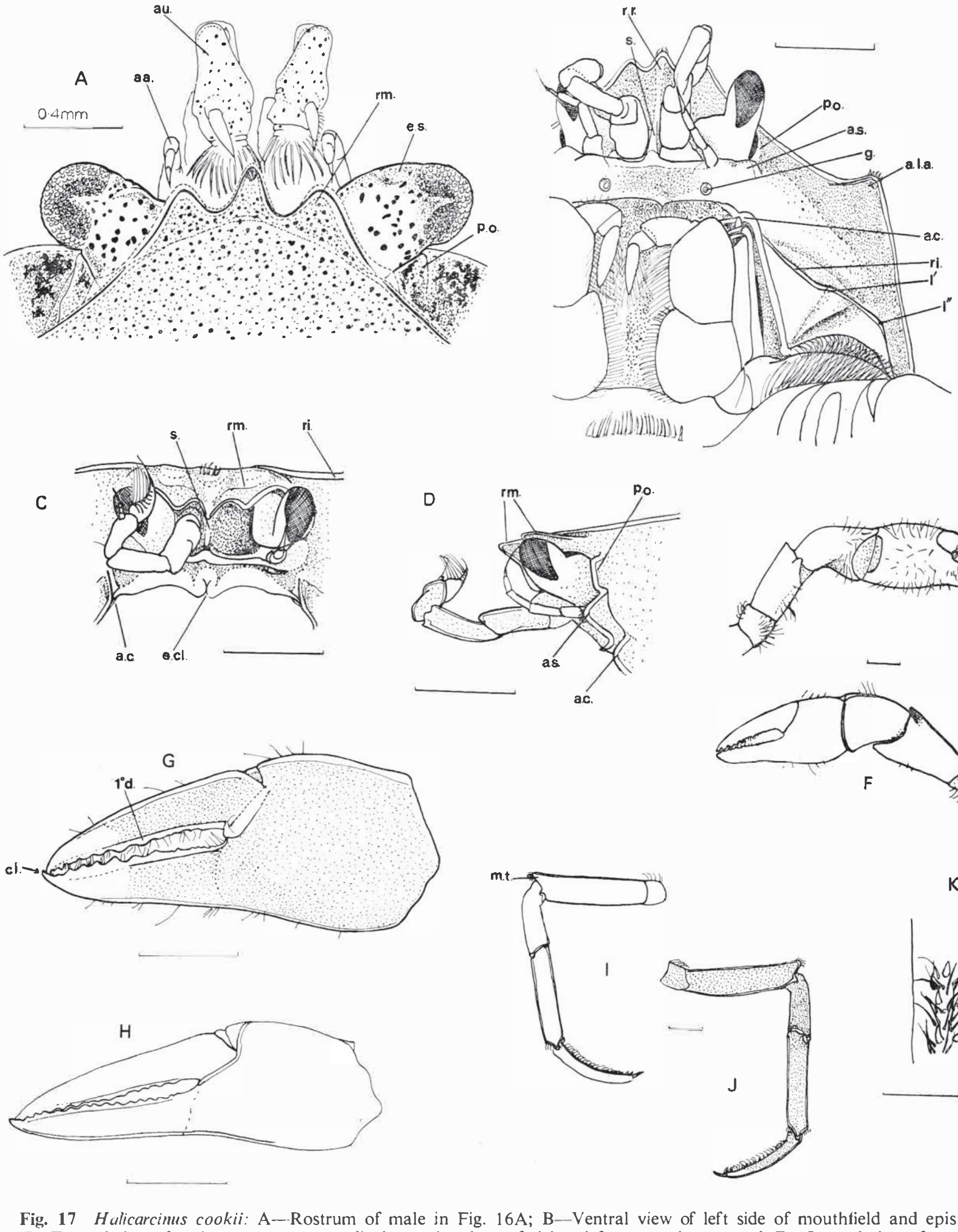


Fig. 17 *Halicarcinus cookii:* A—Rostrum of male in Fig. 16A; B—Ventral view of left side of mouthfield and epistome; C—Frontal view of male carapace, perpendicular to the plane of vision, left antennule removed; D—Lateral view of rostrum; E—Left cheliped of male, anterior view; F—Left cheliped of male posterior view; G—Left chela of male, posterior view; H—Left chela of female, posterior view; I—Left third walking leg of male, posterior view; J—Left 3rd walking leg of male, anterior view, K—Ventral edge of dactylus of left 3rd walking leg. (scales represent 1 mm except where otherwise stated)

ZOEAE: No attempt was made to hatch larval stages of Hymenosomatidae, but one female specimen of *H. cookii* was obtained which had within the abdomen a cluster of unhatched eggs and some eggs which had just liberated young zoeae.

MATERIAL EXAMINED:

Personal collection: Goat Island Bay, Leigh, Auckland, 11/1/1965, 4 ♂ ♂ 3.1–4.0 mm, 1 ♀ 4.7 mm; 8/2/1965, 8 ♂ ♂ 2–5.5 mm, 5 g. ♀ ♀ 5–6 mm, 2 ♀ ♀ 3.0–5.5 mm; 9/2/1965, 2 ♂ ♂ 2.5–3.5 mm, 6 g. ♀ ♀ 4–6 mm, 1 ♀ 4.5 mm. Leigh Harbour, 16/5/1965, 2 ♀ ♀ 4–6 mm. Goat Island Bay, Leigh, Auckland, 17/5/1965, 20 ♀ ♀ 2.0-5.0 mm, 20 ♀ ♀ 3.5–6 mm, 2 g. ♀ ♀ 5.0 mm, 4 s. ♀ ♀ 3–6.5 mm; 10/7/1965, 7 ♂ ♂ 2–4 mm, 49 ♀ ♀ 2.5–5 mm, 1 g. ♀ 5 mm, 3 s. ♀ ♀ 4–5.5 mm; 12/9/1965, 5 ♂ ♂ 3.7–6 mm, 8 ♀ ♀ 3.5–5 mm, 4 g. ♀♀ 4–5.5 mm, 10 s. ♀♀ 4–5 mm; 27/11/1965, 20 ♂ ♂ 1.5–6 mm, 14 ♀ ♀ 2.5–5.5 mm, 9 g. ♀♀ 4–6 mm, 3 s. ♀♀ 4.5–5.5 mm, –/2/1965, 1 ♂ 4.5 mm (from sea water storage tanks in Research Station, coll. B. A. Foster). Clarke Island, Whanganata, Coromandel, 19/4/1965, 6 ♂ ♂ 3.3–7 mm, 1 ♀ 4 mm, 4 s. ♀ ♀ 5.3–6.5 mm. Onemana Beach, Coromandel, 3/1/1965, 6 ♂ ♂ 3.5–7.5 mm, 2 ♀ ♀ 5.5–7 mm, 12 g. ♀ ♀ 5.5–9.5 mm.

University of Auckland Zoology Department Collection: Stewart Island, 1 g. ♀ 8.5 mm.

Auckland War Memorial Museum Collection: Waitangi, Chatham Islands, 9 ♂ ♂ 3–6.5 mm, 5 ♀ ♀ 4.5–6 mm, 3 g. ♀ ♀ 5–7 mm (coll. A. W. B. Powell, with amphipods, *Isocladus* sp., polychaete, *Notomithrax* and *Halicarcinus varius*) Cavalli Island, –/11/1932, 1 g. ♀ 7 mm (coll. A. T. Powell with *Eupagurus*, *Notomithrax*).

Dominion Museum Collection: Cable Bay, Doubtless Bay, 18/11/1963, 1 ♂ 4 mm (coll. R. K. Dell). Tauranga Bay, Whangaroa, 11/11/1963, 1 ♀ 5 mm (coll. R. K. Dell). Long Bay, Auckland, 2 ♂ ♂ 6, 6.5 mm, 1 ♀ 5 mm, 3 g. ♀ ♀ 6–6.5 mm (coll. R. K. Dell, on thalli of *Sargassum sinclairii* at low tide). Lyall Bay, Wellington, 28/12/1948, 1 ♂ 8.5 mm; 27/2/1949, 7 ♂ ♂ 7.5–4 mm, 4 g. ♀ ♀ 7–5.5 mm (coll. R. K. Dell, J. M. Moreland, with *Ozius truncatus*, *Notomithrax* and *Halicarcinus innominatus*). New Plymouth, 29/3/1964, 1 ♂ 4.5 mm (coll. M. A. Crozier). Kaingaroa, Chatham Islands, 1 ♂ 7.5 mm (Chatham Islands Expedition, St. 16, Cr.926). Lottin Point, Cape Runaway, 10/2/1962, 1 g. ♀ 6 mm (coll. R. K. Dell). Waitangi, Chatham Islands, 1, g. ♀ 8 mm (Chatham Islands Expedition, St. 26, Cr.924). Tolaga Bay, East Coast, 28/11/1950, 1 ♂ 7.5 mm, 1 g. ♀ 6 mm (coll. R. K. Dell).

Victoria University of Wellington Zoology Department Collections: Castlepoint, Wellington, 14/1/1964, 2 ♂ ♂ 3–7.5 mm, 1 ♀ 4.25 mm, 1 g. ♀ 5.5 mm, 3 s. ♀ ♀ 4–5 mm; 28/2/1964, 1 ♂ 6 mm; 20-23/12/1964, 7 ♂ ♂ 3–7 mm, 1 ♀ 4 mm (coll. R. Wear). Lyall Bay, Wellington, 29/10/1964, 1 ♂ 11.5 mm (under rocks among weed). Wainui Bay, Wellington, 22/10/1964, 1 ♂ 7 mm (under rocks in sand). Rangi Whakaea Bay, Great Barrier Island, 9/11/1962, 1 ♂ 4.5 mm, 1 ♀ 3.5 mm.

Edward Percival Marine Laboratory Collection: Seal reef, Kaikoura, 3/9/1964, 3 ♂ ♂ 6.5–12 mm, 1 ♀ 6.5 mm (from *Carpophyllum* fronds, K 410 A).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: January, February, April, May, July, September, November.

COLORATION (Plate 2, facing p. 49):

Carapace: The coloration of the upper carapace varies greatly. In males it is black, or brown, usually with splotches of white, yellow, green or orange. The female colour range is from pure white, through yellow-brown or reddish-yellow and green, to pure black. Behind the gastrocardiac groove is a dark-pigmented, irregularly shaped area or "X-mark", which partially covers the cardiac region.

The dark, brown-black pigmentation in the X-mark often spreads over the rest of the rear half of the carapace, while the anterior remains paler brown, green or white. In other specimens the white splotches at the base of the last pair of legs may occupy a quarter of the carapace, or may coalesce with the lateral white markings so that the posterior two-thirds of the carapace is almost white. Usually the X-mark remains dark with traces of orange or green, but some females with a pure white carapace have been found. The lateral teeth on the angles of the carapace are tipped in white, pigmented basally.

The carapace sides are usually darker than the upper surface, although pale or brightly contrasting bands may occur behind and below the eyes. At other times, the carapace sides are similarly coloured to the dorsal surface, especially where this pattern is not very definite, for example, in gravid females.

Ventral surface: Ventrally, pigmentation is reduced. Two white spots are common near the mid line of the anterior border of the sternum of the external maxillipeds. Scattered large black, red and white chromatophores cover these outer maxillipeds but pigmentation does not extend to the other mouthparts.

The male abdomen is sparsely pigmented, while that of the female is often faintly streaked with brown, red or black, usually with a light band of pigment across the centre of each segment.

Antennules: The antennules may be predominantly white, black or red, often contrasting strikingly with the predominant colour of the carapace. Crabs with black carapace may have almost white antennules and legs, those with green or brown carapaces usually have red antennules. Frequently, the antennules match the brown general body colour. The eyestalks are usually splotched with a mixture of colours, with a darker line along the external edge visible from above.

Walking legs: The legs are commonly banded in both sexes, especially in immature specimens. The transparent nature of the cuticle, which is yellow elsewhere, causes the bluish tinge in the proximal halves of the merus and propodus. When pigmentation is reduced to a minimum, blue-white bands are formed.

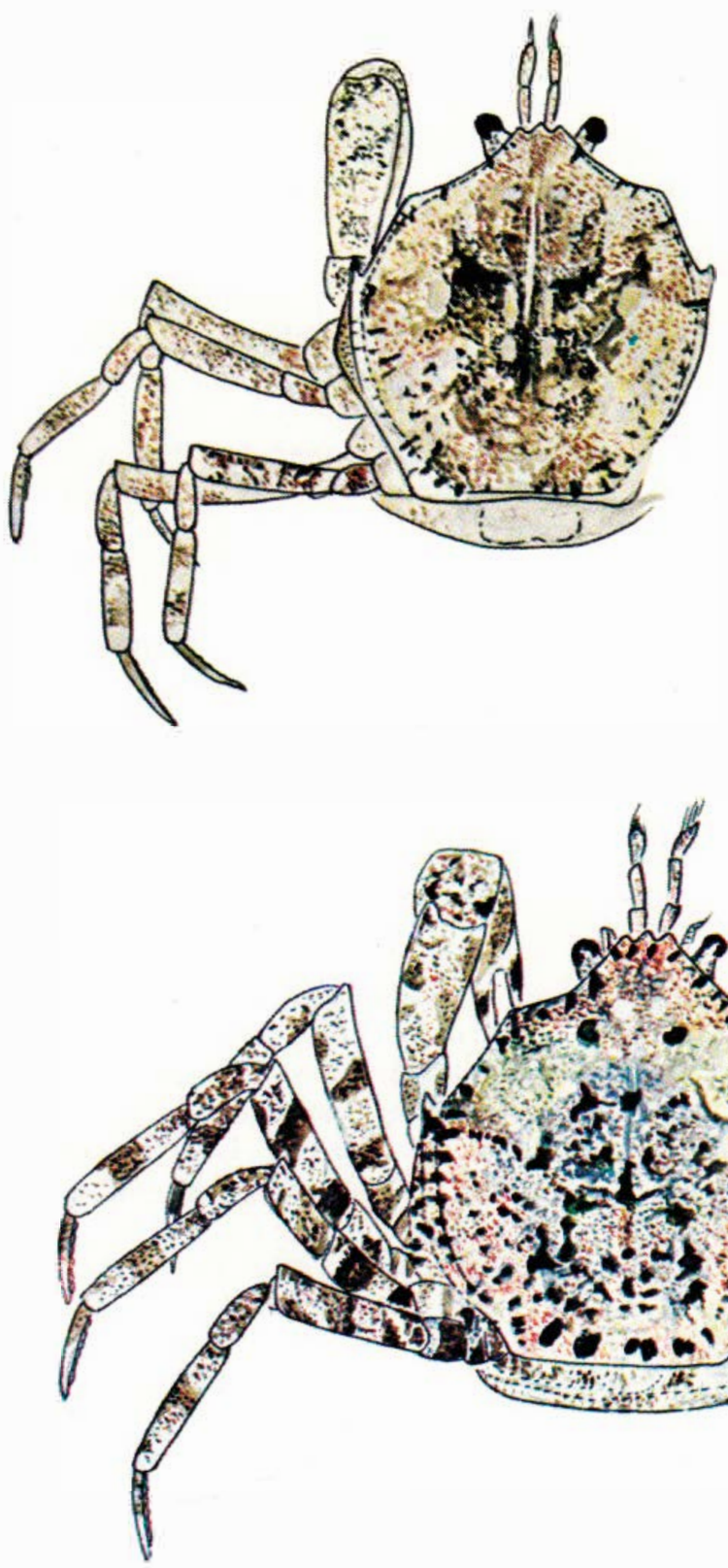
There is a sequence of pigmentation in the walking legs, the posterior pair being most often noticeably banded.

Two-thirds along the merus, a dark band is commonly present, most obviously on the last pair of legs. This band usually becomes progressively fainter anteriorly until it disappears or is represented by scattered brown or orange dots on the first pair of walking legs.

Usually a striking distal white band is present on the propodus of all walking legs. Very frequently an adjacent dark band accentuates this terminal white stripe.

The carpus is commonly speckled in brown or grey, but not distinctly banded. The distal half of the dactyl of all the walking legs is always non-pigmented.

Chelipeds: In some specimens, especially males, the swollen palm of the chela is darker than the rest of the



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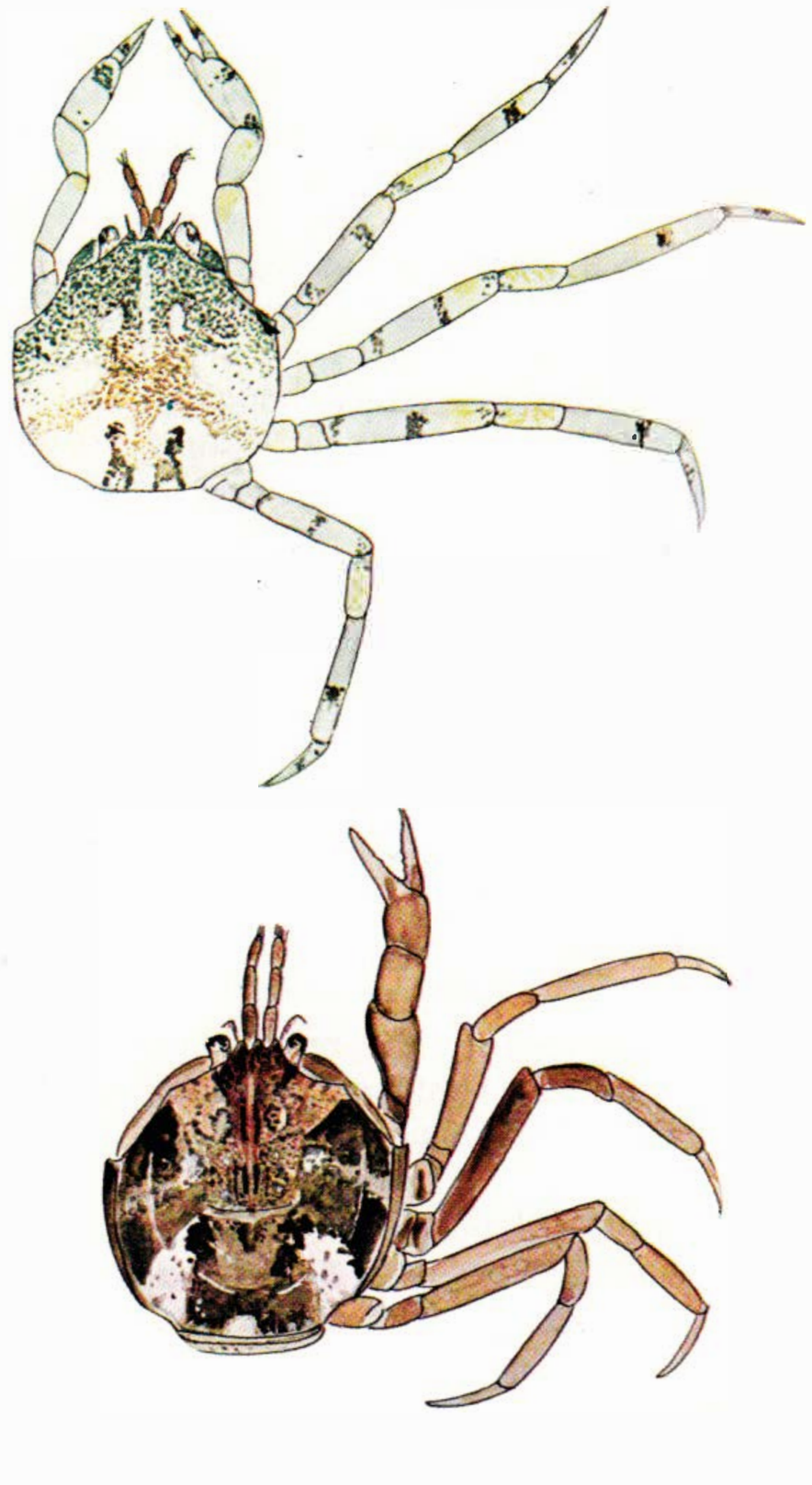

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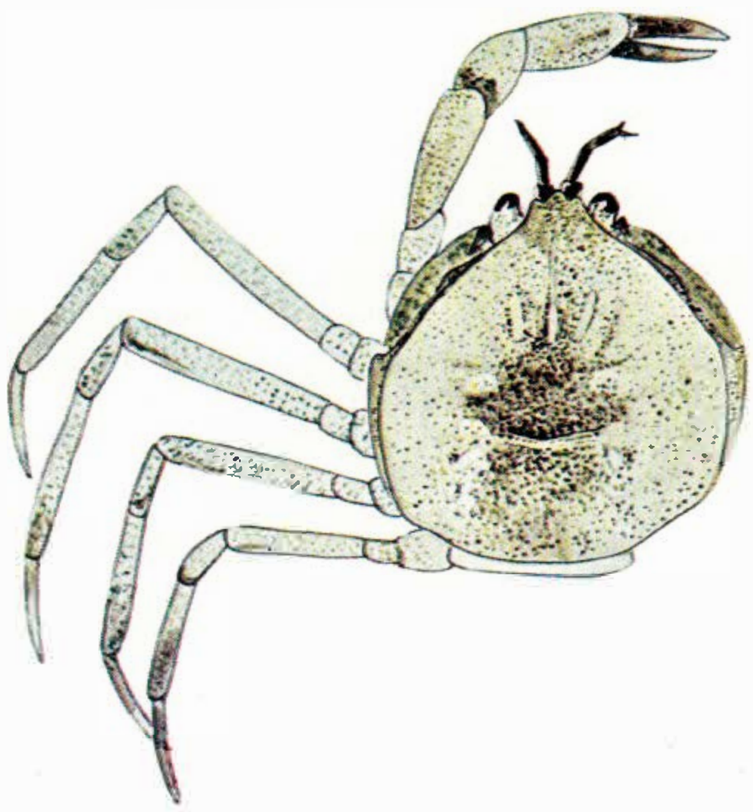

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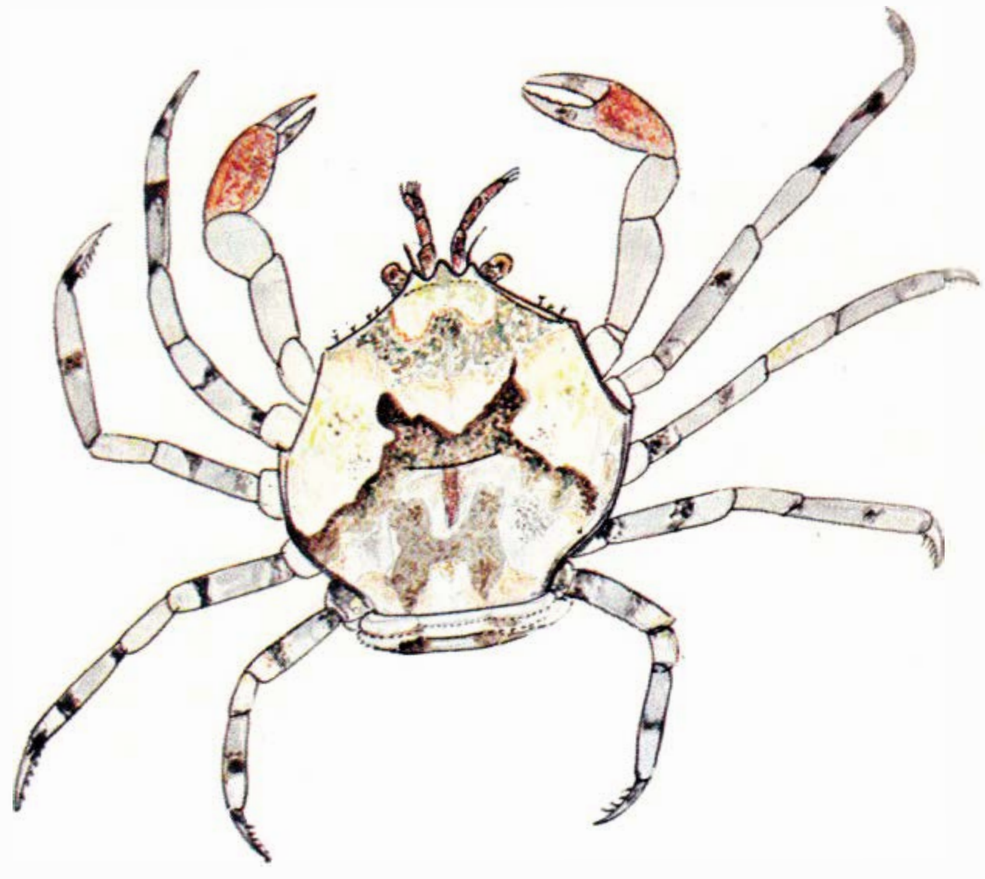


F

Plate 2 A—*Halicarcinus cookii*, gravid female, 6.5 mm; B—*H. cookii*, male, 3.5 mm; C—*H. cookii*, spent female, 5.25 mm; D—*H. cookii*, male, 6 mm; E—*H. varius*, male, 7.5 mm; F—*H. cookii*, female, 4 mm.

[facing page 49]

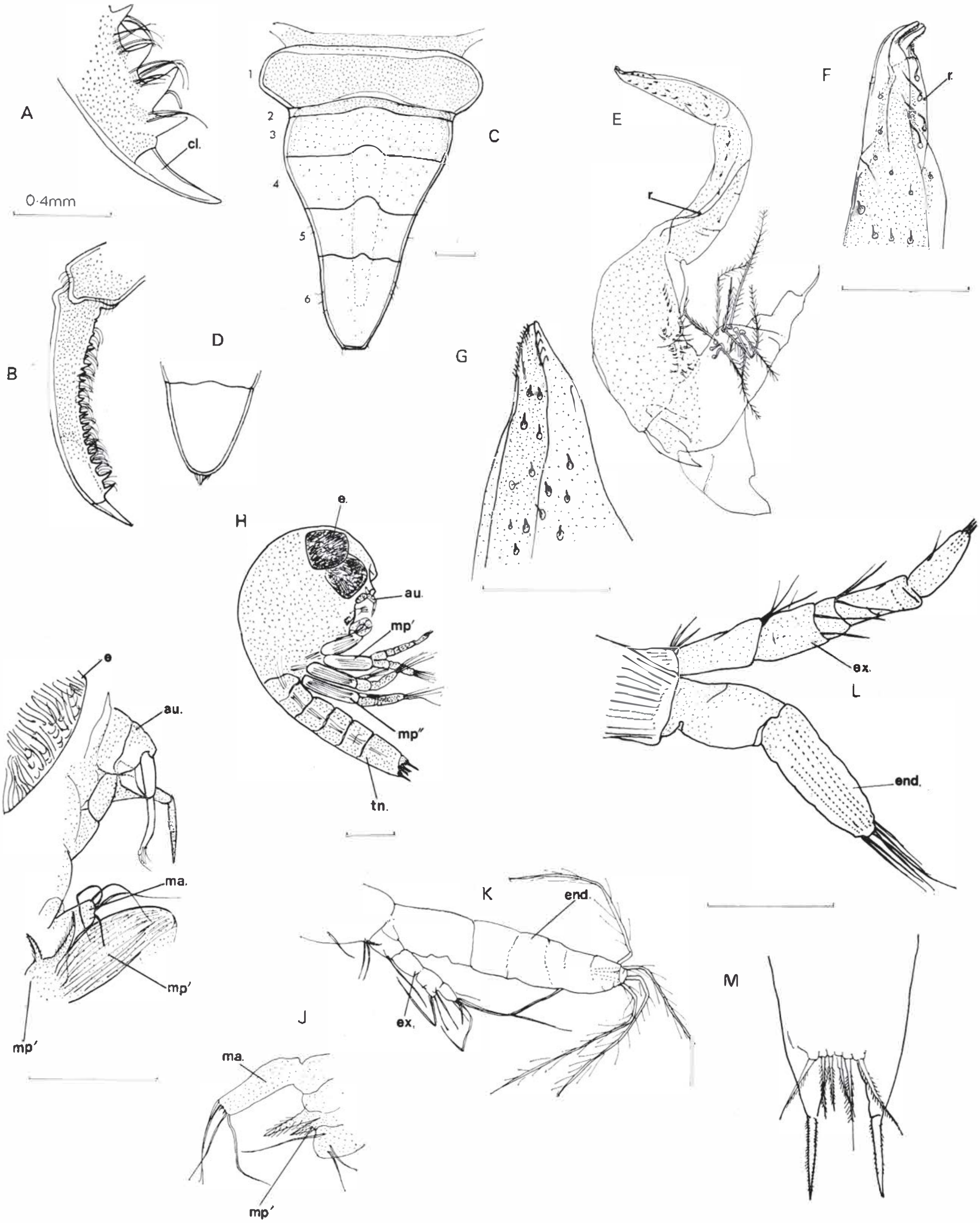


Fig. 18 *Halicarcinus cookii:* A—Tip of dactylus of 3rd walking leg of male, posterior view; B—Dactylus of 3rd walking leg of male, posterior view; C—Male abdomen extended, dorsal view; D—Ultimate segment of abdomen of second male; E—Left 1st pleopod of male, sternal view; F—Tip of left 1st pleopod of male; G—Tip of left 1st pleopod of second male; H—Zoea stage 1; I*—Anterior portion of right side of zoea enlarged, showing antennules, maxilla and 1st maxilliped; J—Left side of a second zoea, showing maxilla and base of 1st maxilliped; K—Exopod and endopod of left 1st maxilliped of zoea; L—Exopod and endopod of left 2nd maxilliped of zoea; M—Telson of zoea. (scales represent 0.4 mm)

*below B

Inset 7*

cheliped, and commonly black or orange-red. There may be a contrasting red or black band halfway along both fingers where the pigmentation has petered out. Other segments may be sparsely pigmented and are usually paler than those of the walking legs and without white bands except sometimes near the joint of the basis and merus. Sometimes abortive dark bands may be present on the merus and carpus but these never completely encircle the perimeter.

Breeding: Many gravid and spent females have extremely disruptive coloration. About half of the females had indistinct patterns on the carapace and leg bands, although present, were diffuse. In males, the colour pattern seems to retain its basic clarity throughout life. In gravid females, there appears to be a breakdown of the pattern, browns and black ceasing to dominate and orange and yellow chromatophores proliferating. Small black specks remain scattered over the carapace, especially near the margins and extending across the rim. Probably the black chromatophores remain but melanic pigment is withdrawn from them and from the whole body of the female, so that the yellow of the cuticle shows through.

The eggs are a faint yellow at first. As pigment enters the chromatophores they become orange and finally brown. This brown appearance is largely due to the formation of the eyes, which are large in comparison with the rest of the embryo. A few scattered black and red chromatophores can also be seen in the embryonic cuticle, especially on the carapace.

Younger specimens tend to have more spectacular, brighter colour patterns, which darken with age, implying deposition of melanin with growth.

After a moult the overall colour pattern was unchanged in 4–5-mm specimens, but usually immediately afterwards the specimen was uniformly paler, probably because the cuticle darkens as it hardens. It is also possible that the moulting hormone and chromatophore hormone interact and moulting causes the white chromatophores to expand and the dark to contract. The white chromatophores are more obvious immediately after ecdysis.

Regeneration: Regenerating legs are much less pigmented than usual. By the second moult, when all leg segments have differentiated, the middle band on the merus is usually represented by a scattered band of red, or red and black chromatophores.

Background: The type of alga in which the crabs lived did not affect their colour patterns. As many red and orange splotched individuals were found on *Carpophyllum* as on *Pterocladia*, and dark brown or olive crabs were found in both Rhodophyceae and Phyophyceae. Hermit crabs in *Pterocladia* and *Carpophyllum* had the same red, white and black banded legs as *H. cookii*, suggesting that these disruptive patterns are advantageous to algal-living species.

Colour changes: In dark-adapted specimens, most of the chromatophores were monochromatic. Black, red and white chromatophores were most common. Yellow, green or blue chromatophores were more rarely encountered. In some specimens a brown colour seemed to be due to dichromatic chromatophores which combined red and black pigment. However, this occurred only on carapaces with densely packed chromatophores. On the antennules and mouthparts of the same specimens it was obvious that the red and black aggregations of pigment had separate collection centres. Similarly green, white and black intermingled at some points so that although the chromatophores appeared to be trichromatic, the colour components probably belonged to separate chromatophores. White and yellow chromatophores often had a central dot of black pigment but monochromatic chromatophores of the same colour could also be found on the same specimen.

The red chromatophores were very variable in different crabs, ranging from scarlet to orange or pink. In any single specimen, the "red" chromatophores were uniformly pigmented throughout the body.

The depth of the chromatophores within the cuticle also varied. White chromatophores usually lay above the rest, so that their expansion masked all traces of any other colour. In the bluish transparent regions of the merus and propodus, the ramifications of large, monochromatic red and black chromatophores could easily be seen, their branches extending well into the leg segments.

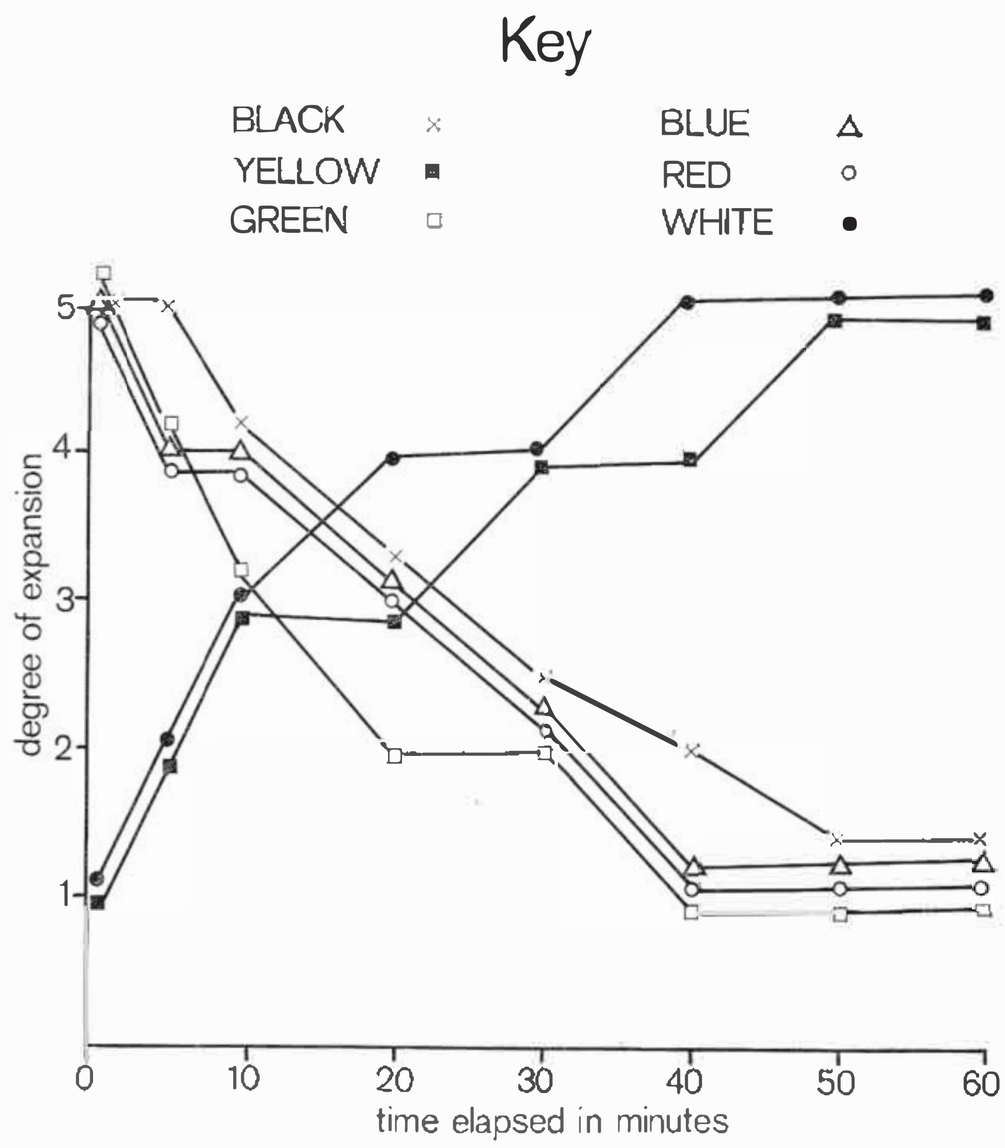
In a dark-adapted specimen placed in light, white and yellow chromatophores expanded and the other colours contracted simultaneously (*see* Fig. 19). The red chromatophores contracted before the black ones, and the white and yellow chromatophores expanded rapidly, the yellow chromatophores lagging a little behind the white.

In a light-adapted crab transferred to darkness, initially all chromatophores react rapidly, the yellow chromatophores contracting faster than the white (*see* Fig. 20). The black chromatophores reached their full expansion sooner than the rest, which took much longer to expand or contract than when the crab was transferred from dark to light. In fact, green, blue, and yellow chromatophores were still not fully expanded or contracted after 2 hours.

The speed of contraction or expansion of chromatophores varies on different parts of the body. Black and red chromatophores in the leg bands react faster than those on the carapace when the crab is transferred from light to darkness, but the reverse is true of white chromatophores in the two areas. The black and red chromatophores on the leg bands contract much more slowly than the same colours on the carapace when the crab is transferred from darkness to light, but the white chromatophores on the leg bands expand faster than those on the carapace.

White chromatophores in the permanently white areas of the carapace are part of the basic colour pattern and never contract completely although they may contract to half their usual size. (Table 2 summarises the results from these experiments.)

Fig. 19 Degrec of chromatophore expansion in relation to time when a dark-adapted specimen of *Halicarcinus cookii* is transferred to light



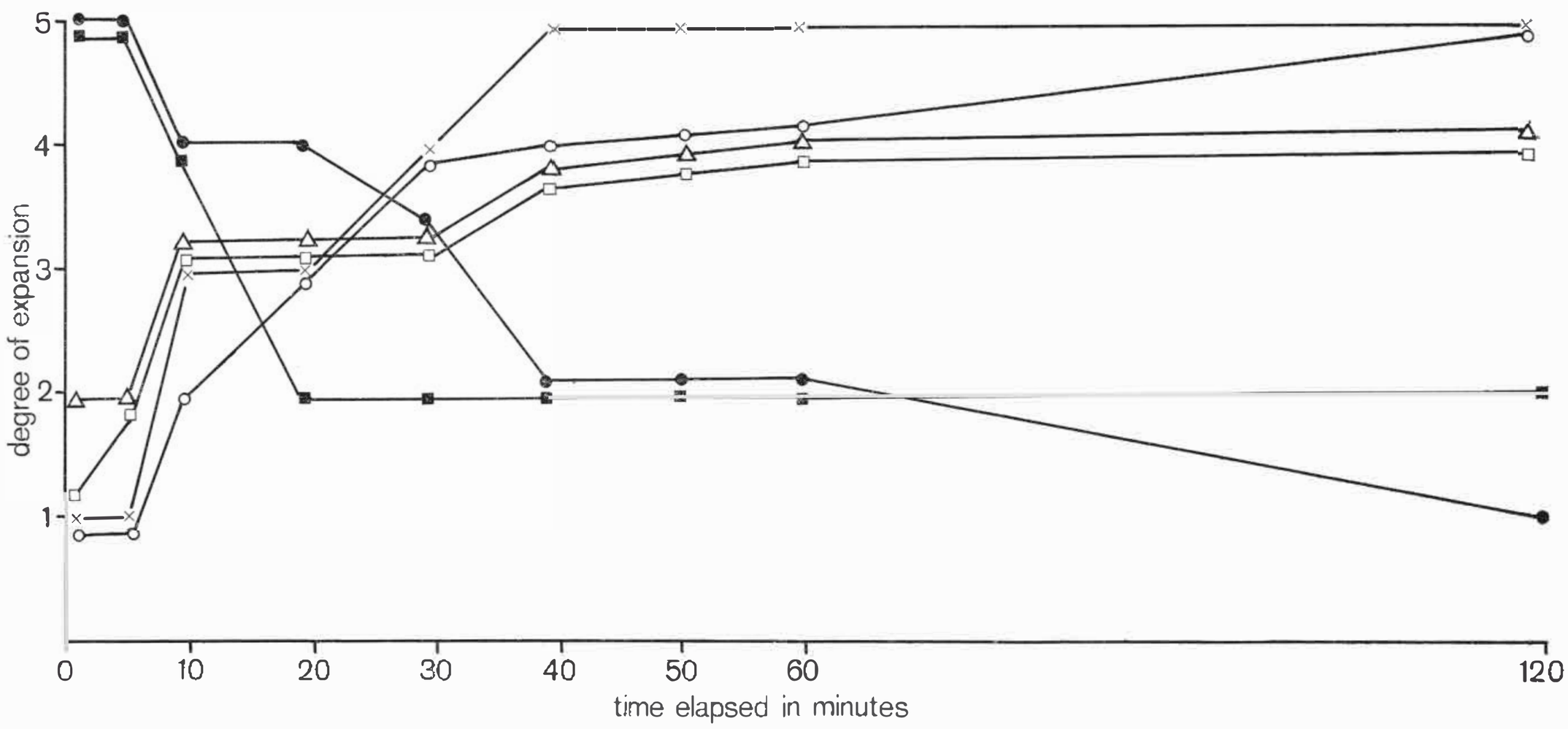


Fig. 20 Degree of chromatophore expansion in relation to time when a light-adapted specimen of *Halicarcinus cookii* is transferred to darkness. Key as in Fig. 19

Table 2 Results of experiments on chromatophore expansion and contraction in *Halicarcinus cookii*
1–5 are states of increasing expansion of any chromatophore

Chromatophore colour	Position	Light adapted specimen transferred to darkness: time elapsed in minutes									Dark adapted specimen transferred to light: time elapsed in minutes								
		0	5	10	20	30	40	50	60	120	0	5	10	20	30	40	50	60	120
Black	carapace	1	1	3	3	4	5	5	5	5	5	5	4	3	2	2	1	1	1
	legs–non-banded areas	1	1	2	3	4	4	4	4	4	5	5	4	3	2	2	1	1	1
	legs–banded	1	3	4	5	5	5	5	5	5	5	5	5	5	5	4	3	1	1
	antennules	1	1	2	2	3	4	4	4	4	4	4	3	3	3	2	1	1	1
	eyestalks	1	1	2	3	4	5	5	5	5	4	4	3	3	3	2	1	1	1
Red	carapace	1	1	2	3	4	4	4	4	5	5	4	4	3	3	1	1	1	1
	legs–non-banded areas	1	1	2	3	3	4	4	4	5	5	4	4	4	3	1	1	1	1
	legs–banded	–	–	–	–	–	–	–	–	–	5	5	5	5	4	4	4	2	2
	antennules	1	1	3	4	4	4	5	5	5	4	3	2	2	2	2	1	1	1
	eyestalks	1	2	3	3	4	4	4	4	4	–	–	–	–	–	–	–	–	–
Green	carapace	1	2	3	3	3	4	4	4	4	5	4	3	2	2	1	1	1	1
Blue	carapace	2	2	3	3	3	4	4	4	4	5	4	4	3	2	1	1	1	1
Yellow	carapace	5	5	4	2	2	2	2	2	2	1	2	3	3	4	4	5	5	5
White	carapace–general	5	5	4	4	3	2	2	2	1	1	2	3	4	4	5	5	5	5
	carapace–permanently white area	5	5	4	4	4	4	4	4	3	3	4	4	4	5	5	5	5	5
	legs–non-banded area	5	5	3	3	2	1	1	1	1	–	–	–	–	–	–	–	–	–
	legs–banded	5	4	4	4	3	3	2	2	1	1	3	4	5	5	5	5	5	5
	antennules	5	5	3	2	2	2	2	2	2	2	3	4	5	5	5	5	5	5
	mouthparts	–	–	–	–	–	–	–	–	–	1	2	4	4	5	5	5	5	5
	eyestalks	5	5	5	5	4	4	3	3	3	2	3	4	5	5	5	5	5	5

REMARKS: The species was initially inadequately described, and until 1949 there was no other account which unmistakeably referred to this species. In his key to the New Zealand Hymenosomatidae, Richardson (1949a, p. 68) gives the following description: "Anterior marginal tooth, rounded; posterior tooth submarginal, acute spine-like; rostral lobes subequal; medial face of the chela hairy; elsewhere hair scanty; digits of chela fully dentate and with full occlusion", and he includes an accurate figure (fig. 46). However, he also adds that *H. cookii* is found "among *Zostera* and other seaweeds on tidal mud-flats". During this present study, all specimens from tidal mud-flats were *Halicarcinus whitei* or *H. varius* (=Richardson's *H. edwardsi*) and *H. cookii* was taken only from seaweed attached to rocks.

Richardson states that since Chilton considered his *H. marmoratus* a possible synonym of *H. varius*, "the original specimen may be referable to *H. cooki*, or to a species (Key 15) which is common but not yet referrable to a named species". (Richardson 1949b later referred "Key 15" to Filhol's *H. edwardsi*.) Although Richardson apparently realised that either his *H. cooki* or his *H. edwardsi* was synonymous with Dana's *H. varius*, he did not suggest which one was the synonym. Chilton's description of *Hymenicus marmoratus* (1882) could apply almost equally well to either *Halicarcinus cookii* or to *H. varius* as described here, but the large size of the second lateral angle (uniformly highly developed in *H. cookii*, less so in *H. varius*), and the colour of Chilton's specimens indicates *H. cookii*. The white and red-brown splotches that Chilton described are common in the more variable colour patterns of *H. cookii*; *H. varius* is most often a uniform dark brown or green or black, more rarely marked with white. The type of *H. marmoratus* is no longer extant, so that it cannot be considered definitely as a prior name for Filhol's species. The species which Filhol (1885a) found in Cook Strait and called "*Hymenicus Cookii*" was described as follows (translation):

"The shape of the carapace resembles that of *Hymenicus edwardsii*. The lateral borders each bear two spines, the posterior long and acute. The front is large and tridentate. The arrangement of these points and lobes greatly resembles that of *Hymenicus varius*. This species differs from the latter in the shape of its carapace but it resembles it in the shape of its front. It resembles the shape of *Hymenicus Edwardsi* and it differs in the shape of its front."

As neither "*Hymenicus varius*", described by Dana, or "*Hymenicus edwardsii*" described by Filhol was well-defined, the above description is unusually vague. In 1886 Filhol added to his description (translation) ". . . the anterior [spine] takes the form of a little projection. The front is prominent, large at its base and tridentate . . . this species differs from *Hymenicus varius edwardsii* [*sic*!] by its very reduced size. The arms are short, the fingers finely dentate. With a magnifying glass one can see some hairs on the internal face of the carapace; the first, second, and third segments of the ambulatory legs are smooth, the fourth exhibits some long isolated hairs over the entire length of its posterior border. The dimensions of the female are 5 mm long, 5 mm broad". The distinctly tridentate form of the rostrum, the emphasis placed on the two well developed lateral angles (the first rounded and the second strongly

Table 3 A comparison of the physical environmental factors tolerated by species of Hymenosomatidae
Salinity of the seawater was determined by titration with silver nitrate

Species	Degree of exposure to wave force	Substrate	Highest position on open shore apart from in pools	Lowest salinity recorded ‰	Average time of survival in tap water	Average time of survival in dry air
Halicarcinus cookii	medium	algae	E.L.W.N.	34.5	1½ hours	1 hour
Halicarcinus varius	shelter	Algae Zostera sand	E.L.W.N.	27.3	6 hours (Eastern Beach) 6 days (Whangamata)	3 hours
Halicarcinus whitei	shelter	Zostera sand	E.L.W.N.	15.8	10 days	6 hours
Halicarcinus innominatus	maximum or medium	near Mytilus canaliculus	E.L.W.N.	24	3 hours	2 hours
Halicarcinus pubescens	shelter or medium	open reef under rocks, algal holdfasts and Corallina	E.L.W.N.	30.5	6½ hours	4 hours
Elamena producta	medium	under rocks in sand at bottom of pools	does not occur	35	—	3 hours

acute), and the scarcity of hair on the walking legs and chelipeds, indicate that Filhol was not describing *H. varius* (= *H. edwardsi*), but this could not be concluded with certainty unless Filhol's type was compared with that of Dana and Dana's types are lost.

ENVIRONMENTAL NOTES (Table 3):

Substrate: The microhabitat of *H. cookii* is within finely divided algal fronds, in holdfasts and also in densely matted growths such as those of *Corallina officinalis*. Specimens of *H. cookii* were frequently collected from under the tangled bladders of *Hormosira* and, more rarely, adults were found under stones near seaweed holdfasts in the low mid-littoral.

Density: In *Corallina* turf and the holdfasts of *Carpophyllum*, a maximum density of 2–4 specimens of *H. cookii* 0.1 m^2 was reached in summer. Then, the *Carpophyllum plumosum* fronds appeared to be swarming with small crabs and careful counts showed approximately one crab in every 100 grams of alga.

Salinity tolerance: Although *H. cookii* is unlikely to encounter any critical fluctuations in salinity of the sea water which regularly covers the low tidal area, some of the rock pools in the lower mid-littoral may be diluted periodically by rain which also falls on the exposed *Hormosira* flat. *H. cookii* was found to be fairly resistant to osmotic stress caused by this dilution of the external medium. Specimens lived indefinitely in 50 percent normal sea water, for an average of 100 minutes in tap water (the period until death varying from 30 to 240 minutes) and for an average of 60 minutes in distilled water (the period until death varying from 15 to 70 minutes).

Respiration: Observations of the mode of respiration in *H. cookii* agreed well with Borradaile's (1922) description for *Carcinus maenus*. The whirlpool exhalent currents were rarely active on both sides of the rostrum at once. Temporary cessation of the respiratory current in response to a sudden change, such as transference from air to water or presentation of a threat stimulus, was common. The highly oxygenated water in which *H. cookii* lives made this behaviour possible. Failure to oxygenate the water in which the crabs lived led to rapid asphyxiation; *H. cookii* succumbing faster than hermit crabs or *Hermigrapsus* from the same habitat. The time taken for death from asphyxiation depended on the size of the container—crabs lived longer in shallower dishes, and indefinitely when these were shallow enough for the crab to raise the anterior part of its carapace out of the water at intervals. Microscopic examination showed that the scaphognathite would beat faster as the water warmed in the light, and the crab would make increasingly vigorous attempts to escape. Strong light and high temperatures caused the crab to leave the water although the risk of desiccation was then increased.

Desiccation: The bulk of the population of *H. cookii* on any beach is found in the sublittoral fringe or lower. The population in the lower mid-littoral (the *Hormosira*

belt) must be exposed to air at most low tides, and those in the sublittorial fringe (the *Carpophyllum* zone) will also suffer from exposure during spring tides. The seaweed substrate must form a water retaining mat which provides a sufficiently moist microclimate when the tide recedes. The longest a specimen in air in the laboratory survived was 1½ hours, but specimens placed in a dry, open bowl with damp seaweed lasted for 12 hours.

Substrate preference: The seaweed substrate is very important in the life of *H. cookii.* Not only does it provide a favourable microclimate, but it reduces the force of the waves which could otherwise sweep the small crabs away. It offers anchorage as they feed and mate, and serves as food or as a home for a myriad of food organisms. The sturdy legs of *H. cookii* end in hooked claws giving a tenacious grip which would prevent them being inadvertently washed away.

Finely divided algae provide more anchorage and break the force of the waves more effectively than others. *H. cookii* reached its greatest population density in *Carpophyllum plumosum.*

To establish whether the crabs were capable of choosing the more favoured algae when the water was comparatively still, bunches of algae of equal size were introduced around the perimeter of a large perspex tank of sea water which was aerated from the centre. A few stones were scattered near the centre, and the tank was evenly illuminated by weak sunlight. The relative positions of the bunches of seaweed were altered between experiments to prevent some constant directional stimulus affecting results. Twenty-five crabs were placed in the centre of the tank, and 2 hours later each piece of alga was carefully searched for crabs. After four experiments, 44 percent of the crabs had selected *Carpophyllum plumosum*, 26 percent were found in *Pterocladia capillacea*, and 18 percent in *Melanthalia abscissa;* 8 percent were in *Carpophyllum elongatum* (holdfast only), 4 percent under stones, and none in *Hormosira banksii. H. cookii* is therefore actively selective.

In catching food, *H. cookii* appears to rely greatly on visual stimuli; it is negatively phototactic in strong light, and is activated by light of moderate intensity.

BEHAVIOURAL NOTES (Table 4):

Thigmotaxis: H. cookii has a strong, tactile response. A solitary specimen dropped into water flexes the walking legs beneath the carapace so that only the distal ends of the meri jut out sharply from the subcircular outline. The chelae are tightly folded, the fingers pointing toward the mid line of the mouthfield. In this position, the crab floats down through the water, like a fragment of brown or red alga with torn edges. After seconds or even minutes have elapsed while the crab rests on its carapace, it extends its legs and runs. When several crabs are present, they move about until they are all in close contact, forming a loose spherical aggregation with their legs linked and bent. If seaweed is provided, the crabs stop when they reach the weed and link the fourth pair of walking legs under a rib of weed. The ischium and merus of the leg lie under the rib, the remainder of the leg is bent inwards and upwards over it. Alternatively the ischium and merus may lie over the rib and the rest of the leg under it. A typical position is shown in Fig. 21c where the crab has just come into contact with a piece of *Cystophora* and the left hind leg has already been bent upward over the seaweed to provide anchorage. The other walking legs are usually hooked haphazardly to the frond, leaving the chelae free for catching food. If no alga is available, *H. cookii* will cling to any other suitable surface such as a pebble. If only small scraps of *Corallina* are available, a piece may be hooked on to the rear half of the carapace with the last pair of legs and held there for a few minutes.

Crabs move about to a limited extent in weed, and naturally come into contact. After contact, each rapidly withdraws the legs which have touched the other individual and moves in another direction. Spacing between individuals in seaweed is therefore a normal situation except when mating occurs, so that the clumping together of individuals in a tank without alga is a simple response to tactile stimuli, not true gregariousness.

Alarm reactions: The tight folding of the walking legs and chelipeds under the carapace and the passive drifting which occurs when *H. cookii* is dropped into water, together with the disruptive banding on the legs and the bright colours on the carapace, which blend with surrounding algae, provide a good example of special resemblance. Predators are presumably deceived into treating prospective prey as a scrap of alga.

Larger males threatened with a needle will sometimes stand on the dactyli of their bent walking legs and brandish their unfolded chelipeds forward and upward, waving them randomly and occasionally advancing to grasp the needle. A male may rear up on its back legs, paddling the other walking legs and chelipeds vigorously.

A crab lifted off a substrate after repeated proddings "plays dead", lying on its back with its legs folded. This position is very transitory. One specimen was observed lying on its carapace, extending and then folding all its walking legs in unison. This convulsive cycle was repeated six times while the crab was being threatened. Such a reaction could be of selective value as a would-be predator might be confused by the changing size and shape of its prey.

H. cookii at Leigh reached a smaller maximum size than most of the other common species. Defensive reactions were therefore predictably more common than threat behaviour. Running sideways or backing was the usual reaction to danger, but even in aquaria this was usually preceded by a period of frozen immobility. The crab crouched low against the substrate, casting no shadow, with some legs bent and some almost straight, spread at random angles.

A crab removed from the water remained stationary for 3 to 10 minutes before running forwards or more rarely, sideways, at speeds of 1.6–2 cm/sec.

Table 4 A comparison of the behaviour of species of Hymenosomatidae

Species	Transferred from water to air	Dropped into water	Threatened with needle	Males meeting	Food eaten (preferred food in *italic*)	Burrowing in sand	Swimming
Halicarcinus cookii	"freezes" for minutes	legs tightly folded under carapace, floats	attacks with chelae	no reaction	*amphipods*, polychaetes (alive)	none	only in unfavourable conditions
Halicarcinus varius	"freezes" for 1½–5 minutes	legs extended or half bent	attacks with chelae	sometines spread chelipeds, anterior surface of palms touching those of other crab	polychaetes, amphipods, small shrimps (*alive* or dead), debris, algae	2.5–5 mm below surface	rare
Halicarcinus whitei	"freezes" for 2–4 minutes	legs extended or half bent	"freezes" then runs or burrows, *or* tucks chelae in sharply, *or* spreads chelipeds	large males spread chelipeds, anterior surface of palms touching those of other crab	*polychaetes*, chopped pipis, debris, sand, *Zostera*	2.5mm below surface	frequent
Halicarcinus innominatus	"freezes" for several minutes	legs tightly folded under carapace, floats	attacks with chelae *or* lies on upper carapace with legs tightly folded	sometimes grip each other's chelae	polychaetes (*dead* or alive), pieces of dead mussel	none	not seen
Halicarcinus pubescens	"freezes" for several minutes	legs tightly folded or half folded overlapping laterally, floats	retreats	no reaction	debris filtered on mouthparts, dead polychaetes	none	occasional
Elamena producta	"freezes" for several minutes	legs half folded and overlapping laterally or legs all straightened and overlapping	chelipeds spread, then all legs straightened and overlapping	no reaction	amphipods and polychaetes (alive)	just below surface	not seen

Normal locomotion: In an aquarium, *H. cookii* walks rapidly forwards for short periods, typically adopting the stance shown in Fig. 21a with the chelae extended in front and held slightly above ground level. The sideways gait usually associated with crabs is observed almost as often as forward movement. When *H. cookii* moves sideways, the chelae are either tucked inward above ground level (*see* Fig. 21b) or less frequently, used alternately like the legs in providing extra sideways thrust.

Forward progression changes to sideways locomotion if the crab is disturbed or if it encounters a barrier such as a large rock. In weed, slow sideways movement is normal.

Swimming: Swimming is rare, but can sometimes be seen as a crab floats down through the water if it unfolds prematurely from the folded position which mimics a scrap of alga. More often *H. cookii* pushes upwards from the substrate and swims a very short distance before touching down. Very rarely, a crab becomes caught at the air-water interface so that it is supported by this tension and can swim along briefly.

Swimming involves basically similar movements of the legs to the sequence employed during forward walking. The chelipeds are held forward and slightly bent, moving a little but not as much as the walking legs. During walking, the coxa-basis joint and the carpus-prodopus joint seem equally important, as both form major planes of movement in effective and recovery strokes. In swimming, most of the thrust comes from movement about the coxa-basis joint, as the walking legs remain relatively

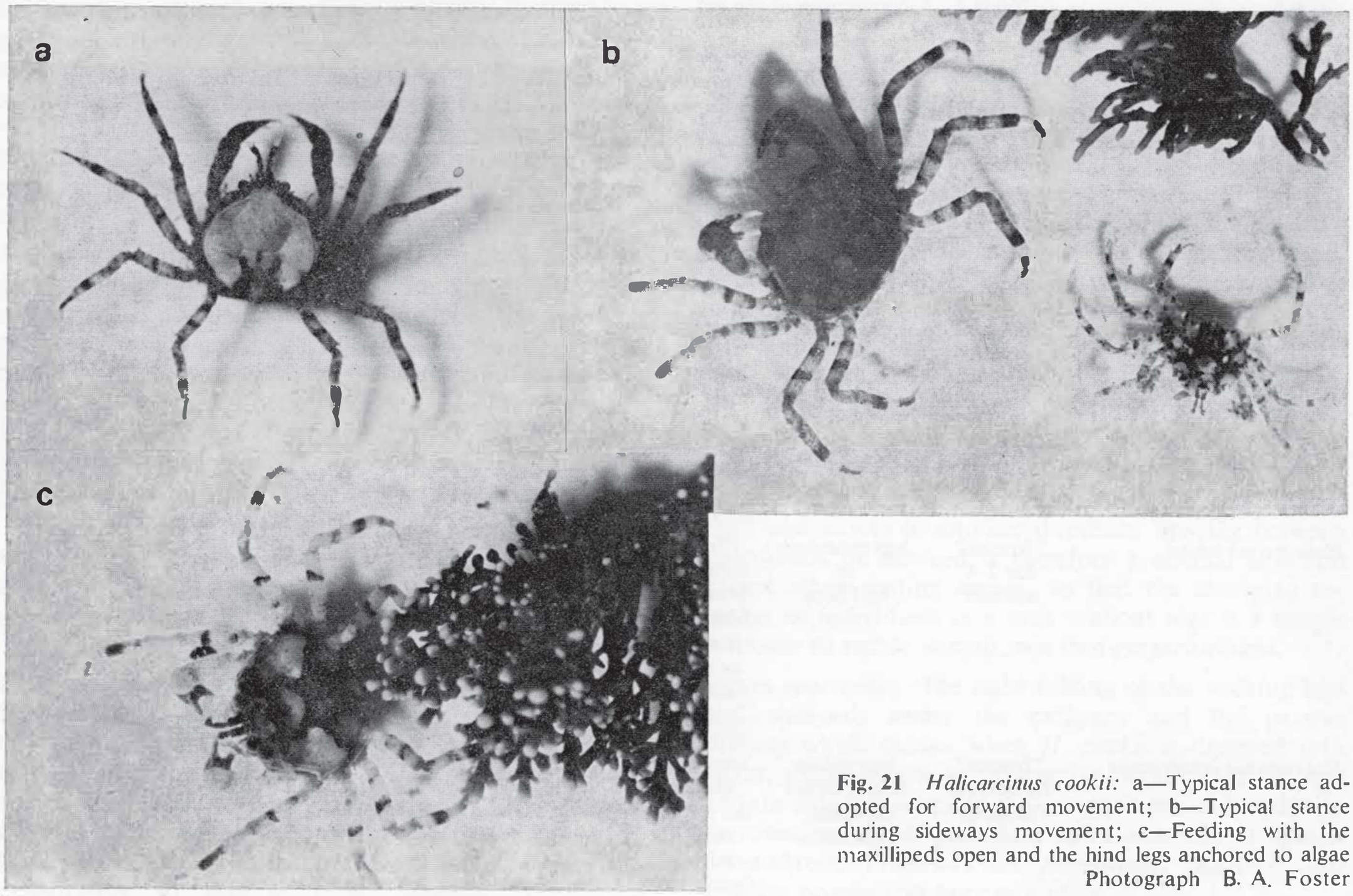


Fig. 21 *Halicarcinus cookii:* a—Typical stance adopted for forward movement; b—Typical stance during sideways movement; c—Feeding with the maxillipeds open and the hind legs anchored to algae
Photograph B. A. Foster

straight. Each walking leg bends upwards, then pushes downwards and slightly backwards. This downward stroke corresponds to the backward thrust in walking and lasts longer than the upward stroke. For both strokes the leg remains approximately at right angles to the edge of the carapace. The individual movements of all the walking legs produce a "fluttering" motion which propels the crab upwards and forwards.

In the laboratory *H. cookii* swam only in adverse conditions when the water became overheated or deoxygenated.

Autotomy: Specimens gripped very tightly to seaweed, so tightly that if they were torn away, one or more legs autotomised. The plane of autotomy in all hymenosomid species is between the basis and the ischium. Contact between this joint and the rim of the carapace causes severance. However, this contact is not essential, and if the leg is bent upwards to a variable degree the leg will snap at this point. With legs missing after autotomy, *H. cookii* can adapt the normal sequence of leg movement and the angle at which the legs radiate outwards when the crab is stationary, so that stability is achieved. When all the walking legs on one side are present and all but one are removed from the other side, the crab frequently rotates in its path. It progresses first forwards and then backwards, but still manages to move in a constant direction at near normal speed. Walking is still possible, but slower, if only one walking leg remains on each side. The crab lurches from side to side and the chelipeds become important in providing thrust and balance.

Display: Only minor display behaviour was observed between males in aquaria. Occasionally two males might meet face to face and stand on the dactyli of the walking legs which splayed out to brace the body upwards, the carapace sloping upward anteriorly and the chelae folded inward or extended forward and brandished upward at intervals. The pair would not touch each other, and usually one would retreat, followed for a short distance by the second, before both wandered off.

Mating: Copulation was observed in June between a male from Whangamata, which had been isolated from other crabs for one month, and a female from Leigh, which had shared a tank with another female for 2 months.

Minutes after the male had been placed in the tank, male and female met among fronds of *Carpophyllum plumosum*. The male clambered on the female's back then manoeuvred sideways and beneath her until their ventral surfaces were together and the female was clasped above the male. Throughout copulation, which took 35 minutes, the male retained a grip on the female by interlocking his last three pairs of walking legs between hers

and flexing them loosely away from the side of both carapaces. The large chelipeds and the first pair of walking legs of the male were clamped over the female's carapace. These chelae almost met in the mid line of the female's carapace, covering the anterior third of her carapace so that the rostrum and eyes were obscured. Infrequently the male lifted both chelae slightly and simultaneously, then clamped the chelae down again. During mating the male maintained an intermittent respiratory current on his left side. The left fourth walking leg of the female and three of her right walking legs anchored the pair to the alga.

A spasm of contraction, a sharp flexing of all the legs of both crabs, was observed 25 minutes after they first came together. Later the third maxillipeds of the male moved apart and swung open, and the chela and first walking leg on the right side flexed abruptly up and down on top of the female's carapace. The male's first walking leg was then stretched sideways to its fullest extent, then bent upwards and backwards before being replaced above the female's carapace but not in contact with it. At this, the female's legs relaxed on her left side, hooking more to the alga than to her partner.

Five minutes elapsed before the male's external maxillipeds began to move, opening and extending downward either alternately or in unison. The antennules of the male flicked rapidly and were cleaned by the palps of the external maxillipeds. The vortex of the respiratory current became more powerful, but was still restricted to the left side. Aimless waving of the male's right chela and right third walking leg occurred before both were violently pushed down to rest on the female's carapace.

Two contractile spasms then occurred. Immediately afterwards all the walking legs of the male were extended and his first pleopods could be seen waving vigorously below the female's carapace. In a series of jerks the male moved forward, the female turning under him until she lay partially under his abdominal region. As the male moved away the female clutched at his right walking legs with her chelae.

The male's abdomen pumped as he rested between fronds of algae. Meanwhile the female sat with her maxillipeds rhythmically clapping in and out, cleaning her antennules. After dropping to the bottom, the male encountered a large piece of shell which he lifted with his back legs and attempted to back under. The female similarly scuttled backwards over the sand, levering shell fragments and scraps of seaweed on to her back. Later, both crabs ran sideways under rocks.

Throughout mating, the male was the more active and dominant partner. Courting was not seen and the male did not exhibit display behaviour towards the female at any stage.

The chain of responses leading up to the spasmic contractions of the male which force sperm along the first pleopods and into the sternal female apertures, occupies a considerable period. After the ventral surfaces of the crabs were pressed together, the whole frond of alga could be pulled from the water and dropped again without disturbing the crabs, other than causing the male to grip the female even more tightly, the usual response of scrambling about and dropping from weed to water being inhibited. Leg movements were minimal and although amphipods swam within catching distance of the male, he showed no response to this food. An irregular flickering of the antennules and waving of the antennae was maintained, but these organs are highly important as chemoreceptors (Waterman 1961, p. 113). After the first spasm of the male, random movements of the legs and mouthparts became increasingly frequent, indicating that the inhibition of responses other than those related to reproduction was beginning to disappear. However, further spasms and increasingly random movements occurred before the crabs finally parted.

Gravid females were seldom seen wandering about and if a stone under which a gravid female was sheltering were removed, the crab scuttled very rapidly for cover.

Food preferences: The algal substrate preferred by *H. cookii* is edible but, whenever possible, this crab is carnivorous. The polychaete genera *Perinereis, Lumbriconereis*, and *Neanthys* were all eaten in the laboratory, but amphipods were the favourite prey. Talitrid amphipods were seen to be eaten and probably most of the amphipods which inhabit seaweed are prey, except caprellid amphipods which were never consumed.

In feeding, a tip-toe stance is adopted, with the hind pair of legs bent sideways and slightly backwards, the first pair of walking legs straight and pointing forward and the whole carapace sloping upward anteriorly at an angle of approximately 45° with the substrate. The chelipeds are raised so that they continue the upward slope of the carapace, and the hand is bent inwards towards the mouthfield with the fingers gaping widely. The antennules keep up a continual flicking (each is capable of independent movement), and the antennae wave. The palps of the third maxillipeds may be extended and folded inwards alternately, either in unison or separately (*see* Fig. 21c).

At intervals the chelae are straightened and raised, waving alternately in an out, the fingers opening and closing. Extension of the chelae occurs especially in response to movements above the eyes, which are directed almost straight up in the feeding pose. Little eye movement other than a small rotation of the eye on the eyestalk is possible in hymenosomatids.

If an amphipod is caught by one of the waving chelae, the cheliped bends inward and stuffs the prey into the mouthfield. As the cheliped swings down, the endopods of the external maxillipeds open to allow the food to pass through. The fingers of the chela manoeuvre the amphipod until it is pointing end-on into the mouthfield. Once the mandibles have grasped the head or tail, the endopodites of the third maxillipeds alternately push the amphipod further in. With each thrust of the palps, the mandibles part and close again with a new grip on the food. Little details of the movement of the remaining mouthparts could be seen, but their structure

agrees with that described for *Carcinus maenus* (Borradaile 1922) and similar functions are likely. The endopod of the second maxilliped has a battery of long, strong spines which probably help to break up the food as well as hold it.

The procedure is almost the same if a polychaete is caught, except that when the first chela grasps the struggling prey, the second chela swings over and inward to gain a grip. Both chelae may then be used to bring the worm towards the mouthparts. The worm is juggled until one end is fed into the mouth by jabbing movements of one chela, while the other chela holds the rest of the polychaete near the mouth.

Chopped pieces of polychaete may be dealt with by one cheliped or by both. A whole polychaete was rarely completely consumed, the corpse being desultorily dropped after some had been pushed into the mandibles.

Polychaetes were accepted most readily by large crabs but only after they were waved above the eyes of the crab, or dropped above it so that they floated down directly in front. Movement of the prey seemed essential to initiate the rapid grasping reaction of the crab. Recently dead amphipods and motionless worms were ignored or pushed away, even when they came into contact with the crab.

There is an interesting similarity between feeding behaviour and the threat reaction shown by large crabs. If *H. cookii* is confronted with a large worm it may at first try to grasp it, but if the prey struggles too vigorously, the crab strenuously pushes it away with its chelae, backing away at the same time and finally scuttling sideways. The difference between a "food stimulus situation" and a "threat situation" would appear to depend on the size of the prey, and feeding behaviour can quickly change to avoidance.

Epifauna: The carapace of *H. cookii* is usually clean of settling organisms, but sometimes isolated *Pomatoceros caeruleus* were found on the carapace or near the mouthfield. Caprellid amphipods frequently clung to the legs and were ignored by the crab. Algal sporelings at the 2–4-cell stage were found on the chitinous exoskeleton in spring. Small molluscs *Dardanula olivacea* and *Microlenchus sanguineus* occasionally grazed on the carapace presumably cropping the algal sporelings and detritus film.

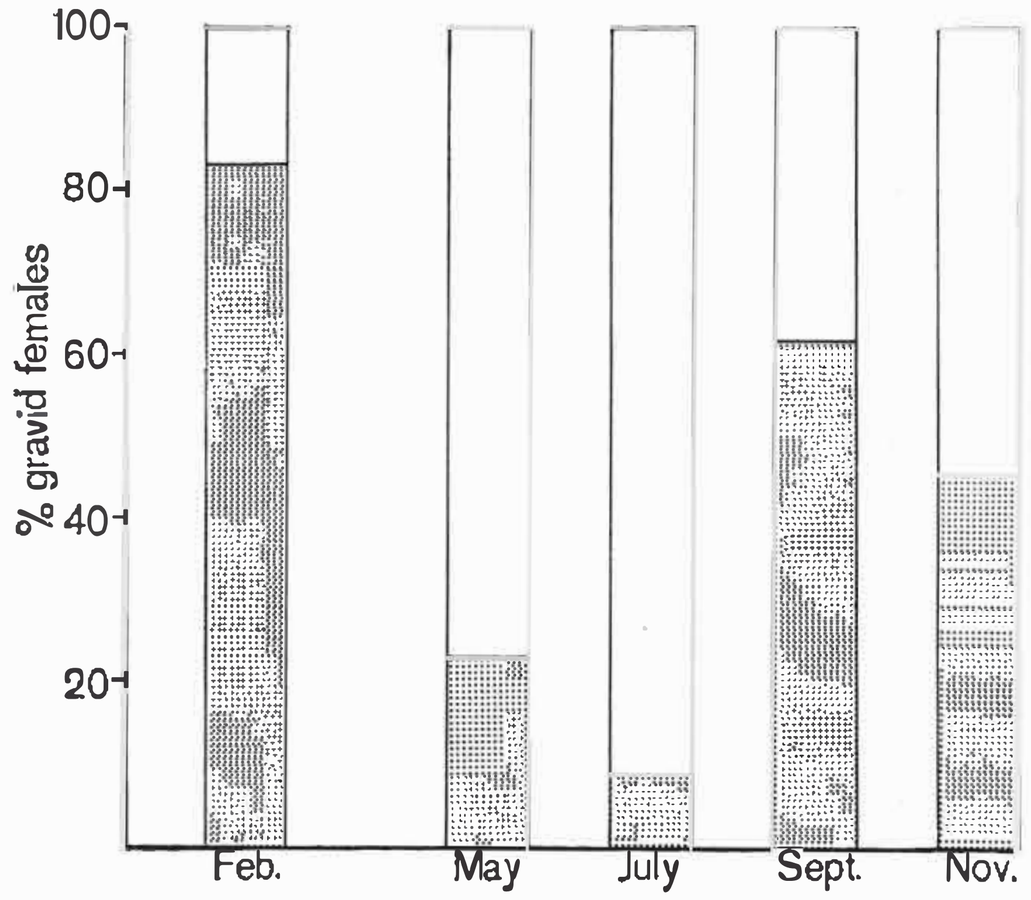


Fig. 22 Percentage of gravid females in the total female population sample of *Halicarcinus cookii* at Leigh

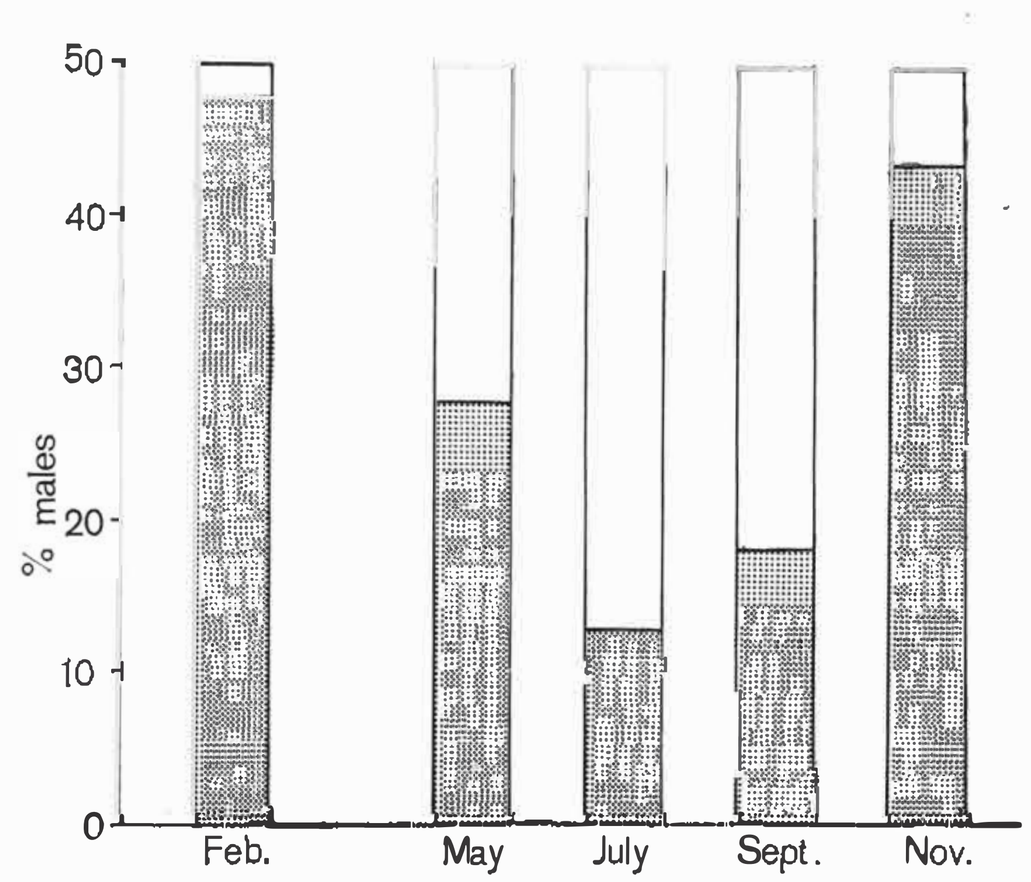


Fig. 23 Percentage of males in the total population sample of *Halicarcinus cookii* at Leigh

POPULATION CHANGES: The population at Leigh was sampled every 2 months by collecting the crabs from a bucketful of *Carpophyllum plumosum* (*see* Figs. 22, 23, and 24). Between 25 and 70 crabs were collected in each sample at Leigh, and the January sample from Whangamata included 20 crabs.

Gravid and spent females were almost always 4 mm or more across the carapace, the smallest spent female being 3 mm. It has been shown by Gurney (1939) that in the moult following egg shedding the condition of the pleopods and abdomen changes to that of an immature female unless more than one batch of eggs is produced at a time. Spent females are therefore those that have just liberated zoeae or that are just about to become gravid again. Spent and gravid females were therefore grouped together. Gurney's findings are confirmed by the collection of non-gravid female *H. cookii* from 2.5–7 mm in size. Several non-gravid females from Leigh were over 5 mm in width. Females in these upper size groups were quite capable of reproduction and were presumably collected after the pleopods had changed in form during the post-hatching moult.

There is probably a residual breeding population of *H. cookii* throughout the year at Leigh where peaks of egg production occurred in spring and mid summer. At Onemana Beach, Coromandel, 87 percent of the female population were gravid in January, which parallels the situation at Leigh in summer.

In winter, males form a smaller percentage of the total population than in November or February. The expected 50 percent ratio of the sexes is almost reached in summer at Leigh, but even then females are slightly more plentiful (*see* Fig 23). Possibly, restriction of the habitat to finely divided seaweed fronds leads to a population density high enough to ensure that a single male can mate with many females. The algae are rich enough in food organisms for crowding of the population without starvation.

GROWTH: Captive individuals moulted only once or twice, usually immediately after capture. Moulting appeared to be inhibited in the laboratory (Waterman 1960, p. 482) making investigation difficult. Crabs 4–5 mm in size gained approximately 0.5 mm in carapace width at each moult.

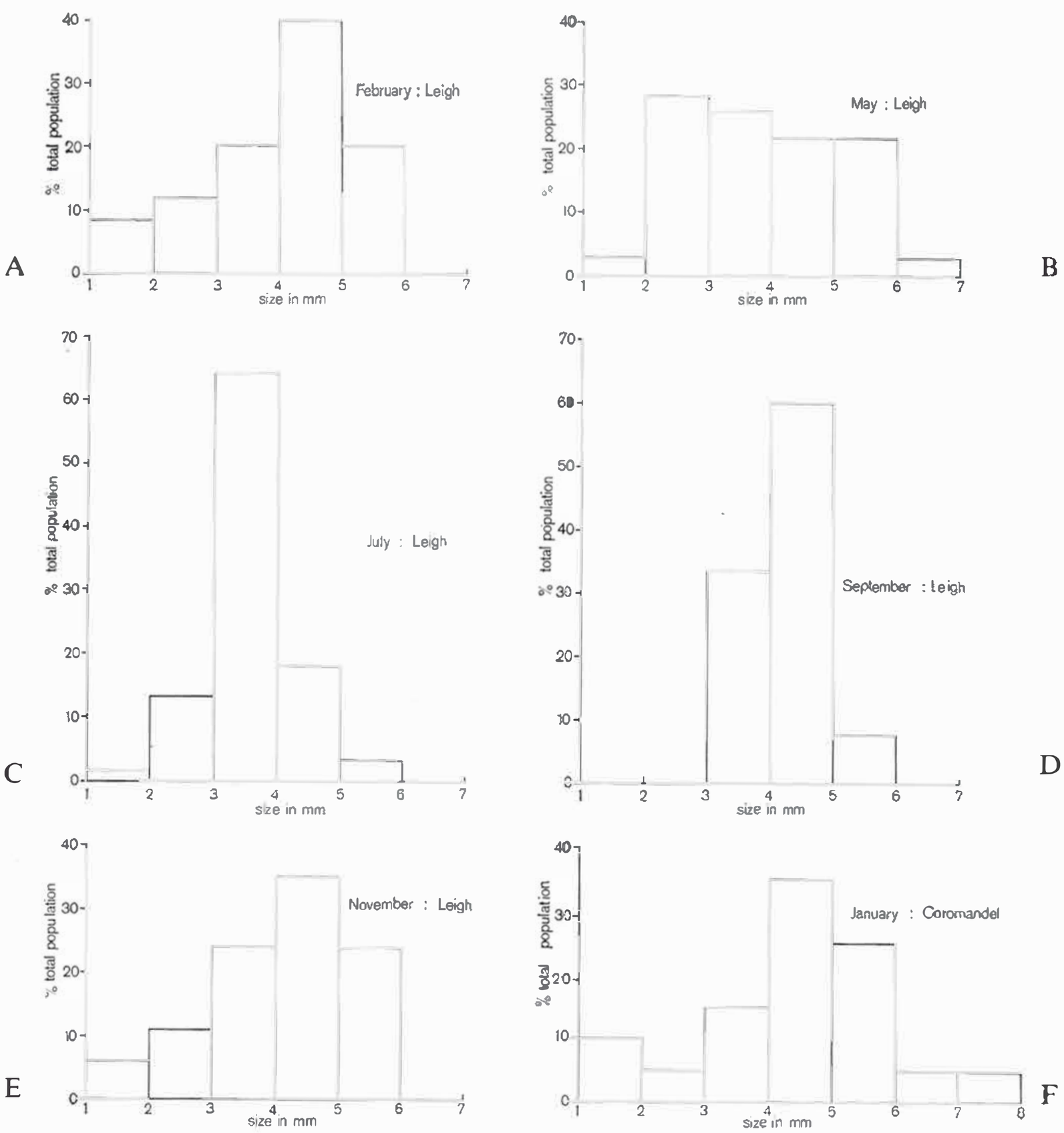
The size distribution of *H. cookii* at Leigh (*see* Fig. 24A–E) may be compared with the size distribution of the January population at Onemana Beach, Coromandel (*see* Fig. 24F). The similarity of Figures 24A and 24F indicates similar size distribution at the two beaches in summer. A larger maximum size is reached at Coromandel. From winter measurements (*see* Fig. 24C, D) it can be seen that the largest number of crabs is found not in the 3–4 mm range but in the 4–5 mm range, implying a growth of 1 mm in the two later winter months.

Halicarcinus varius (Dana)

Figs. 25–30, Plate 2

1851	*Hymenicus varius* Dana, p. 253
1851	*Hymenicus Novi-Zealandiae* Dana, p. 254
1852	*Hymenicus varius*, Dana, pp. 387, 388, pl. 24, figs 9–10
1868	*Hymenicus varius*, Heller, p. 67
1876b	*Hymenicus varius*, Miers, p. 50
1885a	*Hymenicus Edwardsii* Filhol, p. 43
1886	*Hymenicus edwardsi*, Filhol, p. 399, pl. 18, fig. 7
1904	*Hymenicus varius*, Hutton, p. 250
1904	*Hymenicus edwardsi*, Hutton, p. 250
1913	*Hymenicus varius*, Thompson, p. 238
1917	*Halicarcinus varius*, Kemp, p. 247

Fig. 24 Size distribution of *Halicarcinus cookii* in population samples at Leigh and Coromandel



1918 *Hymenicus edwardsi*, Tesch, pp. 13–16, pl. 1, figs 3, 3a–c
1918 *Hymenicus varius*, Tesch, p. 16
1929 *Hymenicus varius*, Chilton and Bennett, p. 776
1936 *Halicarcinus planatus*, Powell, pp. 375, 377, 378
1939 *Halicarcinus edwardsi*, Graham, p. 429
1949a *Halicarcinus* sp. 15, Richardson, p. 67, fig. 45
1949b *Halicarcinus edwardsi*, Richardson, p. 130
?1956 *Halicarcinus cooki*, Ralph and Yaldwyn, p. 74, pl. 6, fig. 40

NOT
1882 *Hymenosoma varium*, Haswell, p. 115

TYPE LOCALITY: Bay of islands, New Zealand.

SUMMARY OF LOCALITIES: Northland: Taurikura Bay, Whangarei Heads; Hokianga Harbour; Goat Island Bay, Leigh; Leigh Harbour; Whangateau; Mahurangi Heads; Ponui Island, Bay of Islands. Coromandel: Whangamata Harbour. Auckland: Auckland Harbour (Westmere, Cheltenham, Chelsea, Eastern Beach, Howick Beach, Motuihe Island, Crusoe Island, Waiheke Island); Manukau Harbour; Ponsonby Reef; Onehunga mudflats. Wellington: Castlepoint; Wellington Harbour (Days Bay, Kau Point, Hope Shoal Light); Lyall Bay. Marlborough: Cape Campbell; Kaikoura (South Bay, Seal Reef, Wairepo Flat). Canterbury: Lyttelton Harbour; Akaroa, Banks Peninsula; Timaru. Otago: Otago Harbour (Port Chalmers, Portobello, Quarantine Island); Dunedin; Brighton. Stewart Island: Oyster beds, Foveaux Strait; Halfmoon Bay. Chatham Islands: Waitangi; Port Hutt.

DISTRIBUTION: New Zealand endemic.

DIAGNOSIS: Carapace subcircular, narrowing a little anteriorly. Short rostrum not projecting past eyes, arising at the same level as carapace, very variable in shape being simple or trilobular, median lobule always longest, all three lobules commonly edged with continuous fringe of short hairs. Ventral rostral ridge pronounced. Suture between carapace and rostrum straight. Anterolateral border of carapace straight or usually convex, never concave, Two pairs of lateral angles always present; first, small, obtuse; second, of medium size, acute, projecting upwards but not reaching the level of the carapace rim, a few curved hairs. Postocular lobe large; antennal spine absent. Chela of male greatly inflated, fingers with a wide basal gape, a large tooth on the base of the movable finger; dense felt of long hairs on anterior face of the palm and base of

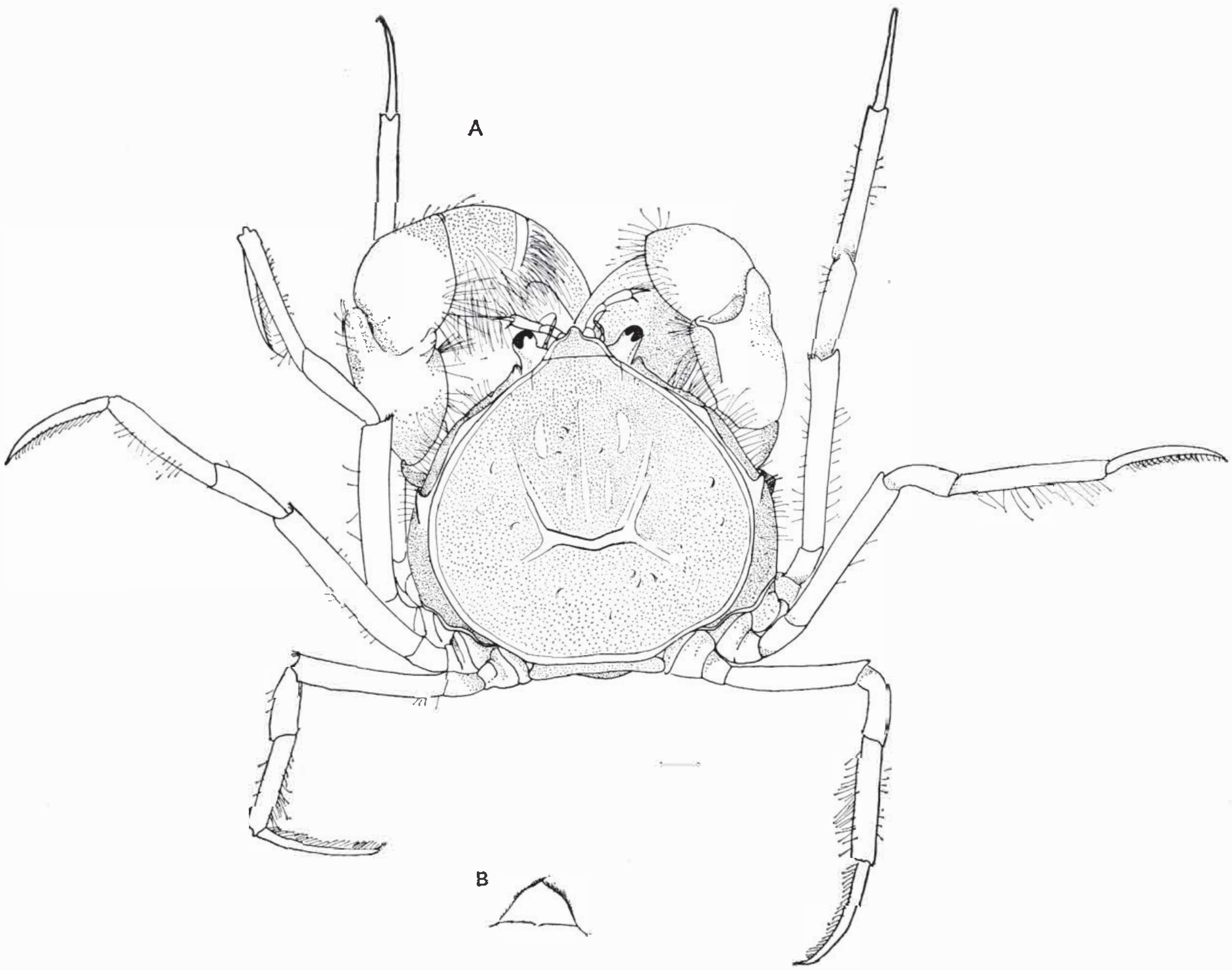
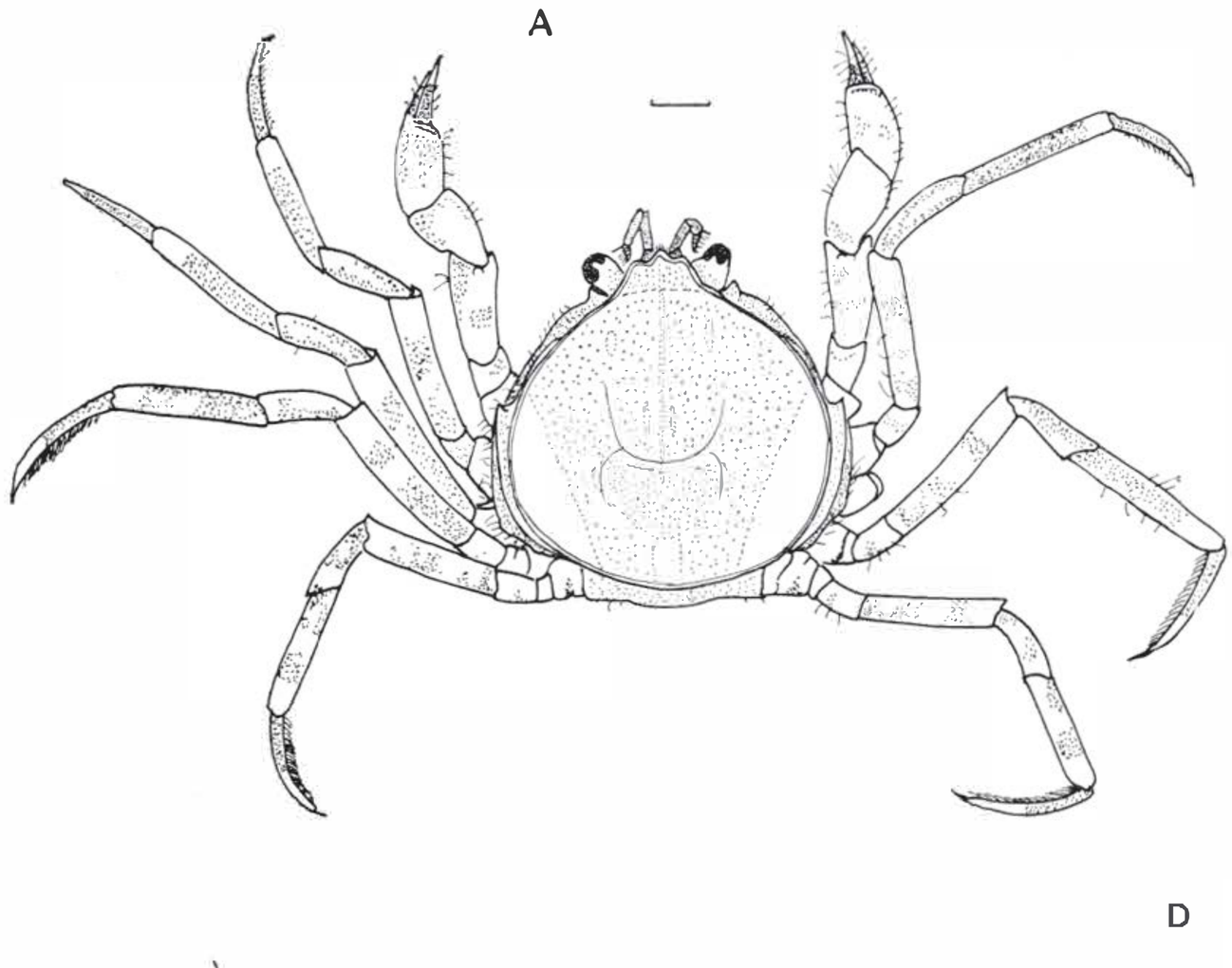
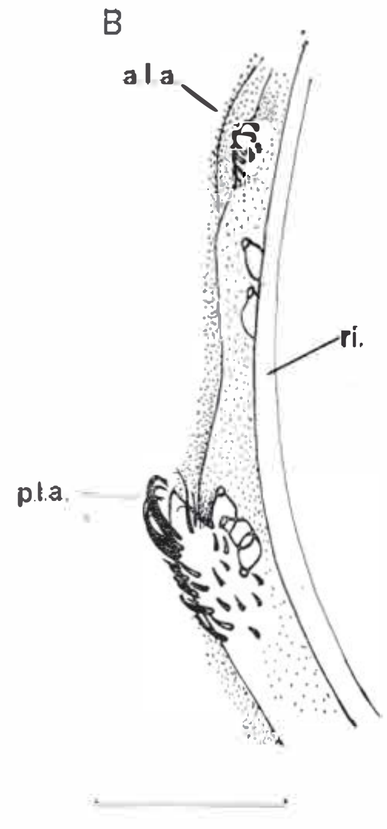
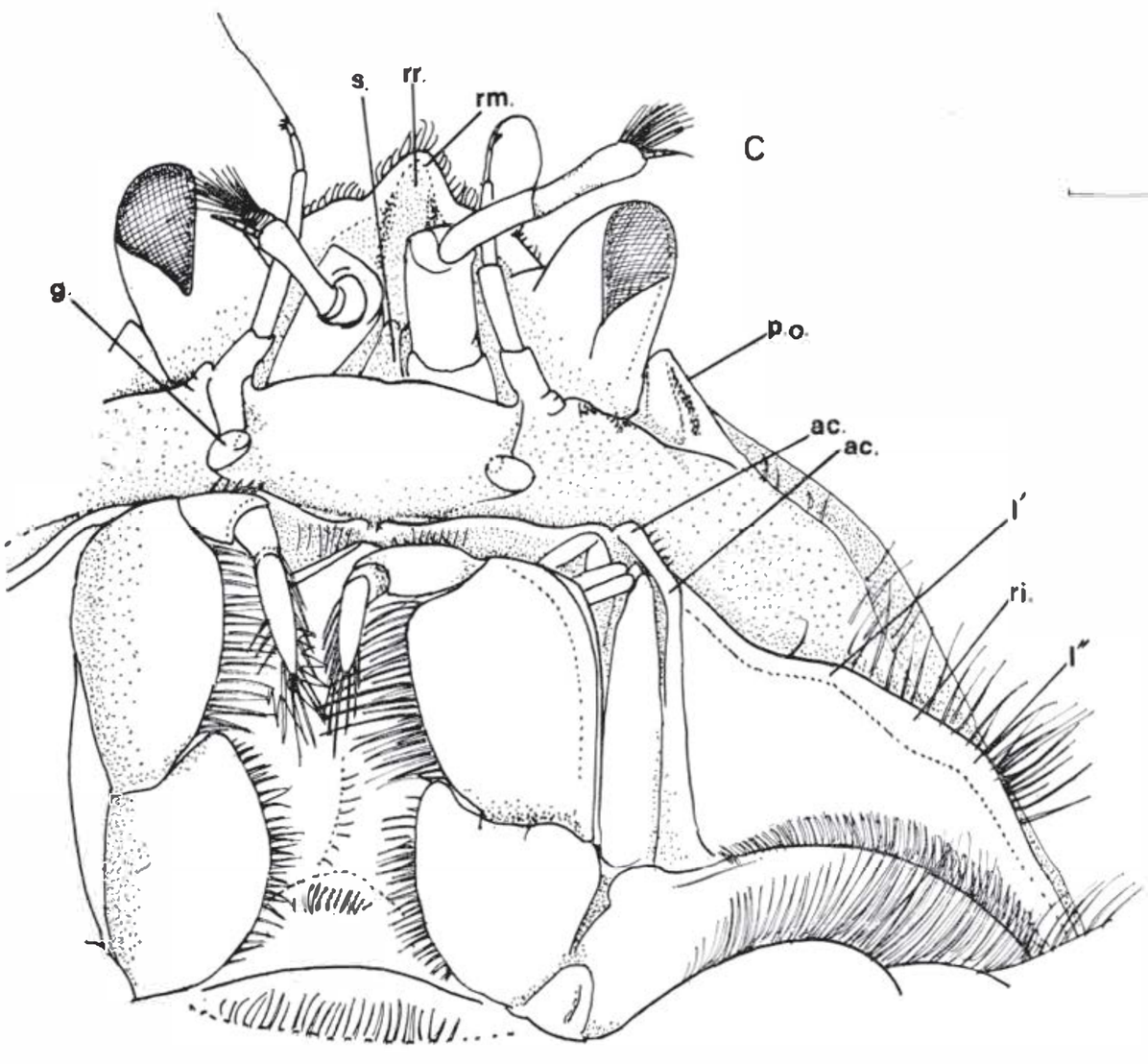
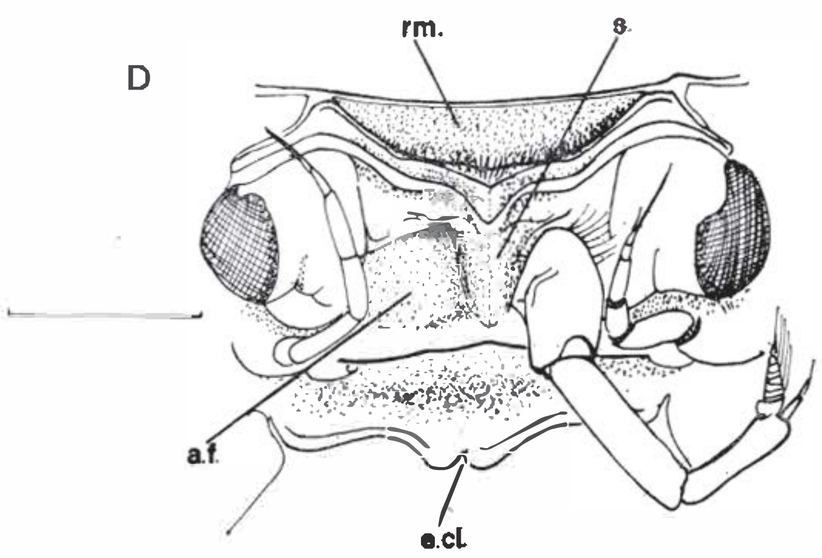


Fig. 25 *Halicarcinus varius:* A—Male, dorsal view; B—Rostrum of a second male. (scale represents 1 mm)









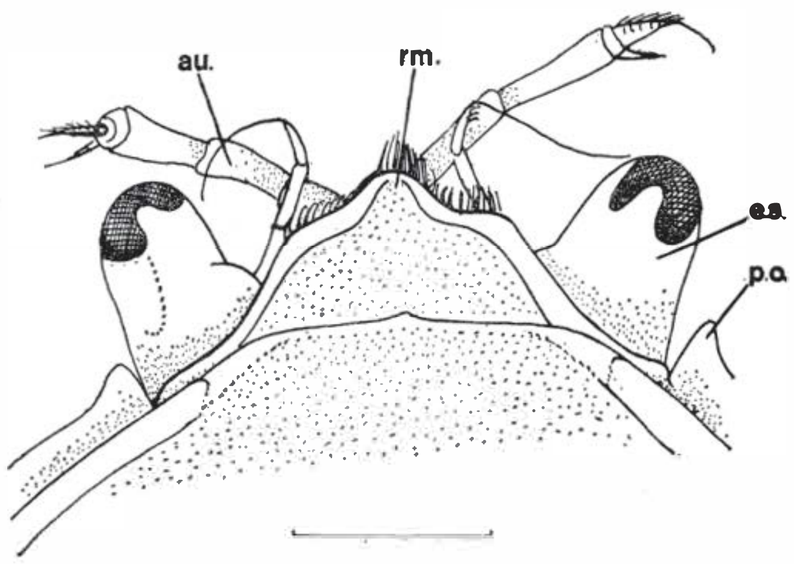


Fig. 26 *Halicarcinus varius:* A—Female, dorsal view; B—Lateral angles of carapace of female with six specimens of a solitary bryozoan attached; C—Ventral view of left side of mouthfield and epistome; D—Frontal view of male in Fig. 25A; carapace perpendicular to the plane of vision, right antennule removed; E—Rostrum of male in Fig. 25A. (scales represent 1 mm)

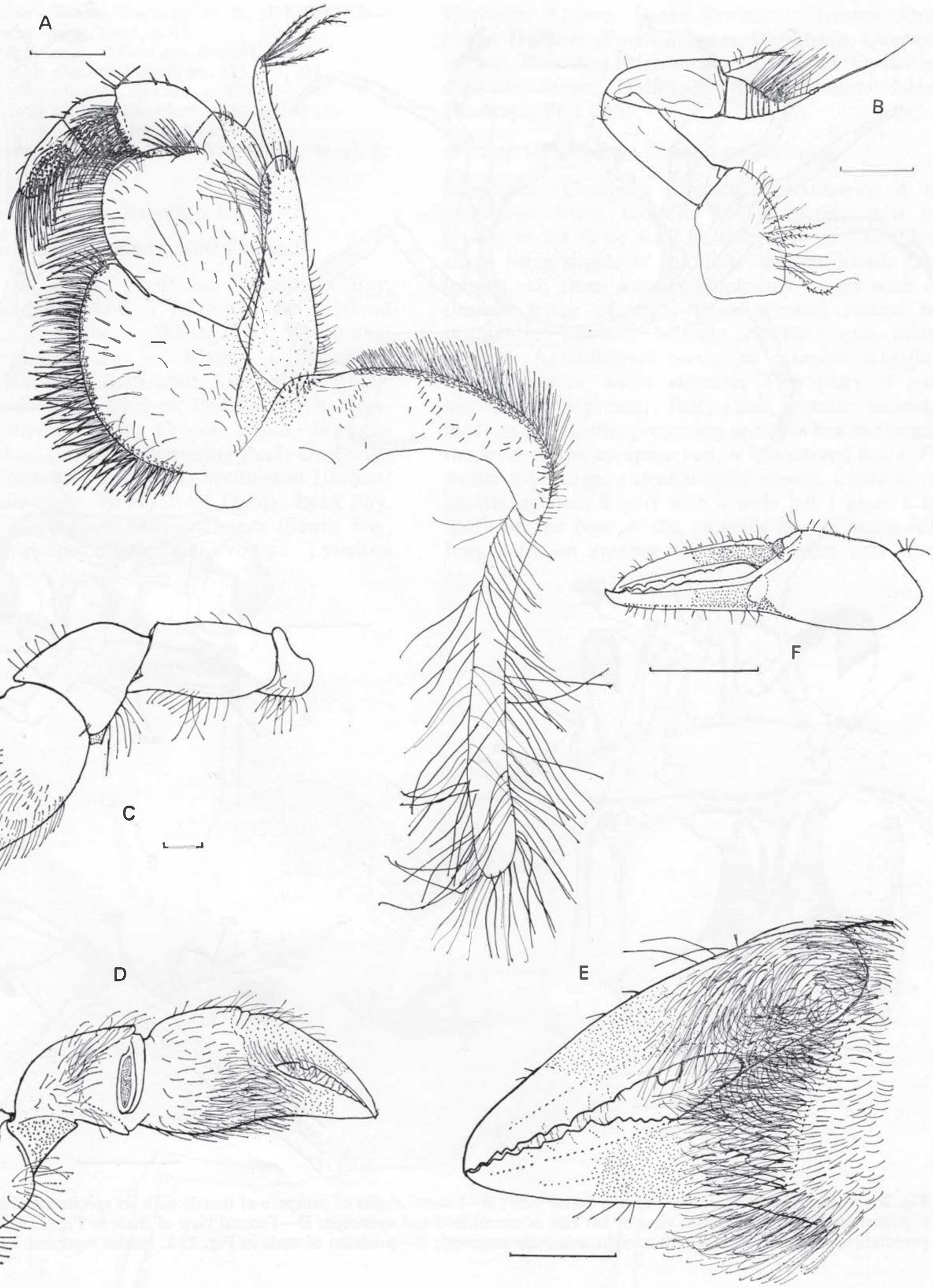


Fig. 27 *Halicarcinus varius:* A—Left 3rd maxilliped of male; B—Left antennule of male, lateral-ventral view; C—Left cheliped of male, posterior view; D—Left cheliped of male, anterior view; E—Fingers of left chela of male, posterior view; F—Left chela of female, posterior view. (scales represent 1 mm)

Fig. 28 *Halicarcinus varius:* A—Left 3rd walking leg of male, posterior view; B—Dactylus of left 3rd walking leg of male, posterior view; C—Tip of dactylus of left 3rd walking leg of male, posterior view; D— Ventral edge of dactylus; E—Abdomen of female extended, dorsal view; F—Abdomen of male extended, dorsal view; G—Left 1st pleopod of male, sternal view; H—Tip of left 1st pleopod of male, sternal view. (scales represent 1 mm except for C, G, and H, where scale represents 0.4 mm)

fingers. Segments of walking legs slender, propodus fringed with long, fine hairs, other segments less hairy. Dactylus armed with small recurved pointed teeth in two very closely approximated rows, with many fine curved hairs; separate claw very short. Ischium and merus of third maxilliped subequal in length and breadth. Male abdomen separated by tiny vertical ledge from carapace. First segment of long male abdomen as long as third and fifth; second almost as long as first centrally; third with straight sides; fourth narrowing distally; fifth segment narrowing distally, almost linear; sixth semicircular. Male first pleopod of average length, sternal edge expanded to form a small shelf subterminally, further constricted below the eave, eave a little recurved.

SIZE RANGE: ♂♂ 2.5 (Wairepo Flat, Kaikoura) – 10.0 mm (Christchurch). ♀♀ 2.5 (Mahurangi) – 8.5 mm (Eastern Beach, Auckland).

DESCRIPTION: Carapace suboval, broadest behind second pair of lateral angles, narrowing anteriorly, length and breadth approximately equal (ratio w.: l.=1.07–0.95). Carapace usually slightly convex, sometimes a little concave; carapace rim of average width in large specimens, uninterrupted by angles. Wide gastrocardiac groove always obvious, deflexed backwards centrally; cervical and thoracic grooves also definite but lacking subdivision, cervicals longer than thoracics. Upper surface of carapace almost always sparsely sprinked with thin, curved hairs. Shallow concavity on either side of the straight posterior border above last pair of legs. Anterolateral border of the carapace straight or convex, never concave. Sides of carapace covered with fine hairs, oblique posteriorly, branchiostegite projections between legs obtuse, with raised marginal rim. Two pairs of lateral teeth on sides of the carapace; first pair frequently reduced, always obtuse and hairy, situated below the level of the carapace rim, which is itself not angled; second pair acute, short, originating well below the carapace rim and not projecting as far upwards as the rim level, curved hairs scattered about the base and near the tip. Suture between rostrum and carapace straight, truncate frontal region not produced.

Rostrum originating at carapace level, forming a horizontal platform, sloping downward a little anteriorly very variable in form, broad basally (ratio carapace w.: rostrum w.=3.5–4.2), narrowing anteriorly. Dorsal surface of rostrum sometimes semicircular with a sharp peak centrally, anterior edge fringed with short straight hairs (*see* Fig. 25B); or distinctly trilobular, median lobe projecting a little further than the laterals but still not reaching past the eyes, sometimes approaching the form shown for *H. cookii* (*see* Fig. 16C). Concavities between the lobes never reach the suture at the rostrum base, lined like the median lobe with short hairs. Deep ventral ridge along the whole length of rostrum. Postocular lobe large with a ventral ridge, concave next to the eyestalk. Eyes directed outward as much as forward; eyestalks short and stout.

Antennules short, slender; basal segment a little longer than wide, many long hairs on external edge. Second peduncular segment longest, third hardly expanded distally. Small ramus with four short terminal hairs; large ramus of moderate size, with five to six small subcircular segments, terminal bulb short and waisted, terminal seta long. Folded antennules just visible dorsally where the rostrum is semicircular, more easily seen if rostrum trilobate. Antennal spine absent.

Interantennular septum has a low ridge. Epistome large, unusually long, length not quite twice breadth, somewhat sunken below the level of the subhepatic regions, divided laterally from these by faint suture. Posterior ridge of epistome deep, central cleft reduced to a small depression. Pterygostomian regions large, broad, a shallow concavity on the long ridged edge, pterygostomial lobes absent, edge straight and very hairy between the usual positions of these lobes. Row of short hairs on the sterna of second and third maxilliped.

Endopods of third maxillipeds gaping widely in mid line. Merus and ischium subequal in length and breadth. Ischium fringed with two to three rows of long setae on the strongly curved median edge, scattered setae present on ventral face but not on outer edge, anteromedian lobe very short and broad, merus articulation broad and oblique. Outer edge of merus much more curved than usual; a sparse, longitudinal row of long, feathery hairs present a short distance from this edge; a single row of hairs slightly longer than those of the ischium on median edge. Carpus large, arising very close to external edge of merus, anterior edge curved. Propodus half as long and not as stout as carpus, two-thirds as long as bluntly rounded dactylus. Ventral setae on palp long, dense. Basal segment of exopod short, tapering markedly throughout its length; short, feathery hairs present on the proximal half of each edge; two irregular rows of longer hairs on inner edge below apex, a horizontal row also at this level. Terminal segment slender, ending in five long hairs.

Basal lobe of epipod very small, sparsely setiferous. Basal portion of epipod long, broad, considerably curved, with up to five rows of fine setae on the anterior edge; fine short hairs scattered elsewhere, completely separated from the lamella. Lamella a little longer than base, broad distally, bluntly rounded, both edges densely fringed with long hairs.

Chelipeds almost twice as long as carapace in large males, only just longer than the carapace is wide in small specimens (l. cheliped: w. carapace = 1.95–1.2); very massive in large males. Ischium very small, subtriangular, hairy. Merus breadth distally half its length, ventral distal projection small. Carpus anterior surface hairy, especially near the edges, as long as merus, expanded distally to two-thirds its length. Palm as long as carpus, as deep as long except in the largest males when it is even deeper and greatly inflated. Fingers longer than palm, broad basally, tapering distally in both sexes. Basal gape wide in both sexes, especially male, large basal tooth on movable finger of male

tuberculate, flattened on the end; fingers occluding along distal third where the dentation is sharp; short, straight hairs between teeth. Palm anterior and posterior faces in male both hairy; dense felt of hairs on anterior face reaching half along fingers and obscuring basal tooth; fingers of female spooned on tips.

First three pairs of walking legs subequal, the third sometimes a little shorter than others, all longer than chelipeds (1.58–1.98 times the width of the carapace), segments very slender but not flattened. Ischium subrectangular, elongate. Merus one-sixth to an eighth as broad as long, tooth reduced, has tuft of hairs. Carpus not two-thirds merus length, ventral distal projection large and blunt. Propodus a little shorter than merus, ending in pronounced V fringed with hairs. Upper and lower edges of leg segments, especially lower edge of propodus, have long, fine hairs. Dactylus longer than propodus, very flattened, slender, parallel-sided, ending in very short, separate claw; ventral edge has very fine small pointed teeth, directed slightly backward but straight, in two very close rows with long fine hairs between and beside them, the tooth adjacent to the claw being enlarged and recurved.

Female abdomen longer than wide, central projections of proximal margins of segments two to six deepening and narrowing until the sixth but broad on all. Sixth segment evenly rounded distally, all but last two segments fringed with hairs.

Male abdomen reaching posterior edge of sterna of chelipeds, separated from carapace by thin, vertical ledge. First segment broadest, as long as third and fifth, slightly expanded laterally into triangular lobes; second almost as long as first centrally, shortening laterally, edges straight; third of equal width throughout, sides almost straight; fourth longer than third, narrowing distally; fifth with barely concave sides, narrowing distally; sixth an elongate semicircle. Central projections on proximal edges of segments two to six successively narrowing, but of similar depth, that on fifth narrowest, that on sixth a little wider and shallower; first segment also has a corresponding bump on proximal edge. First pleopod of male curved over through more than 90°, quite sturdy though long. Sternal edge of distal portion suddenly constricted to form a shelf subterminally, a further small constriction below the slightly recurved eave.

MATERIAL EXAMINED:

Personal collection: Goat Island Bay, Leigh, 17/5/1965, 1 ♀ 5.5 mm, 1 ♂ 5 mm. Laboratory tanks, Leigh, –/2/1965, 1 ♂ 3.5 mm (coll. B. A. Foster). Mahurangi Heads, –/4/1965, –/5/1965, 3 ♂♂ 2.5–5 mm, 1 ♀ 2.5 mm (coll. B. A. Foster). Whangateau, Leigh, 28/7/1965, 1 ♂ 9 mm (coll. B. Rudman). Whangateau, Leigh, 17/5/1965, 1 ♀ 4 mm (coll. P. McGeorge). Mahurangi Harbour mouth, 8/9/1965, 29 ♂♂ 2.5–6 mm, 8 g. ♀♀ 4–5 mm, 2 ♀♀ 3.2–4 mm (coll. W. Ponder, in 3 fm (5.5 m) on *Carpophyllum maschalocarpum*. Taurikura Bay, Whangarei Heads, –/5/1965, 1 ♂ 7.5 mm (coll. P. Warren). Whangamata Harbour, Coromandel, 17/12/1964, 1 ♂ 6 mm. Whangamata, 17/4/1965, 8 ♂♂ 3.5–7.5 mm. Eastern Beach, Auckland, 24/1/1965, 1 ♀ 5 mm, 1 ♂ 7 mm; 28/5/1965, 1 s. ♀ 5 mm; 19/6/1965, 1 ♂ 7.5 mm; 26/6/1965 7 ♂♂ 2.5–9.5 mm, 3 g. ♀♀ 6–7.5 mm, 1 ♀ 6 mm; 17/7/1965, 2 ♂♂ 8, 8.5 mm, 1 g. ♀ 7 mm; 14/8/1965, 2 ♂♂ 4–7 mm; 13/9/1965, 4 ♂♂ 4–10 mm, 3 g. ♀♀ 6–8 mm; 10/10/65, 2 ♂♂ 7.5, 9 mm, 2 g. ♀♀ 5, 7.2 mm, 1 ♀ 5 mm. Westmere, Auckland Harbour, 27/6/1965, 2 ♂♂ 5, 5.6 mm, 3 ♀♀ 5–6 mm. Cheltenham, Auckland Harbour, 26/6/1965, 2 ♂♂ 4.5–5.5 mm, 2 ♀♀ 4–7.5 mm.

Victoria University of Wellington Zoology Department Collection: Castlepoint, Wellington, 20–23/12/1964, 2 ♂♂ 2.5, 5.5 mm. Kaikoura, 8/12/1964, 1 ♂ 10 mm.

Edward Percival Marine Laboratory Collection: Wairepo Flats, Kaikoura, 21/8/1963, 1 ♂ 10 mm (from *Zostera* beds, K 160A). South Bay, Kaikoura, 28/8/1965, 1 ♂ 4 mm (under rocks at low tide, K 160A). Seal Reef, Kaikoura, 3/9/1964, 2 ♂♂ 4, 4.5 mm (*Carpophyllum* fronds, K 410A); 27/8/1965, 1 ♂ 5 mm (K 653 D–F). Kaikoura, –/8/1965, 1 ♀ 3.5 mm.

Auckland War Memorial Museum Collection: Motuihe Channel, between Browns Island and Motuihe, 1 ♂ 4 mm, 1 g. ♀ 5.5 mm, 2 ♀♀ 4, 5.5 mm (coll. A. W. B. Powell, 10 fm (18 m)). Motuihe Channel, between Emu Point and Home Bay, 2 ♀♀ 3.5 mm (coll. A. W. B. Powell, 8–10 fm (14–18 m)). Chelsea Point, Waitemata Harbour 27/2/1926, 2 ♂♂ 3.5 mm, 1 ♀ 3.5 mm (coll. C. Archey, St. A, 14 fm (25 m), with *Pilumnus* sp., and *Elamena momona*). South Shore, Motuihe Island, 13/11/1927, 1 ♂ 7.5 mm, 2 g. ♀♀ 5.5 mm, 1 ♀ 3.5 mm. Crusoe Island, Auckland Harbour, 4 ♂♂ 3.5–5 mm, 3 g. ♀♀ 6–6.5 mm (with a polychaete worm, small ophiuroid, *Petrolisthes elongatus*, talitrid amphipod). Waitangi, Chatham Islands, –/2/1933, 7 ♂♂ 2.5–5.5 mm, 2 ♀♀ 3–5.5 mm, 2 g. ♀♀ 9.5, 10 mm (coll. A. W. B. Powell, with amphipods, *Isocladus* sp., polychaete, *Notomithrax* sp., *H. cookii*).

Dominion Museum Collection: Halfmoon Bay, Stewart Island, 7/4/1965, 6 ♂♂ 5.5–9.5 mm, 4 g. ♀♀ 7.5–8.5 mm, 3 ♀♀ 6–8.5 mm. Oyster Beds, Foveaux Strait, 1961, 2 ♂♂ 4.5, 5.7 mm (coll. M. Stead). Hope Shoal Light, Wellington Harbour, 23/8/1957, 1 ♂ 4 mm (6 fathoms V.U.Z. 91, 41°18′30″, 174°1′24″E). Portobello Station Wharf, Otago Harbour, 10 ♂♂ 8–11 mm, 14 g. ♀♀ 8.5–9.5 mm (coll. R. K. Dell, J. Moreland, 2–4 fm (4–7 m)). Kau Point, Seatoun, Wellington Harbour, 14/10/1954, 1 ♀ 4 mm (coll. R. K. Dell, on algae, with *H. cookii* Cr.635). Purau Bay, Lyttleton Harbour, 22/9/19—, 1 ♂ 4.5 mm, 2 g. ♀♀ 9, 10 mm (dredged, Cr.385). Portobello, Otago Harbour, 10/11/1952, 1 ♂ 9 mm, 1 s. ♀ 9 mm, (coll. J. Moreland). Waiheke Island, 1 g. ♀ 8 mm (coll. G. Chamberlain, with *H. whitei*). Days Bay, Wellington Harbour, 19/1/1953, 4 ♂♂ 3.5–4.5 mm, 2 g. ♀♀ 5.5 mm (coll. R. K. Dell, J. M. Moreland, 9 fm (17 m)). Manukau Harbour, 7/9/1961, 2 g. ♀♀ 6.5 mm (coll. H. J. Chapman, in *Zostera* mud-flat pools). Tauranga Harbour, 25/8/1920, 2 ♂♂ 5.5, 7.5 mm, 2 g. ♀♀ 6, 7 mm (coll. R. B. Oliver, *Zostera* beds). Port Hutt, Chatham Islands, 1 ♂ 9.5 mm, 1 g. ♀ 10 mm (Chatham Islands Expedition, 49, Cr.925).

University of Canterbury Zoology Department Collection: Kaikoura, 23/10/1965, 4 ♂♂ 5–9 mm, 4 ♀♀ 4–7.5 mm (coll. K. P. Jansen, from *Cystophora*, *Hormosira*, etc. under stones). Kaikoura, –/8/1965, 4 ♂♂ 5–9.5 mm, 1 ♀ 5.8 mm (coll. K. P. Jansen, from *Hormosira* and under stones, mid-tidal rock platform).

University of Auckland Zoology Department Collections: Howick Beach, 2 g. ♀♀ 4.5–5 mm, 1 ♂ 5 mm (coll. D. Wood).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: January, February, April–November.

COLORATION (Plate 2, facing p. 49):

Carapace: Large males are predominantly dark brown. Sometimes the convex areas of the carapace before and behind the gastrocardiac groove are a gunmetal shade with tinges of purple, blue or green underlying the brown. There is often a central longitudinal pale streak, like that on *H. cookii*, flanked by a pair of pale spots on the anterior part of the carapace.

White or yellow blotches at the base of the last pair of legs are also common. The branchiostegites are dark brown.

Legs: The basis and ischium are frequently lighter in colour than the carapace or the remaining segments of the legs. In some small specimens with pale brown legs, two faint bands of black chromatophores can be seen at the base and two-thirds along the merus. Almost always, however, the legs are unbanded.

The fingers of the chelae are whitetipped and usually there is a striking red or orange band between the white and brown portions of the fingers of the chelipeds. The distal half of the dactylus of each walking leg is white.

Young: Immature specimens are principally green or grey.

Females: Females are often brown or green, but a few of the females at Eastern Beach had striking brown and white colour patterns. White dominated the posterior half or two-thirds of the carapace, contrasting with the brown anterior and rostrum. Frequently, three distinct patches were present; one centrally behind the gastrocardiac groove, and one on each side reaching forward to the carapace edge between the obsolescent first lateral tooth and the second prominent tooth. This colour pattern is like that sometimes found in *H. cookii* but no specimen of *H. varius* with a pure white carapace was ever found. Nor were the kaliedoscope patterns of vivid red, orange, yellow, green, or blue, common in *H. cookii*, ever encountered in *H. varius*.

REMARKS: The inadequate initial description of *Halicarcinus varius* given by Dana in 1851 and 1852 was:

"Carapace smooth, naked, flat, nearly orbiculate or ovato-orbiculate, very slightly wider than long, front projecting and trilobate, anterolateral margin with two obsolescent teeth. Abdomen of male narrow, oblong sub-triangular, first segment broadest and triangulate on either side, penultimate narrower than preceding, last oblong, sub-triangular, rounded at apex. Anterior feet of moderate size, eight following very slender, nearly or not quite naked. . . . The lobed front occupies the whole space between the eyes and the middle lobe is most projecting . . . the colour various; often greenish-black or black and white in irregular areas, or wholly dirty white or greyish, mottled with brown. Length 2–3 lines." (i.e., 4.5–7 mm).

The colouring, the projecting central lobe of the large rostrum and the slender legs all indicate that Dana's species is that referred to by later authors as *H. edwardsi*. The abdomen figured by Dana (pl. 24, fig. 9d) is very similar to that shown here (*see* Fig. 28F), especially in the relative size of the segments; segment one is much larger in relation to the other segments in *H. cookii*, the species which is most likely to be confused with *H. varius*. Also Dana's figure of the third maxilliped (plate 24, fig. 9c), shows the merus distally as wide as the ischium, as it is here (*see* Fig. 27A). In *H. cookii* the merus remains narrower than the ischium, and the anterior lobes are not as expanded as in *H. varius*.

Finally, Dana remarked that "the two antero-lateral teeth are like those of *Hymenosoma*". Tesch described *Hymenosoma orbiculare* as having "two obtuse prominences, that are themselves minutely tuberculate, the posterior directed upwards, the anterior forward". Specimens of *H. cookii* always have the posterial lateral angles conspicuous and acute. However, although the posterior lateral angle in *H. varius* as described here, is sometimes quite prominent, it may be reduced, especially in young males and females, to an inconspicuous knob (*see* Fig. 26A, B). The second lateral tooth never really becomes "obtuse", but it could sometimes justifiably be called "obsolescent", the term that Dana employed.

The rostrum in *H. varius* is extremely variable, and it is the failure to recognise this which has led to the most confusion in the literature. Richardson described *H. edwardsi* as having a rostrum "ranging from a broad obtusely rounded triangle to minutely tridentate as though eroded". Had he more material, he would have realised that the rostrum is sometimes distinctly tridentate, and sometimes as in *H. cookii* (*compare* Figs. 26A and 16C). The lobes are always apically rounded and the middle lobe is longest in both species. Small specimens of *H. varius* and *H. cookii* are superficially very similar if the rostrum is tridentate. Both may be nearly nude, although there are always fine, long hairs microscopically visible on the leg segments and a dense felt of hairs on the anterior face of the male chelae of *H. varius*, whereas *H. cookii* has sparse hairs. The carapace is subcircular in both, but in *H. cookii* it is relatively wider across the region of the first lateral angle than in *H. varius* and the anterolateral border is always concave in *H. cookii*, straight or convex in *H. varius*. These and other less superficial differences make it clear that there are two distinct, completely non-interbreeding species with overlapping ranges. (The two may sometimes be found together in seaweed.) Large males of *H. varius* are so different from those of *H. cookii* that Filhol (1885a, 1886) and Tesch (1918) both described specimens as a distinct species (*H. edwardsi*) distinguished from Dana's specimens with distinctly tridentate rostrum.

The confusion in the New Zealand Hymenosomatidae is illustrated by the identification in Powell (1936) of *H. varius* from the *Maoricolpus* community of the Auckland Harbour as *Halicarcinus planatus*. (These specimens were identified by Bennett.)

Chilton's *H. marmoratus* (1882, 1906b), because of its colour and large posterior lateral angles, is probably synonymous with *H. cookii* but could possibly be *H. varius*.

Ralph and Yaldwyn's figure of "*H. cooki*" (1956) greatly resembles *H. varius*, and the origin of their specimens in *Zostera* and in the soft bottom community of Otago Harbour also indicates *H. varius*.

An Australian species* (not figured here) which

*Specimens supplied by Dr J. S. Lucas of the James Cook University of North Queensland.

strikingly resembles *H. varius* and is probably that which Haswell (1882a) termed *Hymenosoma varium*, combines some characters of both *H. cookii* and *H. varius*. The three lobes are divided by narrow clefts (narrower than in either New Zealand species), almost reaching the straight suture at the rostrum base. The male chelae are very inflated, the palm sparsely hairy but the fingers widely gaping basally, and the base of the movable finger has a short, square tooth. The carapace angles are pronounced as in *H. cookii*, and the merus tooth of the slender walking legs is sharp. This species does not appear to have been described elsewhere.

ENVIRONMENTAL NOTES:

Substrate: In the littoral zone, *H. varius* was found in four different situations: 1, in algae on a reef; 2, under stones, with algae growing nearby, on a reef; 3, in *Zostera*, on harbour flats; 4, in sand, where the nearest vegetation was hundreds of yards away. It does not thrive under conditions of even medium wave exposure.

It was also common from *Carpophyllum* in dredgings in Auckland Harbour. Powell (1936) reported *H. varius* (as *Halicarcinus planatus*) from the *Maoricolpus* and *Dosinula* association in Rangitoto Channel, Auckland Harbour, from the *Maoricolpus* (*manukauensis*) and *Nucula* association in the Manukau Harbour, and from the *Tawera-Glycymeris* formation in the main channels of the outer Auckland Harbour (Powell 1937, pp. 374–87).

Carpophyllum plumosum, *Carpophyllum maschalocarpum*, *Sargassum sinclairii*, and *Hormosira banksii* of the littoral zone and sublittoral fringe of sheltered reefs were inhabited by *H. varius*. The crabs were almost equally numerous in all four algae but were not found in *Corallina* although it frequently covered the rocks under which *H. varius* lived. At Eastern Beach *H. varius* was common on the *Hormosira* flat and in shallow reef pools.

The substrate below this *Hormosira* belt was dominantly coarse to very fine sand in areas where *H. varius* was living. The crab was never found where the silt content was high, perhaps because silt would clog its gills.

Wood (1968) analysed substrates of stations at Howick Beach where *H. varius* was common (*see* Fig. 29) and samples were taken from other Auckland beaches for this present study (*see* Fig. 30).

Density: Wood (1968) has reported *H. varius* (as *Halicarcinus cookii*) at a maximum density of 4 per 0.1 m^2 on the main beach or sheltered beach at Howick. On the *Zostera* flat at Howick, he found this species in numbers up to 12 per 0.1 m^2, resembling the density of *H. varius* on the *Zostera* flat at Whangamata Harbour where approximately 8 per 0.1 m^2 were present in summer.

At Westmere, where swollen bladders of *Hormosira* lay on the sand and the water lay in small rivulets at low tide, small specimens of *H. varius* reached a density of 5 per 0.1 m^2. In *Sargassum* and the smaller bladders of *Hormosira* at Eastern Beach, four to six specimens were present per 0.1 m^2.

H. varius is most plentiful in *Zostera* where the organic content of the sand is much higher than over the remainder of the beach (Wood 1968), and its food supply would therefore be higher.

Salinity tolerance: Resistance to osmotic stress caused by low salinities is particularly marked in *H. varius*. Specimens from Eastern Beach took 3¼–8 hours to die, with an average survival time of 6 hours, after being placed in fresh water. Specimens from Whangamata, where the water is less saline, showed greater resistance. They survived from 2–20 days in fresh water, with an average period of 6 days before death suggesting physiological adaptation to lower salinities.

Salinities (determined by filtration) recorded from *H. varius* localities were: 39‰ (*Zostera* Flat, Howick); 35‰ (Main Beach, Howick); 35.2‰ (Eastern Beach); 34.2‰ (Whangateau); 31‰ and 32.9‰ (Westmere); 28.4‰ and 27.3‰ (Whangamata).

Desiccation: *H. varius* was frequently found in the lower mid-littoral, but not above this level. The upper fraction of the population must therefore be exposed to air at most low tides.

The burrowing habit of *H. varius* protects it from desiccation. In dry air, *H. varius* shows more initial activity than *H. pubescens* or *H. whitei*, the ranges of which overlap with that of *H. varius* at some localities. *H. varius* succumbs quickly (within approximately 3 hours in winter) when left in air.

BEHAVIOURAL NOTES:

Thigmotaxis: A positive tactile response was present. Specimens tended to cling together in the bottom of any container when seaweed was not available. This response was not however as strong as in *H. cookii* or *H. pubescens*.

Alarm Reactions: When dropped into water, *H varius* usually floated passively down with legs extended, or loosely and partially folded under the carapace. It was never seen to fold its legs tightly as did *H. cookii* in the same situation.

Large males, threatened with a needle, often attacked the source of irritation, walking forward on the tips of the walking legs and grasping the needle in one or both chelae.

Specimens removed from the water remained stationary for 1½–5 minutes before moving, the first pair of walking legs extended forwards with only the dactyli touching the ground. They usually ran away from any light source. One male, 8.5 mm across the carapace, attained a top speed of 14 mm per sec.

Swimming: Swimming was rarely observed, except in some small specimens.

Burrowing: At low tide *H. varius* was often found in the top 2.5–7.5 cm of sand, never deeper. No permanent burrows were constructed. The hind part of the carapace

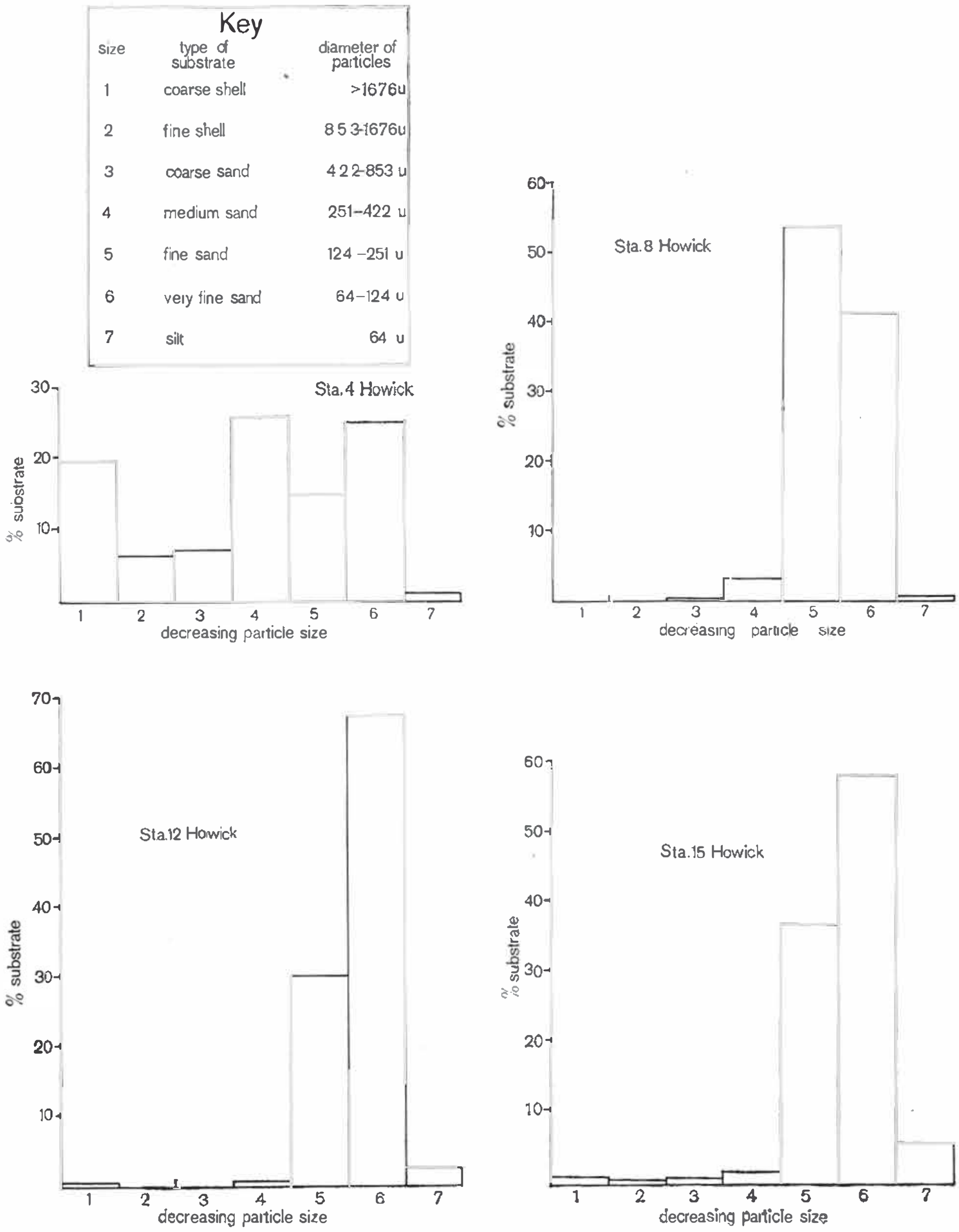


Fig. 29 Grade analysis of sediments at Howick Beach where *Halicarcinus varius* was common (Wood 1968). Sediments were analysed for grade composition with Wentworth sieves

was levered into the sand by thrusting movements of the walking legs. The chelae were used very little in burrowing being loosely folded in front of the crab which rocked back and forth on its splayed walking legs until its carapace was covered by sand.

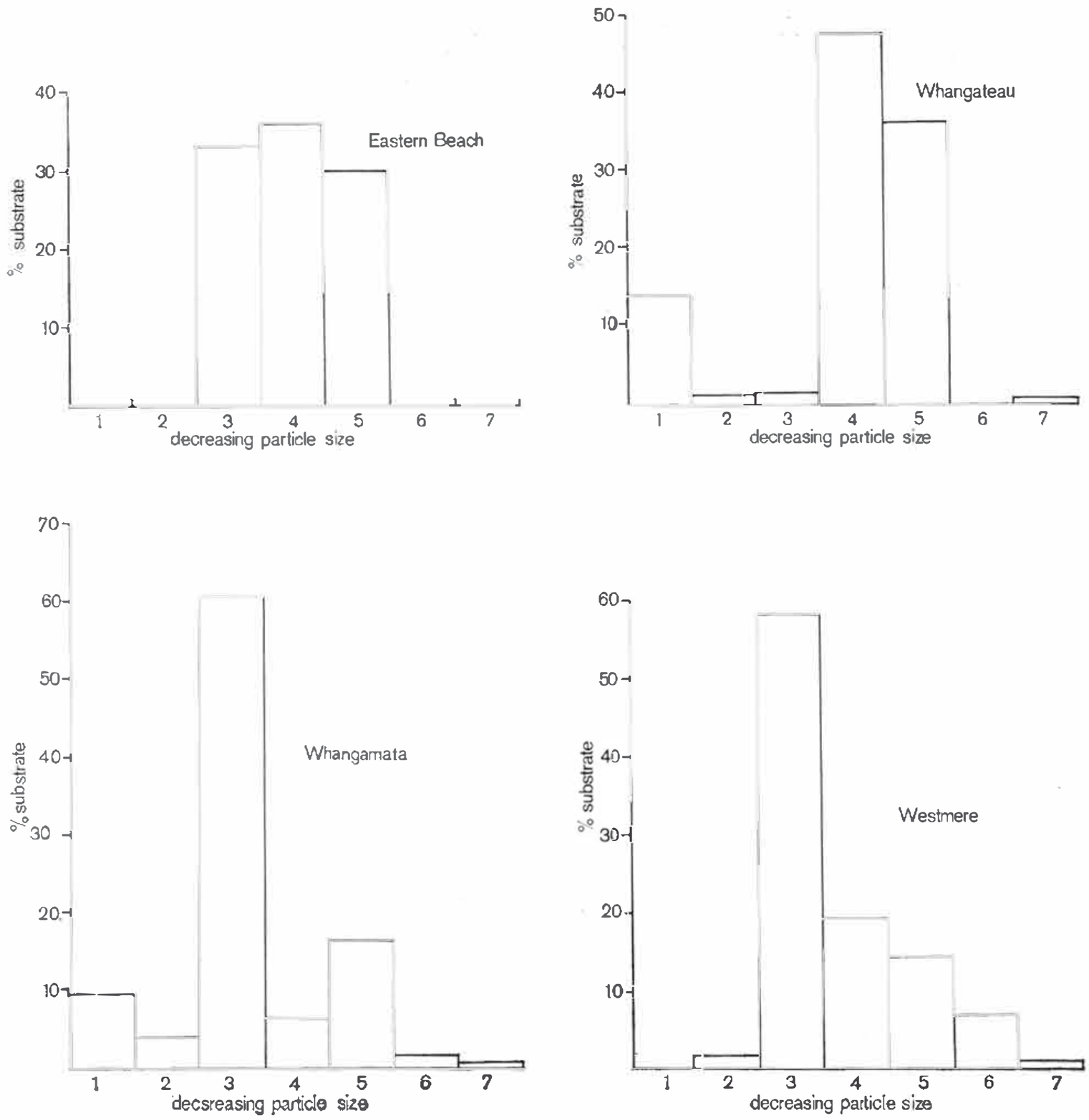
Display: Two males of a similar size, meeting in a confined space, frequently adopted a "threat" posture, with the chelipeds extended outwards almost at right angles to the carapace and the walking legs bracing the carapace upwards anteriorly at an approximate angle of 45° with the ground. They would stand for several seconds with the hairy inner surface of their chelae almost touching and fingers spread. One would then sometimes grasp the opposing chela of its rival, but no vigorous fighting was ever observed. Occasionally, one male would chase another for a short distance across the floor of the aquarium with chelipeds bent and raised, sweeping from side to side.

Food preferences: In the laboratory, *H. varius* ate amphipods, polychaetes, and small shrimps. If starved, it would graze on fronds of *Sargassum*, stripping small pieces off with one chela and cramming these against its mouthparts.

Epifauna: An unidentified species of solitary bryozoan was the only animal found growing on the carapace of *H. varius*.

Breeding: Gravid females have been collected at different localities in every month of the year except March. *H. varius* therefore has an extended breeding period.

Fig. 30 Grade analysis of sediments at some Auckland beaches where *Halicarcinus varius* was common. Key as in Fig. 29



Halicarcinus whitei (Miers)

Figs. 31–35, Plate 1

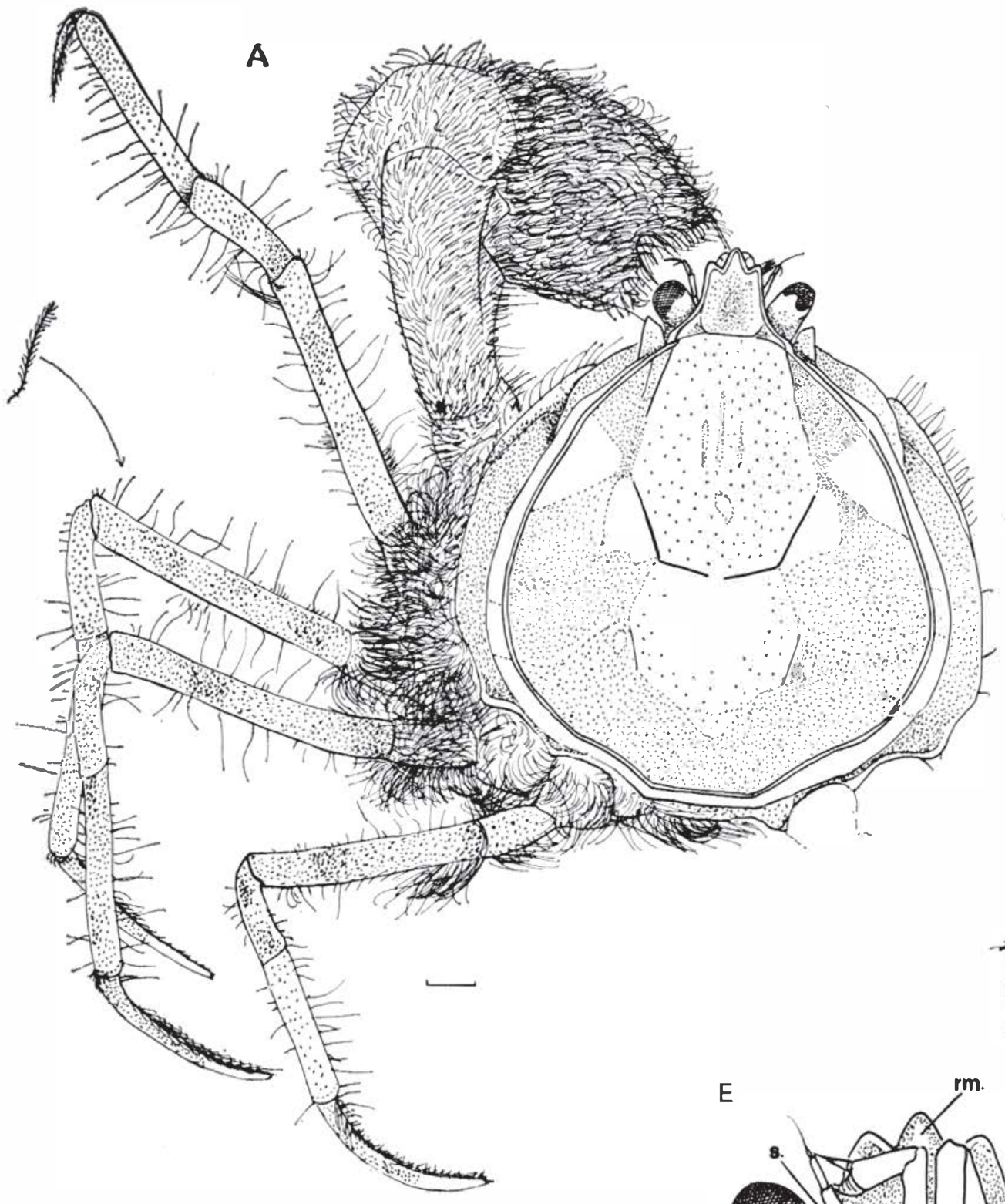
1846 *Halicarcinus depressus* White, p. 187
NOT *Hymenosoma depressa*, Jacquinot, 1853
1847 *Halicarcinus depressus*, White, p. 34
1876a *Elamene whitei* Miers, p. 221
1876b *Elamene whitei*, Miers, p. 52, pl. 1, fig. 4
1882 *Elamena whitei*, Hutton, p. 264
1886 *Elamena whitei*, Filhol, p. 403, pl. 47, fig. 2
1904 *Elamena whitei*, Hutton, p. 251
1918 *Elamena whitei*, Tesch, pp. 20, 24
1929 *Elamena whitei*, Chilton and Bennett, p. 776
1940 *Halicarcinus whitei*, Gordon, p. 73, figs 3d, 8, 9, 10b
1949a *Halicarcinus whitei*, Richardson, p. 68, fig. 47

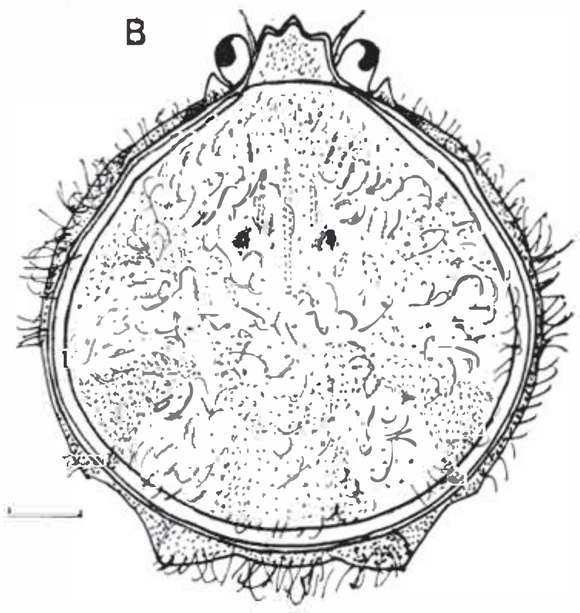
TYPE LOCALITY: Bay of Islands, New Zealand.

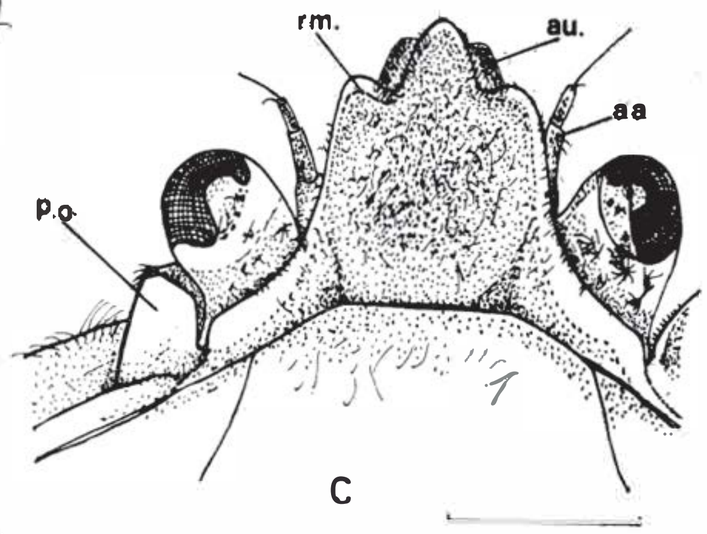
SUMMARY OF LOCALITIES: Northland: Houhora; Te Hapua, Parengarenga Harbour; Tauranga Bay, Whangaroa Estuary; McLeods Bay, Whangarei Harbour. Auckland: Manukau Harbour; Whangateau, Leigh; Pakiri, Leigh; Goat Island Bay, Leigh; Waiheke Island; Bucklands Beach; Howick Beach; Ihumatao, Mangere. Coromandel: Whangamata Harbour. Hawke Bay: Napier Beach. Wellington: Evans Bay; Lyall Bay; Petone; Waitarere. Nelson: Karamea River. Marlborough: Pelorus Sound; Kaikoura. Christchurch: Lyttelton; Heathcote Estuary. Westland: Styx River, Hokitika. Otago: Waitati River; Portobello. Stewart Island.

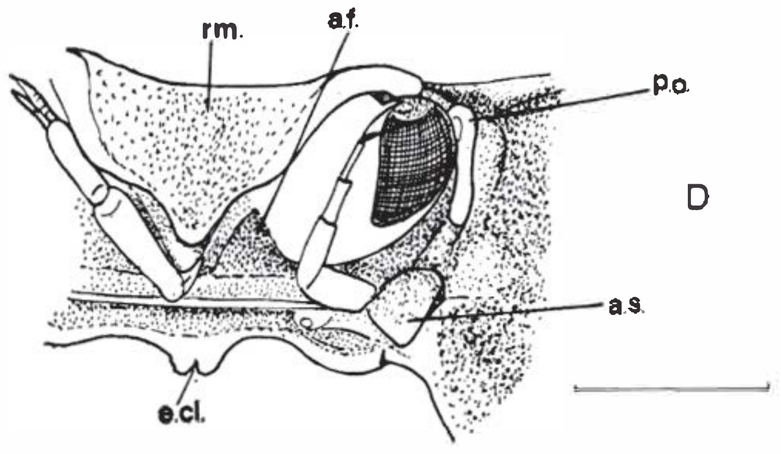
DISTRIBUTION: New Zealand, endemic.

DIAGNOSIS: Carapace suboval, longer than broad, narrowing in front, without lateral angles. True rim very narrow, second false rim present. Frontal region projecting and truncate. Rostrum arising at upper carapace level, extending past eyes, deflexed downward and narrowing anteriorly, concave dorsally from side to side, trilobate terminally, the concavities between the lobes small, not reaching as far back as the extremity of the eyes, central lobule much larger than laterals. Longitudinal central ridge ventrally present along the length of the rostrum. Postocular lobe and antennal spine both well developed. Chela of male moderately inflated, hairy, a large basal gape and a large tooth on the base of the movable finger. Segments of walking legs slender, hairy; dactylus very slender, curved, tapering, with a single row of sharp, recurved teeth.









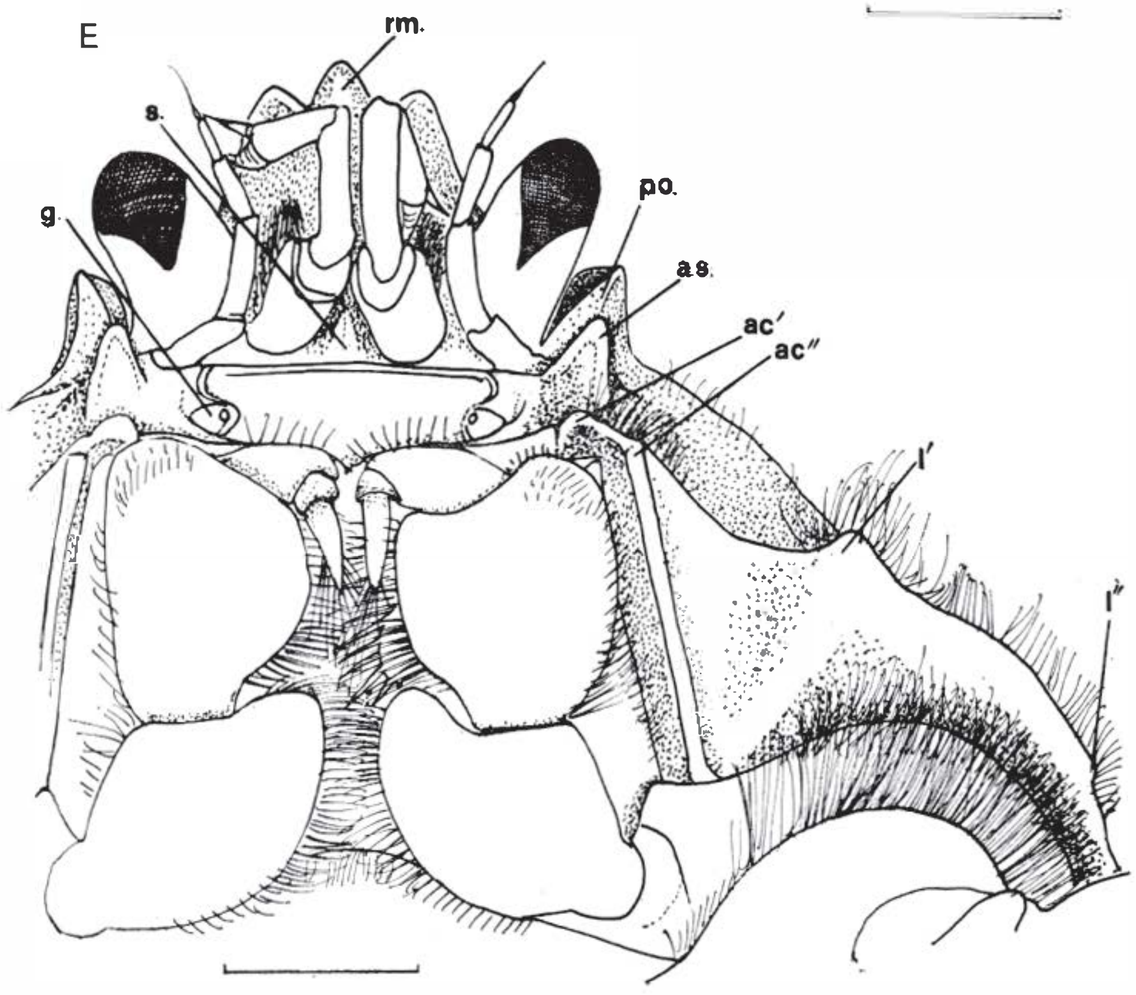


Fig. 31 *Halicarcinus whitei:* A—Male, dorsal view; B—Female, dorsal view of carapace; C—Rostrum of male in A; D—Frontal view of male in A, carapace perpendicular to plane of vision, left antennule removed; E—Ventral view of left side of mouthfield and epistome. (scales represent 1 mm)

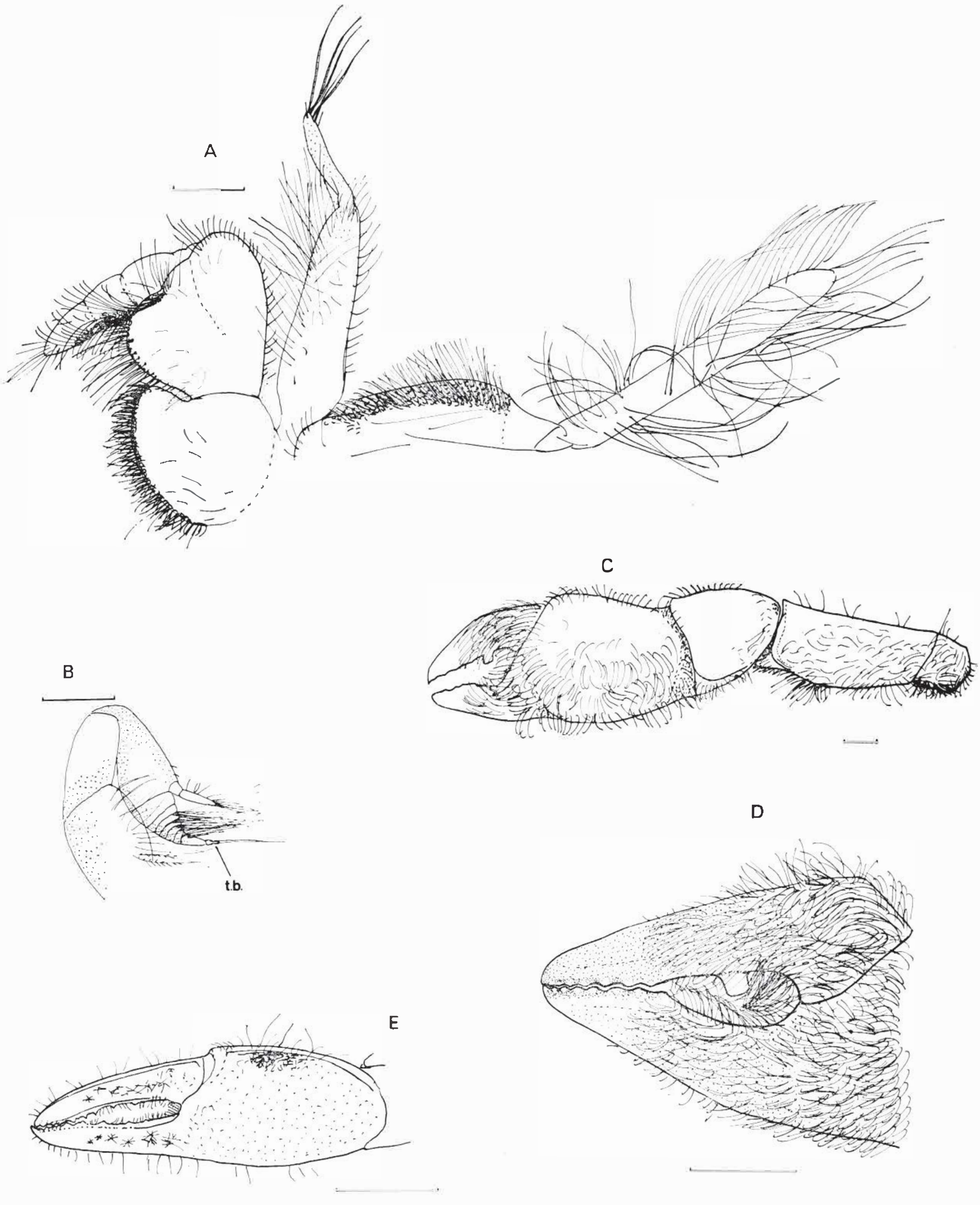


Fig. 32 *Halicarcinus whitei:* A—Left 3rd maxilliped male; B—Left antennule of male, lateral-ventral view; C—Left cheliped of male, posterior view; D—Fingers of left chela of male, posterior view; E—Left chela of female, posterior view. (scales represent 1 mm)

Merus of third maxilliped as broad as ischium, expanded distally. Long male abdomen separated from carapace by false rim, almost as broad between third and fourth segments as across the first segment. First segment much shorter than any other except second; second about half as long as first; sides of third almost straight; sides of fifth just concave; sixth segment semi-elliptical. First pleopod of male long and very slender, tip simple with slightly recurved eave.

SIZE RANGE: ♂♂ 2 (*Enteromorpha* pool, Leigh) – 12.5 mm (Pakiri). ♀♀ 3.5 (Karamea River) – 11 mm (Whangamata).

DESCRIPTION: Carapace suboval, much narrower in front than across branchial region, longer than broad (ratio l. : w = 1.05–1.16). Carapace flat or convex, naked in young specimens; usually, together with the rostrum, covered by felt of fine, short hairs in adults. Carapace rim thin; part of lateral portion of the carapace raised up to rim level forming a broad shelf or second "false" rim. Gastrocardiac groove always detectable if hairs removed, shallowly deflexed backwards in mid line, cervical grooves deeper and longer than thoracic grooves. Paired grooves flanking frontal region, almost meeting cervical grooves. Gastric region elongate; prebranchial region usually distinct, triangular, elongate; postbranchial region sometimes subdivided by parallel backward and outwardly sloping grooves. True rim of carapace not angled laterally, but shallowly concave above last pair of legs, posterior margin straight in males. False rim slightly expanded at normal level of first lateral tooth, no distinct tooth. Sides of carapace very oblique and hairy in large males, branchiostegite projections large, a raised rim marginally.

Variable rostrum of average breadth, arising from upper carapace level, extending well past eyes, concave from side to side dorsally forming shallow gutter, narrowing and sloping downward anteriorly. Rostrum margin raised and thickened behind eyes; rostral tip prolonged centrally into bluntly pointed lobe flanked by pair of much shallower obtuse lobes; this subdivision of the rostrum occurring in front of the eyes. Pronounced longitudinal rostral ridge becoming wider and shallower anteriorly under median lobe. Postocular tooth large, ventral portion forming thick triangular ridge, concave next to the eyestalk, deepest point of the lobe dorsal; eyestalks short and stout, eyes projecting forward more than outward.

Folded antennules just visible between rostral lobes in dorsal view. Basal segment of peduncle subquadrangular, stout, with many long hairs on its external edge; second longer, a little more slender; third expanded distally, as long as second. Small ramus short with three terminal hairs; large ramus short, stout, with six to nine small subcircular segments, terminal bulb of average size, conspicuously waisted. Antennal spine large, acute.

Interantennular septum short, most deeply ridged adjacent to epistome. Epistome broad, very short (width three times length), sunken, separated by suture from subhepatic regions. Anterior rim deeper than usual, posterior ridge also deep, central cleft reduced to small depression. Subtriangular pterygostomian region large and laterally expanded, obtuse but large central lobe present with a ridge from it to the postero-median corner of the mouthfield, preceded by a concavity in long edge of pterygostomian region. Remnant of second lobe present, the edge between central lobe and cheliped fringed with long hairs. Subhepatic regions small but inflated to obscure carapace rim in ventral view. Milne Edwards's opening large, guarded by long hairs. Sterna of third maxilliped naked.

Endopods of third maxillipeds gaping widely in mid line; ischium and especially merus expanded laterally. Ischium as wide as long, median edge of moderate curvature with two to four rows of short setae, antero-median lobe very shallow, narrow merus articulation. Merus broader than wide, shorter on median edge than merus, considerably expanded distally; median edge deeply curved, has row of short setae, outer edge also curved, antero-external lobe large and rounded. Palp, articulating almost centrally on merus, segments all small, short and stout; dactylus longer than propodus, tapering to blunt point. Ventral setae on palp segments sparse but long.

Basal segment of exopod unusually long, reaching past tip of merus, broad throughout, liberally provided with long, feathery hairs, longest on internal edge and densest near apex. End segment long, slender, with five long terminal hairs.

Basal lobe of epipod reduced, hairy. Basal portion of epipod of average length, almost straight, densely hairy on anterior edge, not separated by distinct suture from lamella. Lamella a little longer than the base, broad, rounded distally, densely fringed with long hairs.

Chelipeds of male moderately massive (l. = 1.5–2 times carapace w.). Ischium short, subquadrangular. Merus long, maximum distal width half its length, ventral distal projection large and acute. Carpus as long as or slightly shorter than merus, not greatly expanded. Propodus shorter than or as long as carapus, as deep as long, not much inflated, somewhat pronounced basal gape and large square tooth on movable finger of male, distal third of fingers shallowly dentate. Linear gape of the female fingers also large, lined with hairs. Cheliped progressively hairier with increased size.

First three pairs of walking legs subequal, longer than chelipeds, usually twice carapace width. Fourth walking leg much shorter than other three. Ischium subrectangular, hairy. Merus longest, slender, breadth one-sixth to an eighth length, distal tooth small and blunt. Carpus just over half merus length; propodus a little shorter than merus, distal V pronounced. Merus, carpus, and propodus all with two rows of hairs, one long and straight, one short and hooked, on both edges. Dactylus as long as propodus, very flat and slender, curved, sickle shaped, tapering to long, separate terminal claw. Ventral edge of dactylus with single row of recurved sharp teeth, double row of curved setae either

side of teeth, the teeth absent or reduced near to the claw, a few fine hairs on dorsal edge.

Female abdomen an elongate oval, sixth segment not greatly enlarged, having deepest, narrowest proximal projection centrally; all segments fringed with hairs, hair also on their ventral face.

Male abdomen separated by broad false rim from carapace. Hairy first segment not long or laterally expanded, second only slightly smaller than first, hairy; third longer, sides almost straight; fourth still longer, narrowing distally; fifth as long as third, sides barely concave, narrowing a little distally; sixth segment semi-elliptical, a remnant of the suture cutting off the seventh segment present. Proximal central projections present on segments one to six, deepening and narrowing progressively except for that of the sixth segment which is shallow.

Long first pleopod of male bent through 90°, very slender distally, parallel sides narrowing very little subterminally, sparsely setiferous. Tiny constriction below slightly recurved eave.

MATERIAL EXAMINED:
Personal Collection: Whangamata Harbour, Coromandel, 17/12/1964, 45 ♂♂ 3.5–12 mm, 17 ♀♀ 3.5–8 mm, 10 g. ♀♀ 7–11 mm; 17/4/1965, 3 ♂♂ 6–7.5 mm, 2 ♀♀ 5, 8.5 mm, 1 g. ♀ 8.5 mm. Laboratory tank, Leigh Research Station, –/4/1965, 2 ♂♂ 6, 7 mm (coll. B. A. Foster); 14/5/1965, 2 ♂♂ 10, 9.5 mm (coll. S. J. Whitley). Pakiri, Leigh, 10/2/1965, 34 ♂♂ 8–12.5 mm, 1 ♀ 5.5 mm; 15/5/1965, 6 ♂♂ 6–9 mm, 8 ♀♀ 6–9 mm; –/4/1965, 1 g. ♀ 9 mm (coll. W. Rudman). Goat Island Bay, Leigh, 8/2/1965, 6 ♂♂ 2.5–3 mm (*Enteromorpha* pool). Whangateau, Leigh, 17/2/1965 1 ♀ 4.5 mm, 1 g. ♀ 9 mm (coll. S. J. Whitley); 28/5/1965, 2 ♂♂ 1.5, 11.5 mm (coll. W. Rudman). Karore Bank, Manukau, 6 ♂♂ 2–5.3 mm (with *Chione* and *Helice crassa*, coll. A. Michael). Ihumatao, Manukau, 3/5/1965, 2 ♂♂ 7.5, 8 mm, 2 g. ♀♀ 7, 8 mm; 31/3/1965, 1 ♂ 11 mm (coll. P. McGeorge). Bucklands Beach, Auckland, 21/3/1965, 3 ♂♂ 7–8 mm. Howick Beach, Auckland, 7/3/1965, 2 ♂♂ 5, 7 mm, 1 ♀ 6.5 mm.

Victoria University of Wellington, Zoology Department, Collection: Waitati River, 29/1/1963, 1 ♂ 8 mm (tidal flats, at night). McLeods Bay, Whangarei Harbour, 18/10/1964, 3 ♂♂ 9–11 mm (sand, 2 in. (5 cm) of water). Karamea River, 2 ♂♂ 3–3.2 mm, 2 ♀♀ 3.5, 4.3 mm (tidal reaches).

Edward Percival Marine Laboratory Collection: Rock House Point, Heathcote Estuary, Christchurch, 23/10/1964, 1 ♂ 10 mm, 1 g. ♀ 10 mm, 1 ♀ 8 mm (C 030F).

Dominion Museum Collection: Te Hapua, Parengarenga Harbour, 14/11/1963, 2 ♂♂ 7, 10 mm, (coll. R. K. Dell). Whangateau, Leigh, 24/11/1963, 2 ♂♂ 10.5, 11 mm (coll. R. K. Dell). Waiheke Island, 3 ♂♂ 7–10 mm (coll. G. Chamberlain). Napier Beach, 5/9/1952, 1 ♂ 14 mm (coll. A. M. Russell). Manukau Harbour, 13/10/1961, 2 g. ♀♀ 9, 10 mm (in *Zostera*, coll. H. J. Chapman). Waitarere, 1/8/1954, 1 ♀ 8 mm, 1 g. ♀ 11.5 mm (in sponge, M. Ordish). Waikawa, Wellington, 1954–55, 2 ♂♂ 9.5, 11.5 mm (coll. R. V. Bronson, Cr.1159). Tauranga Bay, Whangaroa, 11/11/1963, 2 g. ♀♀ 8.5, 10 mm, 1 ♂ 9.5 mm (coll. R. K. Dell). Evans Bay, Wellington, 13/10/1954, 1 ♂ 11.5 mm (coll. R. K. Dell, Powerhouse intake).

MONTHS IN WHICH GRAVID FEMALES TAKEN: February, April, May, August, October, November, December.

COLORATION (Plate 1): The basic carapace colours are green, yellow, grey or brown, sometimes finely speckled with white, black, cream or green. There may be a pair of small, white patches at the base of the last pair of legs, and another patch of white centrally on the carapace posterior border. The distal half of the dactylus of the walking legs and chelipeds is white, and a red basal band on the fingers of the chelipeds is common. There are usually dark bands on the walking legs; two on the merus are particularly obvious but the legs may also be uniformly coloured.

REMARKS: An adequate description of this species has been given by Gordon, who correctly transferred it from *Elamena* to *Halicarcinus* in 1940, after examining White's specimens in the British Museum, labelled "*Halicarcinus depressus*". White listed this species with the type of his genus, *Halicarcinus planatus*, when he erected *Halicarcinus* in 1846, so that he fully realised the true position of this species, but not its lack of homology with Jacquinot's *Hymenosoma depressa*. Miers (1876a, b), realised that White's specimens belonged to a separate species, and was the first to note the narrow front, acute rostrum, postocular tooth, lack of lateral teeth on the carapace and long, slender, hairy legs.

Gordon states that Filhol's *Elamena whitei* is not synonymous with Miers' species, but gives no reason for her belief. Filhol's figure is sketchy and fails to show the hairy nature of the legs, but he mentions long hairs on the legs and a light down on the carapace and the rest of his description agrees quite well with Miers'.

Hutton (1882) and later Chilton and Bennett (1929) queried the occurrence in New Zealand of "*Elamena whitei*", but White's type specimens came from New Zealand and Richardson (1949a) had no difficulty in recognising the species here.

ENVIRONMENTAL NOTES:
Substrate: *H. whitei* was found in three types of habitat: 1, among *Zostera nana* on harbour flats; 2, in the sand of sheltered open beaches, hundreds of yards from the nearest vegetation; and 3, in estuaries.

At the three stations where *H. whitei* was plentiful but *H. varius* was absent the dominant sediment particle size was in the coarse to fine sand grade (*see* Fig. 34). *H. whitei* was found with *H. varius* at Station 4, Howick Beach (*see* Fig. 29), Whangamata Harbour and at Whangateau. Both species prefer a substrate where the silt content is negligible and sand rather than shell predominates. *H. whitei*, unlike *H. varius*, never occurs in seaweed.

Density: In the Manukau Harbour and in the estuary at Pakiri, *H. whitei* reached a maximum density of 8 per m^2 in summer. In May, only eight specimens were found at Pakiri where the species was very plentiful earlier in the year.

Salinity tolerance: *H. whitei* is very tolerant of lowered salinities. Specimens were collected from localities where the salinity of the sea water varied from 35.4‰ (Howick Beach) to 15.8‰ (Pakiri Estuary). One small male survived in fresh water for 47 days.

Desiccation: *H. whitei* was more resistant to desiccation than any other species of hymenosomatid examined, the average survival time in air being 6 hours. As *H. whitei* does not burrow as deeply as *H. varius*, and is not

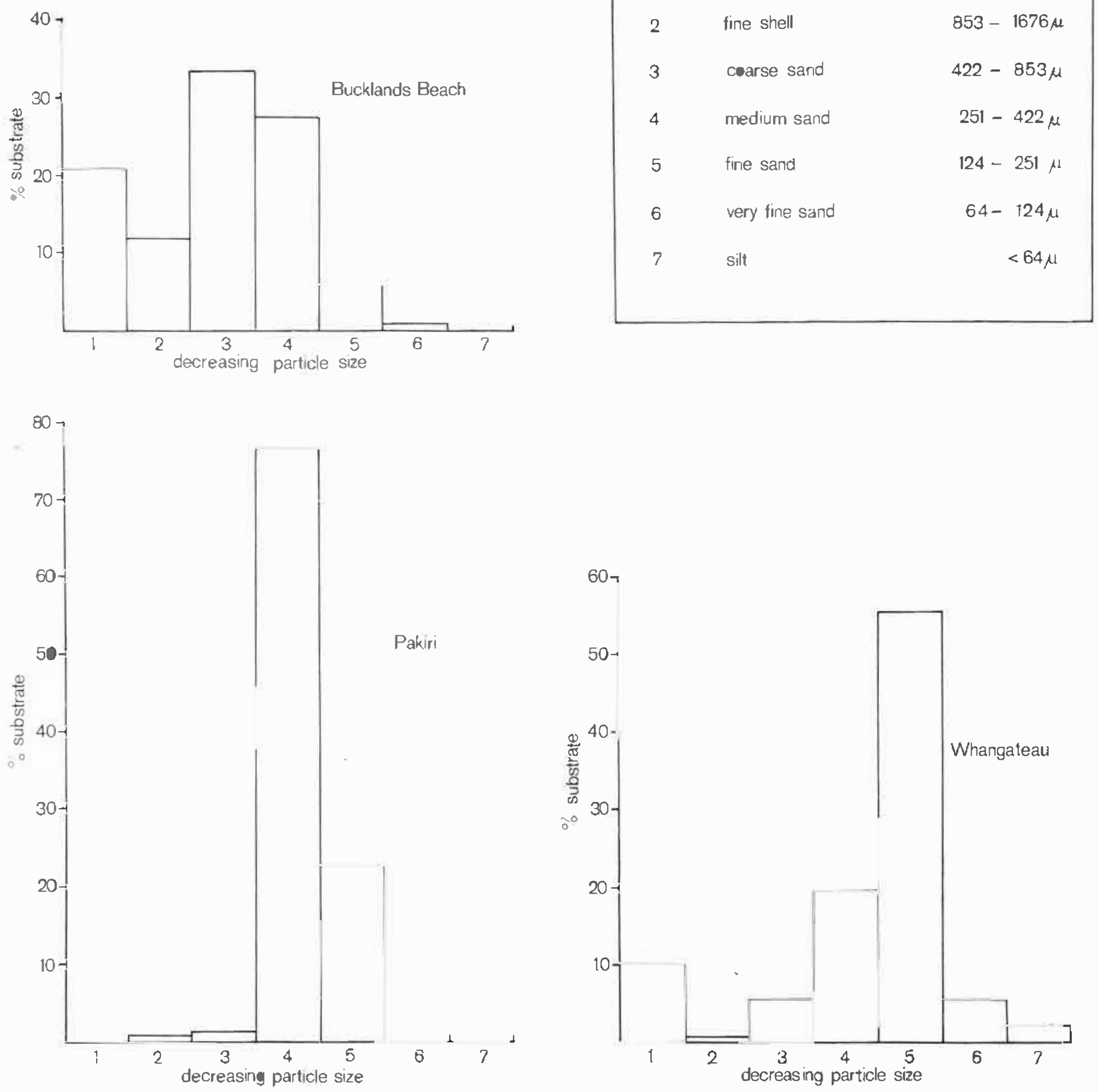


Fig. 34 Grade analysis of sediments at three stations at which *Halicarcinus whitei* was plentiful but *H. varius* was absent

found more than 2.5 cm below the surface at low tide, its superior ability to withstand desiccation must assist it in colonising the lower mid-littoral.

BEHAVIOURAL NOTES:

Alarm reactions: Prodding the crab with tweezers, or suddenly moving a large object in the immediate vicinity, produced complete immobility. If prodding were continued, *H. whitei* moved out of immediate contact with the irritant and then froze into a stationary pose. After 2 to 3 minutes, it moved rapidly to the sides of the aquarium and usually burrowed the rear portion of its carapace into the sand or under a shell.

Prodding a large male with tweezers first resulted in the chelae, which normally rested loosely on the ground, being sharply tucked under the anterior part of the carapace. Further prodding caused the crab to spread its chelipeds (*see* Fig. 35), using the walking legs as braces. Frequently the chelipeds swung so far outwards that they projected at right angles to the carapace, which was then tilted even further upwards anteriorly. When the chelipeds were fully extended, the first and second walking legs projected straight outwards, touching the ground and parallel with the chelipeds which were themselves held above the substrate so that the walking legs provided all the support.

Specimens dropped into water floated down with all legs outstretched and slightly bent and sometimes randomly moving. The legs were never tightly folded under the carapace.

The hairs on the carapace and legs trap debris and crystalline grains of sand so that *H. whitei* blends perfectly with the surrounding fine sandy bottom; coupled with its "freezing" and burrowing reactions to danger, this cryptic coloration makes this species very difficult to detect.

Normal locomotion: When large males walk, the chelipeds are almost invariably used alternately as well as the walking legs. Sometimes *H. whitei* will progress in a

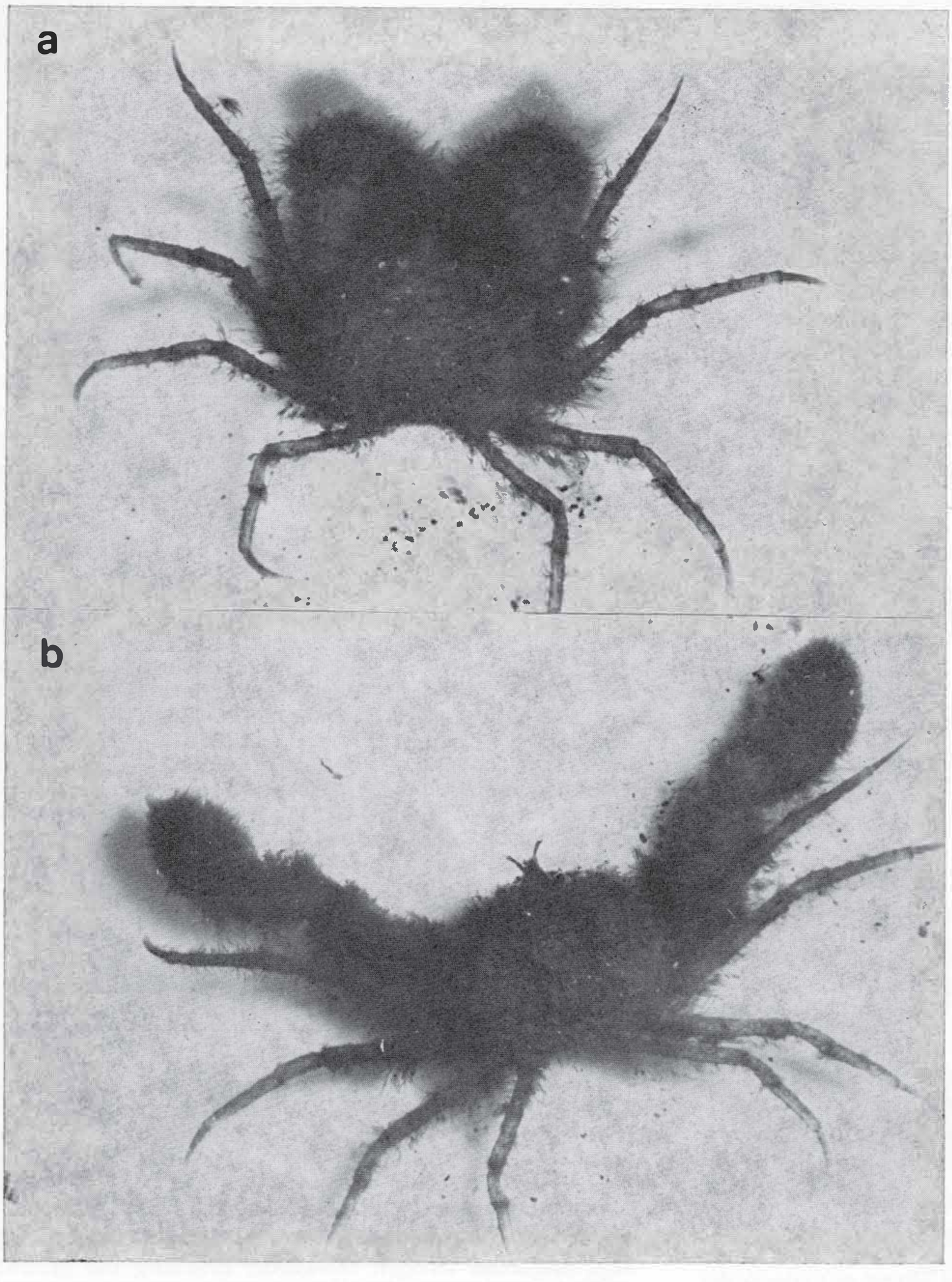


Fig. 35 Large male *Halicarcinus whitei* reacting to prodding by spreading its chelipeds widely *Photograph B. A. Foster*

series of forward jerks; the walking-legs lever the carapace off the ground in front, then the last three pairs of legs thrust the crab forward and it flops on to its folded chelae.

Swimming: Swimming was often observed. Even large, heavy specimens can lever themselves off the substrate and swim for short distances in motions like those of *H. cookii*. Usually *H. whitei* attempts to lift the legs on one side off the ground first, stretching them upwards and then pushing off with the legs of the other side.

H. whitei is very agile and will try to escape from the aquarium by standing on the legs of one side while the legs of the other side scrabble for a foothold on the glass, the whole crab leaving the ground briefly.

Burrowing: *H. whitei* does not construct permanent burrows. It moves about when covered by water, but disturbances will often make it dig its rear carapace and abdomen backwards into the sand. The walking legs radiate outwards and forwards and are used to lever the carapace to and fro in a series of jerks. The chelae are folded in front and provide extra purchase. Burrowing is a gradual process, and the flurry of exploding sand associated with the burrowing of most crabs is absent. The crab's legs press downwards with each rocking motion and the carapace and legs settle beneath the surface, usually leaving the rostrum, eyes, antennules, and part of the folded chelae above ground, but the crab may occasionally retreat until these are also hidden.

Specimens were not found more than 2.5 cm below the surface of the sand, and in the aquarium the crab was still just visible on the surface 30 minutes after the sand had been drained of water.

In the field it was noticed that this species gradually ceased moving and turned to face the incoming sea just after low tide, digging backwards until only the fore-carapace and chelae protruded from the sand.

Display: When a small and a large male encountered each other, the smaller would always retreat. No "threat" display was ever observed. If two large males met, each sat back on its hind carapace and last pair of walking legs, with the other walking legs braced sideways. The chelipeds were lifted, straightened, and spread laterally so that the inner surfaces of the chelae were opposed to those of the other crab. This position was usually held for up to a minute before the crabs retreated or sidled around each other. Fighting was only observed over food.

Food preferences: In the field, specimens were observed eating the polychaete *Perinereis*. *H. whitei* will live for 2 to 4 weeks without food, but during this time it will scoop up handfuls of sand and present these to the mouthparts. Whether this represents vacuum feeding, or whether the crab actually derived some nourishment from the organic content of the sand is difficult to decide. The stomach contents of specimens from Pakiri included sand grains as well as the remains of polychaetes, but this sand may be accidentally introduced with its food. *H. whitei* remains in good condition without plant food. Starved specimens will readily eat *Zostera* or algae.

H. whitei differs from *H. cookii* in consuming motionless food with which it comes into contact. Some indication that this species is capable of learning was also noticed. One specimen which was fed by tweezers for 3 months, reacted at first to the tweezers by freezing, running sideways, or hiding beneath a rock, but after several weeks, would come running to the side of the aquarium to receive its food when the tweezers were dipped in the water.

Moulting: Moulting was common in smaller specimens which usually moulted within 12 hours of a large feed of worms. Immediately after moulting specimens were a pale orange-brown or red-brown. Within 24 hours the colour darkened to grey-green with black banding and the carapace had hardened. Until then *H. whitei* would not accept food, and any movement or disturbance of the water caused it to run or burrow. Moulting was not observed in large males over 10 mm in width.

Halicarcinus pubescens (Dana)

Figs. 36–40

1851 *Hymenicus pubescens* Dana, p. 254
1852 *Hymenicus pubescens*, Dana, pp. 388, 389, pl. 24, figs 11a–c,
(NOT: *Halicarcinus pubescens* Dana, 1851 p. 253, and 1852 p. 386, pl. 24, fig. 8)
?1853 *Elamene quoyi* Milne Edwards, p. 223, pl. 11, fig. 3
1868 *Hymenicus pubescens*, Heller, p. 67
1876b *Hymenicus pubescens*, Miers, p. 51
?1885 *Hymenicus haasti*, Filhol, pp. 43, 44
?1886 *Elamena quoyi*, Filhol, p. 403
1904 *Hymenicus pubescens*, Hutton, p. 250
1913 *Hymenicus pubescens*, Thompson, p. 238
1917 *Halicarcinus pubescens*, Kemp, p. 247
1918 *Hymenicus pubescens*, Tesch, pp. 12, 13
1929 *Hymenicus pubescens*, Chilton and Bennett, p. 776
1949a *Halicarcinus pubescens*, Richardson, pp. 66, 67, fig. 42

TYPE LOCALITY: Bay of Islands, New Zealand.

SUMMARY OF LOCALITIES: Houhora Harbour; Cable Bay, Doubtless Bay; Tauranga Bay, Whangaroa; Whangamumu; Goat Island Bay, Leigh; Opouto, Kaipara Harbour; Hauraki Gulf; Cheltenham Beach, Auckland; North Head, Auckland; Westmere, Auckland; Onehunga mudflats, Auckland; Waihau Bay, Cape Runaway; Mahia Peninsula; Castlepoint, Wellington; Hope Shoal Light, Wellington; Lyall Bay, Wellington; Golden Bay; Cape Campbell; Cape Foulwind; New Brighton Pier; Heathcote Estuary, Christchurch; Otago Peninsula; Pegasus Bay, Stewart Island.

DISTRIBUTION: New Zealand endemic.

DIAGNOSIS: Carapace subcircular, upper surface convex, gastric region strongly outlined. Rostrum short, simple, bluntly pointed, projecting past eyes, slightly deflexed, longitudinally ridged below, convex from side to side above. Rostrum arising at upper carapace level. Frontal region a little produced anteriorly, suture between front and rostrum just convex. Lateral angles on carapace absent or obscure. Postocular lobe well developed, acute. Antennal spine absent. Chela of male not greatly inflated, palm long for its depth, fingers short and broad, closely occluding, the usual basal tooth on movable finger present but fitting obliquely inside immovable finger. Segments of walking legs of average breadth, dactylus short and broad, a single blunt tooth by the claw. Ischium and merus of third maxilliped both narrow. Male abdomen short, separated from carapace by a broad vertical ledge, first segment as long as second, first four segments subequal in width, last two a little narrower. First pleopod of male short, stout, with a longitudinal row of long, sturdy setae subterminally, tiny knob at tip. Whole body densely covered with hairs.

SIZE RANGE: ♂♂ 3 mm – 6.5 mm (Leigh). ♀♀ 2.5 mm (Leigh) – 6.5 mm (Cheltenham).

DESCRIPTION: Carapace subcircular (ratio w. : l. = 1.1–0.95). Upper carapace convex, rim very thin. Wide gastrocardiac groove strongly deflected backward centrally. Cervical grooves distinct, continuing anteriorly to base of rostrum, sometimes dividing to delimitate tiny hepatic regions, a strong, sometimes forked groove cutting off small prebranchial region. Very short thoracic grooves present, sometimes with third short groove between them originating from centre of gastrocardiac groove. Sides of carapace almost vertical; well developed obtuse branchiostegite projections between legs. Lateral teeth absent or represented by tiny expansions of lateral sides of carapace.

Rostrum broad basally, arising at carapace level, separated from front by a suture only slightly more

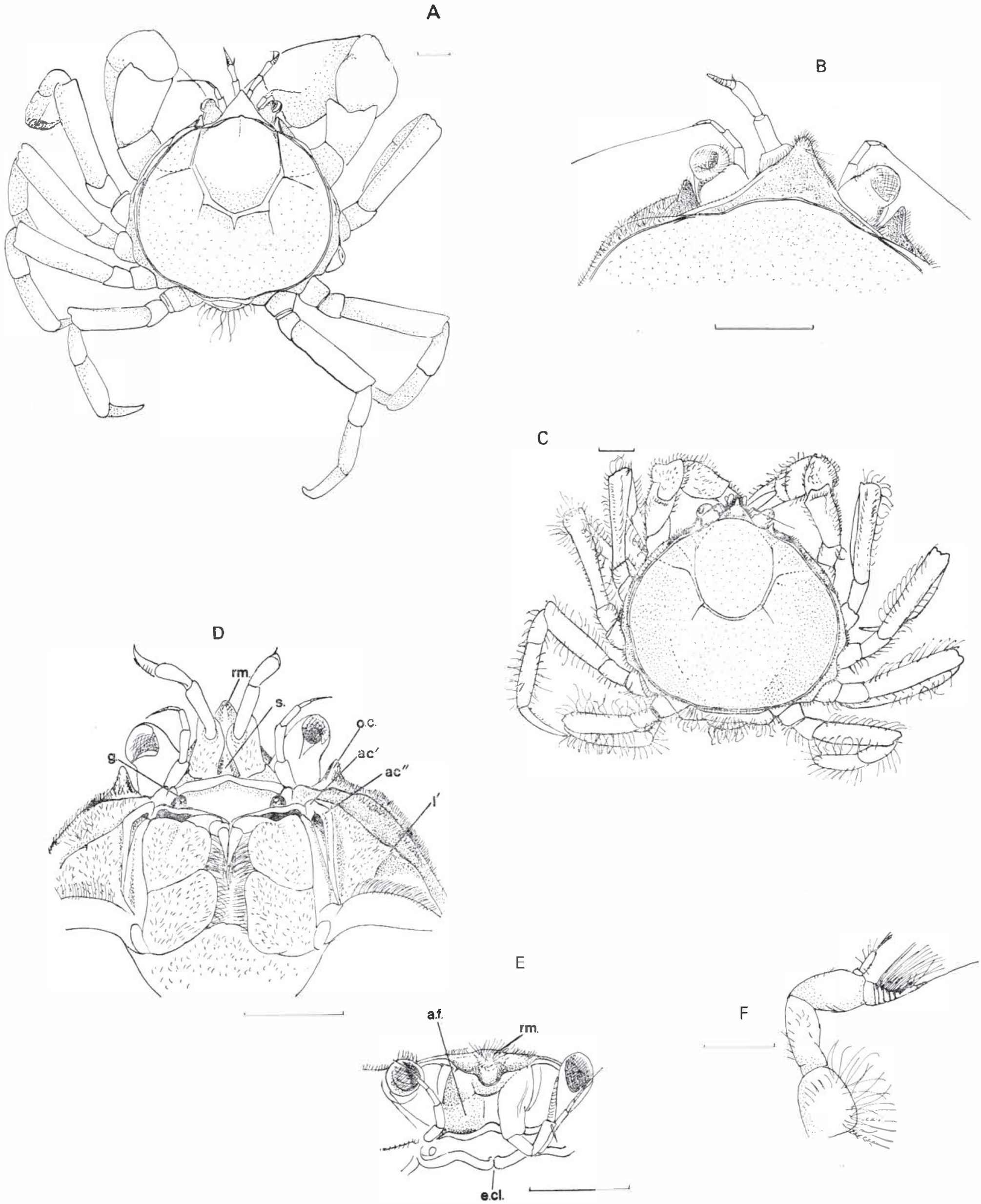
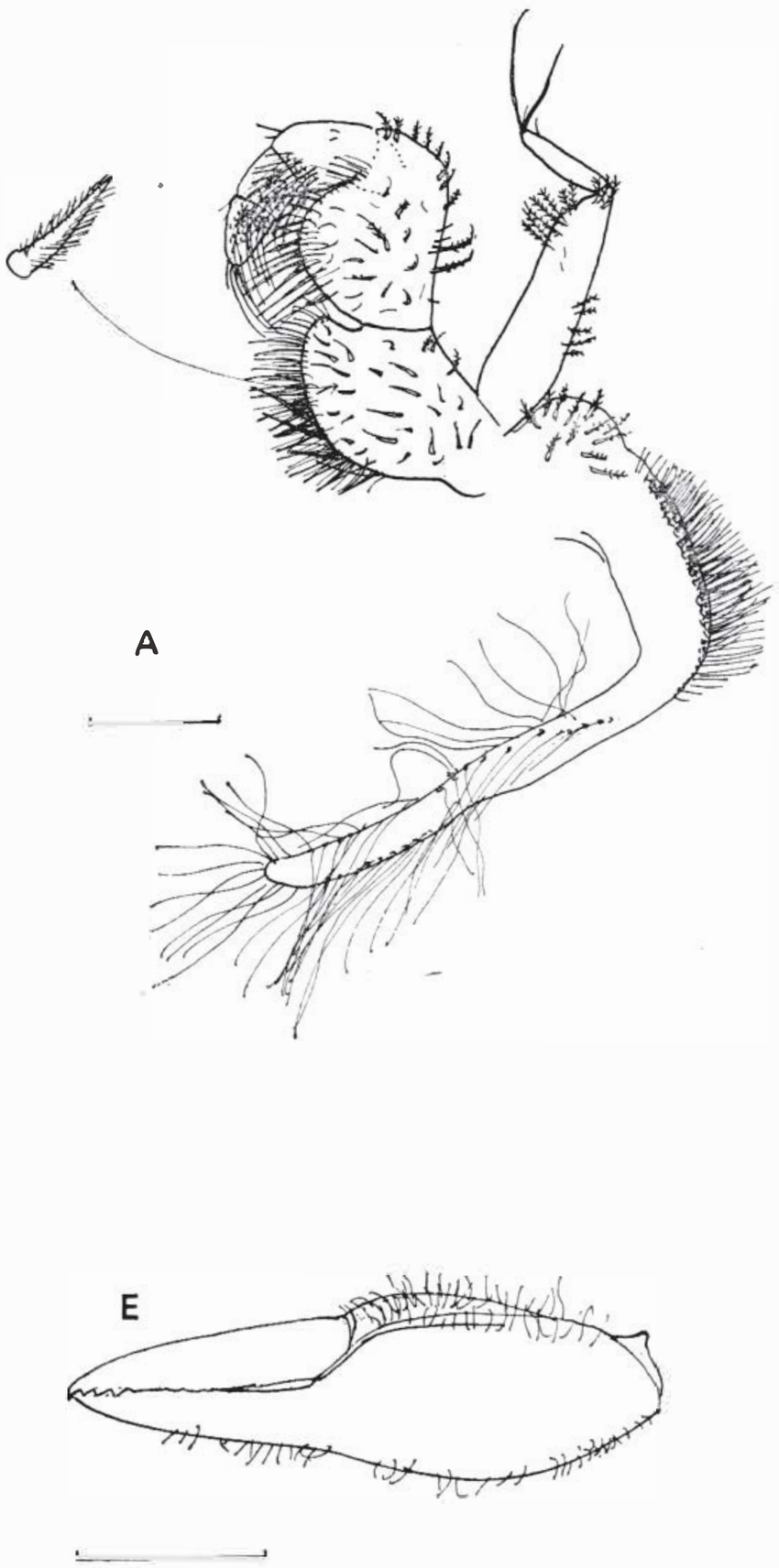
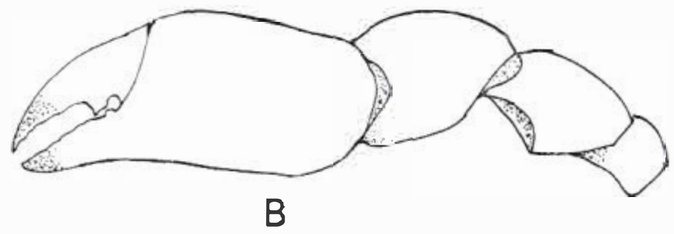
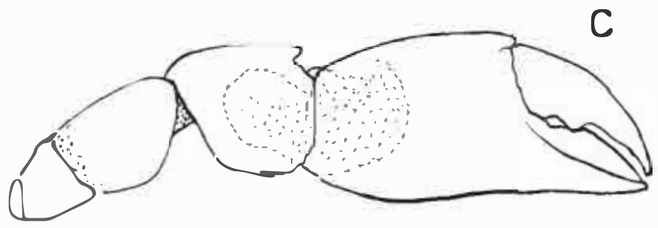
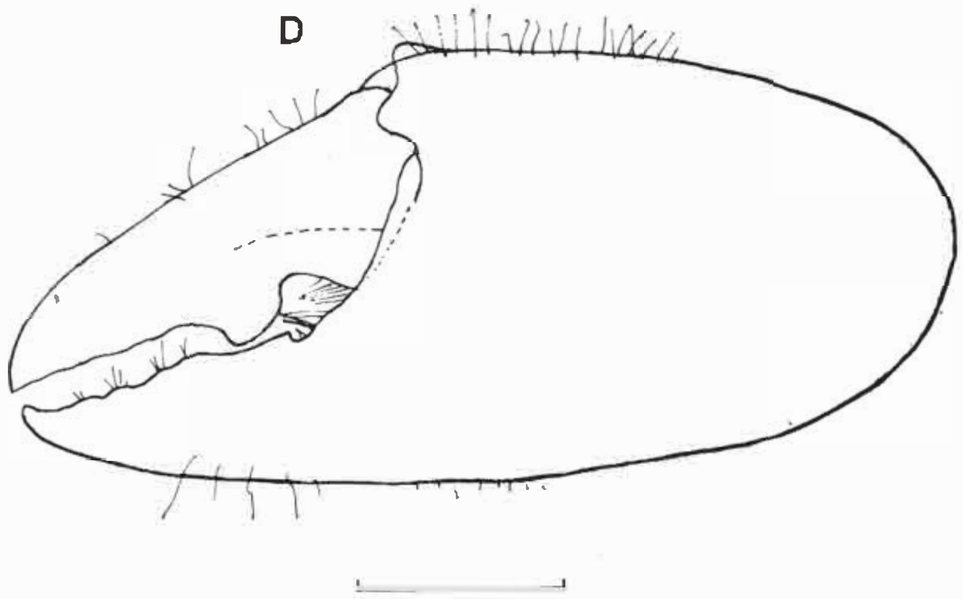


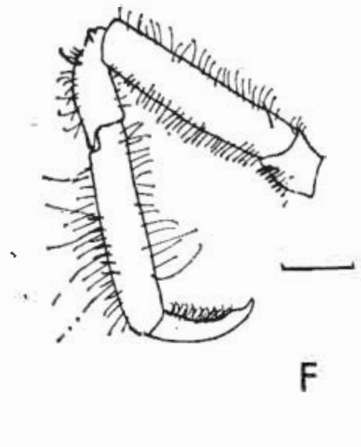
Fig. 36 *Halicarcinus pubescens:* A—Male, dorsal view (directly after moult, hairs not shown); B—Rostrum of male in A; C—Female, dorsal view (hairs not shown on carapace); D—Ventral view of mouthfield and epistome region; E—Frontal view of male in A, carapace perpendicular to plane of vision, right antennule removed; F—Left antennule of male, lateral-ventral view. (scales represent 1 mm)

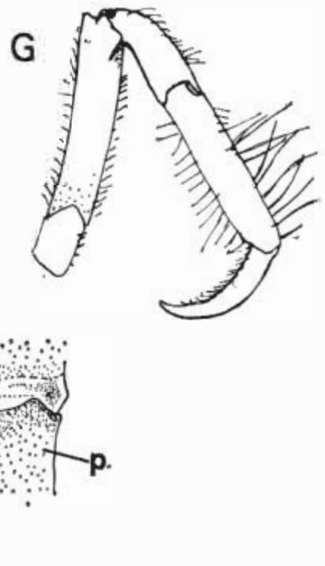












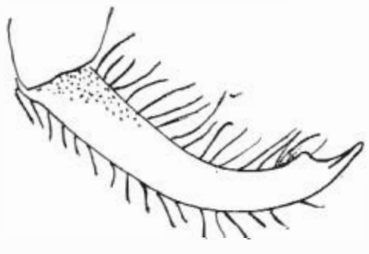
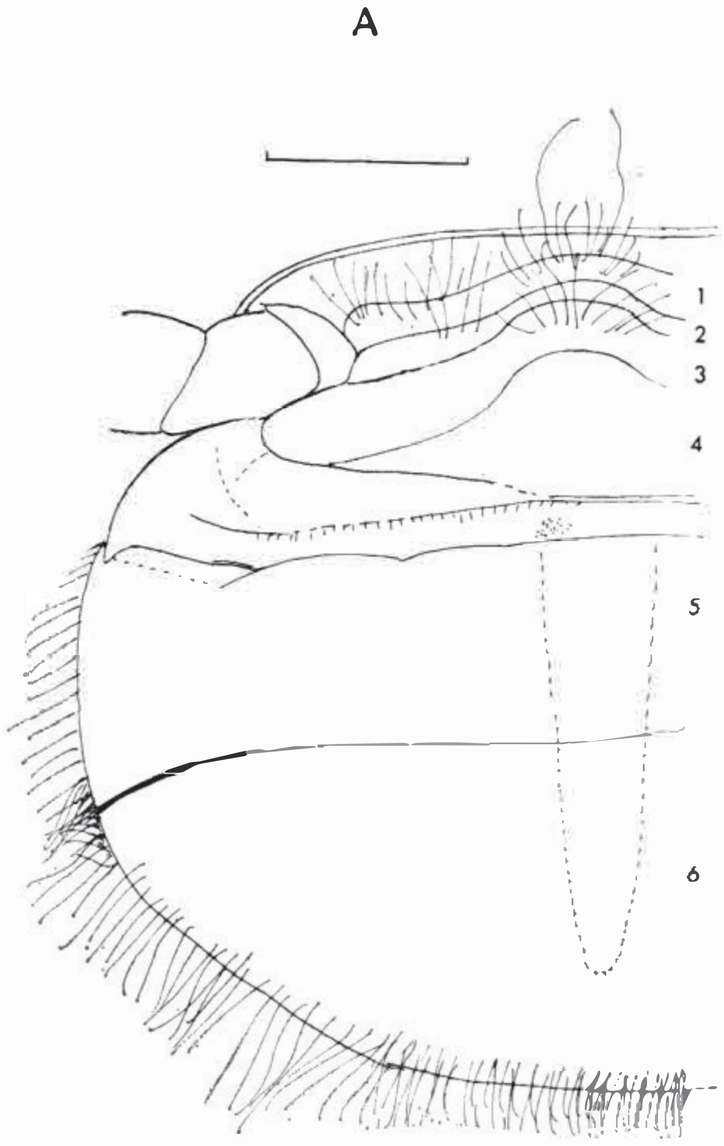
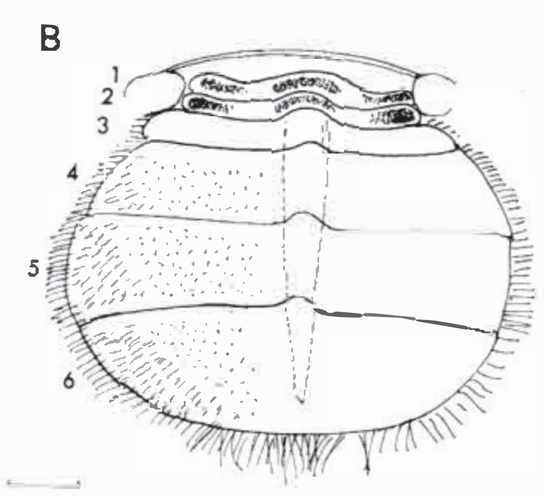
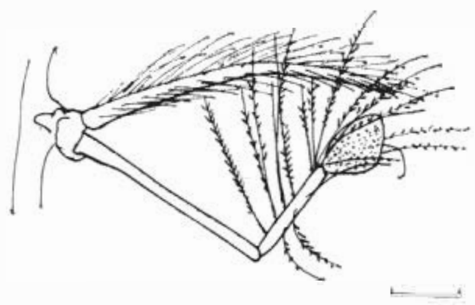
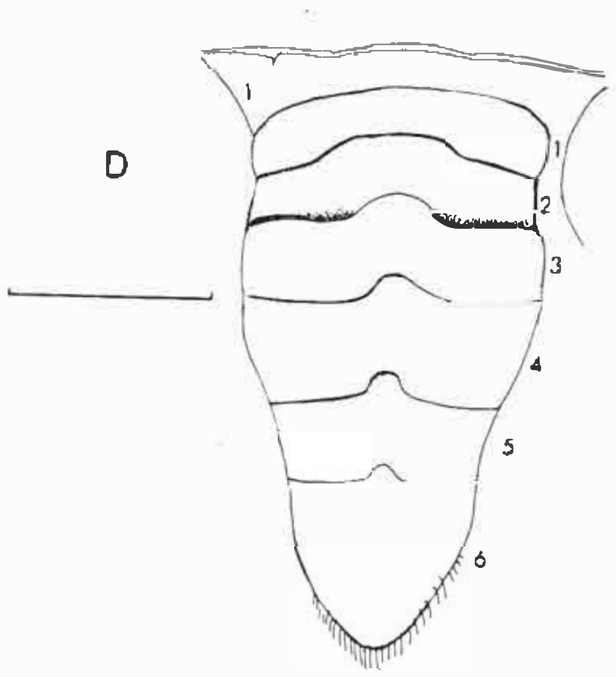


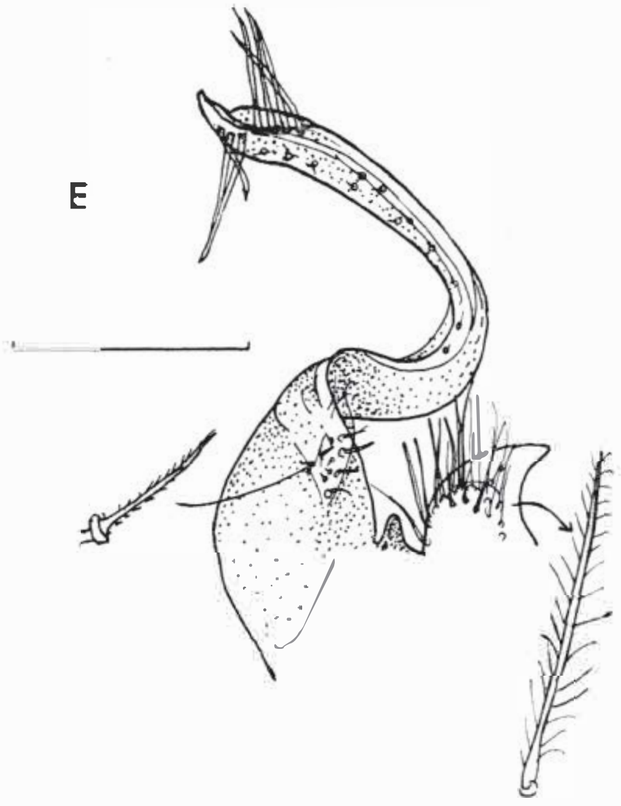
Fig. 37 *Halicarcinus pubescens:* A—Left 3rd maxilliped of male; B—Left cheliped of male, posterior view; C—Left cheliped of male, anterior view; D—Left chela of male, posterior view; E—Left chela of female, posterior view; F—Left 3rd walking leg of male, posterior view; G—Left 3rd walking leg of male, anterior view; H—Joint of carpus and propodus of left 3rd walking leg of male, posterior view; I—Dactylus of left 3rd walking leg of male, posterior view. (scales represent 1 mm)











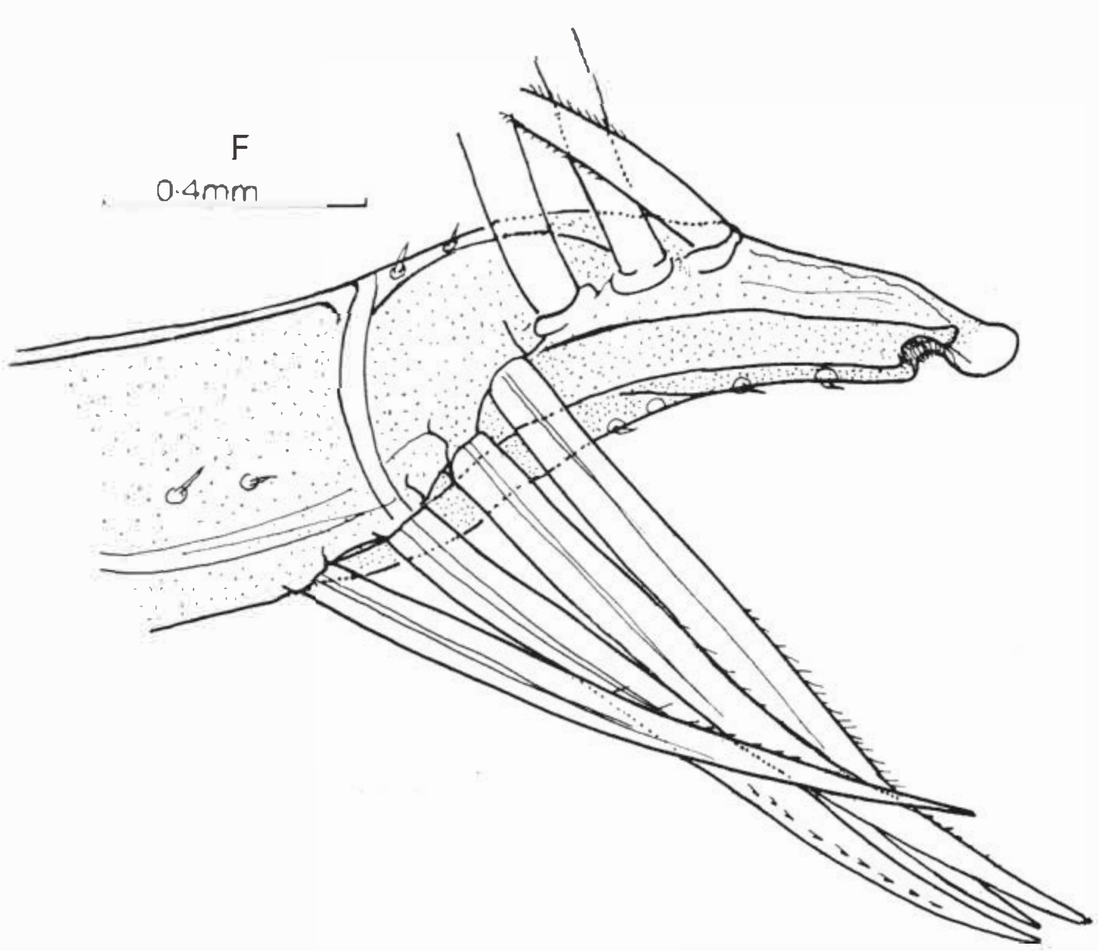


Fig. 38 *Halicarcinus pubescens:* A—Extended abdomen of female, dorsal view of left side showing a freak fold in segment 4; B—Extended abdomen of normal female, dorsal view; C—Left 2nd pleopod of female; D—Extended abdomen of male, dorsal view; E—Left 1st pleopod of male, sternal view; F—Tip of left 1st pleopod of male. (scales represent 1 mm except where otherwise stated)

curved than anterolateral border; frontal region little produced anteriorly. Rostrum simple, edges narrowing evenly between eyes until just below bluntly pointed tip when sides become semiparallel. Rostrum slightly deflexed downward anteriorly, rounded from side to side above, a central longitudinal shallow ridge ventrally. Eyestalks short, of average breadth; eyes angled outward as much as forward. Postocular tooth of moderate size.

Folded antennules just visible on either side of the rostrum in dorsal view, short, slender; the basal segment subquadrangular and hairy. Second peduncular segment slender, hairy; third a little expanded distally, subequal with the second. Small ramus very short, terminating in three hairs; large ramus, short and slender, three to five small subcylindrical segments, terminal bulb long and waisted. Antennal spine absent.

Interantennular septum short and shallow. Epistome small, twice as long as its central depth, shortening laterally, not much sunken but separated by antennal gland covers and their rims from the small, somewhat inflated, subhepatic regions. Anterior ridge on the epistome thick and prominent, posterior ridge not deep, a small central cleft. Subtriangular pterygostomian region small, ridge leading from vestigial central lobe to posteromedian corner. Milne Edwards's opening large, guarding fringes of hairs reduced. Sterna of third maxillipeds large, entirely covered by short fine hairs.

Endopods of third maxillipeds gaping narrowly in mid line. Ischium a little longer than broad, median edge moderately curved, with a double row of setae of medium length, anteromedian lobe reduced. Merus narrow basally, expanded distally, as broad as long, as broad as the ischium, median edge curved with single row of long hairs, outer edge straight proximally, anteroexternal corner rounded and enlarged; ventral faces of ischium and merus with scattered long hairs. Palp articulating centrally on oblique distal end of merus. Carpus large, propodus also stout and square, dactylus not longer than propodus, stout and blunt. Ventral hairs of palp long.

Basal segment of the exopod broad, scarcely tapering until immediately below the apex. Line of short hairs on inner edge below apex, horizontal row adjacent to apex, a few hairs on outer edge. Basal lobe of epipod large, shallow, hairy. Basal portion of epipod long, broad, almost straight, up to four rows of long setae on anterior edge, continuous with lamella which is one-third as long again, of average breadth, distally rounded and fringed on both edges with long hairs. Oblique row of hairs at the base of lamella.

Chelipeds short in both sexes (1.2–1.5 times the carapace width). Segments of male cheliped moderately inflated. Ischium short, subtriangular. Merus also short, little longer than broad, ventral distal projection narrow. Carpus subequal with merus, expanded distally. Palm of male as long as carpus or up to half as long again, depth always less than length. Palm of female up to twice as long as carpus, depth subequal with carpus length. Fingers on both sexes shorter than or subequal with palm; fingers in male very broad, basal gape small even though there is a large, short tooth on the base of the movable finger, dentation rudimentary but fingers occluding almost completely when shut as the basal tooth is set obliquely and fits in front of the movable finger. Movable finger hollowed slightly on its anterior face to receive this tooth. Hairs sparse on inner edge of movable finger and in the sinus between fingers. Palm of female suboval, narrower than long, fingers slender and straight, occluding almost completely, dentation deep only on tips.

First three pairs of walking legs as long as chelipeds, fourth pair shorter. Ischium subquadrangular, an obtuse projection over merus on its anterior face. Merus and propodus lengths subequal, propodus relatively shorter in larger specimens. Merus half to a third as broad as long, merus tooth blunt. Carpus a little less than half as long as merus, distal projection on the dorsal edge long and sharp, projection on opposite edge blunt. Distal end of propodus gently rounded in shallow V. Dactylus broad, five-eighths to two-thirds as long as the propodus, considerably curved, not tapering much, both edges fringed with hairs, those on ventral edge longest. Dactylus has single blunt tooth on ventral edge adjacent to the small claw, claw fused to rest of segment. All segments a little flattened.

Female abdomen broad, sixth segment not greatly longer than the fifth, all except the first two fringed with hairs.

Male abdomen short, reaching to suture between sterna of first and second walking legs, separated from carapace by broad vertical ledge. First segment short, not expanded laterally, second segment as long as first; third segment slightly wider than first two, edges almost straight; fourth segment longer than third, narrowing slightly distally; fifth segment shorter, sides barely concave, narrowing very little distally; sixth segment longest, semi-elliptical a fringe of hairs terminally.

First pleopod of male short, sharply twisted through more than 90°, scattered short setae on the distal portion, obliquely longitudinal row of about seven long, stout setae subterminally; tapering tip ending in tiny knob above aperture of vas deferens.

MATERIAL EXAMINED:

Personal Collection: Goat Island Bay, Leigh, 11/1/1965, 5 ♂♂ 2.5–5 mm, 3 ♀♀ 2.5–4 mm; 8/2/1965, 4 ♂♂ 1.3–4.5 mm, 2 ♀♀ 3.5 mm; –/5/1965, 3 ♂♂ 5–6.5 mm (coll. B. A. Foster). Leigh Harbour, 17/5/1965, 2 ♂♂ 4, 5 mm. Goat Island Bay, Leigh, 17/5/1965, 1 ♂ 3.5 mm. Cheltenham, 26/6/1965, 3 ♂♂ 4–5.5 mm, 1 ♀ 6.5 mm, 2 g. ♀♀ 5.5, 6 mm. Westmere, 26/6/1965, 2 g. ♀♀ 5.5, 6.5 mm, 2 ♂♂ 4, 6 mm.

Victoria University of Wellington, Zoology Department Collection: Castlepoint, Wellington, 14/1/1965, 3 g. ♀♀ 4–5 mm, 1 ♀ 2.5 mm, 2 ♂♂ 3.5 mm; 28/2/1964, 2 ♂♂ 3, 4 mm; 20–23/12/1964, 13 ♂♂ 2–4 mm, 4 ♀♀ 2.5–4 mm, 2 g. ♀♀ 5, 6.5 mm.

Edward Percival Marine Laboratory Collection: Menzies Bay, 22/8/1961, 1 ♂ 6.5 mm.

Auckland Museum Collection: Auckland, 2 ♂♂ 4 mm, 1 g. ♀ 5 mm. North Head, 21/7/1926, 1 ♂ 6 mm (coll. D. H. G., A 5, with *Hemigrapsus edwardsi*).

Dominium Museum Collection: Houhora Harbour, 18/11/1963, 1 g. ♀ 5.5 mm (coll. R. K. Dell); 13/11/1963, 5 ♂ ♂ 2–5.5 mm, 1 ♀ 2.5 mm, 3 g. ♀ ♀ 6–8 mm (coll. R. K. Dell). Tauranga Bay, Whangaroa, 11/11/1963, 1 ♀ 4 mm (coll. R. K. Dell). Cable Bay, Doubtless Bay, 18/11/1963, 8 ♂ ♂ 2.5–6 mm, 4 g. ♀ ♀ 4.5–5 mm (coll. R. K. Dell). Hope Shoal Light, Wellington Harbour, 23/8/1957, 1 ♂ 4 mm, 1 ♀ 5.5 mm (VUZ 91, 41°18′30″ S, 174°51′24″ E, in 6 fm (11 m). Goat Island Bay, Leigh, 10/1/1962, 1 g. ♀ 4.5 mm (coll. R. K. Dell). Waihau Bay, Cape Runaway, 8/3/1962, 1 ♂ 6.5 mm, 1 s. ♀ 6.5 mm (coll. R. K. Dell). From hull of New Plymouth dredge *Porituta* arrived in Wellington 5/5/1954, shipped Evans Bay, 1 ♀ 3.5 mm (coll. J. H. S., with *H. innominatus*, *Notomithrax*).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: January, February, March, June, November, December.

COLORATION: Grey-brown, yellow-brown.

REMARKS: This is almost certainly the species described by Dana (1851, 1852) from the Bay of Islands, North Auckland, as "*Hymenicus pubescens*". The union of the genera *Halicarcinus* and *Hymenicus*, which were regarded as separate by Dana, has caused a problem in the application of the specific name "*pubescens*" to the New Zealand crab. A distinct species, from 50 fathoms (91 m) off Cape Blanco on the east coast of Patagonia, was described as "*Halicarcinus pubescens*" by Dana (1851, 1852). The latter has been regarded as a probable synonym of *Halicarcinus planatus* (*see* Rathbun 1925, p. 563; Garth 1958, p. 31) but the type is no longer extant and its synonymy cannot be finalised. Since Kemp (1917) combined the two genera and used the combination *Halicarcinus pubescens* for the New Zealand species a state of homonymy has existed between it and the Patagonian species. This homonymy is unresolved and potentially threatens the established name of this common New Zealand crab.

The latest edition (1964) of the International Code of Zoological Nomenclature states in Article 24 (a) "If . . . identical names for different taxa, are published simultaneously . . . their relative priority is determined by the action of the first reviser". In this case the names *Hymenicus pubescens* Dana, 1851, and *Halicarcinus pubescens* Dana, 1851, apply to two different species but were published in the same paper; they are now regarded as belonging to the same genus and are thus homonyms. Acting as "first reviser", I reject the name *pubescens* Dana, 1851 (as published in the combination *Halicarcinus pubescens*) and accept *pubescens* Dana, 1851 (as published in the combination *Hymenicus pubescens*) as a valid name. This action leaves the New Zealand species as *Halicarcinus pubescens* (Dana, 1851) and the Patagonian species as a junior secondary homonym. For the latter I propose the replacement name *Halicarcinus patagoniensis* nom.nov. In the absence of the type I follow Rathbun (1952) and Garth (1958) in regarding this species as a probable synonym of *H. planatus*.

Milne Edwards's figure of *Elamena quoyi* (1853, pl. 11, fig. 3), is thought by Tesch (1918, p. 12) to resemble greatly *Halicarcinus pubescens;* there are no lateral angles and the eyestalks and antennules are visible. However, the rostrum of Milne Edwards's species is rather short and there are no grooves shown on the carapace, so that this opinion must be queried.

Halicarcinus pubescens is abnormal in having an almost uniformly narrow short abdomen in the male and a longitudinal row of long, strong setae on the tip of the first male pleopod, and in the absence of dentation on the dactyl of the walking legs except for a single, blunt tooth adjacent to the claw. In these characters it resembles the genus *Elamena*, although in some species of *Elamena* the abdomen is a little more expanded basally and in all species of *Elamena* there are two terminal teeth on the dactylus and the aperture of the vas deferens is distinctly subterminal. The zoea of *H. pubescens* is strikingly different from the zoea of the other marine species of *Halicarcinus* (pers. comm., Dr R. B. Pike). In all other respects *Halicarcinus pubescens* is typical of its genus. The differing but also abnormal shape of the first male pleopod and the male abdomen in another species, *Halicarcinus lacustris*, where even the terminal tooth found on the dactylus of the walking leg in *H. pubescens* has disappeared, indicates that these characters are useful in this family only at the specific level.

Halicarcinus pubescens seems to be closely relate to, but not identical with, the Australian species *Halicarcinus bedfordi* of Montgomery (1931).

ENVIRONMENTAL NOTES:

Distribution: This small species occupies a similar habitat to *Halicarcinus innominatus* on sheltered and on moderately exposed rocky reefs. It was not found in conditions of maximum exposure.

Substrate and density: Young, slender-legged, immature crabs have been found amongst *Sargassum* floating on the open ocean between Great Barrier Island and the coast, as well as in coralline turf and in rock crevices. Adults have been reported from dredgings and are common intertidally, but as *H. pubescens* is small and extremely well camouflaged, it is easily overlooked (*see* Fig. 39).

At Leigh, *H. pubescens* is most abundant from December to April, reaching a density of 2–6 per 0.1 m^2, but it virtually disappears from the open reef platform in winter. In summer, *H. pubescens* may be seen crawling leisurely about in shallow water in the lower mid-littoral on the reef platform, where pinkish-white *Lithothamnion*, corallines, the brown polyzoan *Beania*, *Elminius modestus*, and white whorls of *Spirorbis* dot the rock surface. As the tide retreats, *H. pubescens* hides beneath boulders and in rock crevices which provide a moist shelter from the sun even though the rocks are often not submerged. In winter a few tiny specimens were found below stones in sand well above the *Corallina* zone. These rocks were relatively bare of other animals or vegetation, other than the polyzoan *Beania*.

A very few small specimens were obtained from coralline turf and holdfasts of *Carpophyllum maschalocarpum* on Leigh reef and in Leigh Harbour.

Fig. 39 A group of *Halicarcinus pubescens* on a rock with *Lithothamnion* and the ployzoan *Beania* *Photo B. A. Foster*

In the Auckland Harbour, *Carpophyllum* holdfasts and tufts of *Corallina* yielded four specimens. Evidently the winter density of this species on sheltered reefs remains high, for at Cheltenham and Westmere there were 2-4 specimens per 0.1 m^2 in July below rocks in the mid-littoral.

H. pubescens seems to prefer a solid substrate. It never appears in the fronds of larger algae. The fairly dense substrate formed by *Corallina* must be more favourable for *H. pubescens* than seaweeds that float and shift with the current.

Although found under rocks embedded in sand, *H. pubescens* is found only on those parts of the rock which are not in close contact with the sand. It prefers crevices between neighbouring rocks, or the sides of boulders whose bases are embedded. The frequent presence of sponges under the same rocks indicates a sufficiently strong current to bring food to both these and crabs.

Salinity tolerance: The lowest salinity recorded where *H. pubescens* was found was 30.5‰ (in a pool at Westmere), but it is likely that the crab has to withstand salinities lower than this for brief periods. Specimens from Cheltenham survived for $4\frac{3}{4}$–12 hours in fresh water, with an average survival time of $6\frac{1}{2}$ hours.

In 25 percent sea water and in lower salinities, *H. pubescens* made vigorous attempts to climb from the water. Crabs left in diluted sea water often folded their legs tightly under their carapaces and floated on their backs for a short time.

Desiccation: *H. pubescens* was fairly resistant to desiccation, surviving an average of 4 hours in air.

BEHAVIOURAL NOTES:

Thigmotaxis: Specimens of *H. pubescens* placed together in a bowl without stones curled around one another to form a tightly aggregated grey mass. *H. pubescens* will also cling to other species of *Halicarcinus*, e.g. *H. varius*, in the same situation.

Alarm reactions: When *H. pubescens* is dropped into water, it floats passively downward with the walking legs either tightly folded beneath the carapace so that the distal ends of the meri of the walking legs interrupt the circular outline of the body, or half folded with the posterior faces of the leg segments directed dorsally. Each partially folded walking leg, bent through slightly less than a right angle at the merus-carpus and propodus-dactylus joints, covers the edge of the leg anterior to it so that together the walking legs project to form half of a hollow square on each side of the body. The chelipeds are tucked beneath the rostrum in both poses.

If *H. pubescens* is prodded with a needle and lifted off the substrate, it soon adopts the same folded or partially folded leg position.

H. pubescens is very sensitive to light and will always attempt to crawl under boulders if the light is moderately strong.

Transferred from water to air, *H. pubescens* remains stationary—but not for much more than 1 minute. Although extremely sluggish in aquaria and in the field, remaining almost motionless for long periods, a 6 mm specimen could in air reach speeds of up to 14 mm per sec.

Normal location: As *H. pubescens* moves so slowly in water, the sequence and mode of leg movements during locomotion can be more easily studied than in other species. The chelipeds are usually held forward, roughly parallel with each other and above the substrate. Sometimes they are loosely folded inwards towards the mid line, or may swing alternately with the chelae pushing against the substrate (*see* Fig. 40).

All walking legs begin to move simultaneously though in different phases when the crab first starts to walk. When it is moving very slowly the body lurches from side to side, as though it were being regularly thrown off balance.

The third and fifth legs on one side appeared to be almost in phase, but as the third is longer than the fifth, it swings through a larger arc in the time that the fifth leg takes to execute a forward and backward stroke. The second and fourth walking legs on the same side are in almost opposite phase to the third and fifth.

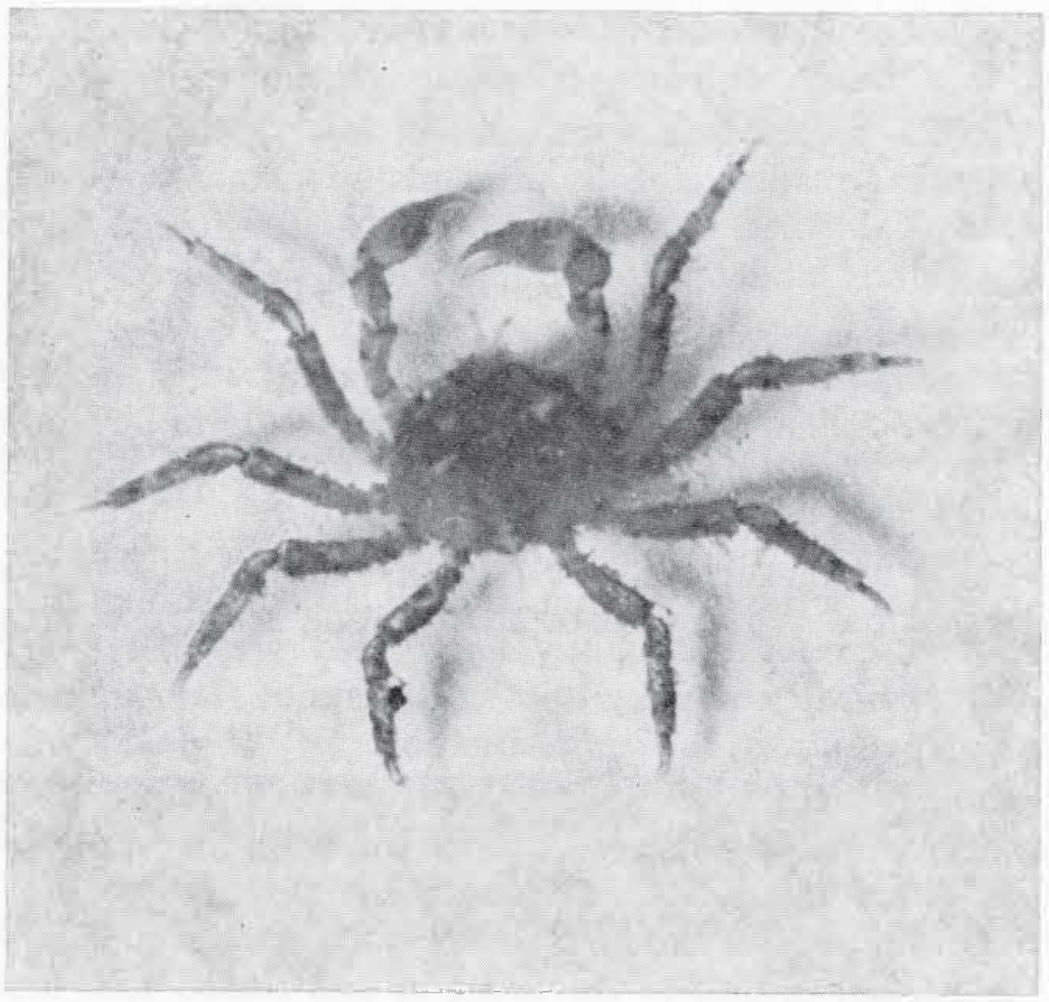


Fig. 40 *Halicarcinus pubescens* walking (photographed by B. A. Foster)

The fourth and fifth legs therefore overlap for that part of their cycle when the fourth almost reaches the limit of its backward stroke and the fifth has just completed its forward stroke.

The forward stroke of the fifth walking legs is slightly shorter in time and distance than the propulsive backward stroke. In general, the recovery stroke and propulsive stroke ratio approximate the ratio for the other walking legs.

Each pair of legs is almost in phase on both sides of the body, both being propulsive together. If the legs were exactly in phase, support would be provided by the four legs R1, L1, R3, and L3, alternating with R2, L2, R4, and L4 (*see* Waterman 1961, Vol. 2, p. 331). This would be an unsteady gait and certainly *H. pubescens* does tip from side and also from rostrum to abdomen as it walks. In *H. pubescens* no two legs appear to be *exactly* in phase.

At any time, the crab may suddenly stop and all the legs then come to rest at whatever point in their sequence they have reached. A single leg may be extended tentatively to touch the substrate ahead and it may be lifted and replaced several times. The whole sequence of leg movement is variable and may alter at random or when the crab encounters any obstacles.

Swimming: Swimming was common in this species.

Food preferences: H. pubescens was not observed catching food or scooping up debris and is presumed to be predominantly a filter feeder. The pronounced hairiness of the mouthparts would assist this. Most of the time, the crab remains motionless in the aquarium, with the maxillipeds open and occasionally rubbing together. At intervals the antennules are brought down to the palps of the external maxillipeds and cleaned and the outer maxillipeds then fold in and out while pieces of debris are transferred from them to the mandibles. Several specimens have been sitting on sponge; the maxillipeds opening into the soft tissue of the sponge and occasionally folding inwards and out again. The sponge-covered area of rocks in an aquarium gradually decreased as though it was being grazed. One specimen was seen with a piece of red nemertean dangling from its maxillipeds, but it is unlikely that the slow movement of *H. pubescens* allows it to catch rapidly moving prey.

Epifauna: Several specimens were found with small patches of sponges growing among the hairs on the carapace.

Halicarcinus lacustris (Chilton)

Figs. 41 and 42

1882	*Elamena ? lacustris* Chilton, p. 172
1883	*Hymenosoma lacustris*, Chilton, p. 69. pl. 1, fig. 2a–e
1902	*Hymenosoma lacustris*, Fulton and Grant, p. 59, pl. 8
1904	*Hymenosoma lacustris*, Hutton, p. 251
1906	*Hymenosoma lacustris*, Fulton and Grant, pp. 16–20
1906a	*Hymenosoma lacustris*, Chilton, p. 703
1911b	*Hymenosoma lacustris*, Chilton, p. 128
1915	*Hymenosoma lacustris*, Chilton, p. 316
1917	*Halicarcinus lacustris*, Kemp. p. 247
1918	*Hymenicus lacustris*, Tesch, p. 12
1919	*Hymenosoma lacustris*, Chilton, pp. 93–5
1949a	*Halicarcinus lacustris*, Richardson, p. 67, fig. 44
1963	*Halicarcinus lacustris*, Dell, p. 39
1968	*Halicarcinus lacustris*, Holthuis, pp. 111–2
1969	*Halicarcinus lacustris*, Walker, pp. 163–73
1970	*Halicarcinus lacustris*, Lucas, pp. 267–78

TYPE LOCALITY: Lake Pupuke, Auckland.

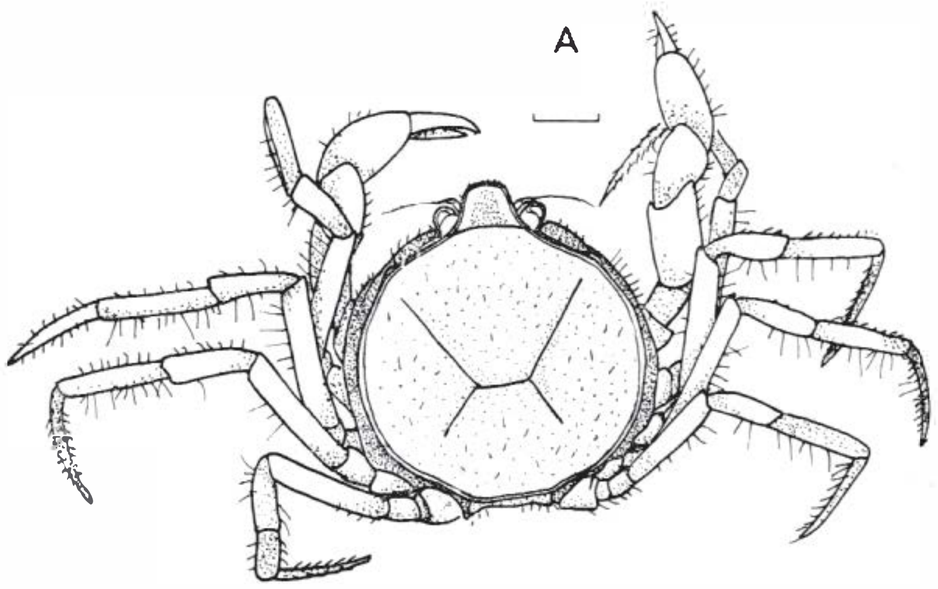
SUMMARY OF LOCALITIES:

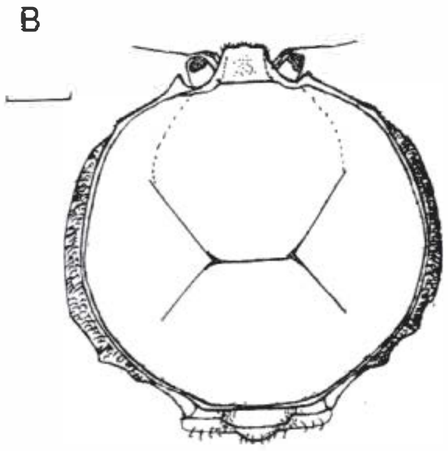
Australia. Victoria: Lake Colac; Moorabool River; Frazer Creek; Wilson's Promontory. (See also localities in Walker 1969, and Lucas 1970.) Lord Howe Island; Norfolk Island.

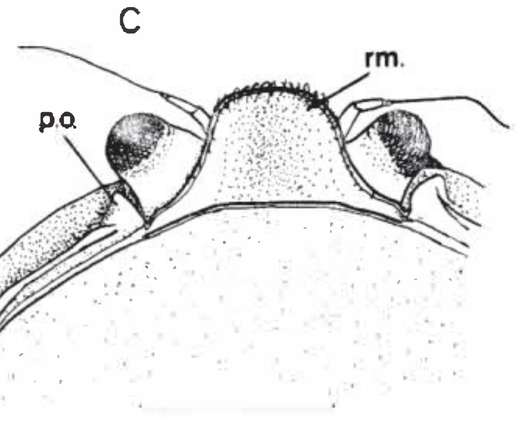
New Zealand. Northland: Lake Waingata and Lake Kanono, Kaipara North Head. Auckland: Lake Waikare; Onehunga. South Auckland: Waipa River; Waikato River.

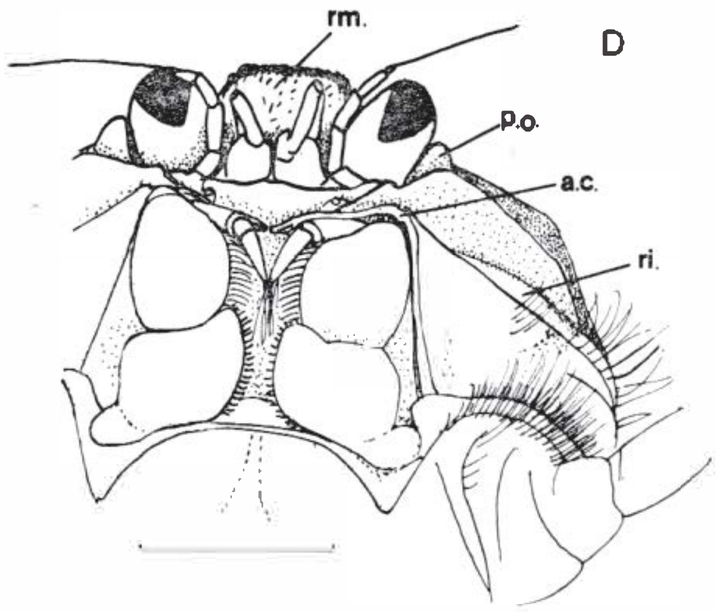
DISTRIBUTION: Confined to freshwater lakes and non-tidal rivers in the north of North Island of New Zealand; south-eastern Australia; Norfolk Island; Lord Howe Island.

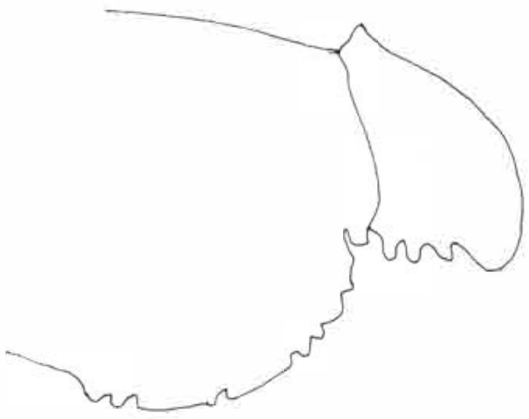
DIAGNOSIS: Carapace subcircular, flat or convex, usually with a single pair of obtuse anterior lateral angles, sometimes a second pair posteriorly. Rim of carapace narrow. Suture between carapace and rostrum almost straight, frontal region not projecting. Rostrum projecting past eyes, obscuring the folded antennules, simple, narrowing little anteriorly, strongly deflexed. Tip of rostrum truncate, broadly rounded or minutely tridentate, Rostrum without ventral ridge, dorsally concave from side to side. Postocular lobe of average size, obtuse. Antennal spine tiny, obtuse. Chela of male not inflated, though large; carpus and palm frequently crenellated on the ventral edge, basal gape and dentation

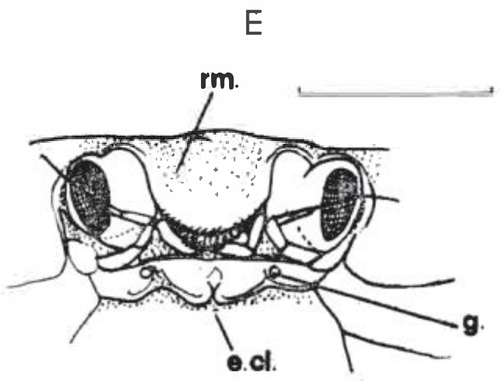


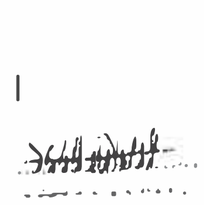


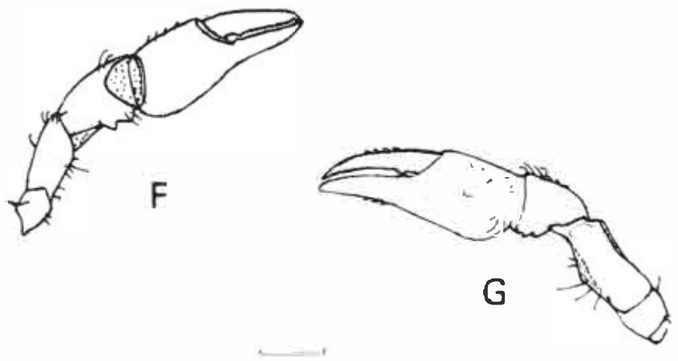












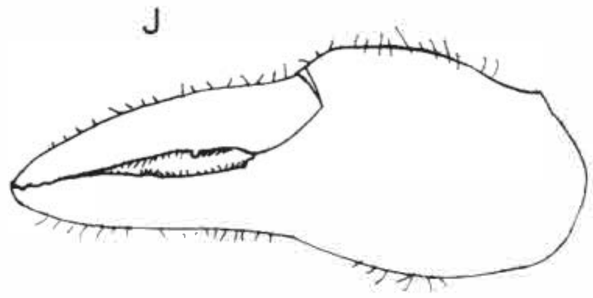


Fig. 41 *Halicarcinus lacustris:* A—Male, dorsal view; B—Female, dorsal view of carapace; C—Rostrum of male in A; D—Ventral view of mouthfield and epistome region, left side; E—Frontal view of male in A, carapace perpendicular to plane of vision; F—Left cheliped of male, anterior view; G—Left cheliped of male, posterior view; H—Left chela of male, posterior view; I—Detail of inner edge of immovable finger of male; J—Left chela of female, posterior view; K (between D and E)—Detail of ventral edge of male palm. (scales represent 1 mm)

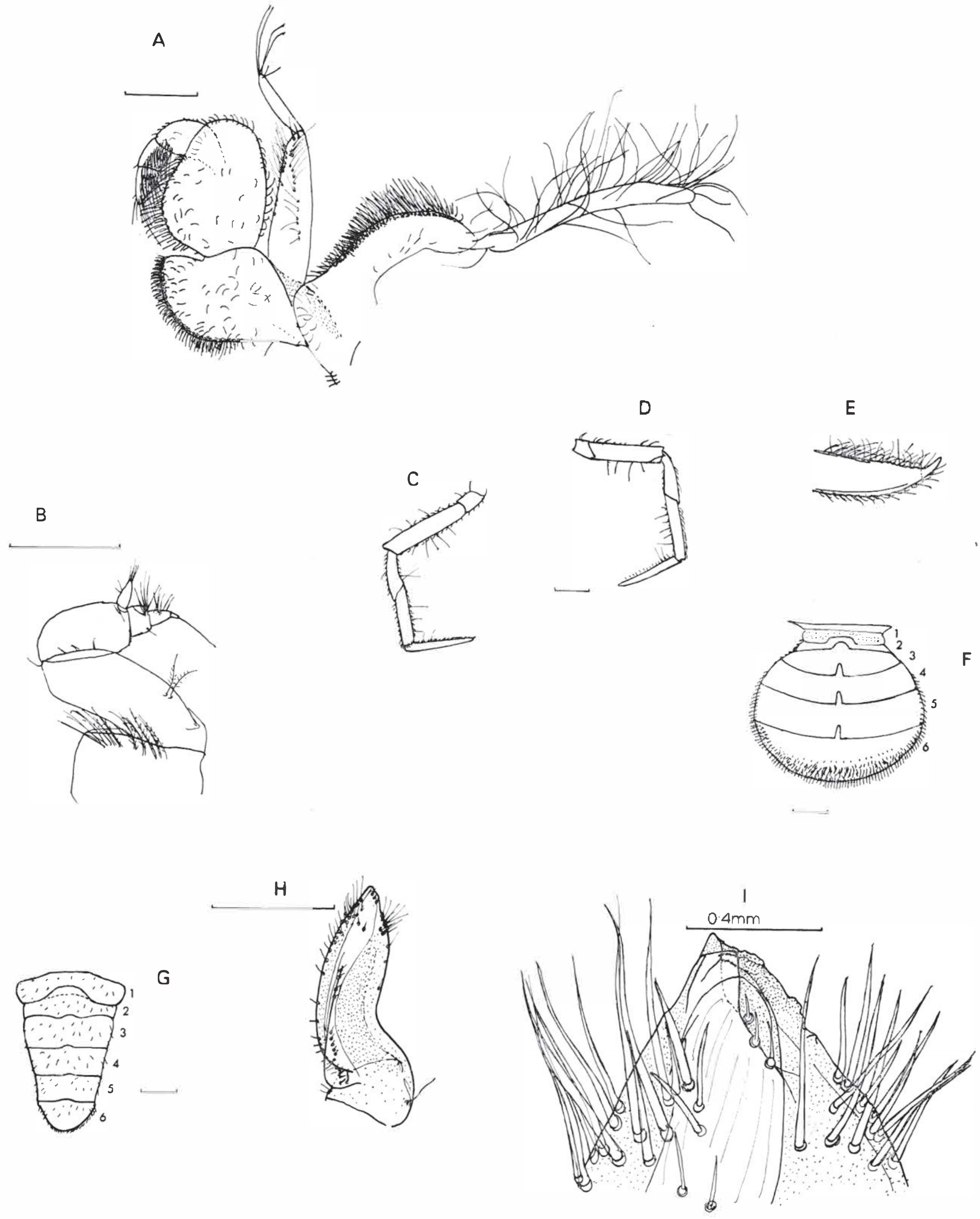


Fig. 42 *Halicarcinus lacustris:* A—Left 3rd maxilliped of male; B—Left antennule of male, lateral-ventral view; C—Left 3rd walking leg of male, posterior view; D—Left 3rd walking leg of male, anterior view; E—Tip of dactylus of 3rd walking leg of male, posterior view; F—Abdomen of female, extended, dorsal view; G—Abdomen of male, extended, dorsal view; H—Left 1st pleopod of male, sternal view; I—Tip of left 1st pleopod of male. (scales represent 1 mm except where otherwise stated)

of fingers reduced, usual basal tooth on the movable finger minute or absent. Segments of the walking legs of average breadth; dactylus straight, devoid of teeth on the ventral edge. Merus of the third maxilliped narrower and longer than ischium. Short abdomen of male adjacent to the carapace rim, segments all subequal in length, their edges all sloping evenly to the rounded tip; sixth segment semicircular. Covered sparsely with short, fine hairs.

SIZE RANGE: ♂♂ 2.5 mm (Norfolk Island) – 11 mm (Kaipara). ♀♀ 2.5 mm (Norfolk Island) – 7.5 mm (Kaipara).

DESCRIPTION: Upper carapace subcircular (ratio w. : l. = 1.05–0.96), flat or convex. Gastrocardiac groove straight and short, cervical grooves long, straight, sloping outward and forward, straight thoracic grooves shorter than cervicals, set at a similar angle to the gastrocardiac groove. No other grooves present. True rim of carapace narrow, angled a little at the level of the first lateral tooth, straighter above the bases of the last pair of legs than on either side. Posterior margin straight. Carapace sides almost vertical, little inflated except along short, straight, anterolateral margin where a knife-edged false second rim is formed outside first, passing back from base of postocular lobe; end of false rim expanded into small, obtuse lateral angle. Second pair of lateral angles absent or very reduced. Branchiostegite projections between legs unobtrusive.

Rostrum originating from carapace level, with almost straight basal suture; frontal region of carapace not prolonged. Rostrum simple. just longer than eyes, wide basally (width = about a third carapace width), narrowing slightly distally, truncate tip gently rounded or minutely tridentate, dorsal surface a little concave from side to side, whole rostrum sharply deflexed downward anteriorly. Ventral surface of rostrum scarcely convex from side to side not ridged. Edge of rostrum separated by tiny cleft from prominent postocular lobe. Postocular lobe obtusely rounded apically, convex against eyestalk. Eyes angles outward as much as forward on short, stout stalks.

Antennules small, not visible dorsally when folded. Basal segment subquadrangular, tuft of hairs on external edge. Second segment of peduncle longest; third has stubby, small ramus with four terminal hairs. Large ramus reduced; without usual small subcircular segments, consisting of only the large basal segment, elongate terminal segment and short terminal bulb. Antennal spine reduced to tiny obtuse lobe.

Interantennular septum reduced to very short, shallow ridge. Epistome short (width=three times length), sunken, separated by ridge from subhepatic regions. Subhepatic regions narrow, not inflated, not obscuring anterior lateral angles from ventral view. Subtriangular pterygostomian regions of average size, without lobes, a sharp rim down longest side, the posterior half of which is hairy. Small Milne Edwards's opening guarded by fringes of long hairs; sterna of third maxillipeds naked.

Endopods of third maxillipeds gaping widely in mid line. Ischium wider than long, median edge strongly curved with three to four rows of short setae, anteromedian lobe short and broadly rounded, articulation with merus of average length, curved, ventral face sparsely setiferous. Merus a little longer than the ischium, as wide as broad, median edge strongly convex with single row of long hairs, curved outer edge elongated with row of setae, antero-external corner expanded into rounded lobe, ventral surface sparsely setiferous. Palp segments all small and stout. Carpus articulating midway along oblique anterior edge of merus, dactylus a little longer than other two palp segments and bluntly pointed.

Basal segment of exopod of average size, narrowing slightly distally, inner edge fringed with single row of feathery hairs, doubled below apex where there is also a horizontal row. Longitudinal row of hairs occurring some distance from the outer edge. Terminal segment long, with four long and two short terminal hairs.

Basal lobe of epipod large, shallow and hairy. Basal portion short, of average curvature, three to four rows of long hairs on anterior edge, separated by suture from lamella. Lamella longer than basal portion, narrowly rounded anteriorly, fringed on both edges with long hairs.

Chelipeds up to twice as long as carapace is wide, massive in large males. Ischium short, subquadrangular. Merus expanded centrally and hairy on ventral edge, distal ventral process long and narrow. Carpus as long as or shorter than merus, not quite as wide distally as long. Palm longer than carpus, depth subequal with or greater than length, but even in large males palm not inflated sideways to form spatulate scoop. Ventral knife-edge of male palm like ventral edge of carpus, frequently deeply crenellated. Rudimentary tooth rarely present on base of movable finger in male. Narrow linear gape present along basal two-thirds of fingers in both sexes, distal one-third occluding and usually shallowly dentate; dentation often reduced, short hairs replacing teeth on inner edges of fingers.

First and second walking legs equal in length, as long as, or slightly longer than chelipeds, third pair of walking legs shorter; fourth pair still shorter. Leg segments a little flattened in cross section. Ischium small, subquadrangular, barely projecting over merus anteriorly, a row of curved hairs on both edges. Merus longest, a little less than one-quarter as broad as long, distal dorsal tooth reduced and obtuse. Carpus three-fifths as long as merus. Propodus as long as carpus, distal V very shallow. Merus, carpus, and propodus with two rows of hairs, one long and straight and one short and hooked, on each edge. Dactylus longer than propodus, straight, tapering, terminating in tiny claw fused with rest of dactylus. Both edges of dactylus hairy; ventral edge with three or more rows of hairs but no teeth, central row of hairs shortest, curved towards claw. Remnants of dentation sometimes present distally.

Female abdomen subcircular, ultimate segment broadly rounded terminally. Central projections on proximal edges of segments three to six very narrow and pointed.

Male abdomen short, reaching to suture between sterna of second and third walking legs, adjacent basally to carapace rim. First segment not enlarged, hardly expanded laterally; second segment longer than the first centrally, shorter laterally; third segment longest; fourth and fifth segments subequal and slightly shorter than third; sixth no longer than previous two, semicircular. Sides of segments 2–5 straight, forming an evenly tapering line, but segment five is little wider distally than the continuance of this tapering would allow. Central protruberance of proximal edge of segment 2 broad and deep, those of other segments are all present, but small and decreasing in size progressively.

First pleopod of the male very short and very stout, little curved, has sparse short setae; longer setae in tufts distally below terminal aperture of vas deferens.

Whole crab setiferous, setae being short and fine, degree of hairiness varying in different specimens.

MATERIAL EXAMINED:

Auckland War Memorial Museum Collection: Norfolk Island, 20/9/1926, 29 ♂♂ 2–7 mm, 7 ♀♀ 2.5–4.5 mm, 2 g. ♀♀ 4.5, 5.5 mm (water mill).
Auckland University Zoology Department Collection: Waikato River, 16/10/65, 1 ♂ 4 mm (coll. D. Cowley, 7 miles north of Hamilton).
Dominion Museum Collection: Lake Kanono, Poutu, Kaipara, 28/9/1953, 8 ♂♂ 6.5–11 mm, 5 ♀♀ 5.5–7.5 mm, 1 g. ♀ 6.5 mm (coll. B. Cunningham, Cr.462); 21/9/1953, 20 ♂♂ 5.5–12 mm, 1 ♀ 6 mm (coll. B. Cunningham, Cr.1630). Lake Waingata, Kaipara North Head, 7/6/1956, 9 ♂♂ 4–11 mm, 2 ♀♀ 4, 5.5 mm (coll. P. J. Burstall, Cr.864). Onehunga Springs, Princess St, Auckland, 5/9/1959, 1 ♂ 4 mm, 1 g. ♀ 5.5 mm, 1 s. ♀ 5 mm (coll. H. J. Chapman, D. M. 964, ovigerous with green eggs when fresh, under overhanging weed, associated with *Paratya curvirostris*, water temp. 60°F).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: August.

COLORATION: Dark brown.

REMARKS: Specimens from Australia and New Zealand have been reported (Fulton and Grant 1902), as varying very little from one another. Not even subspecific divergence has been found in the two countries. *Halicarcinus lacustris* has not been found south of Hamilton in the north island of New Zealand, and reaches its maximum size in the Kaipara Lakes. It differs from most *Halicarcinus* species in possessing an almost uniformly tapering male abdomen, a stout, short, barely curved first male pleopod, and small antennules which are hidden in dorsal view. The crenellation on the ventral edges of the carpus and palm of large males is also unique, as is the absence of dentation on the dactylus of the walking legs. However, other *Halicarcinus* species, notably *Halicarcinus pubescens*, exhibit intermediate conditions of these characteristics, and all other features of *H. lacustris* are in keeping with this genus. Some divergence from the other New Zealand species of *Halicarcinus* would be expected as a result of isolation in fresh water.

H. lacustris is the only New Zealand freshwater crab.

SALINITY TOLERANCE: Only one specimen, collected in the Waikato River among water weed, was obtained alive during this study. It was mid brown with no specific colour pattern. In normal sea water it lived for 5 days, showing a remarkable resistance to osmotic stress.

Halicarcinus tongi sp. nov.

Figs. 43 and 44

TYPES: ♂ holotype w.=4.2 mm, l.=4.6 mm. 2 ♀♀ paratypes, both w.=3.5 mm, l.=4.3 mm (Victoria University of Wellington Zoology Department Collection).

TYPE LOCALITY: Great Barrier Island.

SUMMARY OF LOCALITIES: Little Barrier Island, off Northland; Port Jackson, Coromandel; Mayor Island, Bay of Plenty; off Gannet Island; Wanganui; between Castlepoint and Kahau Rocks, Wellington; Queen Charlotte Sound, Marlborough; Tasman Bay, Nelson; Albatross Point, Antipodes Islands.

DISTRIBUTION: New Zealand endemic, deep water.

DIAGNOSIS: Carapace suboval, longer than broad, narrowing anteriorly, flat or convex. Gastrocardiac and cervical grooves form continuous curve. Two pairs of lateral teeth below very narrow carapace rim; anterior pair small, obtuse; second pair large, acute, arching upward, narrowly rounded apically. Carapace rim itself uninterrupted by angles; suture between carapace and rostrum almost straight, frontal region not produced. Rostrum originating at carapace level, tridentate, the long teeth projecting past eyes. Teeth of rostrum acute, subequal, lateral teeth curving outward and then up, median tooth jutting upwards anteriorly. Single central peak on ventral edge of rostrum, next to the interantennular septum. Postocular lobe of moderate size, acute. Antennal spine absent. Chela of male hardly inflated, small square basal tooth on movable finger in male, other dentation well developed. Segments of walking legs slender, dactylus very narrow and curved with a single row of recurved sharp teeth. Merus and ischium of the third maxilliped subequal in length, ischium wider than merus. Male abdomen short, third segment as wide centrally as first, second segment narrower, third and fourth subequal in length, third with convex edges, fourth narrowing distally as does fifth, sixth an elongate semicircle. First pleopod of male of average length, slender distally with a sparsely setiferous simple tip and a vertical eave.

SIZE RANGE: ♂♂ 4 mm (Little Barrier Island) – 6.5 mm (Castlepoint). ♀♀ 3.5 mm (Great Barrier Island) – 6.5 mm (Nelson).

DESCRIPTION: Carapace suboval, narrowing in front, longer than broad (ratio l.: w.=1.1–1.23). Gastrocardiac groove arching back in mid line, short cervical grooves continuing curve forward, thoracic grooves reduced and sometimes absent. Carapace rim narrow, not angled laterally, shallowly concave above last pair of legs. Posterior margin convex, anterolateral margins short

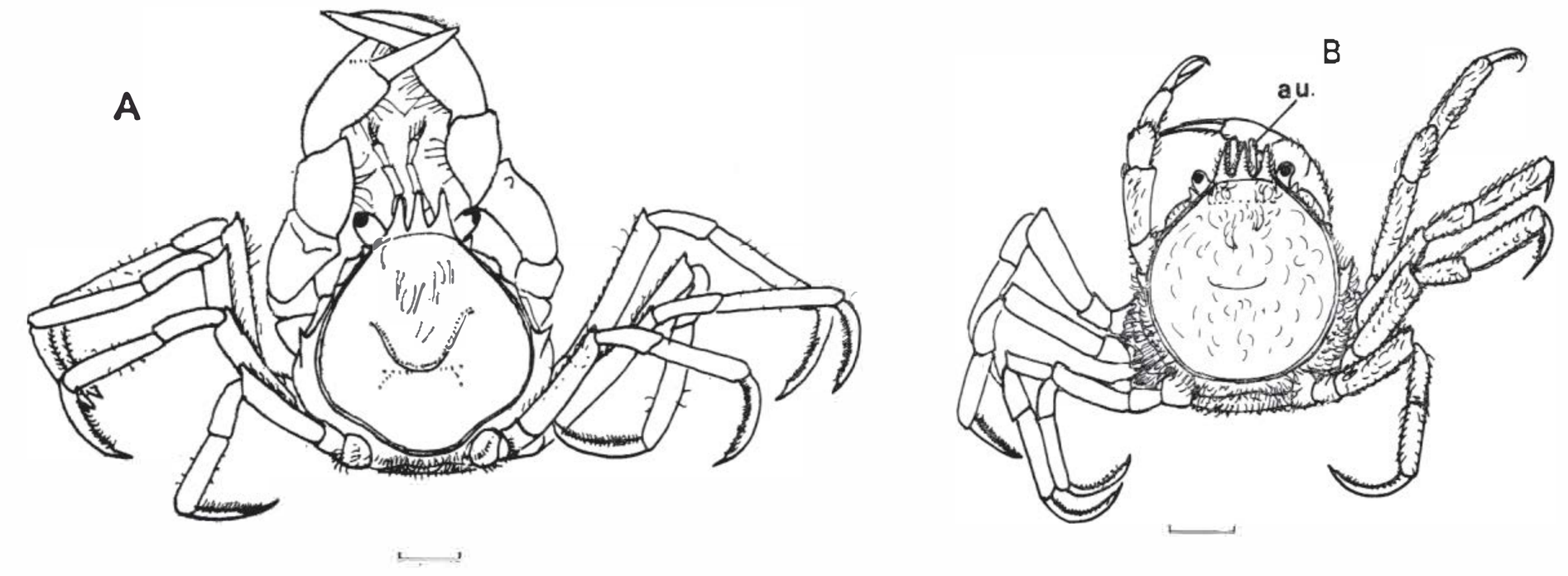


Fig. 43 *Halicarcinus tongi:* A—Male, dorsal view; B—Female, dorsal view; C—Ventral view of mouthfield and epistome region, left side; D—Frontal view of male in A, carapace perpendicular to plane of vision; E—Lateral angles of carapace of male in A; F (bottom left) —Rostrum of male in A; G—Left 3rd maxilliped of male. (scales represent 1 mm except where otherwise stated)

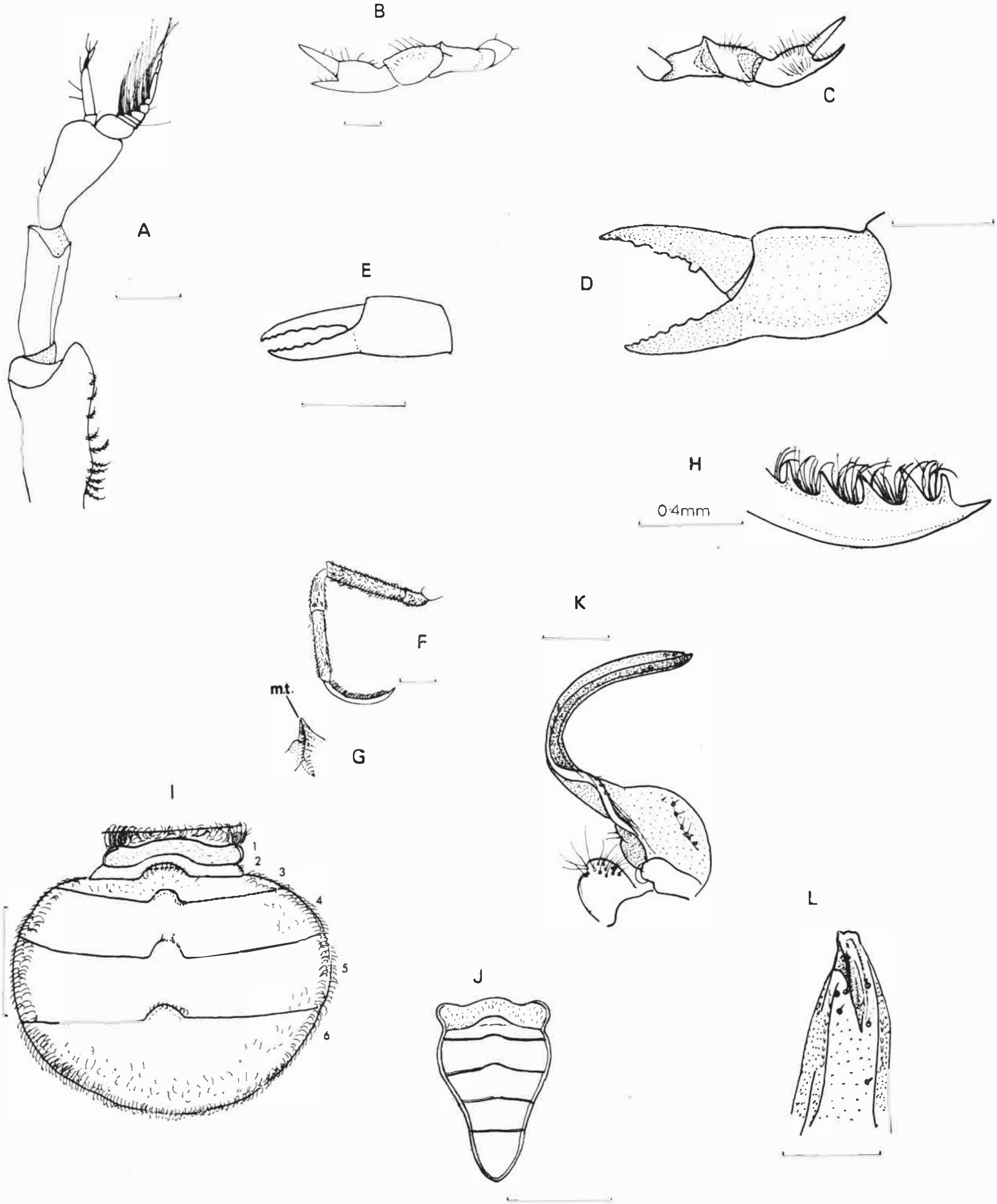


Fig. 44 *Halicarcinus tongi:* A—Left antennule of male, lateral-ventral view; B—Left cheliped of male, posterior view; C—Left cheliped of male, anterior view; D—Left chela of male, posterior view; E—Left chela of female, posterior view; F—Left 3rd walking leg of male, posterior view; G—Joint of merus and carpus of 3rd walking leg; H—Tip of dactylus of left 3rd walking leg of male, posterior view; I—Extended female abdomen, dorsal view; J—Extended male abdomen, dorsal view; K—Left 1st male pleopod, sternal view; L—Tip of left 1st pleopod of male. (scales represent 1 mm except for A (0.5 mm) and for L (0.3 mm))

and straight. Two pairs of lateral angles below the carapace rim; first pair obtuse, hairy; second pair large, slenderly acute, projecting dorsally above carapace rim, sparse scattered hairs below apex. Frontal region of carapace not produced, suture between carapace and rostrum tapering backward a little laterally, straight centrally.

Tridentate rostrum arising carapace level, long, projecting well past eyes. Teeth narrow, bluntly pointed, subequal in length. median tooth slightly shorter than the laterals in dorsal view; concavities between teeth almost reach sutuie at base of rostrum. Laterals bowing outward as well as arching upward and forward, extending level with carapace for the basal one-third of their length, then curving upwards at angle of approximately 45°. Central tooth jutting upward from point of insertion at 45° so that in side view it projects above laterals initially, distal one-third curving downward parallel with carapace again, tip almost level with those of laterals. All three teeth rounded from side to side dorsally and ventrally. Dense row of long, curved setae along outer edge of each lateral tooth, shorter setae forming a row on both edges of median tooth. Ventral posterior edge of rostrum produced in single sharp peak centrally, next to the interantennular septum. Large eyes angled outward as much as forward, on stout stalks. Postocular lobe large and acute.

Antennules dorsally visible when folded. Peduncular segments all more slender in relation to length than usual. Basal segment broader than the others but still elongated, a fringe of short hairs on external edge; second and third segments subequal, third slightly expanded distally. Terminal segment of small ramus long, with four distal hairs; larger ramus reduced, only a few small subcircular segments and an elongated waisted terminal bulb. Antennal spine absent.

Interantennular septum short but prominently ridged. Epistome large, length three-fifths width, not sunken, fused laterally with subhepatic regions, arched along anterior edge and therefore longest centrally. Central cleft on posterior rim large. Subhepatic regions small, expanded into small lobe centrally, not obscuring the anterior angle of carapace. Pterygostomian regions subtriangular, of average size, with both lobes well developed, central lobe in form a bluntly pointed tooth. Fringes of hairs of average length line narrow Milne Edwards's opening. Row of short hairs on anterior edge of septa of third maxillipeds.

Endopods of third maxillipeds gaping moderately in mid line. Ischium subquadrangular, median edge almost straight two to three rows of hairs of average length, anteromedian lobe short and broad, articulation with merus narrow and straight; merus basally narrow, as long as ischium, widening distally until as wide as ischium, median edge strongly curved with single row of long hairs, external edge somewhat curved, anteroexternal corner a little expanded; ventral surfaces of both segments with sparsely scattered setae. Carpus large, articulating a considerable distance from external edge of merus, anterior edge straight. Propodus narrower, subquadrangular. Dactylus long, slender, pointed. Ventral hairs of palp dense and long.

Basal segment of exopod long, slender, tapering a little distally. Internal edge with a row of long hairs, closest together distally. No horizontal row of hairs below the apex, setae sparse near external edge.

Basal lobe of epipod broad, very shallow, sparsely setiferous. Basal portion strongly curved, slender, long, two to four rows of setae of average length on anterior edge, completely separated from the lamella by suture.

Chelipeds not massive, approximately half as long again as carapace is wide. Carpus of male a little longer than merus, both segments extended into peak on dorsal edge where they meet. Palm of male subequal in length and depth with the merus, not inflated laterally, long fingers arching more than palm. Carpus and palm of female subequal in length, slightly shorter than merus, fingers as long as merus. Fingers in both sexes dentate along almost the entire length. Complete occlusion in female; a tiny gape in male, small square tooth on movable finger.

First three pairs of walking legs subequal, length almost twice the carapace width. Fourth pair legs much shorter. Ischium subrectangular. Merus long, width about one-fifth length, tooth acute and large. Carpus half as long as merus, distal projections reduced or absent. Propodus five-sixths merus length, terminating in a pronounced V. Dactylus as long as propodus, strongly curved, flattened, very slender, not narrowing until immediately before the claw. Claw tiny, completely fused with rest of dactylus; dactylus ventral edge has single row of large, narrow, sharp, recurved teeth, increasing in size distally; curved hairs in tufts between teeth.

Female abdomen broad, ultimate segment broadly rounded distally. Central protruberances of proximal edge of segments four to six subequal, that of third wider than rest.

Male abdomen short. First segment hairy, small, not much expanded laterally; second as long, shortening somewhat laterally, edges sloping outward distally; third, fourth, and fifth subequal in length, all longer than first, sides of third convex, widening to be as broad as first; fourth tapering distally; fifth, sides almost straight, narrowing distally; sixth semi-elliptical.

First pleopod of male of average length, distally narrow, bent through more than 90°. Few setae arranged in longitudinal row up ridge, dispersed near aperture of vas deferens. Eave above beginning of opening, short, internally a little ridged, almost vertical.

MATERIAL EXAMINED:

Victoria University of Wellington Zoology Department Collection: Great Barrier Island, –/3/1962, 1 ♂ 4.2 mm, 2 ♀♀ 3.5 mm.
Dominion Museum Collection: Between Castlepoint and Kahau Rocks, 15/8/1956, 1 ♂ 6.5 mm (coll. F. Abernethy, in 70fm (128 m)). Tasman Bay, Nelson, –/11/1934, 1 g. ♀ 6.5 mm (dredged, coll. M. Young). Off Little Barrier Island, –/2/1957, 1 ♂ 4 mm (trawled, attached to *Aphanipathes, Ikatere*). Off Mayor Island, Bay of

Plenty, 27/2/1957, 1 ♂ 4 mm (in 270 fm (494 m), m.v. *Alert*, B.S. of 209 37°20.5′ S., 176°26.5′ E). Off Wanganui, 1/9/1959, 1 ♀ 4.5 mm (coll. Baxter, *Admiral* in 20–30 fm (55–73 m)).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: November.

COLORATION: Not known in life. Greyish brown or yellow brown in preservative.

REMARKS: This small, deep water species shows an interesting transition between the trilobate shelf type of rostrum at carapace level of *H. varius* and the deeply tridentate rostrum depressed below the carapace rim of *H. planatus*. In *H. tongi*, the concavities between the rostral teeth have almost reached the suture at the base of the rostrum. *H. tongi* has well developed teeth or angles on most parts of the body, e.g. the two pairs of well developed lateral angles on the carapace; the long acute rostral teeth; the acute postocular tooth; the recurved, large, sharp teeth on the dactylus. For this reason a Maori adjective meaning "point" was chosen for the specific name.

Genus **Elamena** Milne Edwards

1837	*Elamene*, *Elamena* H. Milne Edwards, pp. 29, 33
	NOT *Elamene* H. Milne Edwards 1853, p. 223
	Elamene A. Milne Edwards 1873, p. 321
?1839	*Ocypode* de Haan, p. 75
1852	*Elamena*, Dana, p. 379
?1853	*Trigonoplax* H. Milne Edwards, p. 224
?1858	*Trigonoplax*, Stimpson, p. 109
1900	*Elamena*, Alcock, p. 385
1906	*Elamena*, Baker, p. 112
?1907	*Trigonoplax*, Stimpson, p. 146
1917	*Elamena*, Kemp, p. 270
1918	*Elamena*, Tesch, p. 19
?1918	*Trigonoplax*, Tesch, p. 4
1927b	*Elamena*, Hale, p. 117
1940	*Elamena*, Gordon, pp. 60–3
1949a	*Elamena*, Richardson, p. 67
1957	*Elamena*, Balss, p. 1632

TYPE-SPECIES: *Elamena mathaei* (Desmarest).

DESCRIPTION: Carapace subcircular, oval, or polygonal. Upper surface flat or concave, without distinct grooves, upturned edges usually forming thin circumscribing rim continuing around rostrum. One or two pairs of lateral angles sometimes present on this rim; lateral teeth below carapace rim completely absent. Never any suture between carapace and rostrum. Simple rostrum broadly truncate or triangular, with a keel ventrally giving rostrum a T-shape in frontal view. (This keel is reduced to a remnant on the posterior half of the rostrum in the subgenus *Trigonoplax*.) Interantennular septum forming pronounced lobe, reduced to a mere ridge in the subgenus *Trigonoplax*. Antennules folding longitudinally beneath rostrum, never visible in dorsal view, basal segment of peduncle with pronounced lobe on anterior outer corner. Corneas of eyes, but not rest of eyestalks, usually visible dorsally at side of rostrum. Eyes angled outward as much as forward. Large epistome almost as long as broad. Endopod of external maxillipeds broad, almost meeting in mid line of mouthfield. Ischium of endopod longer, sometimes much longer than merus, lengthening medially to look like a halberd blade. Merus heart-shaped. Lamella of epipod slightly longer than basal portion. Chelipeds of male more massive than walking legs but not greatly inflated. Dactylus of walking legs with two large teeth beside claw, other dentation absent. Male abdomen with four (?), five, or six segments, female with six. Male first pleopod fringed at tip with longitudinal row of long stout setae. Aperture of vas deferens markedly subterminal.

REMARKS: Although H. Milne Edwards's original description of the genus in 1837 is adequate, both Stebbing (1900) and Kemp (1917) have pointed out that his subsequent reference to the genus in 1953 is almost certainly erroneous, the genus being then credited with a tridentate rostrum. Haswell (1882b) guessed that the "*Elamena mathaei*" described in Milne Edwards's second publication was a young *Halicarcinus planatus* (called "*Hymenosoma planatum*" by Haswell). For that reason, Haswell did not recognise the genus *Elamena* at all.

A comprehensive description of the species of *Elamena* in the British Museum has been provided by Gordon (1940). There is as well Kemp's 1917 account of the Indian species. Both unite the formerly separate genera of *Elamena* and *Trigonoplax*, retaining *Trigonoplax* only as a subgenus. The most important characters separating *Trigonoplax* from *Elamena* sensu stricto are the reduction of the ventral keel on the rostrum to a small posterior tooth (this is absent altogether in one Indian species, *Elamena (Trigonoplax) cimex* Kemp, the slenderness of the male chelipeds, the extremely elongate epistome, and the reduction of the interantennular septum to a ridge rather than to a prominent lobe.

Both New Zealand species belong to *Elamena* sensu stricto. However, they differ from described overseas species in having six separate segments in the male abdomen. In all the British Museum species the abdomen had five segments (Gordon 1940, p. 31), although Kemp maintained that all his Indian species had only four segments. Specimens of *Elamena truncata* from Australia (sent by Dr J. Lucas) have the suture between segments four and five partially obliterated so that Gordon's description of this feature appears to be accurate.

Key to New Zealand Species of *Elamena* (after Melrose 1968)

1 Rostrum broad, rounded; subrostral keel blunt. Carapace rounded. Legs without teeth except one on merus. 2

Rostrum narrow, produced; subrostral keel with strong spine extending from it. Carapace triangular. Legs with many sturdy teeth. . . . . *Elamena longirostris* (off-shore in deep water)

2 Length of rostrum at least half width. Keel deepest anteriorly, tapering behind. Prominent upwardly curved tooth on the distal end of merus of walking legs. Carapace rim produced into two pairs of lateral angles.
. . . . . *Elamena producta*
(littoral)

Length of rostrum less than a third width. Keel shallow, of equal depth throughout. Tooth on merus of each walking leg reduced, obtuse. Carapace without distinct angles. . . . . *Elamena momona*
(deep water)

Elamena longirostris Filhol

Fig. 45

1885b *Elamena longirostris* Filhol, p. 45
1886 *Elamena longirostris* Filhol, p. 403, pl. 46, fig. 7
1916 *Elamena longirostris*, Borradaile, p. 101
1918 *Elamena longirostris*, Tesch, p. 24
1949a *Elamena longirostris*, Richardson, p. 67, fig. 40
1965 *Elamena longirostris*, Griffin and Yaldwyn, p. 43
1969 *Elamena longirostris*, Takeda and Miyake, pp. 181–4, fig. 7

TYPE LOCALITY: On east coast of Stewart Island.

SUMMARY OF LOCALITIES: Off North Cape, off Wanganui, continental shelf off Banks Peninsula, 90–116 m.

DISTRIBUTION: New Zealand, endemic.

DESCRIPTION: "Carapace almost exactly trigonal; its dorsal surface not strongly convex, but nearly flat posteriorly; median gastric region evenly elevated, has scant stout setae; otherwise, cardiac region obscurely demarcated; marginal rim of dorsal surface distinct but not raised; lateral wall of carapace weakly expanded and observable along the anterolateral portion of the marginal rim; a high tubercle, directed obliquely-upwards, on marginal rim near first and second ambulatory legs; sparse short hairs near and at base of present tubercle.

"Front formed by somewhat triangular rostrum which is strongly extended forwards and upwards; rostrum weakly bulged at middle of each lateral border and acute at tip; lower surface of lobe has short but high median crest just near tip; in addition, a very high tubercle, curved forwards near tip and fringed with sparse stout setae at lower surface, is placed medially just in front of antennules.

"Antennular basal segments very stout, each antero-outer angle strongly produced in prominent lobe that is extended forwards; interantennular septum basally developed as blunt septum; accordingly, antennular basal segments not in contact with each other; though they become closer in front; antennular peduncles obliquely folded at each side of median tubercle.

"Antennal basal segment oblique, curved, forming inner part of infraorbital border; second segment longitudinal, hardly reaching anterior margin of antennular basal segment, has fringe of several stout setae along outer border; third segment as long as second, but not as stout; flagellum as long as or slightly shorter than second and third segments.

"Eyestalk short and stout, fringe of several short stout setae at ventral distal margin; anterior border weakly tuberculated in middle, ventral surface near cornea shallowly excavate; its prolongation on to cornea terminally tuberculated. In dorsal view, cornea and distal half of eyestalk observable. Orbit very incomplete, but external angle produced in acute prominent tooth.

"Epistome rather sunken posteriorly. Buccal cavern narrower in front, its antero-external angle produced in tubercular tooth. Third maxillipeds broad so as to close buccal cavern, rather sparsely covered with longish stout setae; antero-inner angle of ischium strongly extended as lobe which is curved obliquely-outwards and somewhat upwards; antero-outer angle of merus also produced in lobe which is greatly extended forwards; carpus expands distally, has prominent spine at distal upper part; propodus crested along entire upper border; dactylus slender, about twice propodus length. Pterygostomian region inflated at the outer middle part, has a high tubercle.

"Chelipeds equal and slender. Merus has terminal tubercle. Carpus swollen distally, as high as palm which is rather slender and covered with more or less longitudinally disposed short setae. Fingers longer than palm, curved inwards near tips; cutting edges microscopically serrated along their whole length; and, in addition, each has three distant, larger spiniform teeth in middle, two smaller ones near tips; tips are sharply pointed and crossing.

"Walking legs very long. Merus covered with several long hairs and short setae, has high terminal tubercle. Carpus also has terminal tubercle, tubercle much smaller than that of merus; a still smaller prominence associated with a tuft of short hairs present near proximal part of upper border. Propodus somewhat depressed, widening distally; its lower border thickly provided with short hairs. Dactylus depressed, slightly curved; both upper and lower borders densely fringed with short hairs or setae; two teeth near the small terminal claw, the main tooth is somewhat directed inwards, the accessory distal tooth somewhat outwards.

"Abdomen roughly eroded, so greatly developed that the whole sternum is covered; it has a median and some transverse elevations; its margin rather irregular, marginal hairs short." (after Takeda and Miyake 1969).

SIZE: Takeda and Miyake's specimen (a female) was 10.6 mm carapace length without rostrum. The male specimen illustrated here is 5.5 mm carapace length including rostrum.

MATERIAL EXAMINED:

Dominion Museum Collection: Trawled between Foxton and Wanganui approx. 50 fm (91 m), m.v. *Admiral*, 14/6/1956, det. J. C. Yaldwyn, 1 ♀ 5.5 mm. Off Hope Shoal Light, Wellington Harbour, Victoria University Zoology Department, VUZ 91, 23/8/1957, from mud and shell bottom, 6 fm (11 m), det. J. C. Yaldwyn, 1 g. ♀ 7.5 mm. Cook Strait area, no detailed locality (L. R. Richardson Collection No. IA), det. J. C. Yaldwyn,

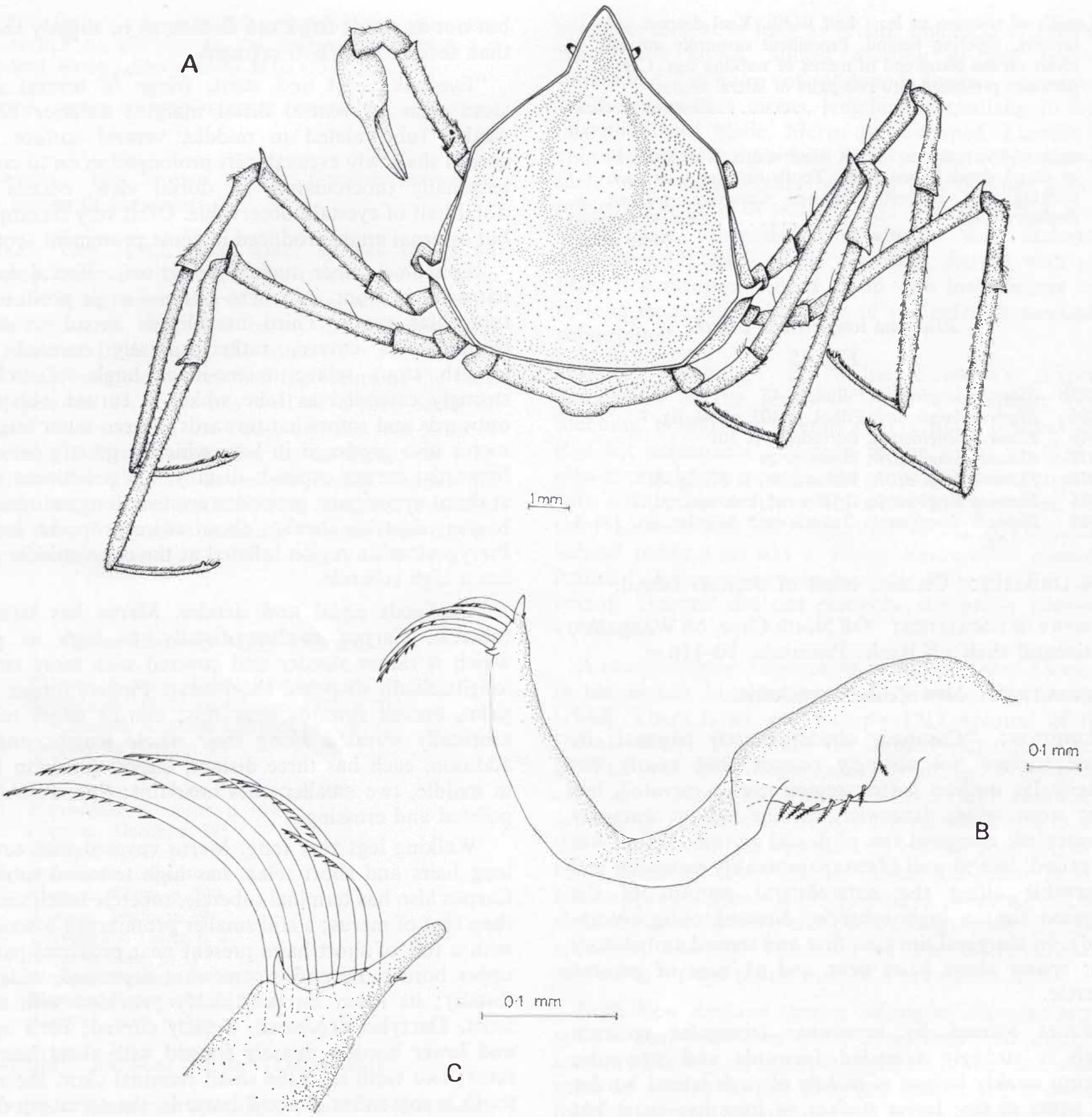


Fig. 45 *Elamena longirostris*: A—Male dorsal view; B—Left 1st male pleopod; C—Detail of left 1st male pleopod

1 ♂ 5 mm, 1 ♀ 6 mm. Trawled Cook Strait approx. 40 fm (73 m), Dec. 1956 (L. R. Richardson Collection No. 10A), det. J. C. Yaldwyn, 1 g. ♀ 10 mm.

MONTHS IN WHICH GRAVID FEMALES COLLECTED: August, December.

REMARKS: This species is evidently rare and was not found in collections made for the present study. Subsequently I have had the opportunity of examining specimens in the Dominion Museum collections from which a figure of an adult male, and details of the first male pleopod has been prepared (*see* Fig. 45). Takeda and Miyake's description is fully adequate for adult female morphology and the general character of the species.

COLORATION: The carapace, chelipeds, and ambulatory legs are generally pale brown; the dorsal surface of the carapace is greyish and the ambulatory legs are somewhat darker (after Takeda and Miyake 1969).

ENVIRONMENTAL NOTES: The species has only been found in moderate depths on the continental shelf.

Elamena producta Kirk

Figs. 46–50, Plate 1

1879 *Elamena producta* Kirk, pp. 395, 396
1886 *Elamena producta*, Filhol, p. 404, pl. 50, figs 1–2
1886 *Elamena kirki* Filhol, p. 405, pl. 47, fig. 6
1901 *Elamena producta*, Lenz. p. 469
1904 *Elamena producta*, Hutton, p. 251
1904 *Elamena kirki*, Hutton, p. 251
1906b *Elamena producta*, Chilton, p. 270
1911a *Elamena producta*, Chilton, p. 294
1913 *Elamena producta*, Thompson, p. 238
1918 *Elamena kirki*, Tesch, pp. 20, 24
1918 *Elamena producta*, Tesch, pp. 20, 24
1929 *Elamena producta*, Chilton and Bennett, p. 777
1929 *Elamena kirki*, Chilton and Bennett, p. 777
1929 *Elamena producta*, Young, p. 152
1949a *Elamena producta*, Richardson, p. 67
1960 *Elamena producta*, Dell, p. 4
1963 *Elamena producta*, Dell, p. 40

TYPE LOCALITY: Wellington, New Zealand.

SUMMARY OF LOCALITIES: Northland: North Cape; Cape Kari Kari; Cable Bay, Doubtless Bay; Goat Island Bay, Leigh. Auckland: Takapuna Reef. Coromandel: Hotwater Beach; Clarke Island, Whangamata. Hawke Bay: Pourerere Reef. Wellington: Castlepoint, East Coast; Riversdale Beach, East Coast; Rona Bay, Eastbourne; Lyall Bay; Island Bay. Cook Strait. Nelson: Totaranui. Marlborough: Queen Charlotte Sound; Kaikoura. Otago: Blueskin Bay; Otago Harbour; Port Chalmers. Stewart Island. Chatham Islands.

DISTRIBUTION: New Zealand, endemic.

DIAGNOSIS: Carapace subheptagonal, two pairs of obtuse lateral angles on carapace rim. Rostrum broadly rounded anteriorly, of medium length, about half as long as wide, a deep keel showing as small central peak dorsally on end of rostrum. Deepest part of ventral keel on rostrum halfway between eye and front of rostrum. Postocular lobe and antennal spine both reduced to obtuse, tiny prominences. Chela of male little inflated, fingers gaping along basal third of length, small rounded tooth on base of movable finger. Segments of walking legs of moderate width, greatly flattened in adults, merus with large sharp distal tooth. Male abdomen long, basally adjacent to carapace, narrowing sharply to penultimate segment which has concave edges, last segment subtriangular. Male first pleopod of moderate length and breadth, single longitudinal row of long stout setae on either side of subterminal aperture of vas deferens, mostly on distal portion past aperture.

SIZE RANGE: ♂♂ 4 mm (Leigh) – 17.75 mm (Lyall Bay). ♀♀ 4 mm (Leigh) – 13 mm (Kaikoura).

DESCRIPTION: Carapace subheptagonal in outline, flat or concave in large specimens, slightly convex in immature ones. Carapace of almost equal length and breadth (ratio w. : l. = 0.89–1.13), narrowing somewhat in front. No distinct grooves or areas on carapace, margin raised upward into a sharp-edged wide rim, continuing round edge of rostrum, commonly with an upper and lower row of curved setae; rest of upper surface naked. Two pairs of lateral angles on carapace rim, always obtuse, variable in size, ridges radiating from these angles toward centre of carapace in young specimens. Anterolateral margin generally more concave than mid-lateral border, posterolateral border convex, posterior border very shallowly convex with suspicion of concavities about bases of last legs, a peak marking outer end of each concavity.

Semicircular rostrum fused with carapace, of average size (width about 1½–2 times as great as length), tipped by a small median peak which indicates end of subrostral keel, flat or slightly convex from side to side, almost horizontal but a little downwardly deflexed anteriorly, rim ringed by hooked short setae which are denser anteriorly and on ventral surface. Ventral keel on rostrum large, thickened, subtriangular; in frontal view, narrowest in middle of anterior edge. Anterior free edge of rostrum making angle of approximately 70° with upper surface, pendulous lobe equivalent to a rounded right angle. Corneas of eyes showing dorsally on either side of rostrum. Postocular lobe small and rounded.

Antennules short, stout, not visible dorsally when folded. First segment subquadrangular, with a large antero-external lobe, tuft of long hairs on ventral surface some distance from edge; second more slender than first; third as stout as first distally; all three subequal in length. Antennal spine reduced to tiny hump.

Interantennular septum large and lobular. Epistome large, almost three-quarters as long as wide, not sunken, continuous with subhepatic regions. Posterior ridge of epistome shallow with small central cleft. Subhepatic regions a little expanded and ridged, not obscuring the anterior lateral angles from ventral view. Pterygostomian regions small and subtriangular, central lobe large, acute, pointing forward, downward, and outward. Smaller second lobe also pointed, projecting almost straight downward. Row of curved setae near anterior edge of sterna of third maxillipeds.

Endopods of third maxillipeds almost meeting in mid line, sturdy and laterally expanded. Ischium shaped like halberd blade, median edge over three times as long as outer edge, gently curved with several rows of short setae. Anteromedian corner of ischium expanded into broad, acute, narrowly rounded lobe, posteriomedian corner prolonged into even larger lobe, articulation with merus broad and subequal with external edge. Merus three-fifths as long as, and narrower than ischium, wider than long, heart-shaped, median edge of inner lobe with a few rows of hairs only slightly longer than on the ischium, following curvature of ischium median edge. Palp segments large. Carpus articulating centrally between two distal lobes of merus, but a little nearer external edge, anterior edge of carpus almost straight. Slender, pointed dactylus almost twice as long as square propodus.

Basal segment of exopod very narrow, tapering anteriorly, inner edge with single row of long, feathery hairs, a second short, longitudinal row below apex. No

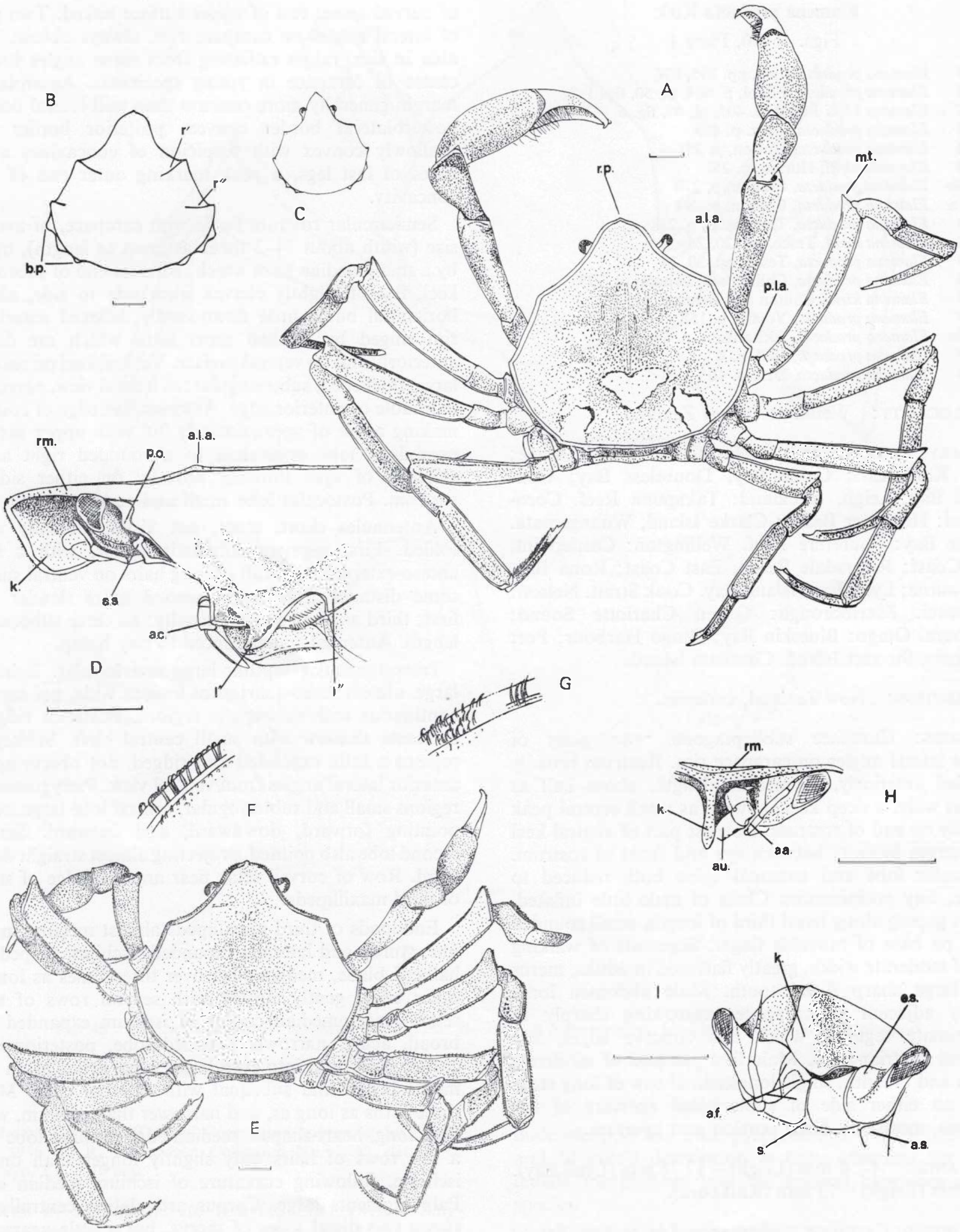


Fig. 46 *Elamena producta:* A—Male dorsal view; B—Immature male, dorsal view; C—Immature male, dorsal view; D—Lateral view of rostrum of male in A; E—Female, dorsal view; F—Rim of carapace along left posterolateral border; G—Rim of rostrum, setae increasing towards tip; H—Frontal view of male in A; I—Frontal and slightly lateral view of male in A, left antennule removed. (scales represent 1 mm)

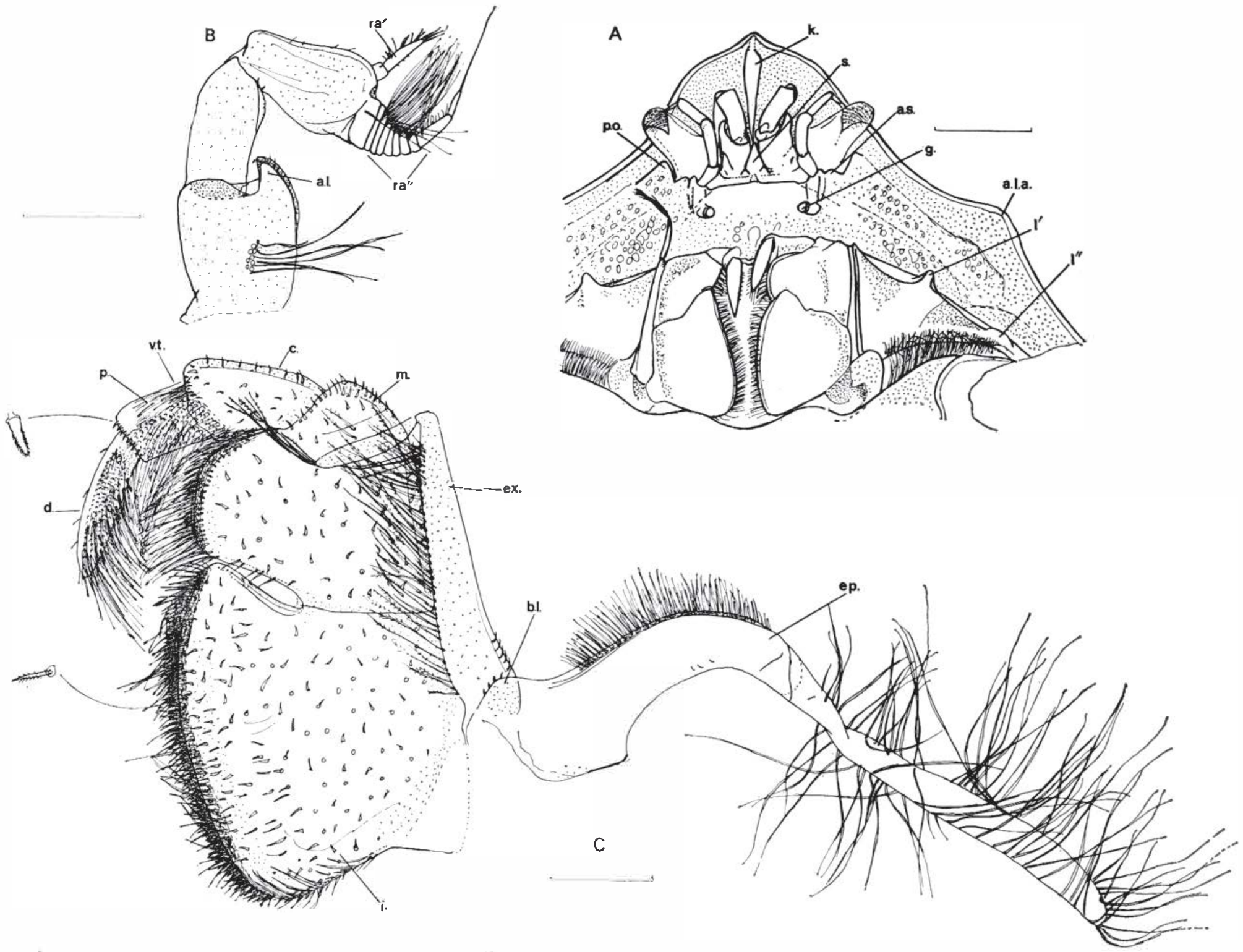


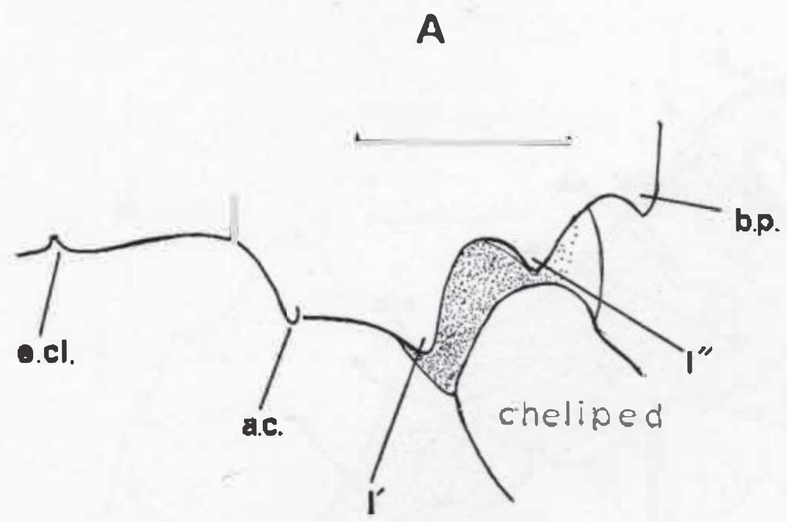
Fig. 47 *Elamena producta:* A—Ventral view of mouthfield and epistome region; B—Left antennule of male, lateral-ventral view; C—Left 3rd maxilliped of male. (scales represent 1 mm)

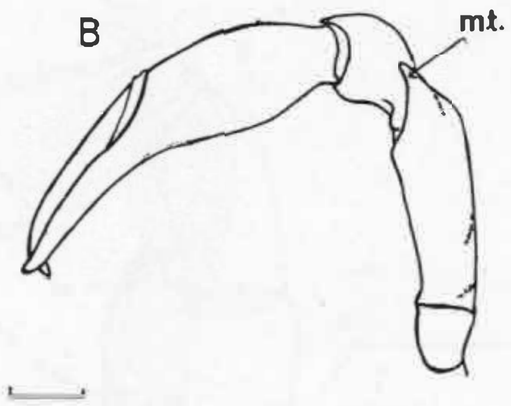
horizontal row of hairs near apex, external edge with a few short setae proximally.

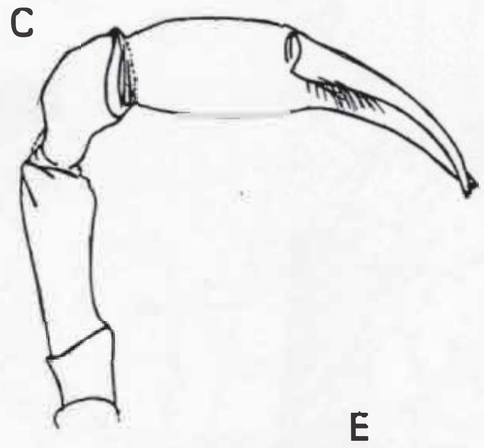
Basal lobe of epipod shallow with few setae. Basal portion deeply curved, slender, a single row of setae on anterior edge. Lamella slightly longer than base, broad, densely fringed with long hairs.

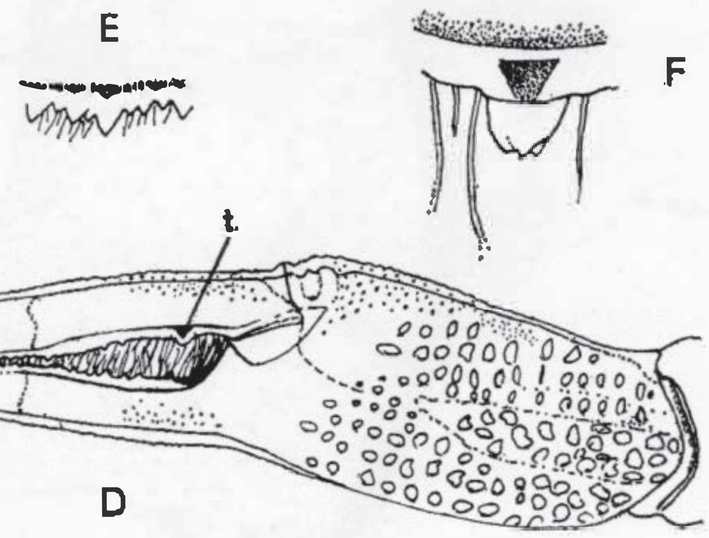
Male cheliped less than twice as long as carapace is wide (1.33–1.69 times carapace width), massive. Female cheliped still shorter, less massive. Ischium short, slight projection of ischium meeting similar projection on merus where their ventral edges meet. Merus long, pronounced ventral projection. Carpus not two-thirds merus length, little expanded distally, Palm as long as, but slightly shorter than merus, much shallower than long, not much inflated sideways. Fingers slender, spooned, as long as palm. Almost perfect occlusion and distinct dentation over distal two-thirds of fingers of females and young males, a basal linear gape. Weaker dentation on margins of fingers in adult males, but occlusion still good, basal gape enlarged, small rounded tooth at base of movable finger.

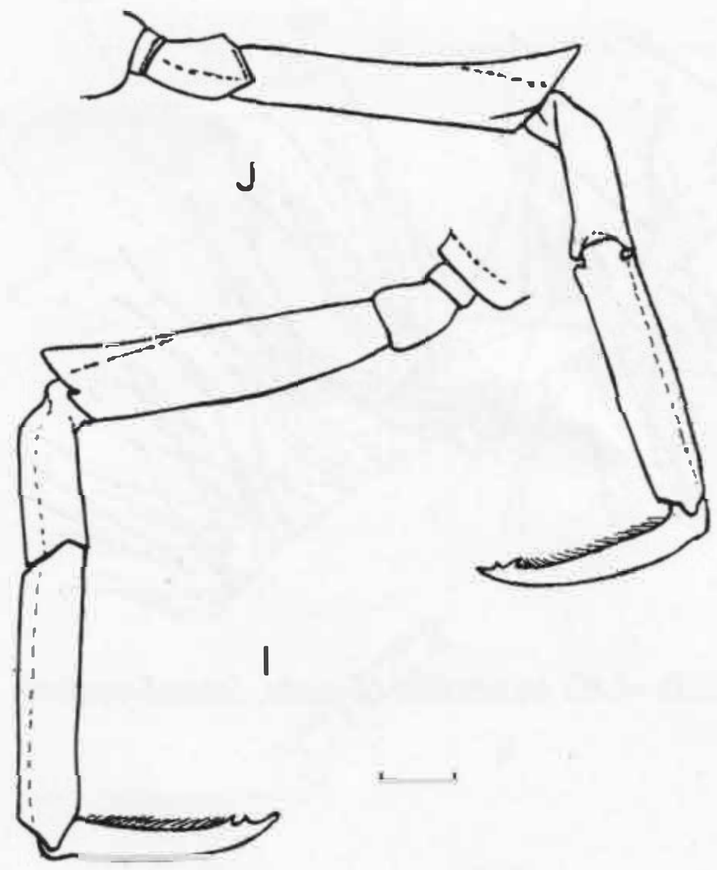
Second pair of ambulatory legs longest, twice as long as carapace is wide. First pair of walking legs barely shorter than second; third pair as long as or a little shorter than the second; fourth pair still shorter (ratio l. of fourth walking legs: w. of carapace=1.2–1.5). Ischium, merus, carpus, and propodus of walking legs all flattened, merus and propodus usually wafer-thin throughout their breadth, often with tiny, hooked setae on ridged dorsal and ventral margins. Ischium shortest on upper edge, a short obtuse projection on anterior face over merus. Merus and ischium meet in peak on dorsal edge. Pronounced keel ending in acute upwardly angled tooth on distal end of merus. Merus broader than any other segment, breadth approximately one-quarter to one-fifth length. Carpus short, about half merus length, distal pair of projections not well developed. Propodus about five-sixths merus length, pronounced distal V. Dactylus flattened, only three-quarters propodus length, almost straight, curving a little distally. Ventral surface has row of short hairs which are replaced by two teeth; first large, recurved; second small, straight,

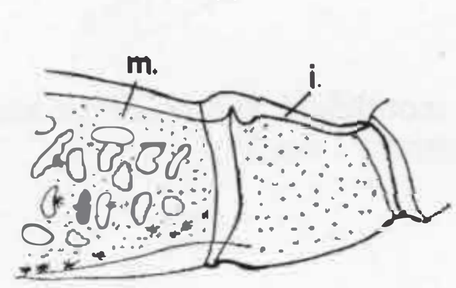


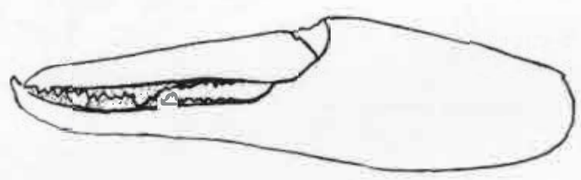


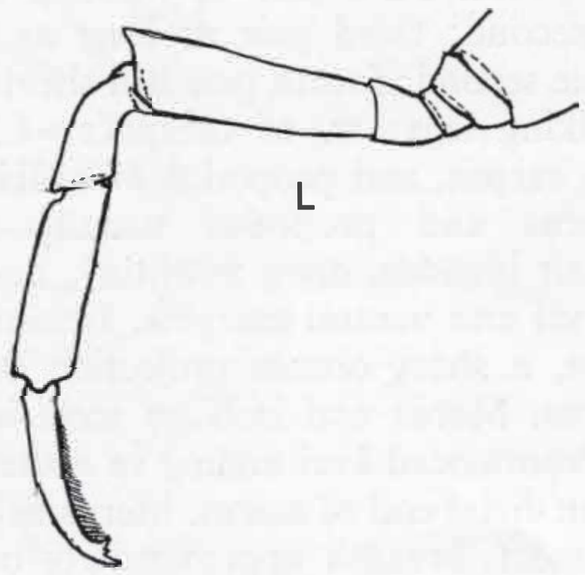












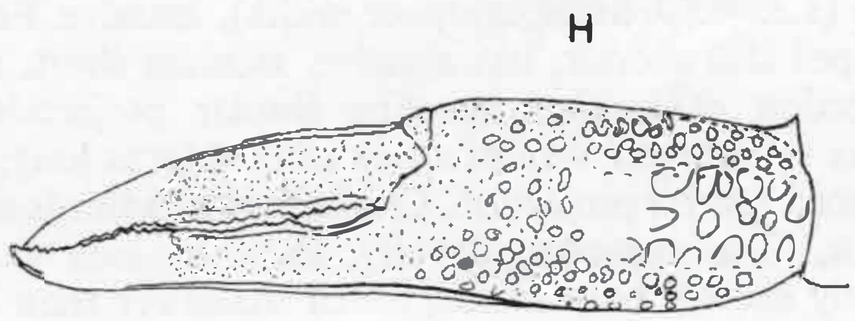
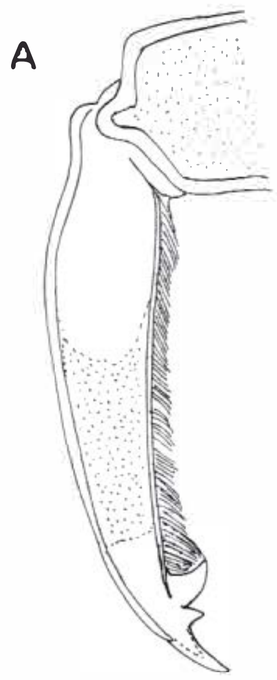
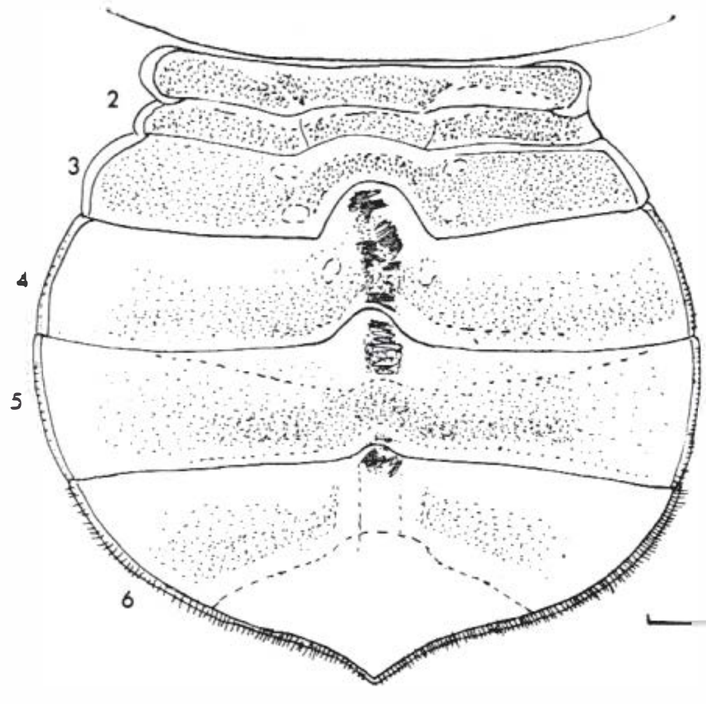
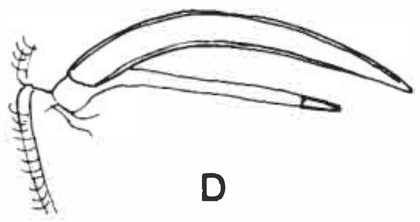
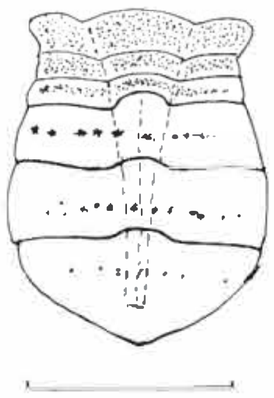


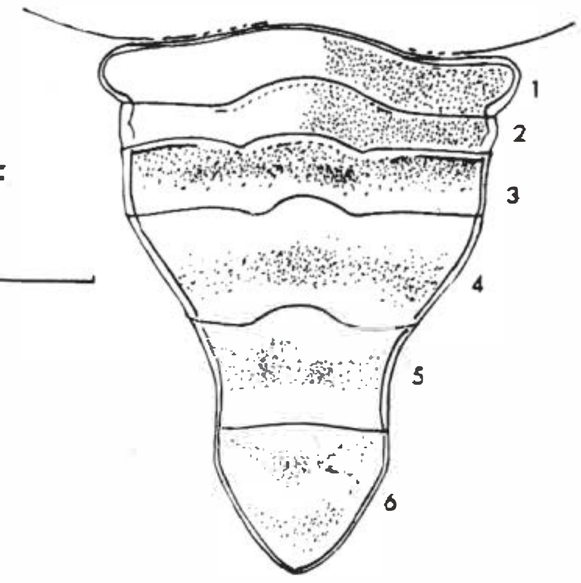
Fig. 48 *Elamena producta:* A—Frontal view of left side of epistome region showing lobes of pterygostomian region and branchiostegite projection behind cheliped; B—Left cheliped of male, posterior view; C—Left cheliped of male, anterior view; D—Left chela of male, posterior view; E—Detail of dentation on distal end of movable finger; F—Detail of basal tooth on movable finger; G—Left chela of immature male, posterior view; H—Left chela of female, posterior view; I—Left 3rd leg of male, posterior view; J—Left 3rd walking leg of male, anterior view; K—Detail of joint of ischium and merus, posterior view; L—Left 4th walking leg of same male. posterior view. (scales represent 1 mm)

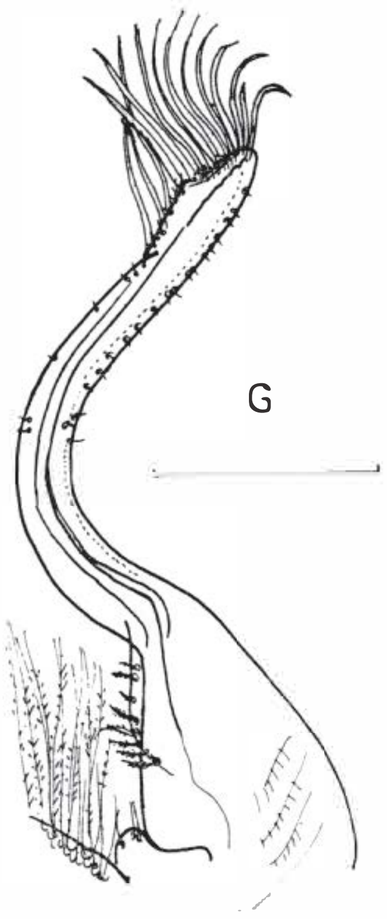


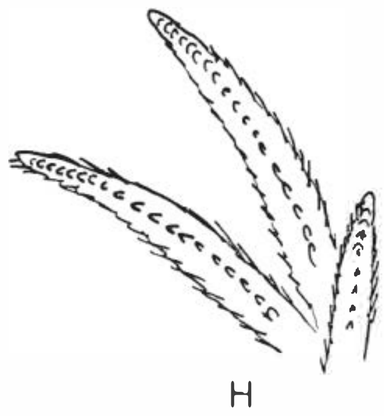












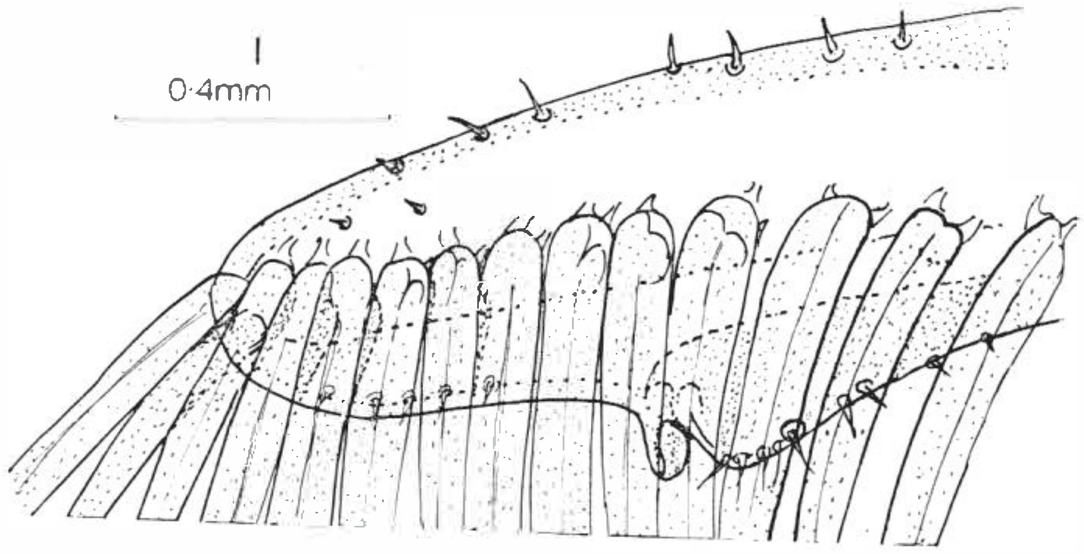


Fig. 49 *Elamena producta:* A—Dactylus of left 3rd walking leg of male; B—Dactylus of left 3rd walking leg of male; C—Extended female abdomen, dorsal view; D—Left 2nd pleopod of female; E—Extended abdomen of immature female (carapace width =4.1 mm), dorsal view; F—Extended male abdomen, dorsal view; G—Left 1st pleopod of male, sternal view; H—Tips of 1st three setae in langitudinal row at end of 1st pleopod; I—Tip of 1st male pleopod showing only the bases of longitudinal row of setae. (scales represent 1 mm except where otherwise stated)

adjacent to small fused claw. Dactylus expanded laterally about one-third from base, this expansion being least on dactyl of fourth walking leg which is smallest.

Abdomen of gravid females sometimes as wide as long, usually narrower. Last segment not greatly longer than rest, ends in central shallow peak. Central concavity on proximal edges of segments two to six, deepest and widest on segment four, decreasing in breadth and depth progressively, very shallow and broad on segments two and three. Male abdomen long, reaching suture behind sterna of cheliped, not separated by ledge from rim of carapace. First segment small, hardly expanded laterally; second segment as long as, but fractionally narrower than first, third segment barely longer than second, not narrowing distally, with straight sides; fourth and fifth segments subequal in length, longer than third; sixth segment barely longer than fourth and fifth; sides of fourth just convex, narrowing markedly distally; fifth narrowing only slightly distally, sides concave; sixth segment subtriangular, rounded apically; central convexity on proximal edge of segments one to five, narrowing progressively, convexities of four and five subequal.

First pleopod of male of average length, bent through less than 90°, moderately slender. Longitudinal ridge on distal portion widening below subterminal aperture of vas deferens which is followed by small acute lobe, pendulous like end of ridge below aperture. Single row of about 14 very long, stout setae on each side of aperture, most setae originating between aperture and rounded tip of pleopod.

MATERIAL EXAMINED:

Personal collecton: Clarke Island, Whangamata, Coromandel, 19/4/1965, 2 ♂ ♂ 7.5 mm, 6 mm. Goat Island Bay, Leigh, 29/11/1964, 1 ♂ 6.5 mm (coll. B. A. Foster); 30/11/1965, 1 s. ♀ 10.5 mm (coll. B. A. Foster); 26/11/1965, 1 ♂ 5 mm (coll. B. A. Foster); 21/12/1965, 1 g. ♀ 7 mm (coll. B. A. Foster); 8/2/1965, 1 ♂ 8 mm, 1 ♀ 6.7 mm; 9/2/1965, 1 ♂ 4.1 mm, 3 ♀ ♀ 4.1–8.3 mm; 8/5/1965, 1 ♀ 6.8 mm; 8/2/1965, 2 ♂ ♂ 5 mm.

University of Auckland Zoology Department Collection: Stewart Island, 2 g. ♀♀ 10, 10.5 mm. Leasks Bay, Stewart Island, 21/8/1963, 2 ♂ ♂ 12.5, 8.5 mm, 3 g. ♀ ♀ 10.2–12.4 mm.

Edward Percival Marine Laboratory Collection: Seal Reef, Kaikoura, 3/9/1964, 1 g. ♀ 8.9 mm (from stipe of *Lessonia*, K 424 E). Seal Reef, Kaikoura, 3/9/1964, 1 ♂ 6.6 mm, 1 g. ♀ 7.9 mm (from *Carpophyllum* fronds, K 410 A). Raramai Tunnel Point, Kaikoura, 22/5/1963, 2 g. ♀ ♀ 12, 12.7 mm (from holdfast of *Durvillea* at low spring tide); 27/8/1965, 9 g. ♀ ♀ 9–13 mm (K 653 D–F).

Victoria University of Wellington Zoology Department Collection: Lyall Bay, Wellington, 29/10/1964, 1 ♂ 17.7 mm (under rocks and among weed). Castlepoint, 1 ♂ 2.7 mm. Wellington, 1 ♂ 3 mm.

University of Canterbury Zoology Department Collection: Kaikoura, –/8/1965, 5 ♂ ♂ 5.5–14 mm.

Dominion Museum Collection: Port Hutt, Chatham Islands, 1 ♂ 7.5 mm (Chatham Islands Expedition, St.49). Kaingaroa, Chatham Islands, 2 ♂ ♂ 8.5 mm (Chatham Islands Expedition, St.16). Pourerere Reef, Hawke Bay, 1959, 1 g. ♀ 8 mm (coll. L. O. Bousefield, found with *Haliotis*, Cr.873). Seatoun, Wellington, –/7/1934, 1 g. ♀ 14.5 mm (Ac 1934/88, Cr.376). Rona Bay, Wellington, 22/8/1964, 1 g. ♀ 12.5 mm (coll. S. G. Sedge, symbiotic in *Haliotis iris*). Lyall Bay, Wellington, 22/8/1954, 1 ♀ 10 mm (coll. F. Demant, symbiotic in *Haliotis iris*). Hotwater Beach, Coromandel, 22/10/1961, 1 ♀ 7 mm (coll. H. J. Chapman, associated with *Haliotis iris*). Riversdale Beach, Wellington, 17/1/1964, 1 ♂ 7.5 mm (coll. M. A. Crozier, in weed at low tide, Cr.1449). Cod stomachs, off White Rocks, Queen Charlotte Sound, 27/9/1963, 1 g. ♀ 13 mm (coll. M. A. Crozier). Cape Kari Kari, Northland, 5/10/1963, 1 ♂ 8.5 mm, 2 g. ♀ ♀ 10.5, 11 mm (rock pool, N.Z. Marine Department, Cr.1437). Stewart Island, 1 ♀ 10 mm (coll. M. A. Crozier in *Ulva*, Cr.1544). Goat Island Beach, Leigh, 10/1/1962, 1 ♂ 10.5 mm. 1 ♀ 4.5 mm, 1 s. ♀ 8.5 mm (coll. R. K. Dell). Cable Bay, Doubtless Bay, 18/11/1963, 1 g. ♀ 9.5 mm (coll. R. K. Dell, Cr.1466). North Cape (rock pool), 18/9/1963, 1 ♂ 6 mm (coll. J. McCallum, N.Z. Marine Dept.). Leasks Bay, Stewart Island, 12/3/1965, 4 ♂ ♂ 12.5–14.5 mm (coll. M. A. Crozier). Totaranui, Tasman Park, Nelson, 19/5/1963, 2 ♂ ♂ 10.5, 11.5 mm, 1 g. ♀ 13.5 mm (on *Haliotis iris*, coll. R. K. Dell, Cr.1310).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: January, May, July, August, September, October, November, December.

REMARKS: Filhol's figures of *E. producta* and *E. kirki* make it clear that only one species was involved. Lenz (1901) observed that the development of the lateral angles of the carapace was very variable in *E. producta;* Filhol's *E. kirki* was differentiated almost solely on the slight difference in shape of the carapace resulting from the reduction of these angles.

E. producta closely resembles the type of the genus *Elamena*, *E. mathaei* (Gordon 1940, pp. 63, 64, 67, figs. 1a, b, 2, 3). However, in *E. mathaei* the carapace is consistently wider than long; the chela of the male is more inflated; the two teeth on the end of the dactylus are subequal; the male abdomen is narrower and reaches its minimum width between the penultimate and preceding segment not halfway along the penultimate segment; the first pleopod of the male is bent further, and the row of 10 to 12 setae near its tip are longer and more slender than in *E. producta.*

COLORATION (Plate 1, facing p. 32):

Carapace: No constant sexual difference in coloration was found; the carapace varying from blackish-brown to olive-brown, red-brown, purple, cream, or white.

Small specimens of *E. producta* often surprisingly resembled those of *H. cookii* with blindingly white carapaces. Where the carapace is principally white, a very blotched effect of grey, yellow, or green, produced by a mixture of chromatophores, is often present. This gives the effect of a lichen or *Lithothamnion* encrustation. Frequently the rim of the carapace and rostrum is disruptively coloured, flecked with white, alternating with dark purple or brown.

Where the carapace is pale brown, longitudinal pale streaks and paired, pale, circular patches can often be seen as in some species of *Halicarcinus.* Striking white patches are often present at the base of the last pair of legs. Sometimes these posterior spots are very regular

in shape; almost invariably there are yellow chromatophores in the centre of each spot. Infrequently, the posterior white patches spread on to larger areas of the carapace and, rarely, there is a central white patch on the posterior edge of the carapace.

Legs: The legs are often purple-tinged, and not conspicuously banded, but the dactylus of each walking leg has two white bands, one distal and one basal, flanking a central, darker strip. The cheliped fingers are white distally. There is sometimes a diffuse white bank two-thirds along the merus of the walking legs and chelipeds.

A pale or white area at the very base of every segment of the walking legs gives them a distinctively segmented appearance.

This very striking coloration would be expected to be conspicuous in its sandy habitat, but it is strangely difficult to detect a specimen on the bottom of a pool, probably because large dark pebbles, small dark gastropod shells, algal fragments and ophiuroids already break up the uniform sandy background.

ENVIRONMENTAL NOTES:

Substrate: At Auckland *E. producta* was taken from a very restricted environment, under large boulders in coarse sand or pebbles on the bottom of pools in the lower mid-littoral or from deeper pools near the mid-tide level. The pools were invariably more than 60 cm across, and over 15 cm deep at all phases of the-tide.

Although coralline cover or turf was invariably present on these rocks and often *Melanthalia*, *Carpophyllum plumosum*, *Carpophyllum elongatum*, *Pterocladia*, and other small seaweeds, *Elamena producta* was never collected from algae. *H. cookii* was frequently found in these algae in the same pool.

The few young specimens of *E. producta* collected also came from the shell on the bottom of pools and not from seaweed.

E. producta like *Halicarcinus cookii* is restricted to hard shores of moderate exposure.

Richardson (1949a) says that *E. producta* is found as a commensal of paua, but I have no further evidence.

Density: Around Auckland, *E. producta* is rather rare. At Leigh, up to three were sometimes found in a single pool in summer. Northern specimens did not approach the size commonly found in southern collections. Colder conditions therefore appear to favour *E. producta.*

Desiccation: *E. producta* dies quickly (within 3 hours) when removed from water.

BEHAVIOURAL NOTES:

Thigomataxis: Specimens kept together without rocks would cling loosely together, sometimes moving away to separate areas of the aquarium. Small specimens would often cling to the carapace of large ones.

Alarm reactions: *Elamena producta* is difficult to see on the bottom of a pool immediately after rocks have been removed. It remains motionless, crouched against the sand while ophiuroids under the same rock writhe away. After 1 or 2 minutes the settling sand reveals a faint red, purple, or brown shape sidling towards the side of the pool. Specimens will also burrow backwards into the sand until partially covered.

E. producta has a very characteristic alarm reaction. When repeatedly prodded and lifted off the substrate, there is a sequence of movements from the normal walking position (*see* Fig. 50) to a posture with chelipeds spread widely and second walking legs pressed against them, and finally with the walking legs and chelipeds all parallel and approximately at right angles to the carapace. The last posture (Fig. 50b) is also adopted when *E. producta* is dropped into water. As the crab floats down with legs extended and pressed together, it turns over and over like a scrap of red alga drifting in the current. Each walking leg lies above and slightly crossed over the previous one; the fourth pair are directed a little forwards, the third pair at right angles to the longitudinal axis of the carapace, the second at a similar angle but fractionally in front and below the third, and the first just slightly backwards. The chelipeds slope back below the walking legs so that the chelae are visible behind the other legs in dorsal view, halfway along the span of the walking legs. The white bands on the dactyli of the walking legs and on the fingers of the chelae resemble the crenellated edge of detached and decaying algal fragments. This posture is held for a minute at most, usually for 30 seconds.

This is the only species investigated showing straightened rigidity of the legs when alarmed. Sometimes the legs overlap but are simultaneously half bent at merus-carpus and propodus-dactylus joints, a posture like that adopted by *H. pubescens*. In *E. producta* this pose is transitory, lasting only a few seconds before the crab unbends its legs and runs around or adopts the straight-legged posture described above.

Very rarely *E. producta* lies on its upper carapace with the legs folded inwards under the carapace. This has only been observed as death from osmotic stress or poisoning approaches.

Both males and females of *E. producta* have essentially the same "threat" posture as large males of *H. whitei* and, to a lesser extent, *H. varius*. The chelipeds are extended laterally and the fingers spread (*see* Fig. 50b). The carapace is raised anteriorly until it is almost vertical and the walking legs arranged to provide support (*see* Fig. 50c). This posture is often a transitory stage in the assumption of the cryptic escape posture (*see* Fig. 50d).

E. producta is a sluggish crab; in the laboratory it clings to the underside of small pebbles with the chelipeds extended and gropes weakly at any food swimming past. It was never seen pursuing food like other more voracious species of Hymenosomatidae, and was the most fragile species examined. Its pebbly substrate is considerably unstable and autotomy is highly developed. Rough handling or addition of alcohol to the water both produce almost instantaneous shedding of most of the walking legs although the chelipeds are usually retained.

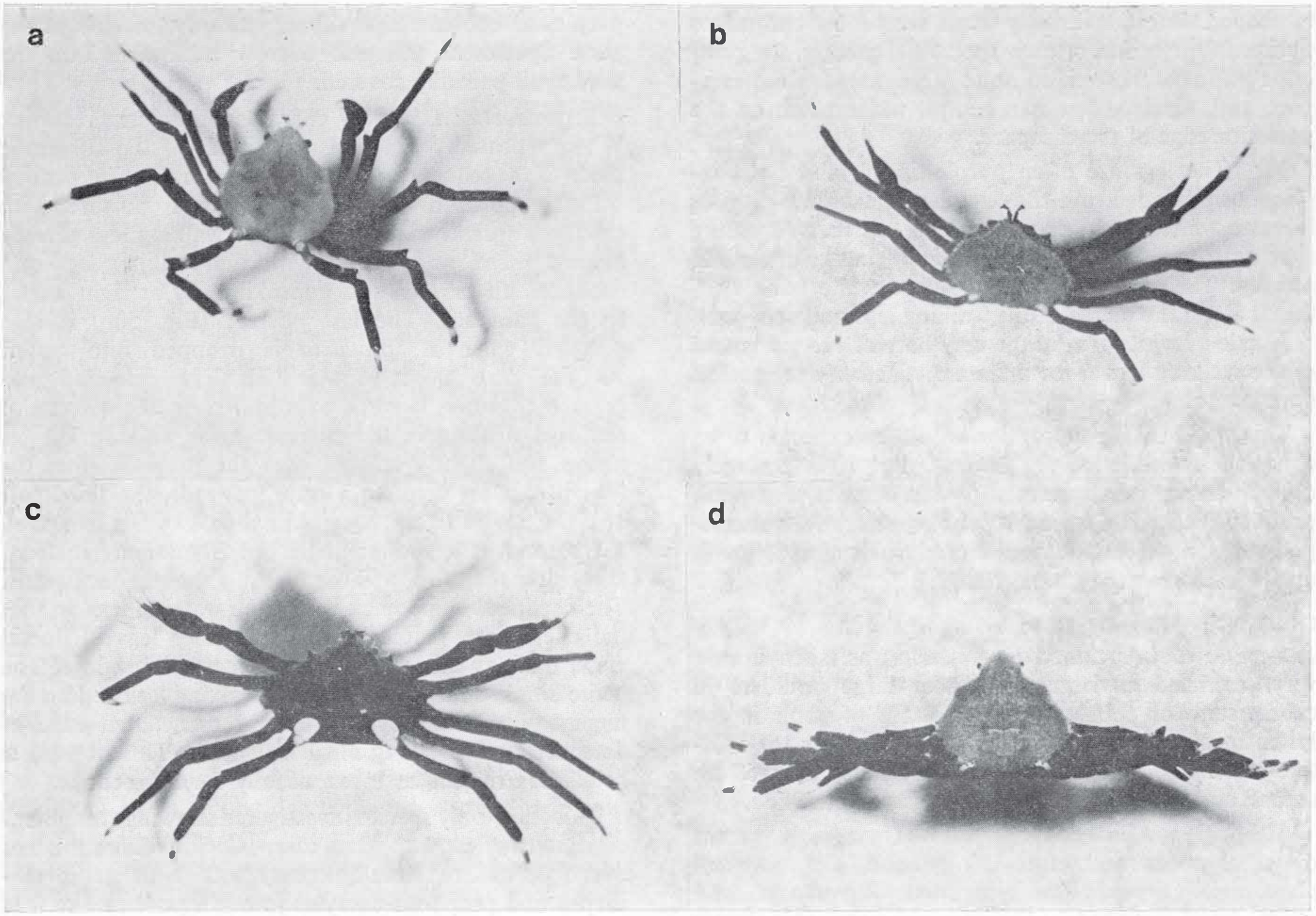


Fig. 50 *Elamena producta:* a—Walking; b—Stage 1 in alarm reaction; c—Stage 2 in alarm reaction with carapace tipped further, the chelipeds straightened and the walking legs directed further backwards than in Stage 1; d—Stage 3 in alarm reaction, or the posture adopted when the species is dropped into water *Photograph B. A. Foster*

Food preferences: In the laboratory *E. producta* ate pieces of polychaete which were held lengthwise in the two chelae and gradually pushed into the mouthparts as in *Halicarcinus cookii.* Large talitrid amphipods were also consumed. No dead amphipods or polychaetes were accepted, and ophiuroid fragments were always rejected even when these were still mobile.

Epifauna: Specimens from Auckland were almost invariably clean of algal growth or sessile animals. One specimen from Leigh had a fragment of a sponge on its carapace. Specimens from Christchurch and Wellington usually had some *Spirorbis* on leg bases and carapace—one crab had as many as 40.

Elamena momona sp. nov.

Figs. 51 and 52

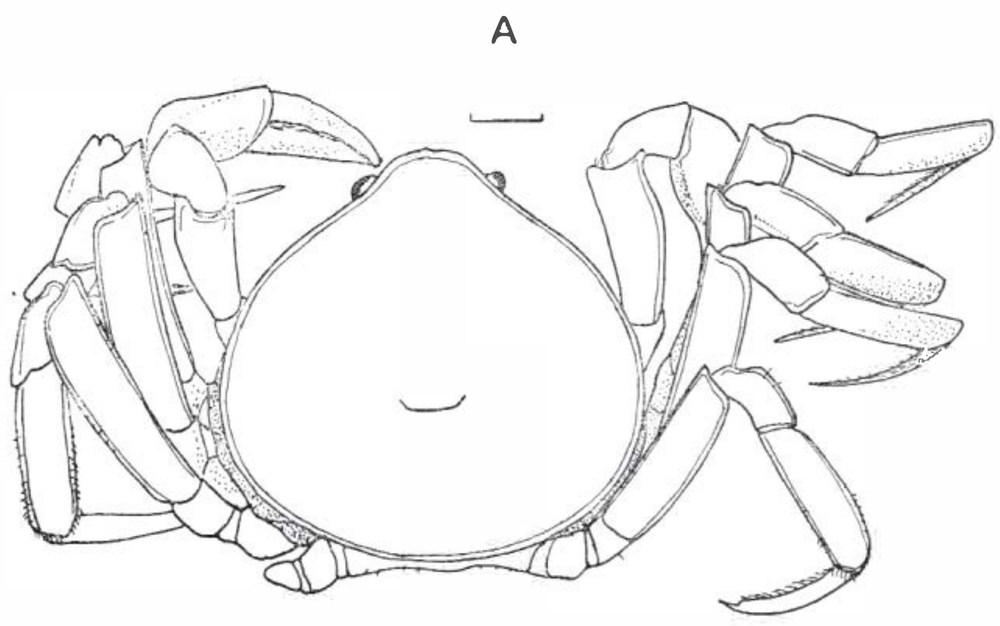
TYPES: ♂ holotype w.=6.5 mm, l.=6 mm; paratypes 1 ♂ w.=4 mm, l.=3.75 mm; 1 g. ♀ w.=9 mm, l.=7.5mm; 1 s. ♀ w.=7.5 mm, l.=7 mm (Auckland War Memorial Museum Collection).

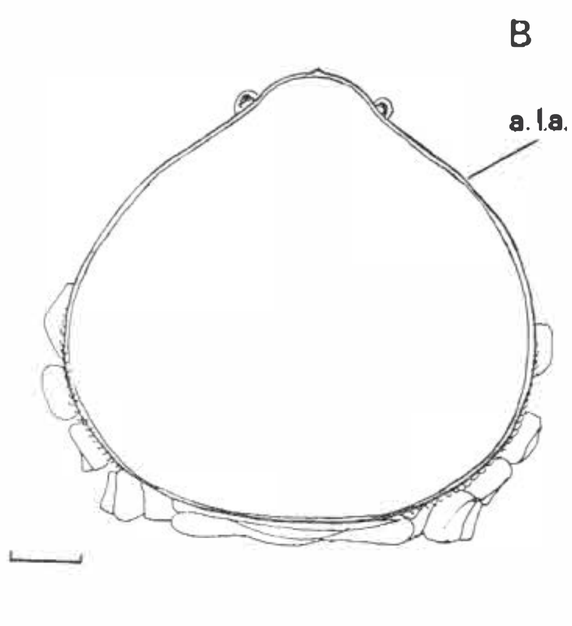
TYPE LOCALITY: Chelsea Point, Waitemata Harbour.

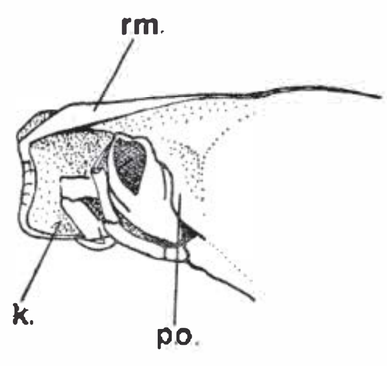
OTHER LOCALITY: Foveaux Strait.

DISTRIBUTION: New Zealand endemic.

DIAGNOSIS: Carapace suboval, broader than long, without lateral angles. Rostrum very short, less than one-third as long as wide, shallowly rounded anteriorly, a tiny central peak dorsally marking end of subrostral keel. Ventral keel on rostrum square anteriorly, of equal depth throughout, not reaching below eyestalks in lateral view. Postocular lobe reduced to small swelling, antennal spine absent. Chela of male little inflated, basal gape elongate, occlusion of fingers limited to their extremities; small, square tooth on base of movable finger. Male abdomen short, basally wide, penultimate segment with barely concave sides, ultimate segment semicircular. Male first pleopod of moderate length and breadth, a single longitudinal row of stout setae of average length on either side of subterminal aperture of vas deferens, most of these setae originating before this aperture.







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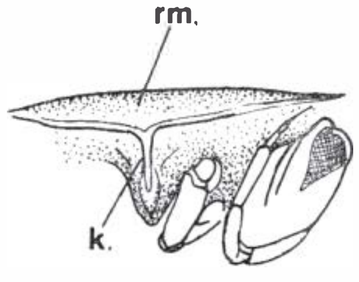

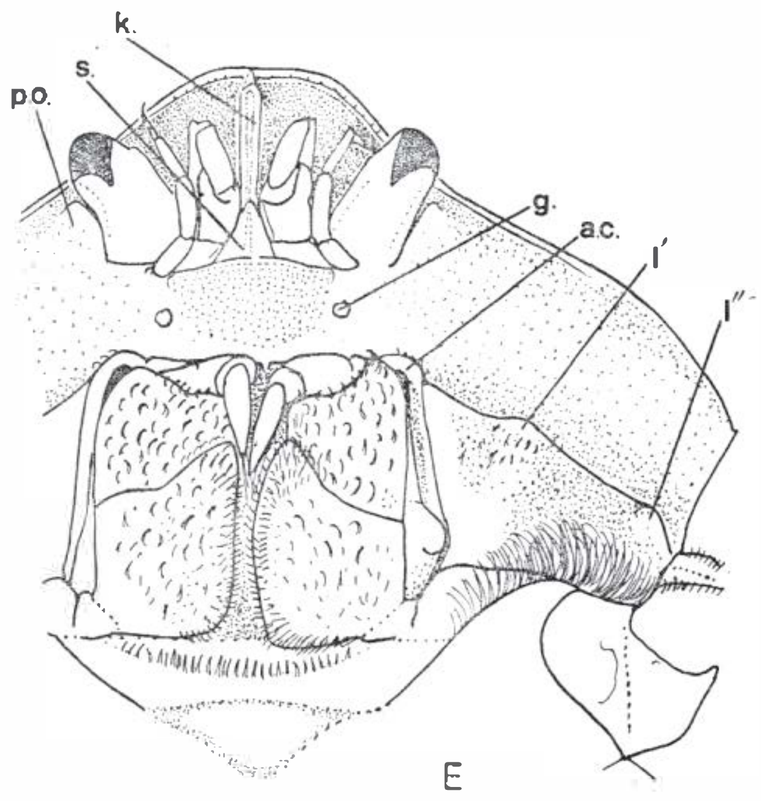

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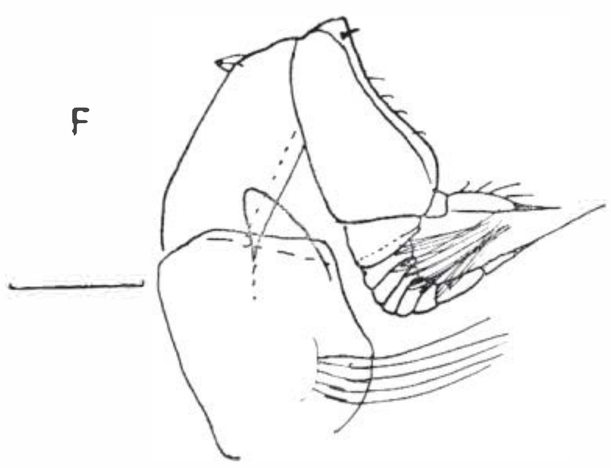


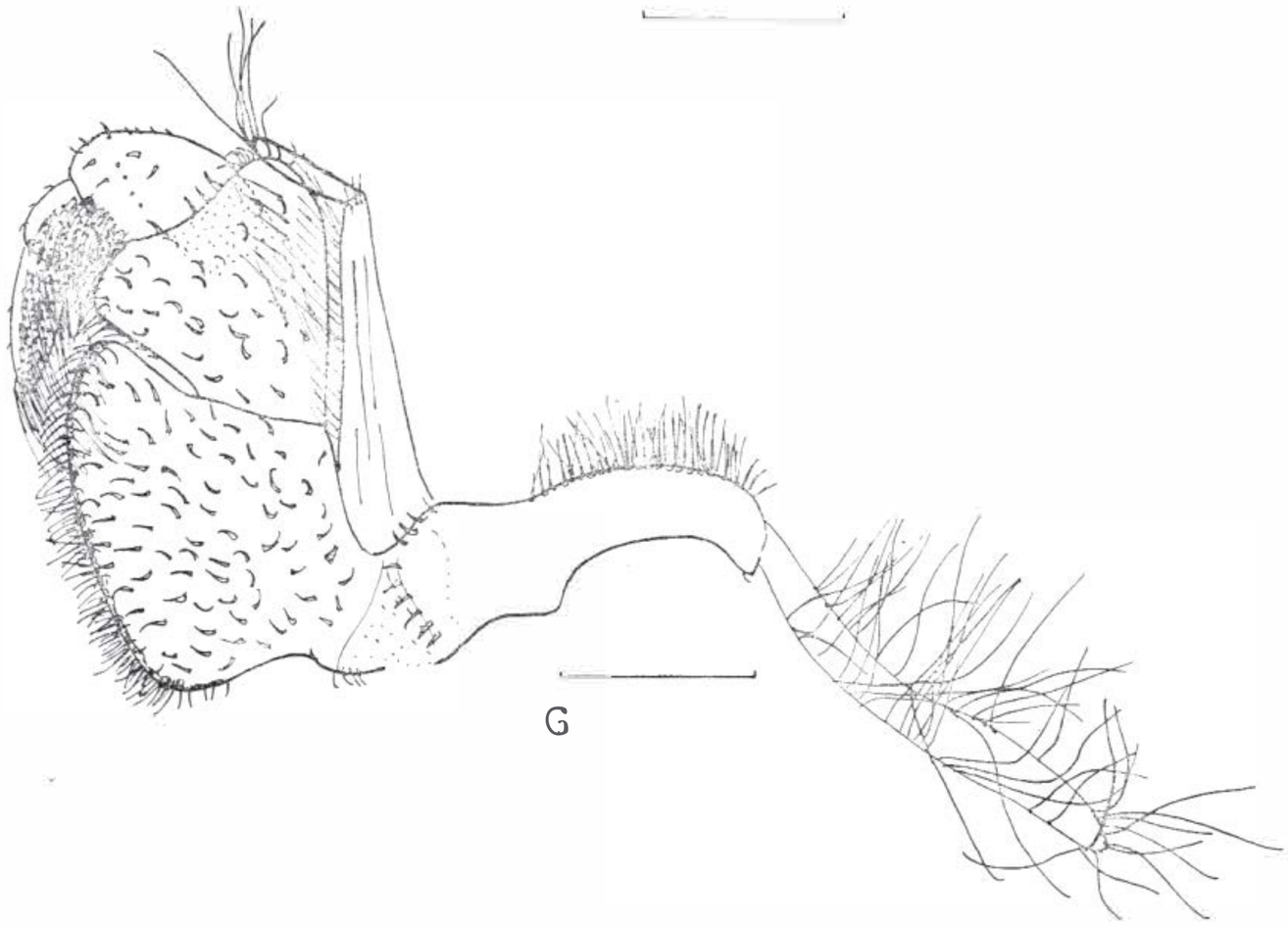


Fig. 51 *Elamena momona:* A—male dorsal view; B—Female dorsal view of carapace; C—Lateral view of rostrum in A; D—Frontal view of rostrum in A; E—Ventral view of mouthfield and epistome region, left side; F—Left antennule of male, lateral-ventral view; G—Left 3rd maxilliped of male. (scales represent 1 mm except for F, where it represents 0.55 mm)

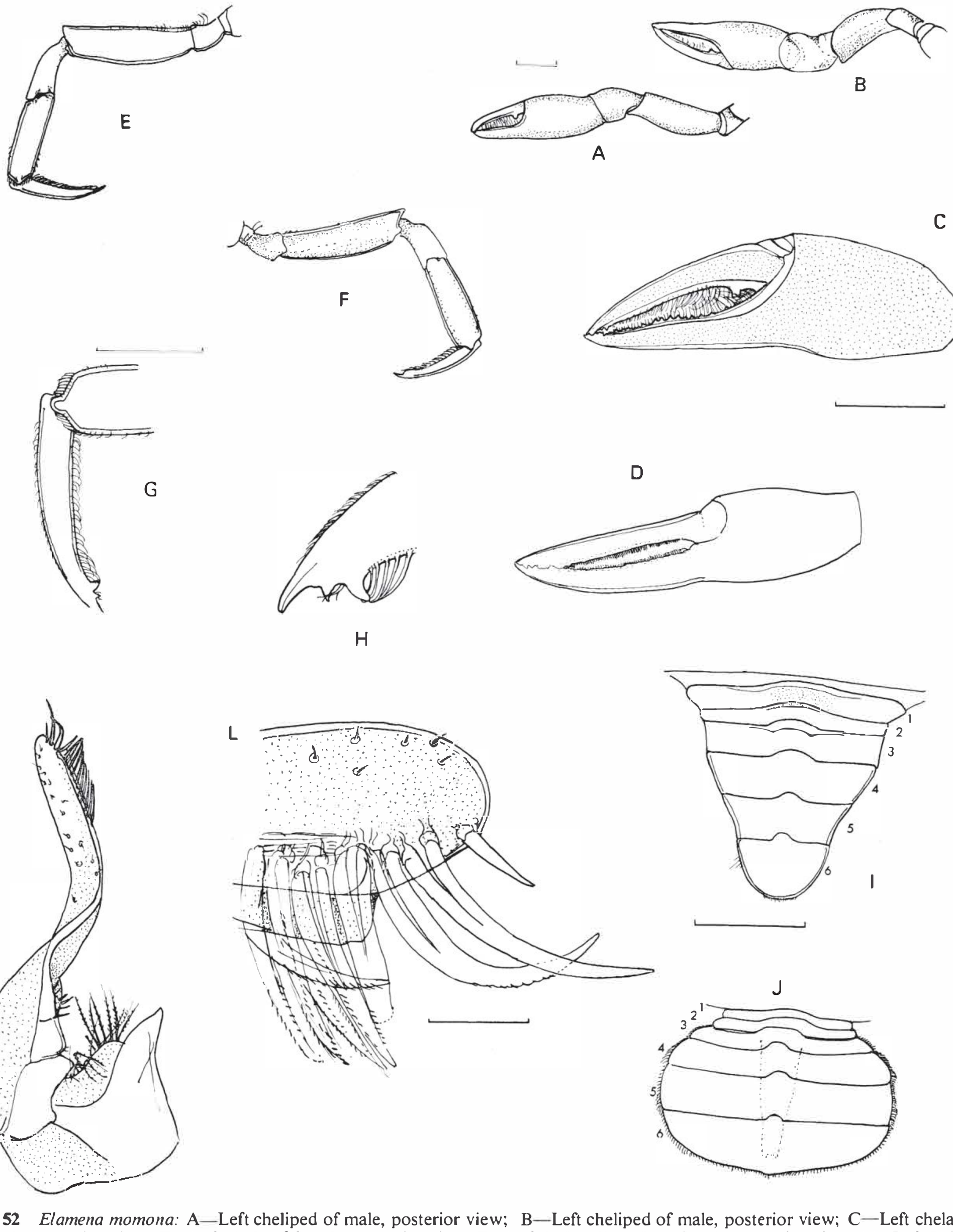


Fig. 52 *Elamena momona:* A—Left cheliped of male, posterior view; B—Left cheliped of male, posterior view; C—Left chela of male, posterior view; D—Left chela of female, posterior view; E—Left 3rd walking leg of male, posterior view; F—Left 3rd walking leg of male, anterior view; G—Dactylus of left 3rd walking leg of male, posterior view; H—Tip of dactylus of left 3rd walking leg; I—Extended abdomen of male, dorsal view; J—Extended female abdomen, dorsal view; K—Left 1st male pleopod, sternal view; L—Tip of left 1st male pleopod. (scales represent 1 mm except for K (0.5 mm) and for L (0.3 mm))

SIZE RANGE: ♂♂ 4 mm (Chelsea Point) – 9 mm (Chelsea Point). ♀♀ 4.5 mm (Foveaux Strait) – 9 mm (Chelsea Point).

DESCRIPTION: Carapace suboval, wider than long (ratio w. : l. = 1.07–1.13) flat or very slightly concave, sometimes with a faint depression but never a definite groove where the gastrocardiac groove would be in *Halicarcinus* (Fig. 51a). Narrow sharp edged rim around carapace and rostrum frequently set with minute curved setae laterally and posteriorly, rest of upper surface naked. Outline of carapace uninterrupted by lateral angles, or with mere suggestion of anterior pair of angles, evenly convex, posterior border a little less curved than sides.

Rostrum completely fused with carapace, broad basally and very short, slight anteriorly, a small central peak visible dorsally where subrostral keel ends. Anterior edge of keel perpendicular, slightly concave centrally (*see* Fig. 51c), hardly swollen ventrally. Antero-ventral angle of keel square, on same level as base of eyestalks. Keel almost uniformly deep its entire length. Corneas of eyes showing dorsally. Postocular lobe reduced to small bulge at edge of eye socket.

Antennules short, stout, not visible dorsally when folded, the three peduncular segments subequal in length, the second a little longer than rest. Basal segment subquadrangular, has large, acute antero-external lobe, a tuft of hairs a short distance from edge of ventral face; second segment about twice as long as wide, more slender than first; third even more slender basally, widening distally until as wide as the second. Antennal spine absent.

Interantennular septum large and lobular. Epistome just two-thirds as long as wide, not sunken, fused laterally with subhepatic regions. Posterior ridge of epistome shallow, central cleft virtually absent. Subhepatic regions not expanded or ridged. Subtriangular pterygostomian region large, expanded laterally, both lobes, especially second, obtuse, reduced to mere interruptions of the long edge of the triangle. Row of short setae on sterna of third maxillipeds.

Endopods of third maxillipeds almost meeting in mid line, sturdy, laterally expanded. Triangular basis more distinct than usual, a few setae bordering its free edge, small ridge between basis and epipod with row of setae. Ischium trapezoid, shaped like axe blade, external edge short, hairless, as long as oblique edge where merus articulates. Median edge of ischium shallowly curved, about three times as long as external edge, two or more rows of short setae. Anteromedian corner broad, deep, obtuse; posteromedian corner hardly produced, broadly rounded. Merus subchordate, three-fifths ischium length, wider than long, short portion of median edge follows curvature of median edge of ischium, has single row of hairs only slightly longer than those on ischium. Carpus articulating centrally between two distal lobes of merus, but a little nearer external edge, anterior edge almost straight. Palp segments all large, ventral hairs long and dense. Dactylus over twice propodus length; fairly stout, bluntly pointed.

Basal segment of exopod wide basally, narrowing considerably to apex of basal segment, below which is a horizontal row of hairs. Internal edge fringed with single row of long, slender hairs; external edge bare.

Basal lobe of epipod shallow with few setae. Basal portion of epipod deeply curved, of average size, a single row of long setae traversing anterior edge, separated by suture from lamella. Lamella longer than base, slender, fringed with long hairs, narrowly rounded terminally.

Cheliped not massive in either sex, short (cheliped l.: carapace w. = 1–1.37), especially in the female. Ischium very short, trapezoid in posterior view, rectangular anteriorly with blunt projection over merus. Merus long, slender; ventral tooth elongate, pointed. Carpus half to two-thirds as long as merus, slight ridge on dorsal edge meeting corresponding one on propodus. Palm narrower than long, hardly expanded laterally, as long as merus. Fingers slender, as long as palm, flattened elliptical gape in both sexes narrowing distally, dentation reduced especially on movable finger, basal tooth on movable finger in male sizable and square. Tips of fingers in male spooned, hardly occluding even at tips. Terminal dentation still reduced, more obvious in female.

Second pair of walking legs a little longer than first not quite twice as long as carapace is wide (ratio l. second leg: w. carapace = 1.57–1.95), third pair shorter, fourth shorter still (length = 1.2–1.54 times carapace width). Ischium, merus, carpus, and propodus all flattened, not wafer-thin, thickened down their central axes, knife-like edges with sparse tiny, curved setae. Ischium subrectangular, squared corner projecting over merus anteriorly. Merus tooth barely acute, hairless, merus longer than other segments. Carpus half merus length, distal projections short and blunt. Propodus approximately three-quarters merus length, distal V blunt. Dactylus as long as propodus, almost straight, curving a little distally, flattened, tapering towards claw but a little expanded about one-third along its length. Ventral edge of dactylus has single row of short hairs, curving towards claw; dorsal edge has row of finer, shorter, denser hairs. Short, fused claw preceded by two teeth, the first large, narrowly rounded and recurved, the second small, acute, and almost straight.

Female abdomen much wider than broad, ultimate segment not much longer than preceding segments, very shallowly rounded terminally with a faint central peak. Central concavity on proximal edges of segments 2–6, deepest and widest on segment four, progressively decreasing in breadth and depth, very shallow and broad on segments 2 and 3.

Male abdomen short, reaching to level of suture between sterna of first and second walking legs, basally broad, separated by small vertical ledge from rim of carapace. First segment short, hardly expanded laterally; second segment a little shorter and narrower; third longer than first, edges straight, barely narrowing distally; fourth half as long again as third, narrowing distally, sides almost straight; fifth as long as third, narrowing

distally, sides slightly concave; sixth just longer than preceding two, semicircular. Central convexity on segments 1–6 becoming progressively narrower.

First pleopod of male of average length and breadth, bent through 90°. Longitudinal ridge on distal portion widening only slightly below subterminal aperture of vas deferens, a short distance from rounded tip. Longitudinal row of approximately eight straight, stout, moderately long setae extending either side of aperture; most of setae arising before opening, only a few behind.

MATERIAL EXAMINED:

Auckland War Memorial Museum Collection: Chelsea Point, Waitemata Harbour, 27/2/1926, 2 ♂ ♂ 4, 6.5 mm, 1 g. ♀ 9 mm, 1 s. ♀ 7.5 mm (in 14 fm (7 m), coll. G. Archey).

Edward Percival Marine Laboratory Collection: Foveaux Strait, 6/11/1965, 1 g. ♀ 4.5 mm (oyster beds).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: February, November.

REMARKS: This species is superficially like *Elamena quoyi* Milne Edwards (1853, p. 223, pl. 11, fig. 3), but in Milne Edwards's figure the rostrum is much narrower, the carapace is interrupted behind by concavities above the last pair of legs, the eyestalks and eyes are visible dorsally, and the leg segments are relatively narrower than in *E. momona*. As Tesch has remarked (1918, p. 12) *E. quoyi* is most likely synonymous with *H. pubescens*.

E. momona also resembles the cosmopolitan *E. truncata*, which occurs in Australia. However, *E. truncata* differs in several important respects: a small, posterior angle and sometimes an anterior one are present on the carapace, the rostrum is truncate in front and the corneas of the eyes are hidden in dorsal view; the male cheliped is longer and more slender; the walking legs are not flattened and relatively longer than in *E. momona;* the male abdomen though similar in shape, shows partial fusion of segments 3 and 4; the first pleopod of the male is pointed with approximately five setae all anterior to the aperture of the vas deferens; and the postocular lobe is prominent.

Genus **Halimena** gen. nov.

TYPE-SPECIES: *Halimena aotearoa* sp. nov.

DESCRIPTION: Carapace suboval or subtriangular, longer than broad. Upper surface shallowly convex, without distinct grooves, the very thick rim continuing round rostrum; one or two pairs of lateral angles on rim; lateral teeth below rim completely absent. Rostrum separated from carapace by suture arising from carapace level. Rostrum simple, elongate, tapering to rounded tip, without keel or narrow ridge ventrally. Interantennular septum tiny but lobular. Antennules folding longitudinally beneath rostrum, never visible in dorsal view, basal segment of peduncle with small lobe on anterior outer corner. Corneas of eyes, but not eyestalks, visible dorsally at side of rostrum. Eyes angled outward as much as forward. Large epistome almost twice as wide as long. Endopods of third maxillipeds of average breadth, not quite meeting in mid line. Ischium of endopod longer than merus, lengthening medially to shape of halberd blade. Merus heart-shaped. Lamella of epipod twice as long as basal portion. Dactylus of walking legs with single large tooth beside apical claw. Abdomen in both sexes of six segments.

REMARKS: This monotypic genus is based on a rare species of which only four specimens, and no mature males, have been found. However, as the characters which distinguish the various genera of Hymensomatidae are present in both sexes, the lack of male specimens does not prevent the definition of this genus. *Halimena* differs from *Elamena* sensu stricto and from the subgenus *Trigonoplax* in having a distinct suture between carapace and rostrum; also, in *Halimena* the epistome is smaller, the endopods of the third maxillipeds are narrower, and the two distal teeth found on the dactylus of the walking legs in *Elamena* sensu lato are reduced to one. The ventral keel which is prominent in *Elamena* sensu stricto and is present as a remnant in all but one species of the subgenus *Trigonoplax*, is altogether absent in *Halimena*. The elongate shape of the carapace in *Halimena* is approached by species of *Trigonoplax*, although in *Elamena* sensu stricto the carapace is always wider than long.

Because of the suture at the base of the rostrum and the relatively short epistome, *Halimena* may be regarded as intermediate between *Halicarcinus* (*see* pp. 24–5) and *Elamena* (*see* p. 92), but closer to *Elamena*.

Two overseas genera of hymenosomatids are monotypic (*Elamenopsis* and *Hymenicoides*), which may indicate that the family has produced several evolutionary blind ends, or that these monotypic genera represent transitional stages between genera which have been more successful in producing a spectrum of species well adapted to various environments.

Halimena aotearoa sp. nov.

Figs. 53 and 54

TYPE: 1 g. ♀ holotype w. =6.2 mm, l. =9 mm (Edward Percival Marine Laboratory Collection K 405 K); paratype 1 ♀ w.=6 mm (Dominion Museum Collection Cr. 377).

TYPE LOCALITY: Seal Reef, Kaikoura Peninsula.

SUMMARY OF LOCALITIES: Leigh, Northland; Castlepoint, Wellington; Cape Runaway, Gisborne; Lyttelton, Canterbury; Potato Point, Otago.

DISTRIBUTION: New Zealand, endemic (rare).

DIAGNOSIS: Carapace oval, longer than wide, two pairs of obtuse, lateral angles on carapace rim, second pair sometimes reduced or absent. Rostrum as long as wide, narrowing anteriorly to rounded tip with ventral tuft of hairs apically. Postocular lobe reduced. Antennal spine large, acute. Both lobes on pterygostomian region reduced and obtuse.

SIZE RANGE: ♂♂ 1.3–1.5 mm, ♀♀ 6–6.2 mm.

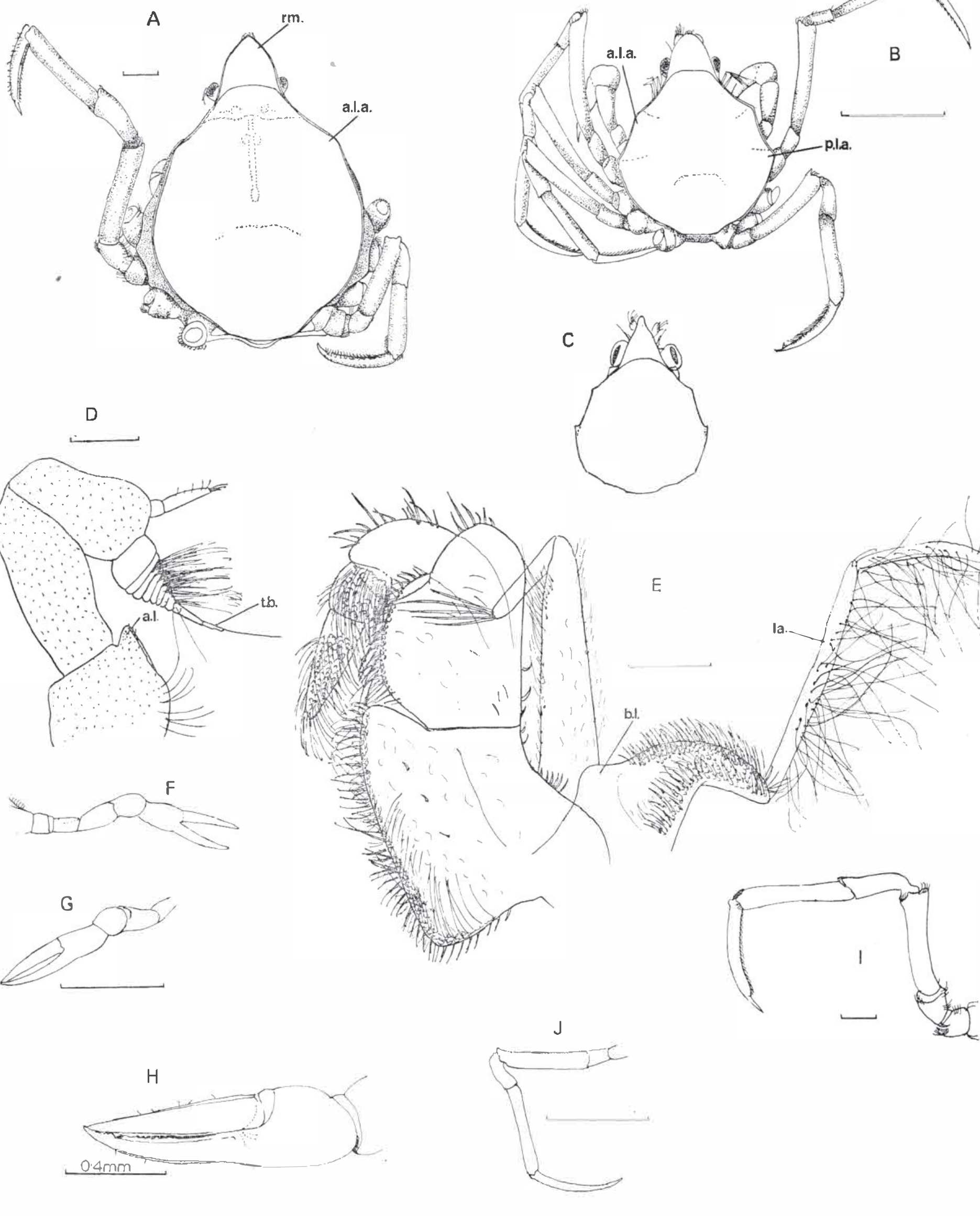
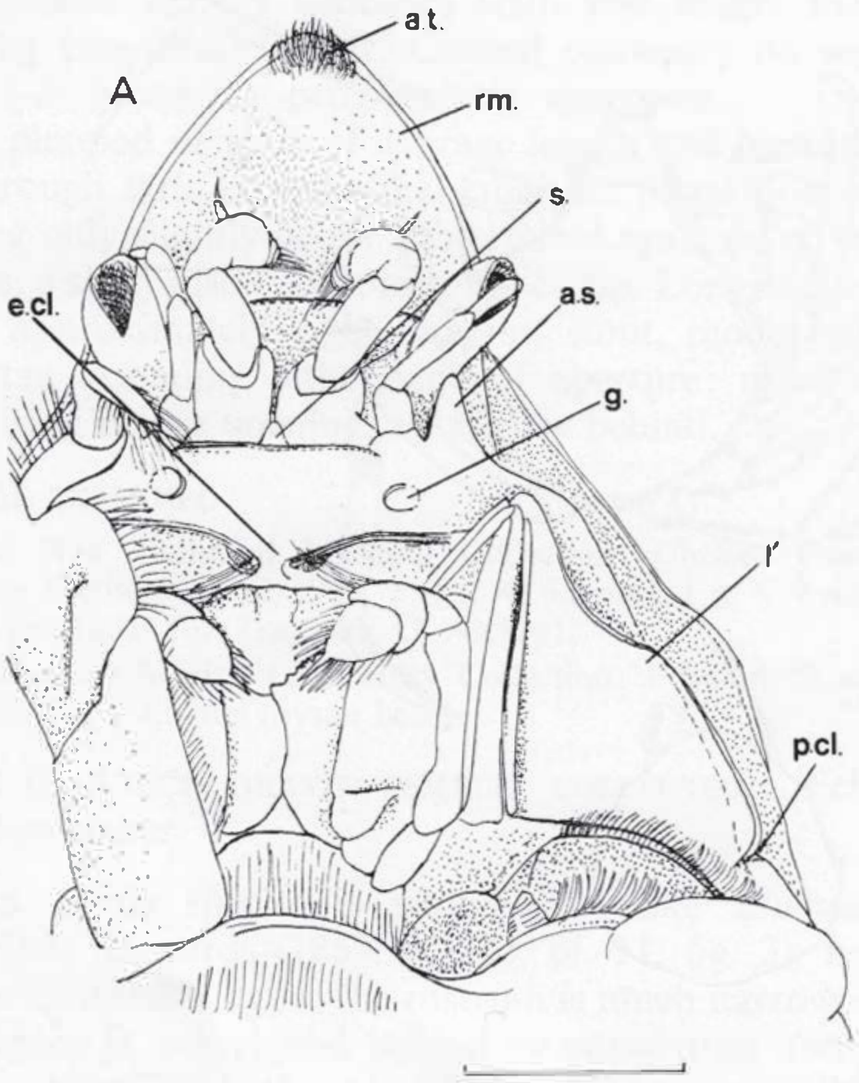
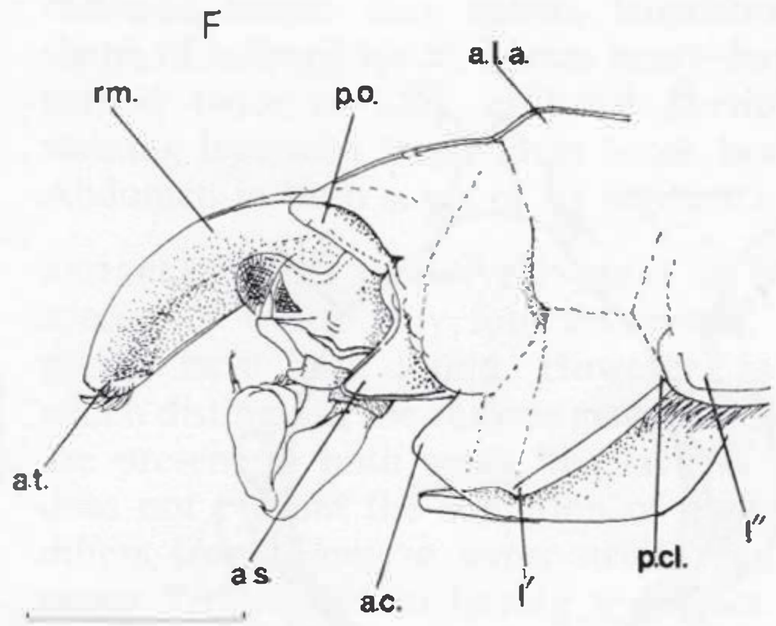
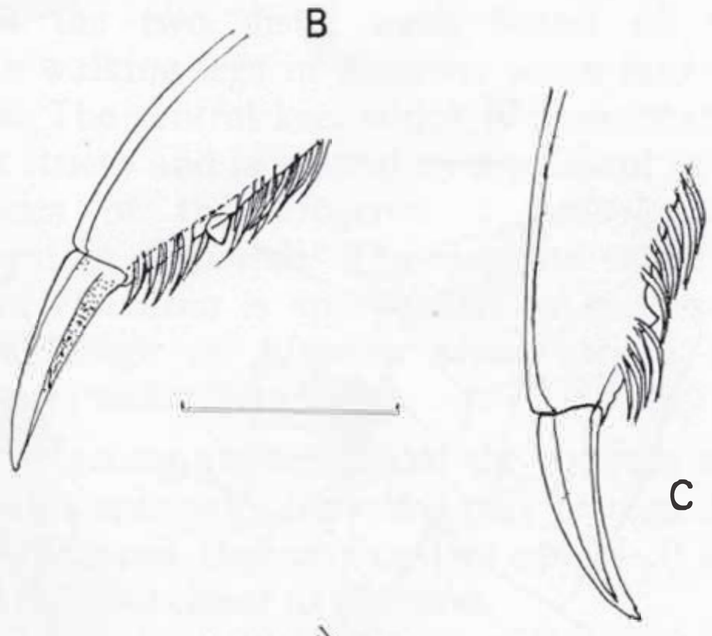
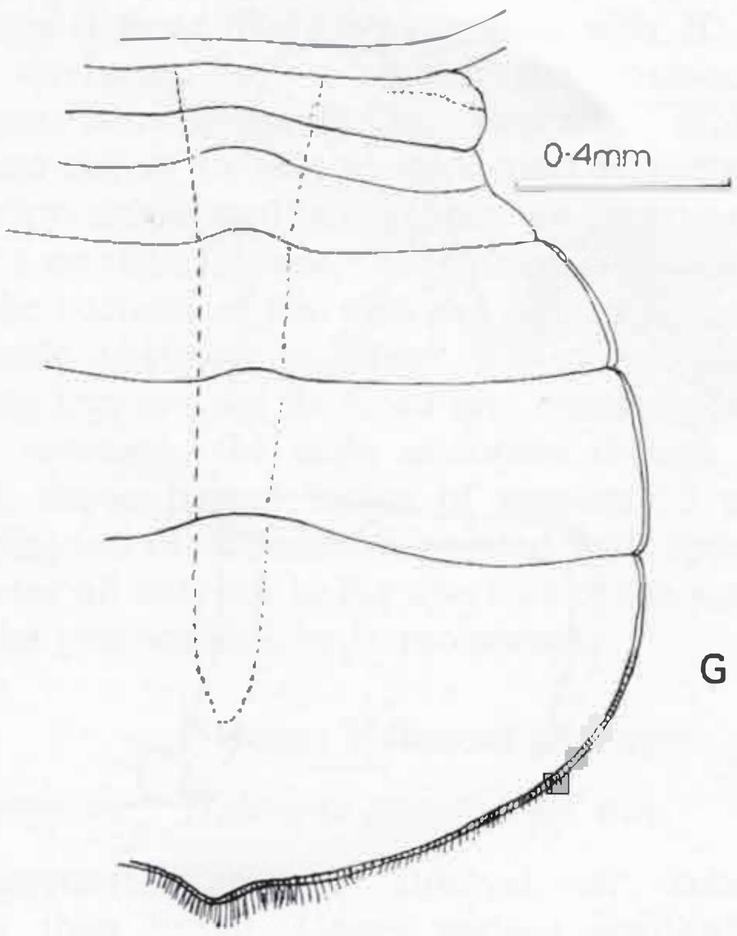


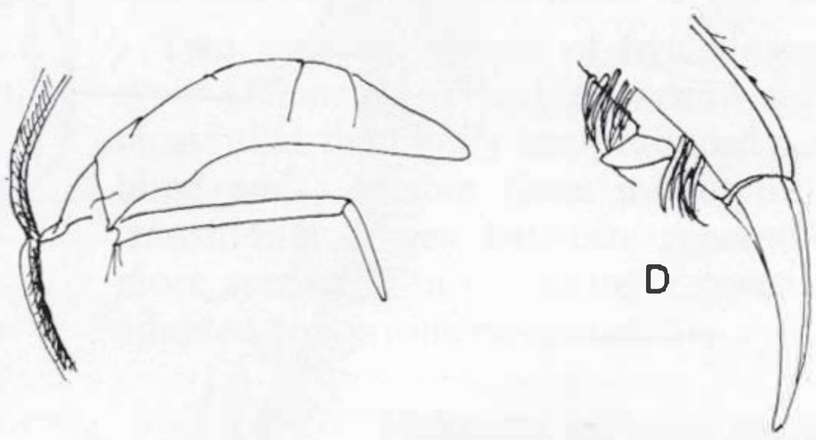
Fig. 53 *Halimena aotearoa:* A—Female, dorsal view; B—Immature male, dorsal view; C—Immature male, dorsal view; D—Left antennule of female, lateral-ventral view; E—Left 3rd maxilliped of female; F—Left cheliped of immature male, anterior view; G—Left cheliped of immature male, posterior view; H—Left chela of immature male, posterior view; I—Left 2nd walking leg of female, posterior view; J—Left 3rd walking leg of male, posterior view. (scales represent 1 mm except for D, where it represents 0.6 mm)

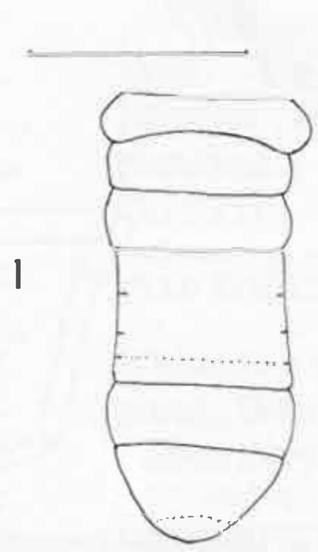












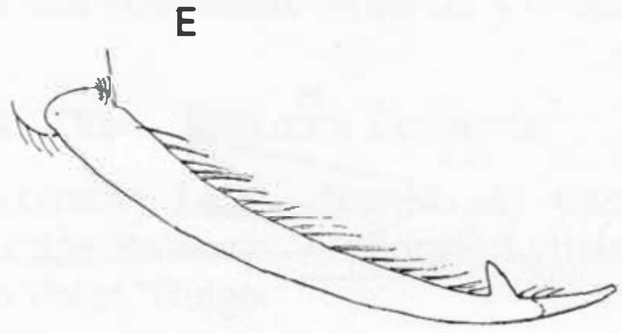


Fig. 54 *Halimena aotearoa:* A—Ventral view of mouthfield and epistome region, left maxilla removed; B—Tip of dactylus of left 2nd walking leg of female, posterior view; C—Tip of dactylus of left 2nd walking leg of female, from slightly different angle; D—Tip of dactylus of right 4th walking leg of female, posterior view; E—Dactylus of left 3rd walking leg of male, shown in Fig. 53B; F—Lateral view of rostrum of female in Fig 53B; G—Extended female abdomen, dorsal view, right side; H—Left 2nd pleopod of female; I—Extended abdomen of immature male, dorsal view. (scales represent 1 mm except where otherwise stated)

DESCRIPTION: Carapace suboval, longer than broad (ratio l.: w.=1.25–1.4), narrowing anteriorly, slightly convex dorsally. Two pairs of obtuse lateral angles on rim in young specimens, reduced in adult females where second pair may be altogether absent. Anterolateral border short and shallowly concave like mid-lateral border, posteriolateral border shallowly convex, rim a little convex above last pair of legs, posterior border almost straight. Carapace devoid of grooves, naked, sometimes with ridges radiating inward from position of lateral angles.

Rostrum as long as wide, simple semi-elliptical lobe tapering to narrowly rounded tip. Distinct groove between rostrum and carapace arising just behind where corneas of eyes are dorsally visible, following a shallow arc flattened anteriorly; frontal region therefore produced a little. Rostrum dorsally convex from side to side, curving steeply downward anteriorly so tip on horizontal level with antennular spine, thickened ventrally about longitudinal axis but without keel or distinct ridge, thick tuft of upwardly curving hairs ventrally on tip. Postocular lobe small and flattened (Fig. 54F).

Antennules short, stout. Basal segment not as long as broad, small acute lobe on anterior outer corner, tuft of hairs on edge below lobe. Second segment of peduncle almost as stout as, but longer than third, both more slender than first; third a little expanded distally. Antennal spine large, narrow, ends in blunt point.

Interantennular septum reduced to very small lobe. Epistome of moderate size, length a little over half width. Posterior ridge of epistome deep laterally. Epistome not sunken, laterally fused with subhepatic regions, central cleft much wider than usual. Subhepatic regions very small. Pterygostomian region large, subtriangular, somewhat elongated, obtuse central lobe present, reduced more in female than in immature males, second lobe almost absent but preceded by a cleft.

Endopods of third maxillipeds meeting in mid line, of average breadth, basis and ischium completely fused. Ischium large, longer than wide, lengthened medially especially anteriorly, anteromedian lobe of average size, obtuse; median edge very shallowly curved, several rows of short hairs which lengthen posteriorly; posteromedian corner expanded; articulation with merus quite broad. Merus shorter than the ischium, subequal in length and breadth, heart-shaped, outer lobe long, inner lobe shallow, fringed with one to two rows of shorter hairs than those on posterior part of ischium, part of inner lobe follows curvature of ischium median edge. Carpus articulating nearer external edge of merus than median edge. Palp segments all very large, dactylus extending back past point of articulation between merus and ischium. Carpus inflated, anterior edge curved. Propodus subquadrangular, slighter than carpus, dactylus twice as long as propodus, slender, bluntly pointed. Ventral setae on palp dense, of average length.

Basal segment of exopod of average size, scarcely tapering to apex, lateral edges fringed with fine, short hairs, inner edge with second row of hairs a short distance below apex, no horizontal row.

Basal lobe of exopod naked, shallow. Basal portion of epipod short, densely hairy on both edges, deeply curved, divided from lamella by septum. Lamella very long, twice as long as basal part, slender, fringed on one edge and medially by long, fine hairs, ending in a blunt point.

Chelipeds a little longer than carapace is wide, slender. (The female specimens examined lacked chelipeds.) Fingers completely occluding, nearly twice as long as palm.

Segments of walking legs slender and cylindrical. First pair of walking legs the longest, approximately twice as long as carapace is broad; second and third subequal; fourth only one and half times as long as carapace is wide. Ischium small, subtriangular, expanded distally, scattered curved hairs on upper edge, a few on ventral edge. Merus, propodus, and dactylus subequal in length, twice as long as carpus. Merus tooth reduced, obtuse, hairy. Distal projections of carpus blunt, upper with a few hairs dorsally. Propodus ends in a shallow, hair-fringed V. Dactylus flattened, of average curvature, tapering a little to long, strong, distinctly separate claw ventral edge with row of curved short hairs, interrupted near claw by single small blunt tooth, directed slightly backward from claw.

Female abdomen of six segments, of equal length and breadth, basally close to the carapace rim without an intervening shelf. Ultimate segment much longer than preceding segments, ending in a central obtuse peak, hair-fringed. Central convexities on proximal edges of abdominal segments but very shallow on segments 2–6.

MATERIAL EXAMINED:

Personal Collection: Goat Island Bay, Leigh, 11/12/1964, 1 ♂ 1.5 mm (in holdfast of *Carpophyllum plumosum*).

Victoria University of Wellington Zoology Department Collection: Castlepoint, 1 ♂ 1.3 mm (coll. R. B. Pike).

Edward Percival Marine Laboratory Collection: Seal Reef, 3/9/1964, 1 ♀ 6.2 mm (from among *Caulerpa*, brownish).

Dominion Museum Collection: Cape Runaway, –/8/1950, 1 ♀ 6 mm (coll. A. S. Voss, in 50 fm (91 m), Cr.377).

COLORATION: Similar to that of *Elamena producta* in the one specimen obtained alive. Reddish-brown ends of the dactyli white, parts of the upper carapace paler brown or cream, a dark red stripe across the region of the suture at the base of the rostrum.

REMARKS: More specimens of this very interesting and apparently rare species would allow investigation of the shape of the male abdomen, first pleopod and chela of the male.

Genus **Cyclohombronia** gen. nov.

1938 *Hombronia* Graham, p. 429
1949a *Hombronia*, Richardson, pp. 59, 65, 67
1963 *Hombronia*, Dell, p. 41
NOT
1853 *Hombronia* Lucas, p. 62

TYPE-SPECIES: *Cyclohombronia depressa* (Jacquinot),

DESCRIPTION: Carapace suboval, upper surface flat or convex, without distinct grooves, encircled by very thin rim. Lateral angles or teeth absent. Rostrum short, simple, bluntly pointed, divided from carapace by suture. Interantennular septum absent. Eyes close together, directed almost straight forward; eyestalks entirely visible dorsally. Epistome very small, length a third as great as width. Endopods of external maxillipeds narrow, gaping widely in mid line. Subtriangular ischium, longer and narrower than merus, expanded distally. Merus subrectangular, narrower than long. Lamella of epipod much longer than basal portion. Chelipeds of walking legs more massive than walking legs but not greatly inflated. Walking legs over twice as long as carapace is wide, very slender, fringed with long hairs. Dactylus of walking legs straight, has two rows of long, fine hairs, no teeth. Male abdomen short; abdomen of six segments in both sexes. Male first pleopod stout, terminal aperture of the vas deferens encircled by tumid lip.

REMARKS: The genus is monotypic. The sole representative species was discovered by Jacquinot and called *Hymenosoma depressa* in his atlas, *Hymenosoma depressum* in Lucas's notes. Subsequently the species was retained in the genus *Hymenosoma*. As late as 1918 Tesch followed this practice, although previously Kemp (1917) had placed the species tentatively in *Halicarcinus*. Bennett in 1930 considered that this species "requires a new genus", while Montgomery (1931) noted that "the position of *H. depressum* is doubtful, but it is certainly not a *Hymenosoma*". In 1939 Graham finally placed the species in a separate genus, *Hombronia*, writing: "The name *Hombronia* is revived for a swimming crab hitherto regarded as rare, but now recognised to be not only generically separable from other members of the family, but ecologically of major importance". Richardson (1949a) agreed, saying: "It seems best here to return the species to the earlier-proposed and apparently still valid g. *Hombronia*".

Both Kemp (1917, p. 246) and Richardson (1949a, p. 59) noted that *Hombronia* had previously been suggested as a generic name for Jacquinot's *Hymenosoma depressa*, Kemp giving as his reference Lucas, in Hombron and Jacquinot's "Voyage au Pole Sud", Zool. III, p. 62 (1853). Only two new species of hymenosomatid from New Zealand were described in this work. Lucas was dubious about the identity of the first of these, which he called *Hymenosoma* ? *tridentatum;* he remarked on the (in translation) "great differences that it presents compared with . . . the genus *Hymenosoma*" and he considered these differences important enough to propose the new generic name *Hombronia*. Lucas's second species was called *Hymenosoma depressum*, without a query, as he considered that it undoubtedly belonged to the same genus as *Hymenosoma obiculare*. Kemp was therefore the first to connect Lucas's name for the first species incorrectly with the second, previously positively assigned species.

As Lucas's *Hymenosoma* ? *tridentatum* is now regarded as a synonym of *Halicarcinus planatus* (*see* Milne Edwards 1853, and Garth 1958), then *Hombronia* Lucas becomes an objective synonym of *Halicarcinus* White, and Graham's and Richardson's use of *Hombronia* cannot stand. A new name, *Cyclohombronia* is therefore given to the genus containing Lucas's "*Hymenosoma*" *depressum.*

Cyclohombronia agrees closely with Stebbing's (1905, p. 50), Miers's (1886, p. 279) and Tesch's (1918, pp. 4–6) descriptions of the genus *Hymenosoma.* Both genera have a carapace of suboval shape with the lateral regions oblique and inflated, a simple, pointed rostrum, short, forwardly directed exposed eyestalks, narrow external maxillipeds, a short six-segmented male abdomen, the first two of which segments are fused to the sternum, and long legs. *Hymenosoma* differs from *Cyclohombronia* in: 1, possessing clear grooves and regions on the carapace; 2, having sharp, spine-like bifid postorbital lobes; and 3, completely lacking an epistome, the external maxillipeds almost enroaching on the base of the antennules, and the buccal cavity not being limited by a ridge anteriorly. *Hymenosoma* Desmarest is now considered monotypic as Stimpson's *H. geometricum* (Stimpson 1858, p. 108) is synonymous with Desmarest's *H. orbiculare* (Desmarest 1825, p. 163) and according to Kemp (1917, p. 245) other species previously referred to this genus do not belong to it.

Cyclohombronia depressa (Jacquinot)

Figs. 55–58

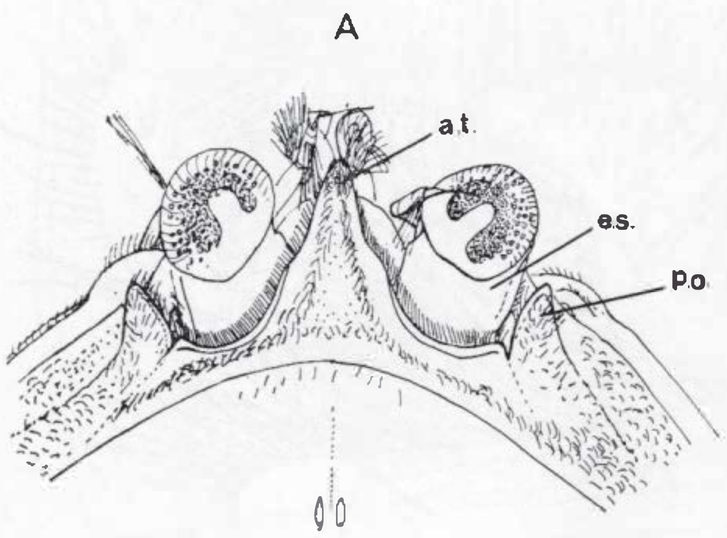
1842–53	*Hymenosoma depressa* Jacquinot, pl. figs 34–9
1853	*Hymenosoma depressum*, Lucas, p. 62
1876b	*Hymenicus depressus*, Miers, p. 41
1886	*Hymenicus depressus*, Filhol, p. 402
1907	*Hymenosoma depressum*, Chilton, p. 146, pl. 5
1909	*Hymenosoma depressum*, Chilton, p. 610
1912	*Hymenosoma depressum*, Thompson, p. 238
1917	*Halicarcinus* ? *depressus*, Kemp, p. 246
1918	*Hymenosoma depressum*, Tesch, p. 6, 8
1930	"*Hymenosoma*" *depressum*, Bennett, p. 258
1938	*Hombronia depressa*, Graham, p. 429, 430, 331
1949a	*Hombronia depressa*, Richardson, p. 59, 65, 67, fig. 39
1963	*Hombronia depressa*, Dell, p. 41
1964	*Hombronia depressa*, Bennett, p. 109, fig. 129

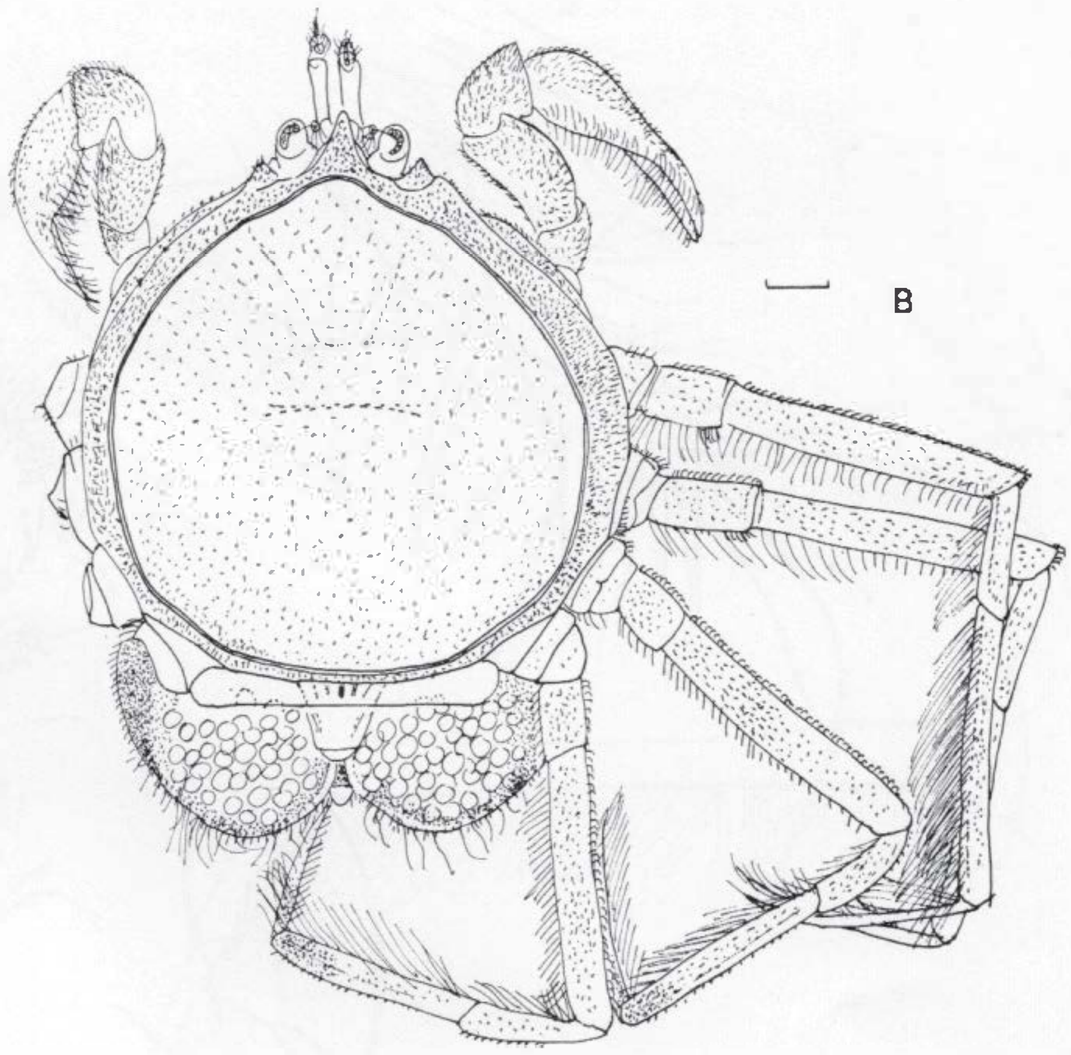
TYPE LOCALITY: Auckland Islands, under stones.

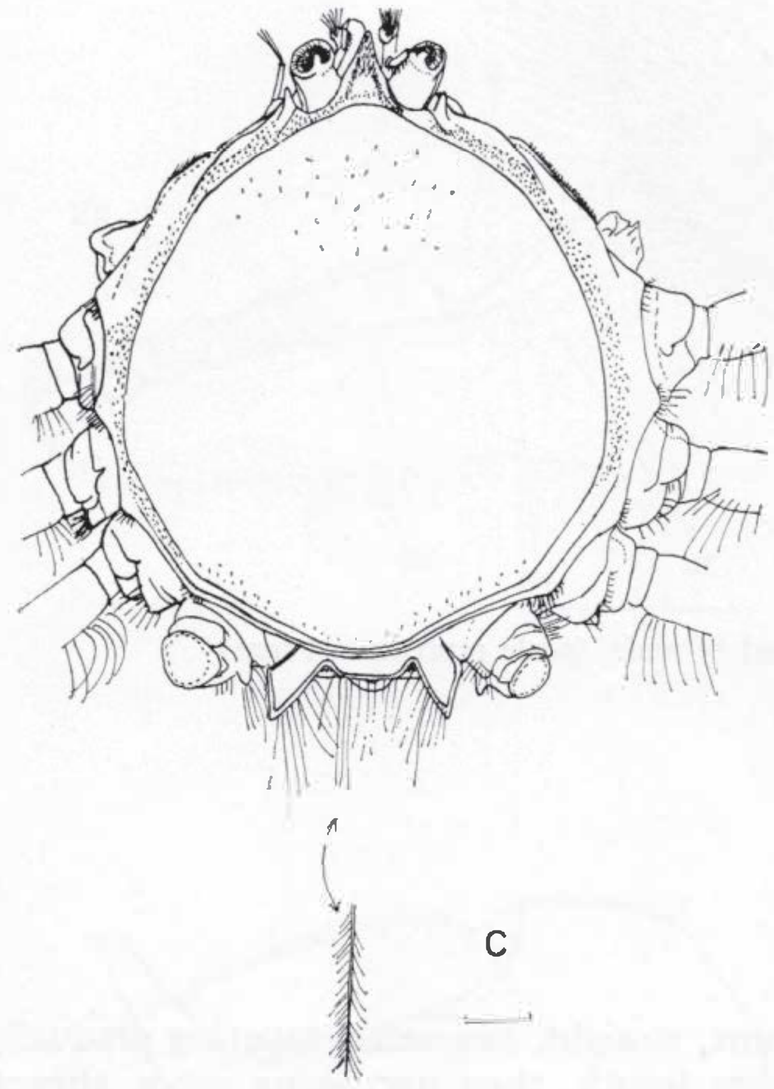
SUMMARY OF LOCALITIES: Waiuku, South Auckland; Napier; Waikawa Beach, Wellington; Lake Ferry, Palliser Bay; Kaikoura, Marlborough; Greymouth, Westland. Christchurch: Sumner; Lyttelton. Otago: Blueskin Bay; Otago Harbour; Portobello; Dunedin.

DISTRIBUTION: New Zealand, endemic.

DIAGNOSIS: Carapace suboval, longer than wide, without lateral angles. Rostrum not extending past eyes, wider along its basal half, then abruptly tapering. Postocular lobe large, acute, curving away from the eyestalk. Antennal spine reduced to an obtuse lobe. Chela of male with a basal rounded tubercle on movable finger, a small linear gape.







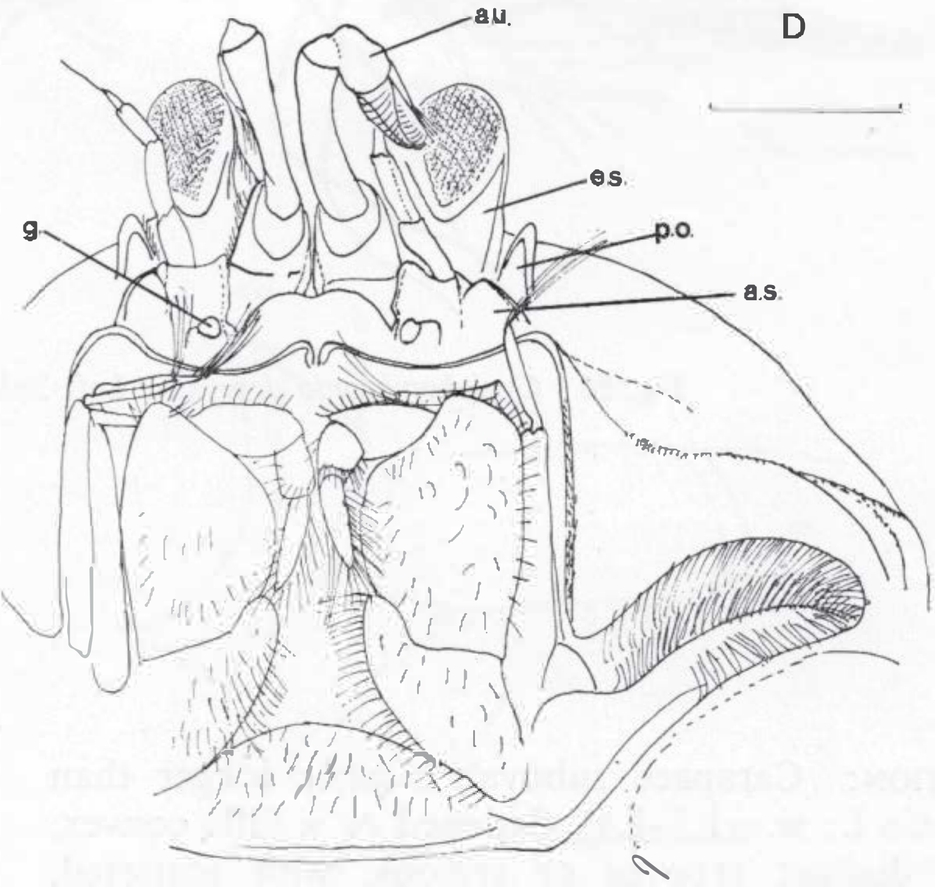


Fig. 55 *Cyclohombronia depressa:* A—Rostrum of male in C; B—Female, dorsal view; C—Male, dorsal view of carapace; D—Ventral view of mouthfield and epistome region, left side. (scales represent 1 mm)

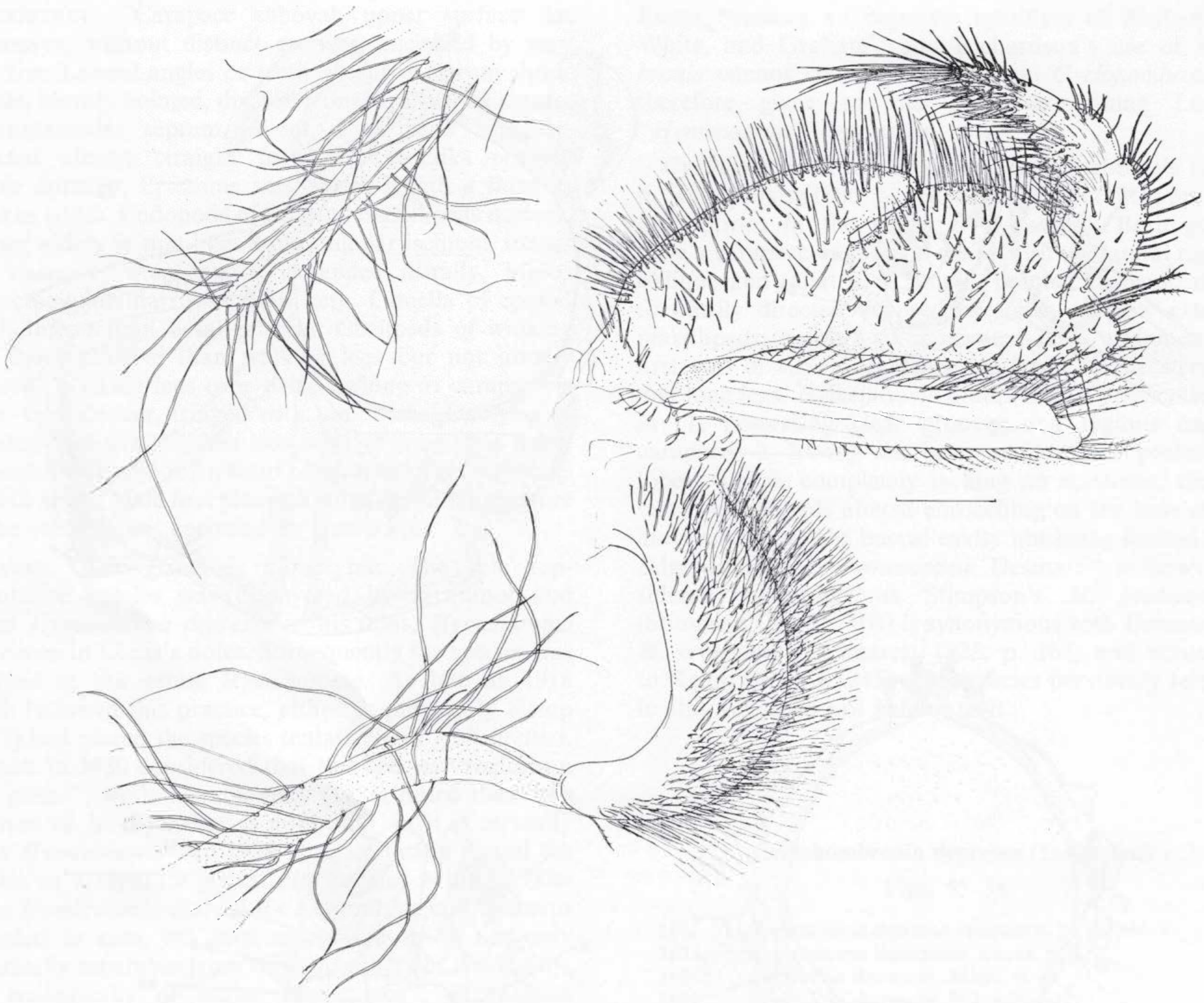
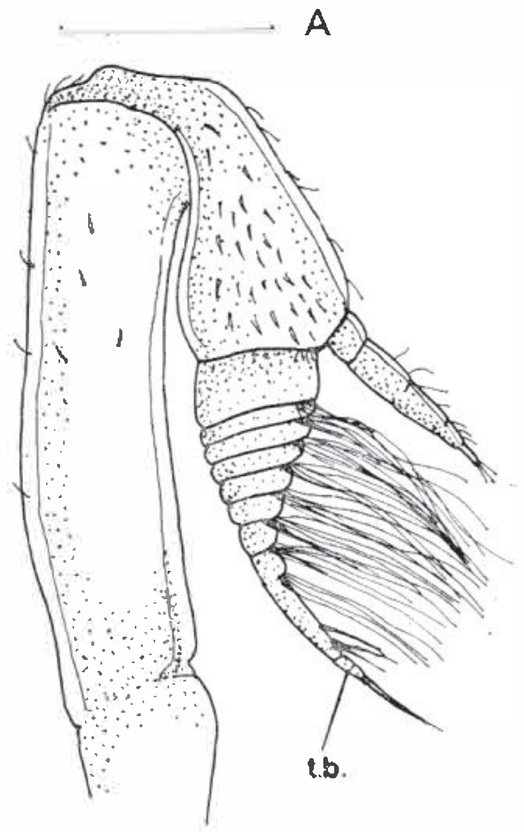


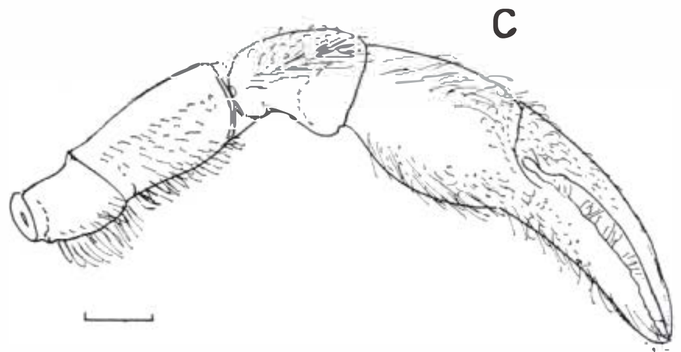
Fig. 56 *Cyclohombronia depressa:* Left 3rd maxilliped of male, (scale represents 1 mm)

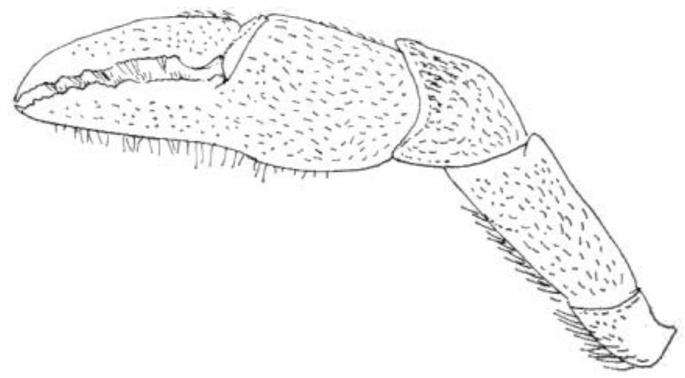
DESCRIPTION: Carapace suboval, slightly longer than wide (ratio l.: w.=1.1–1.4), flattened or a little convex, without distinct grooves or regions, with scattered, short, fine hairs, rim minute and continuous but more deeply arched at rostrum base than along the antero-lateral border; frontal region therefore prolonged a little, sides of carapace oblique especially anteriorly, more densely setiferous than dorsal surface of carapace, branchiostegite projections obtuse and marginally hairy. Lateral borders of carapace smoothly convex, posterior border shallowly convex, flanked by pair of very shallow concavities above last pair of legs.

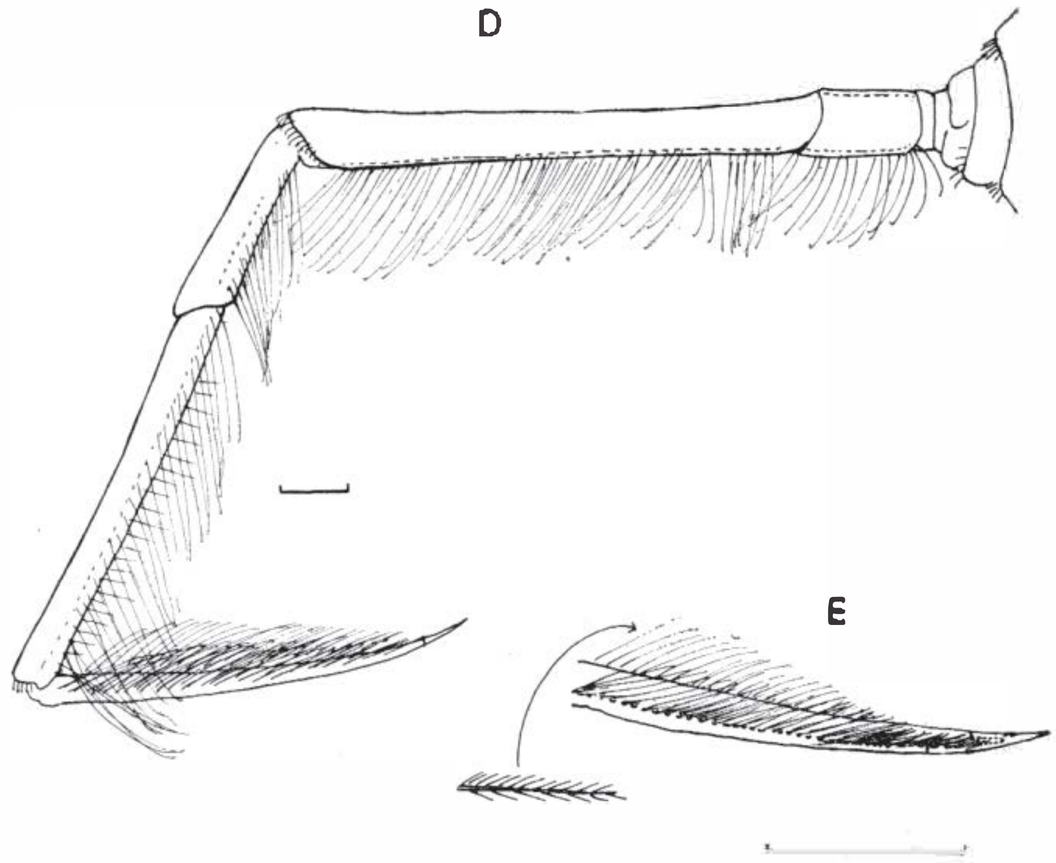
Simple, small, bluntly pointed rostrum not reaching past eyes, somewhat deflexed anteriorly, arising at carapace level, thickened along central axis, setiferous on either side and sometimes all over. Edges have a row of short, straight, fine setae, tapering gradually for half rostrum length, then narrowing more abruptly to tip to form shallow angle in side of rostrum, tip hairy. Small cleft between thickened base of rostrum and postocular lobe. Eyestalks short and stout, eyes close together, directed almost straight forward. Hairy postocular lobe variable in size but always noticeable, acute but bluntly pointed, inner surface concave next to eyestalk, sloping outwards, rounded ridge from its base to carapace rim.

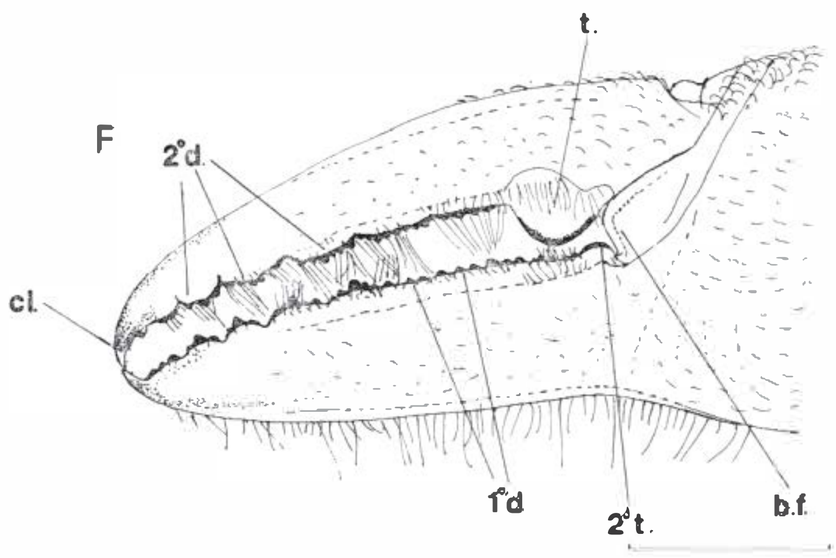
Folded antennules visible dorsally either side of rostrum. Basal segment small and subquadrangular, without any expansion of antero-external corner. Second segment very long and slender, third segment shorter and widening distally. Both rami large, long, moderately slender. Antennal spine reduced to small, obtuse prominence.

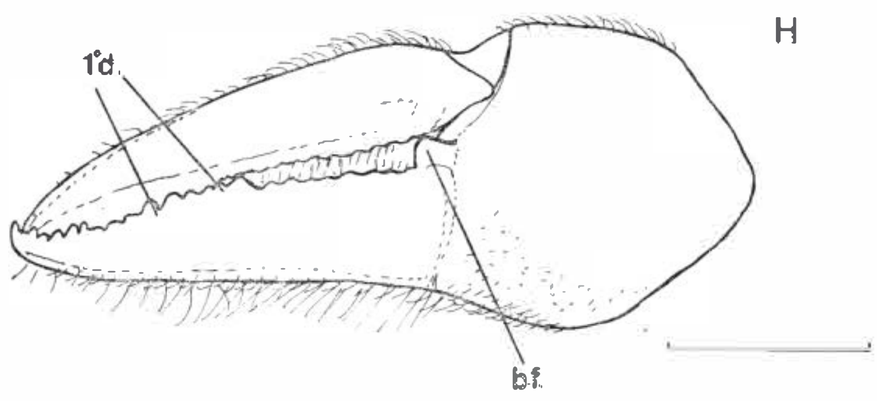


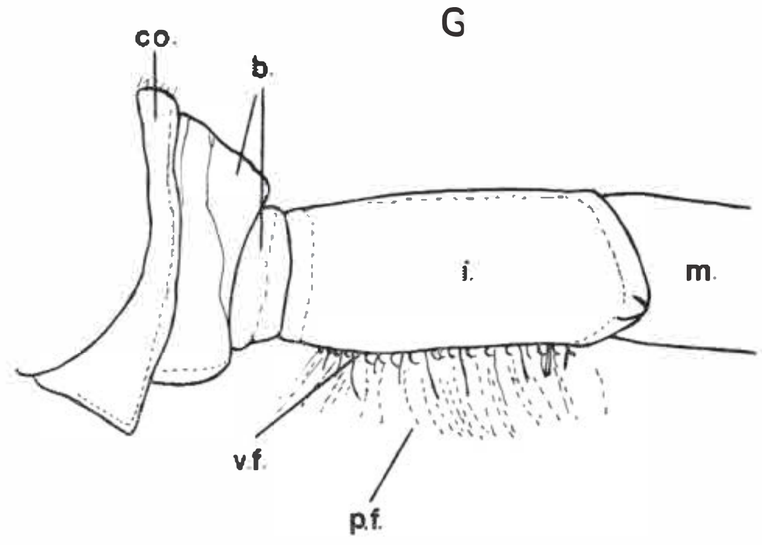












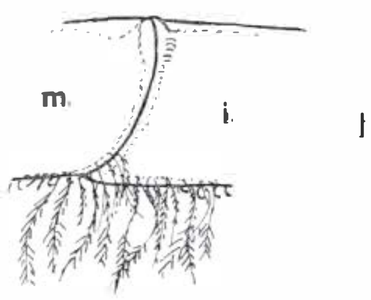
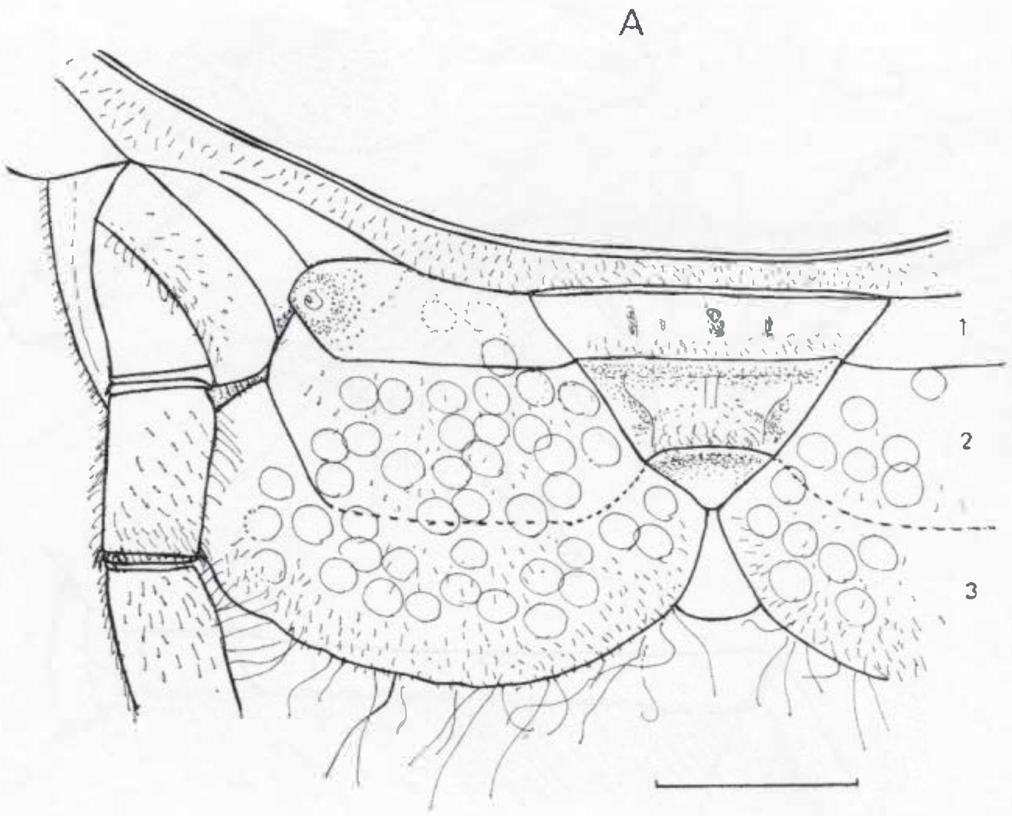
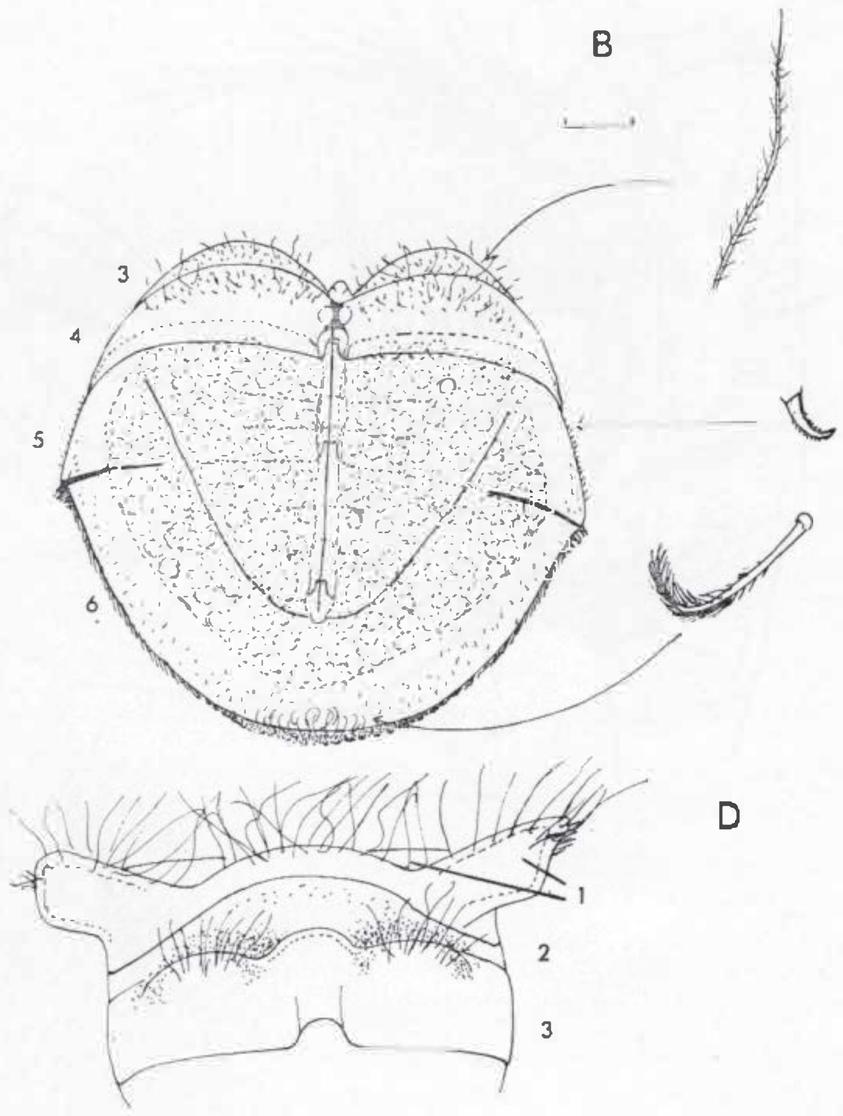
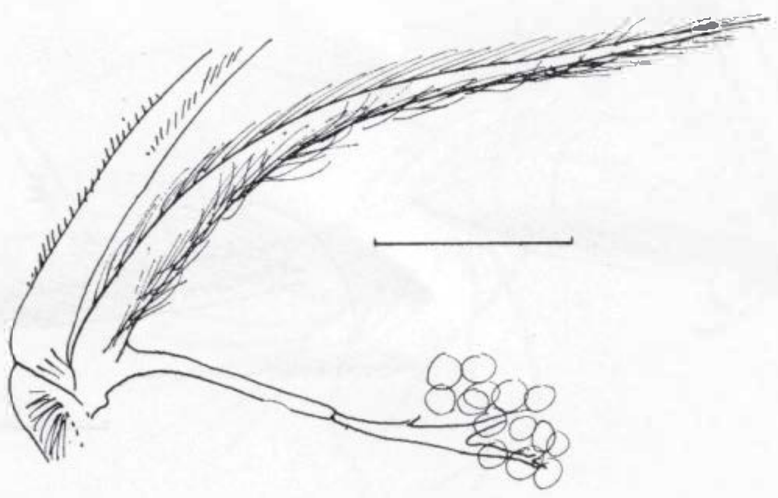
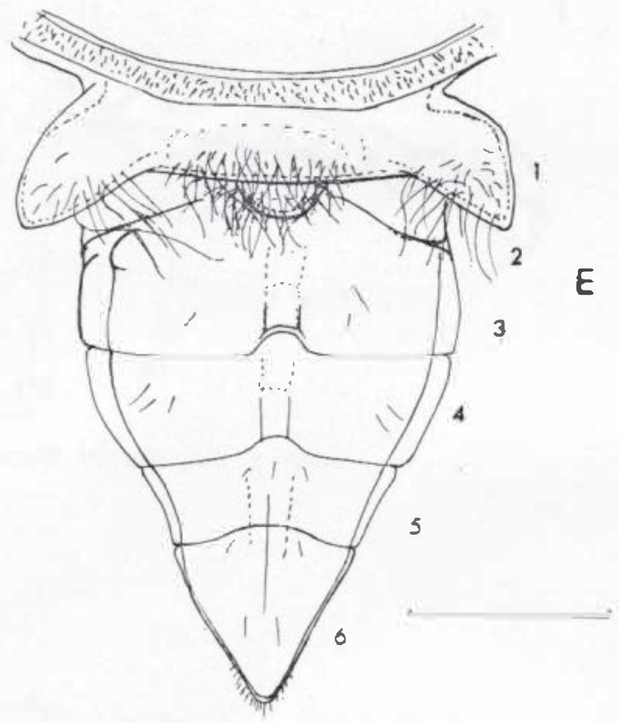


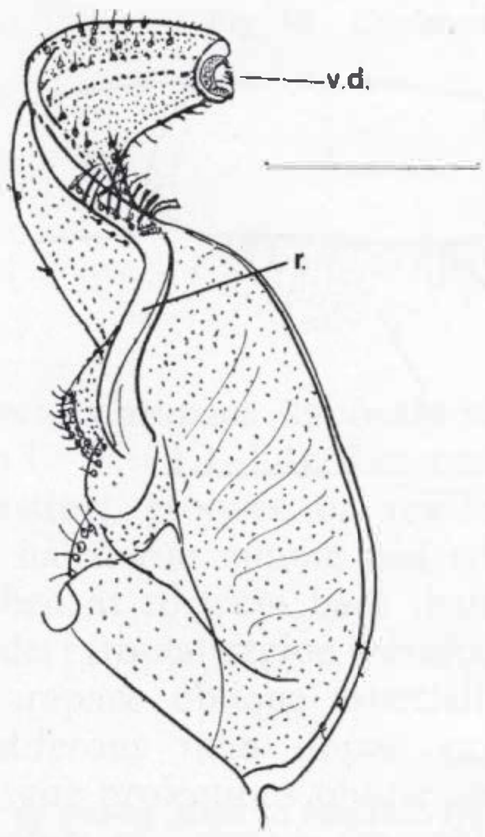
Fig. 57 *Cyclohombronia depressa:* A—Left antennule of male, lateral-ventral view; B—Left cheliped of male, posterior view; C—Left cheliped of male, anterior view; D—Left 3rd walking leg of male, posterior view; E—Tip of dactylus of walking leg, posteroventral view; F—Finger of male chela, posterior view; G—Chela of female, posterior view; H—Detail of first three segments, of male 3rd walking leg, anterior view; I—Detail of joint of ischium and merus, posterior view. (scales represent 1 mm)

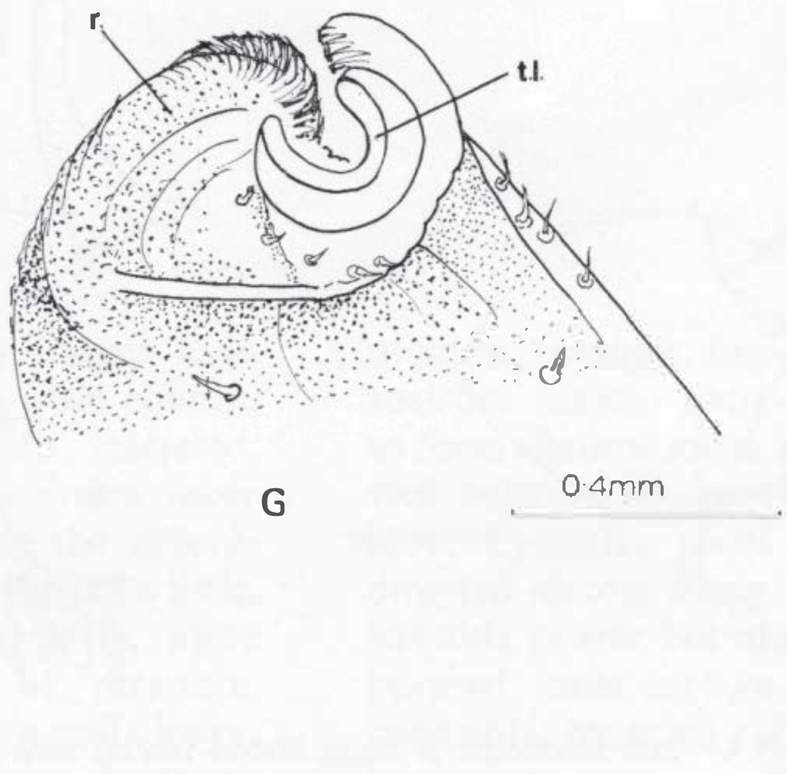












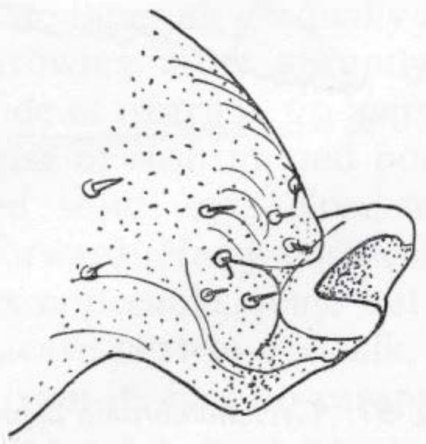


Fig. 58 *Cyclohombronia depressa:* A—Female abdomen in situ, dorsal view; B—Female abdomen in situ, ventral view (on smaller scale); C—Left 2nd female pleopod; D—Male abdomen in situ, ventral view; E—Male abdomen extended, dorsal view; F—Left 1st pleopod of male, sternal view; G—Tip of left 1st pleopod of male; H—Tip of left 1st pleopod of male, from different angle. (scales represent 1 mm except where otherwise stated)

Interantennular septum absent. Epistome narrow, very short, only a third as long as wide, concave centrally. Anterior edge of epistome bow-shaped, without ridge adjacent to bases of antennules. Very deep posterior ridge between epistome and endostome, deepest towards corners of mouthfield, shallowest halfway towards centre where there is a deep narrow cleft. Subhepatic regions not expanded. Subtriangular pterygostomian regions very broad and short; longest edge concave near mouthfield, without lobes, sparsely hairy. Milne Edwards's opening wide, oblique, fringed by rows of shorter than usual hairs. Sterna of third maxillipeds covered with scattered, short hairs.

Endopods of third maxillipeds slender, gaping widely in mid line, especially posteriorly. Subtriangular small basis fused with ischium, anterior edge marked by a row of setae. Ischium longer than merus, subtriangular, narrow basally, expanded distally to merus width; median edge gently curved with three to four rows of long setae; anteromedian lobe large, long, narrowly rounded apically; articulation with merus at right angles to axis, of average length. Merus subrectangular, longer than wide, outer edge straight for most of length, curving to form a shallow lobe anteriorly, median edge following curvature of ischium, with one to three rows of setae no longer than those on ischium. Median portion of face of these two segments with quite dense long setae. Palp segments very large; carpus articulating centrally on oblique anterior edge of merus, between vestigial lobes, twice as long as broad, anterior edge curved and setiferous; propodus short, subquadrangular, half carpus length; dactylus a little longer than propodus, stout, tapering to rounded end; ventral setae on palp segments of average length, longer on the dactylus.

Basal segment of exopod long, wide, not much tapered, row of long, feathery hairs on both edges, the longest near the apex, a few scattered hairs forming second row on inner edge, no horizontal row below apex, a few on extreme tip; second segment short, ending in five long hairs one short hair.

Basal lobe of epipod much shorter than lamella, thick, strongly curved, densely covered with long setae, separated by septum from narrow lamella. Lamella end acutely pointed, long hairs on both edges. Cheliped short moderately massive but not inflated (1.5–1.65 times as long as the carapace is wide). Merus barely more than twice ischium length, distal projections reduced and rounded. Carpus as long as merus, expanded distally. Palm and fingers arched; palm of male as long as carpus, half as deep as long, fingers nearly twice as long as palm; palm of female nearly twice carpus length, depth half length, fingers shorter than palm. Pair of broad, hairy tracts on upper and lower portions of male palm anterior face, short hairs on basal part of anterior faces of fingers and along rounded edges. Fold between bases of fingers in both sexes; movable finger of male has long, rounded tubercle beside fold, rest of edge finely dentate, tiny teeth along edge of rounded projections which represent primary dentation. Small rounded projections at base of fixed finger, behind and below large tubercle on movable finger; rest of immovable finger indented similarly. Distal half of fingers occluding, basal half with narrow linear gape. Fingers of female without secondary dentation, occluding for their distal half, a linear gape basally.

All walking legs very long, second pair 2.2–3 times as long as the carapace is wide; second and third pairs longest subequal, first slightly shorter, fourth shortest of all (2–2.8 times the carapace width). All five terminal segments flattened, fringed very near ventral edge on posterior face with row of long, feathery hairs, set at angle with face of approximately 45°, pointed slightly away from carapace. Propodus and dactylus with second row of shorter hairs on ventral edge itself, almost at right angles to first. Tiny hooked setae interrupted by a few longer hairs represent second row on ischium, merus and carpus. Ischium subrectangular, anterior face projecting very slightly over merus, fractionally wider than other segments. Merus tooth reduced, obtuse, hairy; distal projections of carpus reduced as is the V at propodus end. Carpus two-fifths merus length, propodus nine-tenths merus length, merus breadth one-seventh length. Dactylus as long as propodus, very slender, almost straight, tapering to fine short claw which is distinct from rest of segment. A few tiny setae on dorsal edge; ventrally the two fringes of hairs slope toward tip and become shorter distally.

Female abdomen very abnormal for family. Central portions of first three segments form a triangular chitinous plate, its apex directed posteriorly, visible in dorsal view. Second and third segments partially fused each side of centre, third greatly constricted centrally and folded over on itself so that half is visible dorsally, half ventrally, the ridge so formed having very long hairs; folding preventing abdomen from being lifted and straightened out. Fourth segment somewhat constricted centrally, convex each side, as long as total length of third; fifth longer than fourth, sides sloping outward distally to meet side base of sixth; sixth semicircular, fringed with short hairs. Raised ridge down centre of fifth and sixth segments, a central narrow square projection on proximal edge of each; square groove at end of raised ridge which ends half along sixth segment; presumably represents suture between sixth and original seventh segment. (The abdomen is primitively of seven segments in Brachyura.) Central portion of fifth and sixth segments fused; only outer part of these segments is convex, so that a U-shaped concavity occupies their centre.

Male abdomen short, reaches suture between sterna of second and third walking legs, separated from carapace by very narrow rim. First segment short, sharply convex, hairy in centre, expanded laterally into rectangular or rounded projections fringed with hairs; second partly hidden by first when abdomen straightened, otherwise as long centrally; third segment longest, sides almost straight, surface bulging, hairy each side of mid line; fourth a little shorter, sides convex, narrowing distally; fifth still shorter, sides faintly concave narrowing

distally; sixth subtriangular, elongate, twice as long as fifth segment, bluntly pointed. Central arcuate projection of proximal border of segments 2–5 very pronounced on third segment, progressively becoming shallower and broader, represented by gentle curve on sixth.

Distal portion of first male pleopod very short, base expanded. Broad tip bent through 90°, half along longitudinal ridge, setae amassed below twisted portion. Aperture of vas deferens terminal, with thickened chitinous half-ring forming semicircular swollen lip below.

MATERIAL EXAMINED:
Edward Percival Marine Laboratory Collection: Kaikoura, 2/2/1965, 1 ♂ 7.2 mm, 1 g. ♀ 7.8 mm (from old wharf, at night, K 405 K).
Dominion Museum Collection: Napier, –/9/1953, 1 ♂ 8.5 mm (trawled, coll. A. G. Clark). Waikawa Beach, 6/11/1955, 3 ♂♂ 5.5, 7.5, 8 mm, 5 ♀♀ 6.5, 5.5, 5.5, 6.6 mm (amongst fine driftwood and algae, coll. J. Moreland). Lake Ferry, Wairarapa, 4/10/1953, 1 ♂ 11.5 mm (coll. J. Heath); 1 dried ♂ 12 mm (labelled "*Hombronia depressum*" N.Z. Cr. 432).

MONTHS IN WHICH GRAVID FEMALES COLLECTED: February.

COLORATION: Not known from life. Pale brownish-yellow in preservative.

REMARKS: This description agrees well with that of Chilton (1907). However, Chilton denied the presence of a postocular lobe in this species, although Miers (1876b) had reported one. Chilton noted "the lateral portion of the orbit separated by a slight cleft from the upper portion so that the lateral portion in dorsal view gives almost the appearance of a small tooth outside the eyes". Chilton's figure shows a lobe like that on the specimens examined for this study, and in all specimens a true postocular lobe was present and obvious, although it varied in size.

Richardson (1949a, p. 65) gave as a characteristic of the genus "External maxillipeds concealed beneath a wing-like plate". The dried specimen in the Dominion Museum, labelled "*Hombronia depressum* N.Z. Cr. 432", appears to have this plate on the left side of the mouth-field, with the remnants of the palp of the left maxilliped but all the other mouthparts have been removed, leaving only the labrum. The pterygostomian regions are fragmented; the right pterygostomian region is almost complete and of the usual shape but on the left a large piece of the pterygostomian region appears to have broken away from in front of the cheliped and been put back in the wrong place before the specimen was dried. If there were a genuine deformation of the pterygostomian region, it is likely that this would interfere with feeding and make survival impossible. No other specimens possessed such a deformation.

ACKNOWLEDGMENTS

I thank Professor J. E. Morton, who suggested this topic for study, for his continued interest and encouragement.

My grateful thanks are also offered to: Dr R. K. Dell and Dr J. C. Yaldwyn, of the Dominion Museum, and Dr A. W. B. Powell, of the Auckland War Memorial Museum, who provided facilities for the examination of hymenosomatid material at these museums; Dr R. B. Pike and Dr R. G. Wear, of Victoria University, Wellington; Dr J. F. C. Morgans and Dr P. Jansen, then of the University of Canterbury, and Dr J. S. Lucas, then of the University of Western Australia, all of whom sent valuable collections; Dr D. J. G. Griffin, of the Australian Museum, and Mr D. H. Wood, of the University of Queensland, who gave permission to refer to their M.Sc. theses; Mr B. A. Foster, who photographed some species and contributed material; Dr W. F. Ponder, who gave advice on taxonomic procedure, identified Mollusca and collected specimens; Messrs J. S. Melrose, S. J. Whitley, P. Warren, A Michael, P. McGeorge, W. Rudman, D. Cowley and Mr and Mrs J. R. Gordon, who assisted on collecting trips or contributed material; Miss J. Hogg, who identified Porifera; and Mrs M. Borowska, of the interloan Department of the University of Auckland library.

Dr J. C. Yaldwyn offered invaluable advice on the manuscript.

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1979 A—1500/5/73A A. R. SHEARER, GOVERNMENT PRINTER, WELLINGTON, NEW ZEALAND—1975