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SPIDER CRABS OF THE FAMILY HYMENOSOMATIDAE (CRUSTACEA; BRACHYURA) WITH PARTICULAR REFERENCE TO AUSTRALIAN SPECIES: SYSTEMATICS AND BIOLOGY

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SUMMARY

The family Hymenosomatidae is revised as a result of discovering a large range of species in Australia. Three new genera and seven new species are described from the Australasian region. The genera *Rhynchoplax* Stimpson, *Neorhynchoplax* Sakai and *Cyclohombronia* Melrose are relegated to junior synonomy of *Halicarcinus* White, *Elamenopsis* A. Milne Edwards and *Hymenosoma* Desmarest, respectively. *Trigonoplax* H. Milne Edwards, treated by some authors as a subgenus of *Elamena* H. Milne Edwards, is given generic status on the basis of crab and larval morphology. The family now consists of ten genera and sixty-four species; seven genera, including all multispecific genera, and twenty-two species occur in Australia. An annotated key to all genera and species is provided. Diagnostic features for hymenosomatid larvae are given and larval morphology is considered in resolving several taxonomic problems. Absence of a megalopa larva is a notable family feature. Data on the life-cycles, reproduction, behaviour and ecology of hymenosomatids are reviewed. Fecundity is limited by the small sizes of these crabs and some females show morphological adaptations to increase shallow coastal waters and there has been a number of independent invasions of low fecundity by increasing larval survival. The majority of hymenosomatid species occur in shallow coastal waters and there have been a number of independent invasions of low salinity habitats. Twenty-four species, from six genera, occur in fresh and brackish water. Hymenosomatids reach high densities in some habitats and frequently occur in fish gut contents at various localities: they may play significant roles in some food webs. Most hymenosomatid species occur in the tropical and sub-tropical shelf waters of the Indo-West Pacific region and adjacent inland waters. Because they are inconspicuous, geographical distributions of many species are poorly known; the Indo-Malayan Region, which is central to their distribution, is particularly poorly collected.

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INTRODUCTION

The family Hymenosomatidae consists of small to very small spider crabs (maximum carapace width 3-26 mm), which occur mainly in the Indo-West Pacific region. Major revisions of the family have been undertaken by Kemp (1917), Tesch (1918) and Sakai (1938). Each of these authors was disadvantaged by having access to a limited range of hymenosomatid species and the taxonomy of the family is unstable at the generic level. Kemp (1917) had mainly Indian species and a number of genera were not represented in his material. Tesch (1918) examined five species in the Leyden and Amsterdam Museums and two species from the "Siboga" expedition. Sakai (1938) had access to six Japanese species. There was a further major study of hymenosomatid taxonomy by Melrose (nee Gordon) (1975), which was limited to New Zealand hymenosomatids, consisting of fourteen species in four genera. Melrose (1975) was based on a thesis, Gordon (1966), part of which was published as keys to New Zealand Hymenosomatidae (Melrose, 1968). This study by Melrose clarified the confused literature on New Zealand species and was particularly helpful in considering the Australian hymenosomatids.

In contrast to the substantial, though confused, literature on New Zealand hymenosomatids, knowledge of the Australian species has suffered most from neglect. There has been only one attempt at a comprehensive survey of Australian species:

Haswell (1882c) included five species in his catalogue of Australian "stalk- and sessile-eyed" Crustacea. Two of these species, *Hymenosoma planatum* (Fabricius) and *H. varium* (Dana) (Haswell considered that all hymenosomatids belonged in one genus, *Hymenosoma*), are now known to be invalid records and one species, *H. krefftii* (Hess), has not been reported since. Hymenosomatids were also included in three later studies of crustacean faunas of particular regions of Australia. Fulton and Grant (1906b) listed five species from Victoria; Hale (1927) and Griffin (1972) gave the same five species for South Australia and southern-S.E. Australia, respectively. In a study of the physiology and ecology of Australian species of *Halicarcinus* White, Lucas (1968) included a review of their taxonomy and gave eight *Halicarcinus* species known to occur in Australia. Thus, after Lucas (1968), eleven hymenosomatid species were known to occur in Australia: eight *Halicarcinus* species, two *Elamena* species and one *Trigonoplax* species. All except *Elamena truncata* (Stimpson) were from southern (temperate) Australia.

Examination of the Australian museum collections and other collections from northern (tropical) Australia during this study revealed that there are many unrecorded and undescribed hymenosomatid species in Australia and that all the multispecific genera of Hymenosomatidae are represented by species in Australia. For the first time there was the opportunity to review the taxonomy of the family with a representative range of species at hand. A review of all the biological data on hymenosomatids was also undertaken to make a comprehensive study of the family.

PART A, SYSTEMATICS

MATERIAL, METHODS AND ABBREVIATIONS

Most of the specimens examined in this study are kept in the six major Australian museums. Unless otherwise indicated, specimens are preserved in alcohol. Since some preserved specimens shed limbs with any handling, many of the specimens have detached chelipeds and walking legs. Diagnoses and descriptions are based on mature females and large males unless otherwise indicated. Allometric growth occurs in these species: carapace width to length ratio changes during growth, and rostrum, eyes and walking legs usually become relatively smaller. The onset of maturity in females is marked by an abrupt expansion of the abdomen, curvature of the abdomen to create a cavity between the abdomen and sternum (the abdominosternal or brood cavity), and development of the pleopods. (These comments do not apply to *Elamenopsis* females.) Males also show morphological changes at a late instar, but they may be sexually mature before this instar. Hence "large" is used instead of "mature" in describing late-instar males. The morphological changes in large males usually take the form of one or more of the following: elongation of the rostrum, elongation of body spines, and elongation and expansion of the chelipeds, compared to small males and females.

Measurements were made with vernier calipers or an eyepiece scale according to size. The general measure of size is given as maximum carapace width, which is usually about the level of the posterior lateral carapace angles. The rostrum is included in measurements of carapace length unless otherwise indicated. Walking leg length is measured from the longest leg, usually the second walking leg.

The terminology used in descriptions follows Melrose (1968, 1975) and is illustrated in Fig. 1.

The following abbreviations are used in giving details of specimens examined:

im.,	immature
juv.,	juvenile (could not be sexed)
ov.,	ovigerous
AHF,	Allan Hancock Foundation, California, U.S.A.
AM,	Australian Museum, Sydney, N.S.W.
BM,	British Museum (Natural History), London, U.K.
CSIRO,	Moreton Bay Collection, CSIRO Fisheries and Oceanography, Cronulla, N.S.W.
IFCT,	Inland Fisheries Commission of Tasmania, Tasmania
JCU,	School of Biological Sciences, James Cook University, Queensland.
MHN,	Muséum d'Histoire Naturelle, Paris, France
NMV,	National Museum of Victoria, Melbourne, Victoria
QM,	Queensland Museum, Brisbane, Queensland.
SAM,	South Australian Museum, Adelaide, South Australia.
TM,	Tasmanian Museum, Hobart, Tasmania.
WAM,	Western Australian Museum, Perth, Western Australia.
ZLKU,	Zoology Laboratory, Faculty of Agriculture, Kyushu University, Japan.

Family **HYMENOSOMATIDAE** MacLeay, 1838

Hymenosomidae MacLeay, 1838:68.— Alcock, 1900:285, 291.— Borradaile, 1907:480.— Rathbun, 1925:561.— Sakai, 1938-:193.— Garth, 1950:30.

Hymenosomatidae.— Stebbing, 1905:49.— Barnard, 1950:66-7.— Balss, 1957:1632.— Holthuis, 1968:109-10.— Melrose, 1975:7-8.

See Rathbun (1925) for other synonyms of the family name.

DIAGNOSIS: Cephalothorax thin dorso-ventrally, cuticle not heavily calcified, without hooked setae; dorsal carapace surface flat or nearly flat, often with strong gastro-cardiac groove and contiguous grooves; without orbits or with very incomplete orbits, eyes exposed and little retractile; antennular fossae shallow and poorly defined; antennae fused with epistome (when present), second segment slender; ischium of 3rd maxillipeds well developed, palp articulating near antero-lateral angle of merus; chelipeds not longer than twice carapace width in females and most males, fingers not bent at an angle to palm; male and female abdomens with not more than five segments, excluding telson; male genital apertures sternal; female genital apertures on sternites of 1st walking legs (2nd pereiopods). (Based on Alcock (1900), Borradaile (1907), Barnard (1950) and Balss (1957).)

REMARKS: Hymenosomatids differ from the usual malacostracan pattern of six abdominal segments in never having more than five abdominal segments. Since in female hymenosomatids pleopods occur on abdominal segments 2-5, which are followed by the telson, it appears that the 6th abdominal segment has been lost or obscured by fusion with segment 5 or the telson. Evidence for fusion of the 6th segment and telson is the unusually long proximal portion of the telson in hymenosomatid zoeae. The pattern of five abdominal segments is regarded as normal for hymenosomatids and references to fused and unfused abdomens refer to this basic condition of five segments and telson.

The name of this family (Hymenosomidae versus Hymenosomatidae), the source of the name and the location of the family within Section Brachyura, Order Decapoda, have varied between authors. Recently, Holthuis (1968) found that the oldest known use of the family name was by MacLeay (1838) and Holthuis established that the grammatically correct version of the name is Hymenosomatidae.

Melrose (1975) traced the history of positioning the Family Hymenosomatidae within the Section Brachyura. The hymenosomatids were initially regarded as catometopous crabs; then, later, they were placed in the Superfamily Oxyrhyncha. This is not accepted by some authors as an ideal location. For example, Aikawa (1929), Gurney (1938, 1942) and Wear (1967) saw more affinities of hymenosomatid larvae with larvae of Pinnotheridae (Brachyrhyncha) and Leucosiidae (Oxystomata) than with the larvae of the other oxyrhynchan families; while Richer de Forges (1976, 1977) considered that positioning of the Hymenosomatidae with the catometopous crabs should be reconsidered, particularly in view of the positions of genital apertures and larval morphology. Now Guinot (1977) has proposed a completely new classification of the Brachyura based on positions of genital apertures. In her classification the Hymenosomatidae are included in a Superfamily, Hymenosomatidea, which with six other superfamilies, Gecarcinoidea, Grapsoidea, Mictyroidea, Pinnotheroidea, Hexapodoidea and Ocypodoidea, is in a new taxon, Thoracotremata Guinot, 1977. The Thoracotremata have male and female sternal openings. As well as recognising the affinity of hymenosomatids with catometopous crabs, seen by some previous authors, Guinot's classification expresses the lack of close affinity with any other brachyuran family by placing the hymenosomatids in a separate superfamily.

LARVAL CHARACTERS OF HYMENOSOMATIDAE AND GENERA

Diagnosis of the larval morphology of the family Hymenosomatidae, based on Wear (1967) and Lucas (1971):—telson elongate trapezoidal, wider anteriorly; telson-fork short and straight, with three pairs of close-set spines; 2nd maxillae with single coxal and basial endites, coxal endite vestigial, with a single seta or, less commonly, with two setae; antennae simple, varying from inconspicuous blunt lobes to conspicuous pointed lobes, pointed form with a fine basal hair or terminal spine which tends to be eccentric; abdomen of 5 segments with no traces of pleopods; with three zoeal stages and without pre-zoeal and megalopa stages.

The distinctive telson and telson fork of hymenosomatid larvae are the most useful characters for identifying these larvae in plankton samples.

There is much variation in the development of carapace spines within this family. In addition to the rostral spine, which is always present, mid-dorsal and inferior-lateral spines may also be present. The rostral spine varies from a short blunt lobe to an elongate spine, three times the length of the carapace. As a rule the hymenosomatid species occurring in brackish water have greater development of the larval carapacial spines than do the marine species.

The number of hymenosomatid species for which the larval morphology is known will be substantially increased with the publication of descriptions of most of the fourteen New Zealand species (R. G. Wear, pers. comm.). At this stage larval morphology is not known for enough species in most genera to give generic diagnoses. Details of larval morphology are known for the following species:—

Hymenosoma Desmarest: Broekhuysen (1955) figures lateral views of two larval stages of *H. orbiculare* Desmarest. The larvae have an elongate rostral spine and a mid-dorsal spine. The appendages are not detailed.

Elamena H. Milne Edwards: *E. mathaei* (Desmarest), described by Gurney (1938, 1942) and Al-Kholy (1959); *E. sindensis* Alcock by Prasad and Tampi (1957); *E. cristatipes* Gravely by Hashmi (1970); *E. producta* Kirk and *E. longirostris* Filhol by R. G. Wear (unpublished data); *E. abrolhensis* Gordon by Lucas (unpublished data). Sufficient species are now known to give a diagnosis for larvae of this genus:— globular carapace, without spines except for a short rostral spine; antennules and antennae short; 5th abdominal segment with prominent lateral expansions. From this diagnosis, the "Hymenozoea abdominalis" of Aikawa (1933) is identified as *E. truncata* (Stimpson), since this is the only *Elamena* species occurring in Japan.

Halicarcinus White: *H. messor* (Stimpson) described by Aikawa (1929) and Muraoka (1977); *H. coralicola* (Rathbun) described by Aikawa (1929); *H. varius* (Dana) figured by Wear (1965); *H. cookii* (Filhol) figured by Melrose (1975); *H. planatus* (Fabricius) described by Boschi, Scelzo and Goldstein (1969) and Richer de Forges (1976, 1977); *H. ovatus* Stimpson and *H. rostratus* (Haswell) described by Lucas (1971); *H. orientalis* Sakai by Muraoka (1977); *H. afecundus* n.sp. has large eggs, indicating abbreviated larval development. Larvae of this genus have globular carapaces, although the rostral spine may be of moderate length and there may be small spines on the inferior-lateral margins of the carapace.

Trigonoplax H. Milne Edwards: Aikawa (1929) described a larva of *T. unguiformis* (de Haan). The rostrum, antennules and antennae are of moderate length and the abdomen has no lateral expansions. The larva of this *Trigonoplax* species is unlike the larvae of *Elamena* species. Larval morphology does not support treatment of *Trigonoplax* as a subgenus of *Elamena,* e.g. by Alcock (1900), Kemp (1917) and Gordon (1940).

Elamenopsis A. Milne Edwards: *E. lineata* A. Milne Edwards has been studied by Lucas (unpublished data); *E. bovis* (Barnard) has suppressed larval development — Barnard (1950) described a female with thirteen 1 mm juveniles in its abdominosternal cavity; a freshwater species, *E. kempi* (Chopra and Das), probably has suppressed larval development — Abele (1972) described larger than normal eggs on ovigerous females. The larvae of *E. lineata* are striking, with very long mid-dorsal and rostral spines, two and three times the carapace length, respectively. Another feature of *E. lineata* larvae is the presence of two setae (not one) on the coxal endite of the 2nd maxilla.

Amarinus n.gen.: Lucas (1971) described larvae of *A. laevis* (Targioni Tozzetti) and *A. paralacustris* (Lucas); *A. lacustris* (Chilton) and *A. angelicus* (Holthuis) have no free larval stages (Lucas, 1971; J. C. Yaldwyn, pers. comm.). The larvae of *A. laevis* and *A. paralacustris* have well-developed carapace spines: rostral and inferior-lateral (both species) and mid-dorsal (*A. laevis* only) spines are present.

Neohymenicus n.gen.: Larvae of *N. pubescens* (Dana) have four short carapace spines and an abdomen with a laterally expanded 5th segment (Wear, 1968).

Larvae have not been described in three monospecific genera, *Hymenicoides* Kemp, *Halimena* Melrose and *Halicarcinides* n.gen.

ANNOTATED KEY TO ALL GENERA, SPECIES AND INFRASPECIES OF HYMENOSOMATIDAE

The page number in brackets following each generic name in the key refers to further treatment of the genus in this text. After each species name in the key the following data are provided: size range (carapace width) of mature females, or other specimens as indicated; known geographical distribution; brief habitat details, where available; major references giving descriptions and figures of the species; comments on the species, including major synonyms; page number of further treatment in this text (Australian species).

Many of the non-Australian species of Hymenosomatidae were not examined during this study and the characters used in the key are derived from published descriptions.

1	Rostrum present; carapace of various forms	2
—	Rostrum absent; carapace almost circular (two rare species only)	11
2(1)	Rostrum continuous with dorsal carapace surface, not separated by a ridge or groove; rostrum triangular or truncated; dorsal carapace surface without grooves except for a faint gastro-cardiac groove in some species	3
—	Rostrum separated from the dorsal carapace surface by a ridge or groove or both; rostrum of various forms; dorsal carapace surface usually with a distinct gastro-cardiac groove and contiguous grooves	4
3(2)	Carapace, with rostrum, approximately triangular; Milne Edwards apertures fused laterally for more than half their length (see Fig. 5F) .... *Trigonoplax* H. Milne Edwards, 1853 ... (p.186)	12
—	Carapace, with rostrum, polygonal to pear-shaped; Milne Edwards apertures not fused laterally for more than half their length ...... *Elamena* H. Milne Edwards, 1837 ... (p.170)	14
4(2)	Epistome present	5
—	Epistome absent ...... *Hymenosoma* Desmarest, 1825 ... (p.166)	67
5(4)	Dorsal carapace surface with a distinct gastro-cardiac groove and contiguous grooves	6
	Dorsal carapace surface without distinct grooves	10
6(5)	3rd maxillipeds narrow, not covering three-quarters of mouth-field, ischium much shorter than merus along lateral edge; with fused segments in male or female abdomen or both ... *Elamenopsis* A. Milne Edwards, 1873 ... (p.190)	26
—	3rd maxillipeds broad, covering three-quarters or more of mouth-field, ischium not much shorter than merus along lateral edge; usually without fused segments in male and female abdomens	7
7(6)	Dactyli of walking legs with one or two rows of teeth .....*Halicarcinus* White, 1846 ... (p.176)	44

— Dactyli of walking legs without teeth or with one or two subterminal teeth . 8

8(7) Rostrum distinctly trilobate ..... *Halicarcinus* White, 1846 ... (p.176) 44

— Rostrum not distinctly trilobate, rostrum triangular to spade-shaped..... 9

9(8) Rostrum more triangular than spade-shaped; male 1st pleopod strongly curved, with a single row of long setae subterminally; gastric region of dorsal carapace surface strongly outlined by grooves extending to base of rostrum, gastric region much more indicated by grooves than other regions of carapace .... *Neohymenicus* n.gen. ... (p.208) .(monospecific)

N. pubescens (Dana, 1851); 4-8 mm; New Zealand; *Sargassum,* coralline algae turf and rock crevices, sheltered littoral and sublittoral to 11 m; Melrose 1975: 77-84, figs. 36-40.

— Rostrum more spade-shaped than triangular; male 1st pleopod little curved, not with a single row of long setae subterminally; gastric region of dorsal carapace surface not more strongly outlined by grooves than other carapace regions .... *Amarinus* n.gen. ...(p.198)................................. 61

10(5) 3rd maxillipeds narrow, well separated medially .... *Hymenosoma* Desmarest, 1825 ...(p.166).. 67

— 3rd maxillipeds broad, almost meeting medially .... *Halimena* Melrose, 1975 ...(p.197)..(monospecific)

H. aotearoa Melrose, 1975; 6 mm; New Zealand; on algae, littoral and sublittoral, to 91 m; Melrose 1975: 106-9, figs. 53-54.

11(1) 3rd maxillipeds narrow, well separated medially; palp of 3rd maxillipeds elongate, reaching down to posterior edge of mouth-frame ... *Hymenicoides* Kemp, 1917. (p.196) ....(monospecific)

H. carteri Kemp, 1917; 6 mm (large ♂); Hughli, R., N.E. India; brackish; Kemp 1917: 268-70, figs. 17-21.

— 3rd maxillipeds broad, almost meeting medially; palp of 3rd maxillipeds not elongate, not reaching near posterior edge of mouth-frame ... *Halicarcinides* n.gen ...... (p.206) ....(monospecific)

H. nuytsi (Hale, 1927); 4.9-5.8 mm; S.E. Australian mainland; littoral and sublittoral; Hale 1928: 98-9, fig. 22; page 207

12(3) Rostral keel deep, extending to tip of rostrum, generally visible dorsally; rostrum often strongly upturned ....*T. spathulifera* n.sp.

8-14 mm; northern Australia; variable habitat, from littoral zone on coral reefs to 130 m; page 188.

— Rostral keel shallow, not extending near tip of rostrum, not visible dorsally; rostrum never strongly upturned.. 13

13(12) Carapace width to length ratio approximately 1.0, less than 1.1...*T. longirostris* McCulloch, 1908

13-17 mm; southern Australia; sublittoral, to 20 m; Hale 1924: 70-1, fig. 1; Hale 1927: 120-1, fig. 118; page 187.

— Carapace width to length ratio greater than 1.1 .*T. unguiformis* (de Haan, 1839)

13-17 mm; widespread Indo-West Pacific distribution, excluding Australia; sublittoral, to 100 m; Kemp 1917: 277-8, figs. 28, 29; Tesch 1918: 25-6; Sakai 1938: 201-2, pl. 20 fig. 4; shows some morphological variation over its range (see page 187).

14(3) Rostrum triangular; carapace, with rostrum, tending to be pear-shaped; carapace width often less than carapace length in large specimens; with or without rostral keel forming a distinct T-shape with rostrum rim in anterior view ("triangular" species) 15

— Rostrum truncate and broad; carapace, with rostrum, tending to be polygonal; carapace width often greater than carapace length in large specimens; with rostral keel forming a distinct T-shape with rostrum rim in anterior view ("truncate" species) 21

15(14) Rostral keel forming a distinct T-shape with rostrum rim in anterior view 16

— Rostral keel absent or not forming a distinct T-shape with rostrum rim in anterior view 18

16(15) Posterior portion of rostral keel developed into a long spine projecting anteriorly and ventrally; posterior lateral angles of carapace with a spine or tubercle projecting dorsally (approximately dorsal to base of 2nd walking leg)..*E. longirostris* Filhol, 1885a

7.5-10 mm; New Zealand; sublittoral, 11 m-116 m, on substrates of mud and shell, and sand and small stones; Takeda and Miyake, 1969: 181-4, fig. 7; Melrose 1975: 93-4, fig. 45.

— Posterior portion of rostral keel not developed into a spine; posterior lateral angles of carapace without a spine or tubercle 17

17(16) Carapace width usually greater than carapace length; pterygostomial lobe not prominent; male abdomen very broad at base; male 1st pleopod with two groups of subterminal setae ....*E. gracilis* Borradaile, 1903

6 mm; Maldive Archipelago; coral reef; Borradaile 1903: 684-5, fig. 122*; Gordon 1940: 71-3, figs. 1c, 6a, 6d, 7d; *Gordon (1940) states that both cotypes which she examined were "considerably more narrowly triangular" than Borradaile's figure.

— Carapace width usually equal to or less than carapace length; pterygostomial lobe prominent; male abdomen moderately broad at base; male 1st pleopod with one group of subterminal setae..*E. sindensis* Alcock, 1900

6.6 mm (♂); India and Sri Lanka; Alcock 1900: 386; Alcock and McArdle: 1902, pl. 64 fig. 4; Gordon 1940: 66-7, fig. 4.

18(15) Anterior lateral angles of carapace very prominent; antero-lateral carapace borders at right angles to longitudinal body axis.....*E. umerata* n.sp.

2.8 mm; northern Australia; among sessile invertebrates, littoral, sublittoral; page 175.

— Anterior lateral angles of carapace not prominent, only slightly indicated; antero-lateral carapace borders not at right angles to longitudinal body axis..19

19(18) Dactyli of walking legs with row of small teeth; rostrum parallel sided at base..*E. cimex* Kemp, 1915

6.5 mm; Bay of Bengal and Madagascar; euryhaline marine or brackish; Kemp 1915: 216-18, figs. 4, 5, pl. 12 fig. 3; Barnard 1962: 239; Barnard's specimens differ from those of Kemp in the extent of teeth on dactyli of walking legs and also in type of habitat; there may be two species represented here.

— Dactyli of walking legs without a row of small teeth, but with one or two subterminal teeth; rostrum completely triangular, sides convergent from base 20

20(19) Abdomen of mature female relatively very large, broader than body and conspicuous laterally in dorsal view, pleopods extending laterally from abdomen; rostral keel absent; lobes in pterygostomial and subhepatic regions prominent and visible dorsally.................*E. gordonae* Monod, 1956

2.3-3.0 mm; western Africa, N.E. Australia; sublittoral, 18-40 m; Monod 1956: 469-72, figs. 629-37; page 174.

— Abdomen of mature female of normal size, not broader than body, not conspicuous laterally in dorsal view, pleopods not extending laterally from abdomen; rostral keel present as a small tooth; lobes in pterygostomial and subhepatic regions not prominent and not visible dorsally..*E. xavieri* Kemp, 1917

8.5 mm; Mandavi R., India; brackish; Kemp 1917: 275-7, figs. 24-27.

21(14) Male abdomen without fused segments, consisting of 6 pieces including telson; terminal border of telson of mature female convex (New Zealand species)... 22

— Male abdomen with segments 3 and 4 fused and suture obscure, consisting of 5 pieces including telson; terminal border of telson of mature female concave or truncate (not from New Zealand) 23

22(21) Merus of walking legs with a prominent acute tooth on distal edge; anterior lateral and posterior lateral carapace angles distinct; rostral keel deepest anteriorly..*E. producta* Kirk, 1879

7-14.5 mm; New Zealand; under boulders in sandy or pebbly pools in mid to low littoral; Melrose 1975: 95-102, figs. 46-50, pl. 1B.

— Merus of walking legs with a small obtuse or barely acute tooth on distal edge; anterior lateral and posterior lateral carapace angles indistinct; rostral keel not deepest anteriorly, of uniform depth along its length...*E. momona* Melrose, 1975

4.5-9 mm; New Zealand; shallow sublittoral, oyster beds; Melrose 1975: 102-6, figs. 51, 52.

23(21) Dactyli of walking legs with a single subterminal tooth, dorsal margin of propodus strongly compressed to a ridge and finely serrated; dactylus of chela of large males without a large basal tooth ....*E. cristatipes* Gravely, 1927

5 mm; India; sublittoral; Gravely 1927: 150, pl. 21 fig. 24; Chopra and Das 1930: 425-8, figs. 11-15.

— Dactyli of walking legs usually with two subterminal teeth, dorsal margin of propodus not strongly compressed to a ridge and not finely serrated; dactylus of chela of large males with a large basal tooth..................... 24

24(23) Male 1st pleopod with narrow distal portion approximately C-shaped, with approximately 5 subterminal setae; posterior lateral angles of carapace usually rounded and not evident......................*E. truncata* (Stimpson, 1858)

5.6-9.3 mm; Indo-West Pacific, northern Australia to Japan; coral reefs, coral rubble, weedy and rocky shores, littoral and shallow sublittoral; Sakai 1938: 201, pl. 20 fig. 3; Gordon (1940) considers "it is highly probable ... that more than one species is represented"; page 172.

— Male 1st pleopod with narrow distal portion approximately S-shaped due to recurvature at apex, 8-12 subterminal setae; posterior lateral angles of carapace evident as pointed obtuse angles...................................... 25

25(24) Subterminal setae on male 1st pleopods elongate, reaching or nearly reaching thick basal portion of pleopod if turned down towards basal portion; rostral keel not meeting interantennal septum; postocular lobes with an indistinct tooth or with no tooth..........*E. mathaei* (Desmarest, 1825)

4.5-7 mm; Red Sea, S.E. Africa, Mauritius; marine shallow sublittoral (?); Gordon, 1940: 63-4, figs. 1a, 1b, 2, 3a-3c; Barnard 1950: 73-5, figs. 15g-o.

— Subterminal setae on male 1st pleopods not elongate, not nearly reaching thick basal portion of pleopod if turned down towards basal portion; rostral keel continuous with interantennal septum; postocular lobes with a small acute tooth..*E. abrolhensis* Gordon, 1940

6.8-8.4 mm; southern Australia; on hard substrates, rock or limestone, in littoral or shallow sublittoral; Gordon 1940: 70-71, figs. 6b, 6c, 7a, 7c, 10a; page 173.

26(6) Dactyli of walking legs without teeth 27

— Dactyli of walking legs with a subterminal tooth or a row of teeth........ 35

27(26) Rostrum consisting of a single deflexed lobe 28

— Rostrum trilobate, although lateral lobes may be partially fused with medial lobe and very short... 29

28(27) Walking legs broad and laterally compressed; fused section of male abdomen tapering, not constricting abruptly; male 1st pleopod without a spine-like apex......................................*E. lineata* A. Milne Edwards, 1873

3-4 mm; New Caledonia, northeastern Australia, Philippines; brackish, muddy substrates; Tesch 1918: 26-8, pl. 1 fig. 5; page 192.

— Walking legs not broad and laterally compressed; fused section of male abdomen constricting abruptly; male 1st pleopod with a spine-like apex..*E. inermis* (Takeda and Miyake, 1971a)

3.6 mm; Palau Islands; fresh water; Takeda and Miyake 1971a: 1-7, fig. 1; the ♂ paratype is much smaller than the ♀ holotype and its 1st pleopods, figs. 1f, 1g, may be stouter than in larger males.

29(27) Dorsal carapace surface with one or four large tubercles, one tubercle occurring medially on gastric region .... *E. tuberculata* (Chopra and Das, 1930)... 30

<5-7.2 mm; southern India and Sri Lanka; brackish; Chopra and Das 1930: 419-24, figs. 6-10; Pretzmann 1975: 607-8, pl. 1 figs. 1-5; the variety, *E. t.* var. *attenuipes,* which is sympatric with the *forma typica,* and the subspecies, *E. t. pageti* from Sri Lanka, differ in important features from the *forma typica* and may be separate species.

— Dorsal carapace surface without large tubercles 32

30(29) With three large tubercles on cardiac region of dorsal carapace surface 31

— Without tubercles on cardiac region of dorsal carapace surface ....*E. tuberculata pageti* (Pretzmann, 1975)

31(30) Walking legs broad, propodus of 2nd walking leg ca. 4 X as long as broad ....*E. tuberculata tuberculata* (Chopra and Das, 1930)

— Walking legs not broad, propodus of 2nd walking leg ca. 6 X as long as broad ....*E. tuberculata* var. *attenuipes* (Chopra and Das, 1930)

32(29) Walking legs broad and laterally compressed; lateral lobes of rostrum broad, short to very short, and obtuse... 33

— Walking legs slender; lateral lobes of rostrum narrow, short and acute. 34

33(32) Medial rostral lobe almost square, a little longer than broad; deflexed; carapace nearly circular..*E. demeloi* (Kemp, 1917)

4.4 mm (♂); Goa, India; brackish, under stones on mud; Kemp 1917: 258-60, figs. 6-9.

— Medial rostral lobe triangular, not deflexed; carapace oval-octagonal, broader than long ....*E. ariakensis* (Sakaï, 1969)

3.5 mm; Nagasaki Prefecture, Japan; commensal with holothurian, *Protankyra bidentata,* on mud flats; Sakai 1969: 250-51, figs. 2, 3; Sakai 1976: 150-1, figs. 79, 80a-d, pl. 47 fig. 1.

34(32) Rostrum consisting of three rounded lobes, fused at base; posterior lateral angles of carapace with a small acute tooth (approximately above base of 1st walking leg) ....*E. sinensis* (Shen, 1932)

2.3 mm (♂); Shantung Peninsula, China; littoral, under stones on mud flats and attached to echinoids; Shen 1932: 58-62, figs. 33-36, pl. 2 fig. 7.

— Rostrum consisting of three spine-like lobes, well separated, not fused at base; posterior lateral angles of carapace without a tooth...*E. aspinifera* n.sp.

3 mm; northeastern Australia; brackish-marine, muddy substrates; page 195.

35(26) Rostrum consisting of a single lobe, a pointed horizontal lobe approximately twice as long as wide.........................*E. nasalis* (Kemp, 1917)

4 mm; West Bengal, India; brackish; Kemp 1917: 265-7, figs. 12-15.

— Rostrum trilobate 36

36(35) Posterior lateral angles of carapace with a spine below carapace rim (approximately dorsal to base of 1st walking leg) 37

— Posterior lateral angles of carapace without a spine 40

37(36) Rostral lobes fused at base; dactyli of walking legs 2-4 with a row of small teeth; antero-lateral borders of carapace with one or two short teeth ... 38

— Rostral lobes not fused at base, lateral lobes well separated from medial lobe; dactyli of walking legs without a row of teeth, with a subterminal tooth; antero-lateral borders of carapace without teeth .... *E. octagonalis* (Kemp, 1917)

2.5-3 mm; Goa, India, and Moreton Bay, Queensland, Australia; littoral, muddy substrates; Kemp 1917: 256-8, fig. 5; page 193.

38(37) Medial lobe of rostrum much longer than broad; male telson subequal in length and breadth 39

— Medial lobe of rostrum almost as broad as long; male telson distinctly longer than broad .... *E. kempi* (Chopra and Das, 1930)

4-6 mm; Basra, Iraq, and Panama Canal, Central America; fresh water, on plants; Chopra and Das 1930: 416-19, figs. 2-5; Abele 1972: 211-15, figs. 1-3; Abele suggests that *E. kempi* was introduced into the Panama Canal with the water plant *Hydrilla verticillata,* after 1939.

39(38) Carapace length, excluding rostrum, to width ratio approximately 1.1:1; antero-lateral borders of carapace with two small teeth; fingers of chelae of large males not widely gaping at base......... *E. woodmasoni* (Alcock, 1900)

6 mm (♂); Andaman Islands and West Bengal, India; marine (?); Alcock 1900: 388; Alcock and McArdle 1902: pl. 64 fig. 3; Kemp 1917: 252-3, 255-6, fig. 4a-c.

— Carapace length, excluding rostrum, to width ratio approximately 1:1; antero-lateral borders of carapace with one small tooth; fingers of chelae of large males widely gaping at base .... *E. alcocki* (Kemp, 1917)

4 mm; west coast, India; brackish, muddy substrates and on fouling organisms; Kemp 1917: 253-6, figs. 3, 4d-g; Chopra and Das 1930: 414-16, fig. 1; Abele 1972: 215, figs 2A, 3A.

40(36) Dactyli of walking legs with a row of teeth; lateral lobes of rostrum not widely separated from medial lobe, not pointing inward 41

— Dactyli of walking legs without a row of teeth, with one subterminal tooth; lateral lobes of rostrum widely separated from medial lobe, pointing inward .... *E. torrensica* n.sp.

4.3 mm; Thursday Island, northern Australia; marine (?); page 194.

41(40) Rostrum consisting of three elongate spines, length of medial lobe of large male approximately one third of carapace length, excluding rostrum .... *E. inachoides* (Alcock, 1900)

6 mm (♂); West Bengal, India; marine (?); Alcock 1900: 388-9; Alcock and McArdle 1902: pl. 65 fig. 1; only known from ♂ holotype.

— Rostrum not consisting of three elongate spines, at least medial lobe with rounded apex, length of medial lobe usually much less than one third of carapace length, excluding rostrum 42

42(41) Branchiostegites with strong crest projecting dorsally and reaching higher than postero-lateral border of carapace; rostral lobes not fused or barely fused at base in dorsal view ....*E. introversa* (Kemp, 1917)

<5.4 mm (♂); Kiangsu Province, China; fresh water; Kemp 1917: 262-4, fig.11.

— Branchiostegites without a strong crest projecting dorsally; rostral lobes substantially fused at base in dorsal view... 43

43(42) Fingers of male chelae gaping at base, meeting only in distal third, without teeth; male telson much longer than broad; with an obtuse tooth at anterior lateral angles of carapace; sometimes with very prominent spines on postocular lobes ....*E. bovis* (Barnard, 1947)

<5.5 mm; South Africa; sublittoral to 68 m, brackish; Barnard 1950: 72-3, fig. 15c-f; considering the range of habitats and morphological variation described by Barnard (1950), several taxa may be represented here; without free larval development.

— Fingers of male chelae meeting along most of their length, with approximately 5 teeth (each?); male telson slightly shorter than broad; without a tooth at anterior lateral angles of carapace; never with very prominent spines on postocular lobes......................*E. exigua* (Kemp, 1917)

3.3 mm; Thailand; brackish; Kemp 1917: 260-2, fig. 10.

44(7&8) Rostrum distinctly trilobate or tridentate, concavities between lobes reaching almost to carapace rim... 45

— Rostrum not distinctly trilobate or tridentate, concavities between lobes not reaching near carapace rim... 53

45(44) Medial rostral lobe much longer than lateral lobes 53

— Medial rostral lobe subequal with or shorter than lateral lobes 46

46(45) Dactyli of walking legs with one or two rows of small teeth................ 47

— Dactyli of walking legs without a row of small teeth, but with one or two subterminal teeth 51

47(46) With an acute spine on lateral carapace walls or carapace rim at posterior lateral angle (approximately dorsal to base of 1st walking leg); rostral lobes arising at level of carapace rim or slightly below............................... 48

— Without an acute spine on lateral carapace walls or carapace rim at posterior lateral angle; rostral lobes arising well below carapace rim ....*H. innominatus* Richardson, 1949b

6.5-15.5 mm; New Zealand, Chatham Islands, Tasmania; associated with mussels, *Perna canaliculus,* in littoral zone (Melrose, 1975); Melrose 1975:

26-34, figs. 5-11, pl. 1C-F; specimens of *H. innominatus* from New Zealand have generally been called *H. planatus* (Fabricius), however this latter species occurs south of New Zealand (Melrose, 1975); page 182.

48(47) Rostral lobes extending well beyond eyes — thin and well separated .... *H. tongi* Melrose, 1975

6.5 mm; New Zealand; deep sublittoral, to 500 m; Melrose 1975: 88-92, figs. 43, 44.

— Rostral lobes not extending beyond eyes; *or* if extending beyond eyes, rostral lobes moderately broad and set close together 49

49(48) Medial rostral lobe shortest, lateral lobes sloping downward; anterior lateral angles of carapace not marked by angles in carapace rim .... *H. planatus* (Fabricius, 1775)

3.5-6 mm (Chile), 8-11 mm (Strait of Magellan), 8-19 mm (Auckland Islands), 12-14 mm (Kerguelen Island); circum-polar subantarctic; under rocks and among fronds of algae *Macrocystis pyrifera* in littoral zone, in sublittoral to 270 m; Garth 1958: 31-5, fig. 1, pl. 1; Melrose 1975: 34-9, figs. 12, 13; Richer de Forges 1977: 74-81, figs. 1-5.

— Medial rostral lobe slightly longer than lateral lobes, lateral lobes not sloping downward; anterior lateral angles of carapace marked by obtuse angles in carapace rim 50

50(49) Large males with basal tooth on dactylus of chela; concavities between rostral lobes usually at least reaching carapace rim; rostrum often arising slightly below level of carapace rim; antero-lateral carapace borders slightly concave to straight .... *H. ovatus* Stimpson, 1858

4-10 mm, mostly 5-6 mm; southern Australia; rocky substrates, among mussels and algae, littoral and sublittoral, to 60 m; Hale 1927: 117, fig. 113; Melrose 1975: 39-44, figs. 14, 15; very variable species (see p.179), Hale and Melrose do not show the range of variation; page 179.

— Males without basal tooth on dactylus of chela; concavities between rostral lobes not reaching carapace rim; rostrum at level of carapace rim; antero-lateral carapace border concave .... *H. cookii* (Filhol, 1885b)

3-8.5 mm; New Zealand; on algal substrates, littoral and shallow sublittoral; Melrose 1975: 44-59, figs. 1-4, 16-18, 21, pl. 2.

51(46) Lateral lobes of rostrum distinctly longer and broader than medial lobe .... *H. afecundus* n.sp.

5.4 mm; Great Barrier Reef, Australia (one locality); marine, sublittoral; page 185.

— Lateral lobes of rostrum not longer and broader than medial lobe........ 52

52(51) With an acute spine on lateral carapace walls, approximately dorsal to base of 1st walking leg .... *H. minutus* (A. Milne Edwards, 1873)

5.4 mm; New Caledonia; marine; A. Milne Edwards 1873: 324, pl. 18 fig. 5; Takeda and Nunomura 1976: 65-6, fig. 2.

— Without an acute spine on lateral carapace walls....... *H. orientalis* Sakai, 1932

4-6 mm (?); Japan; shallow beaches, under stones and weeds (Sakai); Sakai 1932: 42-3, fig. 1, pl. 2 fig. 1; Sakai 1938: 195, pl. 20 fig. 1.

53(44 & 45) Rostrum extending beyond eyes, deflexed or upturned, not forming a short, almost horizontal platform 54

— Rostrum not extending beyond eyes, forming a short, almost horizontal platform ....*H. varius* (Dana, 1851)

4-10 mm; New Zealand; sheltered littoral and sublittoral to 18 m, on stones, algae, *Zostera* or buried in sand; Melrose 1975: 59-68, figs. 25-28, pl. 2E; rostrum variable in form, which has caused confusion with *H. cookii* (see Melrose 1975: 66).

54(53) With an acute tooth or spine on lateral carapace walls at posterior lateral angles of carapace (approximately dorsal to base of 1st walking leg)..... 55

— Without an acute tooth or spine on lateral carapace walls at posterior lateral angles of carapace 58

55(54) Medial lobe of rostrum spatuliform, broadest about halfway along its length and broadly rounded apically..................*H. messor* (Stimpson, 1858)

5 mm (♂); Japan; littoral zone of rocky beaches, under stones or in algae; Sakai 1938: 197-8, fig. 1, pl. 20 fig. 2; Sakai 1965: 63, fig. 9, pl. 25 fig. 2; previously known as *Rhynchoplax messor.*

— Medial lobe of rostrum styliform, broadest at base and tapering to apex. 56

56(55) Rostrum with one or more long hairs arising from apex; abdomen of mature female broader than body, conspicuous laterally in dorsal view, with segments 3 and 4 fused; walking legs moderately stout ....*H. hondai* (Takeda and Miyake, 1971b)

2.6 mm; Ryukyu Islands, Japan, and Great Barrier Reef, Australia; coral rubble and green algae on coral reef flats, littoral; Takeda and Miyake 1971b: 168-70, fig. 3; page 183.

— Rostrum without long hairs arising from apex; abdomen of mature female not broader than body, not conspicuous laterally in dorsal view, without fused segments; walking legs slender 57

57(56) Lateral margins of rostrum fringed with setae; anterior lateral carapace angles with an obtuse tooth; posterior lateral carapace angles with an acute tooth ....*H. setirostris* (Stimpson, 1858)

4.4 mm; China, Japan; muddy and shelly substrates, sublittoral 25-110 m; Sakai 1938: 198-9, fig. 2; Sakai 1976: 148-9, figs. 76b, 77, pl. 46 fig. 3; previously known as *Rhynchoplax setirostris;* = *Halicarcinus yangi* Shen, 1932 (Sakai, 1965).

— Lateral margins of rostrum not fringed with setae; anterior lateral carapace angles without an obtuse tooth; posterior lateral carapace angles with an acute spine pointing vertically ....*H. rostratus* (Haswell, 1882a)

3-5.5 mm; southern Australia; often on algae, sublittoral, to 90 m; Hale 1927: 117-18, fig. 114; page 180.

58(54) Medial rostral lobe fringed with short setae along lateral edges; lateral rostral lobes terminating in an acute point.. 59

— Medial rostral lobe not fringed with short setae along lateral edges; lateral rostral lobes with rounded apex or completely fused with medial lobe . 60

59(58) Anterior lateral angles of carapace with an acute tooth; base of rostrum not fused with postocular lobes in a broad band above eyestalks; medial rostral lobe without long terminal hairs............*H. coralicola* (Rathbun, 1909)

3.6 mm (♂); Japan, Taiwan, Singapore; coral reef, rocky substrates and algal holdfasts; littoral; Sakai 1938: 199-200; Sakai 1976: 144, figs. 76a, 78a-e, pl. 46 fig. 4; previously known as *Rhynchoplax coralicola;* = *Halicarcinus septentrionalis* Yokoya, 1928 (Sakai, 1965).

— Anterior lateral angles of carapace without an acute tooth; base of rostrum fused with postocular lobes in a broad band above eyestalks; medial rostral lobe with several long terminal hairs
....*H. keijibabai* (Takeda and Miyake, 1971b)

1.9 mm; New Caledonia; Takeda and Miyake 1971b: 165-8, figs. 1,2; abdomen of mature female broader than carapace and with pleopods extending beyond abdomen.

60(58) Rostrum approximately triangular, narrowing abruptly about half-way or further along its length where lateral lobes terminate, lateral lobes completely fused with medial lobe; body and legs not covered with long dense hairs...*H. bedfordi* Montgomery, 1931

4-6.7 mm (Swan River), 3-4 mm (northern localities); northern Australia, but extending to Swan River on west coast; muddy substrates and algae, littoral and shallow sublittoral, euryhaline marine; Montgomery 1931: 425-6, pl. 27 figs. 3, 3a, 3b; page 181.

— Rostrum approximately spade-shaped, not narrowing abruptly along its length, terminally trilobate; body and legs covered with long hairs in large specimens ....*H. whitei* (Miers, 1876)

7-11.5 mm; New Zealand; littoral, sheltered marine and estuarine localities, among *Zostera* or buried in sand; Melrose 1975: 69-77, figs. 31-33, 35, pl. 1A.

61(9) Antero-lateral margins of carapace with a row of conspicuous teeth; walking legs with long, dense hairs; chelae of large males with dense hairs on posterior side of propodus ....*A. woltereckі* (Balss, 1934)

11 mm (large ♂); Mindanao, Philippines; freshwater lake; Balss 1934: 181-3, figs. 3-5.

— Antero-lateral margins of carapace without a row of conspicuous teeth; walking legs without dense hairs; chelae of large males usually without dense hairs.. 62

62(61) With numerous thin spines (or spinules) on carapace margins, rostrum, pterygostomial regions, walking legs and chelipeds
....*A. pilosus* (A. Milne Edwards, 1873)

26 mm (large ♂); New Caledonia; fresh water, sandy substrates; Milne Edwards 1873: 322-3, pl. 18 fig. 6; Holthuis 1968: 117-19, fig. 3.

— Without numerous thin spines on body and legs.............................. 63

63(62) Mature females generally greater than 10 mm; antennal spines acute and prominent; male 1st pleopods not tapering to a point, apex with a large blunt lobe and smaller curved lobe; chelae of large males with a pulvinus (a sac arising between the bases of the fingers) ....*A. laevis* (Targioni Tozzetti, 1877)

10-18 mm; southern Australia; brackish water, estuaries; Montgomery 1931: 423-5, pl. 27 figs. 4, 4a; largest Australian hymenosomatid, readily distinguished from other Australian *Amarinus* n.gen. species by its size; generally known as *Halicarcinus australis* (Haswell) in previous literature; page 199.

— Mature females generally less than 10 mm; antennal spines small and obtuse; male 1st pleopods tapering to a point; chelae of large males without a pulvinus.. 64

64(63) Rostrum strongly deflexed, almost vertical; orbits well separated from carapace rim by lateral extensions of rostum base ....*A. angelicus* (Holthuis, 1968)

8 mm; Southern Highlands, Papua-New Guinea; freshwater swamp; Holthuis 1968: 112-16, figs. 1, 2.

— Rostrum deflexed, but not near vertical; orbits usually reaching near to carapace rim.. 65

65(64) Postocular lobes large, prominent in dorsal view, extending laterally along antero-lateral borders of carapace, and, with slightly deflexed rostrum, forming a shield across anterior of carapace ....*A. latinasus* n.sp.

4 mm; North Queensland; brackish; page 205.

— Postocular lobes moderate sized, not prominent in dorsal view, not extending laterally along antero-lateral borders of carapace, and not forming a shield with rostrum.. 66

66(65) Female genital apertures 0.4-0.5 mm wide, generally with a curved medial prominence (absent in North Queensland specimens); eggs less than 0.4 mm diameter; telson approximately 0.35 of total abdomen length in mature females...*A. paralacustris* (Lucas, 1970)

5-8 mm; eastern Australia; brackish water, estuaries; Lucas 1970: 275-7, figs. 3c, 3e; *A. paralacustris* and *A. lacustris* can only be distinguished by egg size and the morphology of mature females; page 204.

— Female genital apertures 0.65-0.8 mm wide, without a curved medial prominence; eggs approximately 0.7 mm diameter; telson approximately 0.25 of total abdomen length in mature females.....*A. lacustris* (Chilton, 1882)

5-8 mm; southeastern Australasia; freshwater streams, freshwater and low salinity lakes; Melrose 1975: 84-8, figs. 41, 42; see comment above on *A. paralacustris;* page 201.

67(4 & 10) Epistome present, but short and narrow; without well defined grooves on dorsal carapace surface ....*H. depressum* Jacquinot, 1853

5-8 mm; New Zealand; littoral and sublittoral; Melrose 1975: 110-16, figs. 55-58; see p. 168 for comment on its inclusion in *Hymenosoma.*

— Epistome absent; with well defined grooves on dorsal carapace surface 68

68(67) Dactyli of walking legs with a row of fine teeth ....*H. hodgkini* n.sp.

4-7 mm; temperate eastern Australia; coastal, marine habitats; page 169.

— Dactyli of walking legs without teeth..............*H. orbiculare* Desmarest, 1825

6-24 mm; southern Africa; littoral and sublittoral, to 80 m, brackish and fresh water; Tesch 1918: 6-8, pl. 1 fig. 1; Barnard 1950: 68-71, fig. 15a, b; 1955: 19, fig. 5; very variable in morphology and habitat; this taxon probably represents several species, see page 168.

HYMENOSOMA Desmarest, 1825

Hymenosoma Desmarest, 1825: 163 (type species, by designation of H. Milne Edwards (1837), *Hymenosoma orbiculare* Desmarest, 1825).

Cyclohombronia Melrose, 1975: 109-10 (type species, by original designation, *Hymenosoma depressa* Jacquinot, 1835).

DIAGNOSIS: Carapace elongate oval or subcircular, with anterior lateral and posterior lateral carapace angles not evident; dorsal carapace surface flat, with well defined or very weak grooves; rostrum triangular with rounded apex, separated from dorsal carapace surface by a groove, concave laterally, usually deflexed and shorter than eyes, with lateral portions extending over prominent eyestalks; epistome absent or narrow and very short; pterygostonial region plain; Milne Edwards apertures with wide gape; 3rd maxillipeds not meeting medially, narrow to moderately broad, ischium subequal or shorter than merus along lateral edge, palp large and conspicuous, epipodites conspicuous in wide Milne Edwards apertures; chelipeds stouter than walking legs, especially in large males, but not greatly inflated; walking legs slender or moderately stout, length 2 to 3 X carapace width, dactyli with a row of fine teeth or without teeth, with dense long setae; female abdomen without fused segments, with medial portions of segments 1-3 making a triangular or trapezoidal plate, segments 1 and 2 and part of 3 visible dorsally, abdomen not strongly convex laterally making abdominosternal cavity (brood cavity) broad and shallow; male abdomen without fused segments; male 1st pleopod with stout base, distal portion of moderate and relatively uniform thickness, distal portion almost straight or strongly curved, with at least one longitudinal row of long setae, terminating in a blunt apex with wide aperture, apex complex, with a dense zone of denticles or short setae.

SPECIES OF *HYMENOSOMA:*

Species	**Distribution**
H. orbiculare Desmarest, 1825	southern Africa and Zanzibar
H. depressum Jacquinot, 1853	New Zealand
H. hodgkini n.sp.	eastern Australia

REMARKS: *H. depressum* has been variously treated as congeneric with *H. orbiculare* and as a separate genus (see Melrose, 1975). Recent authors, commencing with Graham

TABLE 1. Morphological features in which *Hymenosoma orbiculare, H. depressum* and *H. hodgkini* differ. (+, present; −, absent).

	Feature	H. orb.	H. depr.	H. hodg.
(a)	subcircular dorsal carapace	−	−	+
(b)	distinct grooves on dorsal carapace	+	−	+
(c)	rostrum reaching corneas of eyes	+	+	−
(d)	rostrum extending over eyestalks	+	−	+
(e)	very prominent postocular lobes	+	−	−
(f)	elongate eyestalks	+	−	+
(g)	antennal spines	−	+	−
(h)	epistome	−	+	−
(i)	very prominent mouth-frame angles	+	−	+
(j)	narrow 3rd maxillipeds	+	+	−
(k)	long slender walking legs	−	+	+
(l)	teeth on walking leg dactyli	−	−	+
(m)	posterior bulges on ♀ abdomen	−	+	+
(n)	arcuate ♀ telson	−	−	+
(o)	subtriangular ♂ abdomen	−	+	−
(p)	elongate seg. 5 in ♂ abdomen	−	−	+
(q)	distally curved ♂ 1st pleopod	−	+	−
(r)	intercalated plates in ♂ abdomen	−	−	+

(1938), have favoured the latter course, calling the species *Hombronia depressa*. However, Gordon (1966) established that *Hombronia* Lucas is an invalid generic name for this taxon, since *Hombronia* is a junior synonym of *Halicarcinus*. Melrose (1975) proposed a new genus, *Cyclohombronia*, for *Hymenosoma depressum*. The reason for the separation is mainly that the New Zealand species has a very small epistome, while the type species, *H. orbiculare*, has no epistome. The epistome of *H. depressum* is, however, unlike any other hymenosomatid: it is so small that the green gland apertures are on the basal segments of the antennae. Melrose (1975) also indicated other differences between *H. depressum* and *H. orbiculare* in the grooves of the dorsal carapace surface and postocular lobes.

H. depressum is here restored to its original genus as a result of finding a species in Australia which shows affinities with *H. orbiculare* and *H. depressum*. *H. hodgkini* n.sp. is clearly a *Hymenosoma* species on the basis of having no epistome. However, it differs from *H. orbiculare* in a number of features and in some of these it is more like *H. depressum*. For example, *H. hodgkini* n.sp. shares with *H. depressum* an unusual modification of the female abdomen in which the abdomen is projected posteriorly at segment 3 into two lateral bulges (Fig. 2E). Table 1 gives a series of features in which the three species differ. Summarizing the data of this table, *H. orbiculare* and *H. hodgkini* n.sp. are most alike in eight features, *H. orbiculare* and *H. depressum* are most alike in seven features and *H. hodgkini* n.sp. and *H. depressum* are most alike in three features. *H. orbiculare* and *H. hodgkini* n.sp. are similar in more conservative features: epistome, carapace grooves and male 1st pleopod. Hence, in dividing these species into two groups, *H. depressum* would be the separated species. However, the three species are much more closely related to each other than to any other hymenosomatid species and the affinity warrants recognition as one genus. This has necessitated a modification of the diagnosis of the genus *Hymenosoma* Desmarest to encompass the three species.

Specimens of *H. orbiculare* have now been reported from localities in southern Africa ranging from the sublittoral, down to 80 m (Barnard, 1950), to estuaries, to a freshwater lake (Allanson et al., 1966; Boltt, 1969); a surprising distribution even for a euryhaline species. There are morphological differences between specimens from deep sublittoral habitats and inshore or estuarine habitats. The specimens from deeper water mature at a smaller size, are more granulose, their rostrum is trilobate, through development of the lateral portions above the eyestalks, and the rostrum projects upward and beyond the eyes in some specimens, e.g. Barnard (1955, Fig. 5). Not all specimens from deeper water are as extreme as the specimen figured by Barnard (1955): the specimens from 9-37 m in Simon's Bay examined in this study (see Material Examined) are intermediate between Barnard's specimen and the "inshore" *H. orbiculare*, but in these Simon's Bay specimens the rostrum is distinctly trilobed. Stimpson (1858) described a granulose specimen as *H. geometricum*, which was subsequently treated as a junior synonym by Stebbing (1914) on the grounds that it was within the variability of *H. orbiculare*. Later workers, e.g. Barnard (1950) and Broekhuysen (1955), have tentatively come to the same conclusion. The size differences at maturity may be phenotypic variation, but the other morphological variation is genetic. It is a greater degree of morphological variation than in any other hymenosomatid and this, with the great range of habitats, makes it quite possible that several species are represented.

MATERIAL EXAMINED: (other than Australian specimens) *Hymenosoma orbiculare:* Simon's Bay, Cape of Good Hope, South Africa, undated, 3 ov.♀♀, 5-20 faths, ex British Museum "Challenger" Collection, June 1897 (AM G.1641); Simon's Bay, South Africa, undated, ♂♂ and ♀♀, 5-20 faths, "Challenger" Collection (BM 84.31). *Hymenosoma depressum:* Blueskin Bay, near Pt. Chalmers, New Zealand, Dec. 1918, C. Hedley, ♂ (AM P.4432); Akaroa Heads, New Zealand, undated, 4♂♂, 2 im.♀♀, in eight faths, Suter

Collection (BM 99.7.18.15).

HYMENOSOMA HODGKINI n.sp.

Figs. 2E, 6H, 7I, 10B, 10C

TYPE LOCALITY AND TYPES: Budgewoi Lake, Toukley via Wyong, N.S.W., Australia. HOLOTYPE: Mar. 1947, I. Bennett, ♂ (7.5 mm, 1st pleopod detached and mounted on slide), tow-netted (AM P.11723); PARATYPES: collection details as for Holotype, 10♂♂ (3.5-<7.5 mm, one male with 1st pleopod detached and mounted on slide), 4 ov. ♀♀ (5.7-7.2 mm), 2 im. ♀♀ (4.7, 5.4 mm) (AM P.11723); Lake Macquarie, N.S.W., Nov. 1894, M. Waite, ♂ (AM G.1210); Narrabeen Lakes, near Sydney, N.S.W., 12.i.1940, H. E. Smythe, im. ♀ (AM P.11260); The Gut, Brooklyn, Hawkesbury R., N.S.W., 6.ix.1975, ♂, ov. ♀, Transect A (through mangrove stand, *Avicennia marina*) Australian Littoral Society (AM); Moreton Bay, undated, ♂, 2 ov. ♀♀, from sample 925 location 94A mud and from sample 448 location 35A mud (CSIRO).

DISTRIBUTION: Coastal marine lakes and Hawkesbury River, N.S.W., and Moreton Bay, Queensland, Australia.

DIAGNOSIS: Dorsal carapace surface with well defined grooves; rostrum much shorter than eyes, not reaching corneas; without an epistome; dactyli of walking legs with a row of fine teeth; mature female abdomen projecting posteriorly in two large bulges at segment 3.

DESCRIPTION: Carapace width to length ratio 0.92-1.07; dorsal carapace surface subcircular (Fig. 2E), with a distinct rim and groove around circumference, with gastro-cardiac, cervical and thoracic grooves well defined, other grooves weak; lateral carapace walls shallow, sloping out ventrally; rostrum deflexed with broad lateral processes over eyestalks; eyestalks elongate, largely visible dorsally; acute postocular lobes adjacent to eyestalks; antennules elongate, reaching far beyond eyes; without an epistome and consequently without an interantennular septum or antennal spines; rostral keel absent; subhepatic regions visible dorsally, with an obtuse tooth located behind postocular lobe, immediately beneath antero-lateral carapace rim; anterior of mouth-field marked by a small sunken ridge below antennules, antero-lateral margins of mouth-field developed into acute rounded prominences, conspicuous dorsally and projecting more anteriorly than rostrum; 3rd maxillipeds more than ¾ filling mouth-field, ischium subequal with merus along lateral edges; length of male chelipeds between 1.5-2 X carapace width, merus long, propodus inflated, fingers occupy ca. ⅓ total propodus length, fingers gape proximally, dactylus with a long basal tooth in gape, fingers meet distally with fine serrations on cutting edges; length of female chelipeds less than 1½ X carapace width, with fine tubercles on anterior surfaces, fingers occupy ca. 0.4 of total propodus length, fingers not gaping, cutting edges with fine serrations; walking legs slender, length 2.5-3 X carapace width, dactyli elongate and slightly curved (Fig. 6H), tapering gradually to a point, ventral margin with a row of very fine teeth getting progressively longer distally, dense long setae on ventral edges of dactyli (not figured); female abdomen conspicuous dorsally (Fig. 2E), eggs visible through segment 3 of ovigerous females in dorsal view, with two submedial grooves extending from distally on segment 3 to telson, segments 5, 4 and telson progressively shorter, telson broad, arcuate, abdomen broadest at segment 5; female genital aperatures not covered by abdomen in large immature females (small immature females?); eggs ca. 0.3 mm diameter; male abdomen sculptured making segmentation difficult to distinguish (Fig. 7I), abdomen broadest at segment 1, segment 1 with a medial prominence, conspicuous in dorsal view, segment 2 short, almost concealed by segment 1 when abdomen straightened, segment 3 of similar breadth to segment 2, slightly longer than segment 1, with a small medial prominence, segment 4 narrower and shorter than segment 3, segment 5 elongate narrow, constricting to narrowest point of abdomen then expanding slightly, telson trapezoidal, with rounded angles distally, with small intercalated plates laterally; distal portion of male 1st pleopod relatively straight (Fig. 10C), with a row of long setae on sternal side, apex partially rimmed with curved setae and with a dense zone of denticles on abdominal side (Fig. 10B); colour pale (preserved specimens); sparse long setae on walking legs, dense setation on mouthparts around Milne Edwards apertures and on dactyli of walking legs; males up to 7.5 mm, mature females 5.7-7.2 mm.

REMARKS: In *H. orbiculare* and *H. hodgkini* the most anterior structures, excluding the eyes, are acute lobes situated ventral to the eyes. These lobes are called exterior orbital angles by Stimpson (1907), Tesch (1918) and Barnard (1950). I consider that they are projections of the antero-lateral angles of the mouth-frame, rather than parts of the orbits. These angles of the mouth-frame are prominent in the other species, *H. depressum,* but not visible in dorsal view; and in the two species without epistomes the angles are considered to have become very prominent. This may be an academic point, since, in the absence of an epistome, the mouth-frame is continuous with the subhepatic region bordering the eyestalks. However, these acute lobes should not be confused with postocular lobes in *H. orbiculare,* as in Gordon (1966). *H. hodgkini* has acute postocular lobes in the normal position as well as the prominences ventral to the eyes. *H. orbiculare* does not have normal postocular lobes; there is an acute tooth on the subhepatic region somewhat lateral to the eyestalks and this may be homologous to the acute postocular lobes of *H. hodgkini* and *H. depressum.*

H. hodgkini has intercalated plates between segment 5 and the telson of the male abdomen, a unique feature which is also shown by the *Amarinus* n.gen. species. Among Brachyura it is only known from one other family, Dromiidae (Holthuis, 1968). Intercalated plates are not present in *H. orbiculare* or *H. depressum.*

H. hodgkini has been collected from five localities in a section of the eastern Australian coast between Sydney and Brisbane. At these localities marine salinities prevail, but salinity is lowered during summer months by freshwater discharge.

H. hodgkini is named in honour of Dr E. P. Hodgkin, who, as Reader in Zoology, University of Western Australia, supervised my Ph.D. studies on hymenosomatids.

MATERIAL EXAMINED: Type specimens listed above.

ELAMENA H. Milne Edwards, 1837

Elamena H. Milne Edwards, 1837: 33-4 (type species, by monotypy, *Hymenosoma mathaei* Desmarest, 1825).

DIAGNOSIS: Carapace, with rostrum, polygonal to pear-shaped; dorsal carapace surface without well defined grooves except for a gastro-cardiac groove present in some species; rostrum truncated or triangular, continuous with carapace surface, concealing antennae, antennules and most of eyes; rostral keel deep, forming a distinct T-shape with rostrum rim anteriorly (all species with truncated rostra and three with triangular rostra), rostral keel poorly developed, or absent; epistome long, usually almost as long as broad; pterygostomial regions often with one or two prominent lobules; 3rd maxillipeds broad, almost completely filling the mouth-field, ischium subequal to or longer than merus along lateral edge; chelipeds stouter than walking legs, particularly in large males; length of walking legs 1½-3 X carapace width, dactyli usually with two subterminal teeth; female abdomen circular to ovate, without fused segments except in two very small species, terminal edge of telson often concave; male abdomen without fused segments (two species) or with segments 3-4 (or 3-5?) fused; male 1st pleopods strongly curved and twisted above a stout base, usually bearing large subterminal setae.

SPECIES OF *ELAMENA:* Based on Kemp (1917), Chopra and Das (1930), Gordon (1940), Monod (1956), and Melrose (1975).

Species	**Distribution**
**E. mathaei* (Desmarest, 1825)	Red Sea; S.E. Africa; Mauritius
**E. truncata* (Stimpson, 1858)	Indo-West Pacific
**E. producta* Kirk, 1879	New Zealand
E. longirostris Filhol, 1885a	New Zealand
E. sindensis Alcock, 1900	India; Sri Lanka
E. gracilis Borradaile, 1903	Maldive Archipelago
E. cimex Kemp, 1915	Chilka Lake, India; Madagascar
E. xavieri Kemp, 1917	Mandavi R., India
**E. cristatipes* Gravely, 1927	India
**E. abrolhensis* Gordon, 1940	southern Australia
E. gordonae Monod, 1956	W. Africa; N.E. Australia
**E. momona* Melrose, 1975	New Zealand
E. umerata n.sp.	northern Australia

REMARKS: The *Elamena* species can be grouped according to the shapes of their rostra into "truncated" species (indicated with an asterisk in the preceding list) and "triangular" species, with *E. cristatipes* being closest to an intermediate condition. Species in the two groups tend to differ in body form (polygonal versus pear-shaped), development of the rostral keel and armature of the pterygostomial region, but the differences are inconsistent and no separate taxonomic status for these groups is proposed. The "triangular" species resemble the *Trigonoplax* species and have been included within this taxon by authors who treated *Trigonoplax* as a subgenus of *Elamena*. In this study *Trigonoplax* is recognised as a genus with three distinctive species which are clearly distinguished from "triangular" *Elamena* species (see Remarks on the genus *Trigonoplax*).

Some authors, e.g. Kemp (1917), consider that fusion of male abdominal segments is a diagnostic character of the genus *Elamena*. However, in two New Zealand species described by Melrose (1975) there is no fusion. Chopra and Das (1930) and Gordon (1940) together describe six *Elamena* species in which they consider that segments 3-4 are fused; Kemp (1917) and Barnard (1950) together describe five species (three in common with the previous authors) in which they consider that segments 3-5 are fused. This discrepancy probably arises from different interpretations of five articulated portions present in the male abdomen and telson of all these species. Depending on whether the author considered that there were normally six or seven segments present, two or three segments respectively were considered to be fused and the sutures obliterated. Hymenosomatids have five abdominal segments plus the telson (see Remarks, page 9) and it is likely that only two medial segments are fused in the male abdomen of *Elamena* species.

Zoeae are known for a surprising number of *Elamena* species: five "truncate" species and two "triangular" species (page 153). Their expanded abdomens are a distinctive character, only known in some zoeae of two other brachyuran families, Pinnotheridae and Ocypodidae (Wear, 1968); and, with the exception of *Neohymenicus pubescens,* only present in *Elamena* species within the family Hymenosomatidae. *H. pubescens* zoeae differ from *Elamena* zoeae in having dorsal and lateral carapace spines. Larval morphology supports the *Elamena* taxon presented here.

ELAMENA TRUNCATA (Stimpson)

Figs. 2D, 6D, 8B, 10H

Trigonoplax truncata Stimpson, 1858:109; 1907:146-7.

Elamene truncata A. Milne Edwards, 1873:323.— Henderson, 1893:395.

Elamena truncata. —Kemp, 1917:272-4, figs. 22, 23.—Sakai, 1932:44, fig. 2; 1938:201, pl. 20 fig. 3; 1976:152-3, pl. 47 fig. 2.— Gordon, 1940:67-8, fig. 5.— McNeill, 1968:47.

[?] *Elamena truncata.* —Tesch 1918:22-24, pl. 1 figs. 4, 4a-c (confused with several *Elamena* species).

[not] *Elamena truncata.* (=*E. abrolhensis*) — Baker, 1906:112-3, pl. 2 figs. 2, 2a-c. — Hale, 1927:119-20, fig. 117. — Montgomery, 1931:426-7, pl. 27 fig. 2.

TYPE LOCALITY AND TYPES: Amami Ohsima and Loo Choo, Japan. No type specimens are extant. They were probably lost in the 1871 Chicago fire with nearly all of the invertebrate collections of the North Pacific Exploring Expedition (see Introduction of Stimpson (1907) and Garth (1958)). None of Stimpson's hymenosomatid types is in the Smithsonian Institution (F. A. Chace, pers. comm.) nor in Peabody Museum of Natural History (W. D. Hartman, pers. comm.), other possible locations of Stimpson's types suggested by Evans (1967).

DISTRIBUTION: Japan, India, Indonesia (?), New Caledonia, and N.E. Australia.

DIAGNOSIS: Carapace width greater than length; posterior lateral angles of carapace rounded and not evident; dorsal carapace surface usually without ridges extending in from angles; rostrum truncated; rostral keel deep, discontinuous with interantennular septum; terminal spine on carpus of walking legs subequal with terminal spine on merus of walking legs; male 1st pleopods bent at ca. 90°, with four or five subterminal setae.

DESCRIPTION: The following are additions to the descriptions of *E. truncata* by Kemp (1917), Sakai (1938) and Gordon (1940) and the Diagnosis:— carapace width to length ratio 1.06-1.22 (Fig. 2D); dorsal carapace surface slightly concave or convex, a faint gastro-cardiac groove sometimes present; rostral keel deep, triangular in lateral view; 3rd maxillipeds often with a well-defined longitudinal ridge on merus, extending to ischium; largest male 6.2 mm, mature females 5.6-9.3 mm.

REMARKS: This species has the greatest reported distribution of the *Elamena* species, being reported from widely separated localities in the Indo-West Pacific region. However, reports of *E. truncata* from Zanzibar, Sri Lanka and southern Australia are considered erroneous and they are referred to *E. mathaei, E. sindensis* and *E. abrolhensis,* respectively (Gordon, 1940). The specimens of *E. truncata* described by Tesch (1918) are unusual. A female figured (Tesch, pl. 1 fig. 4b) is like *E. abrolhensis,* but the posterior lateral carapace angles are even more pronounced and pointed, while a male figured (Tesch, pl. 1 fig. 4) is more like a typical *E. truncata.* In Tesch's general description of the specimens, he gives three features which differ from both *E. truncata* and *E. abrolhensis:* three lobules in the pterygostomial regions, exopodites of the 3rd maxillipeds well exposed, and penultimate segment (5) of the male abdomen shorter than the two preceding segments (3 and 4, or 2 and fused 3-4?) and the telson.

The type specimens of *E. truncata* are not extant and it was not possible to obtain Japanese specimens with which to compare the Australian material. However, Sakai (1932, 1938) figures and describes Japanese specimens and by comparison with Sakai's descriptions, and following Gordon (1940) and McNeill(1968), *Elamena* specimens from northern Australia are attributed to *E. truncata*.

MATERIAL EXAMINED: Lifton, Loyalty Islands, Aug. 1925, A. F. Bassett Hull,♂, 2 ov.♀♀ (AM P.8279). New Caledonia, 1926, A. F. Bassett Hull, ov. ♀ (AM P.8889). QUEENSLAND: Port Denison, 1918, ♂, ov.♀, 2 im.♀♀(AM P.4232); Holbourne Island, Nov. 1921, E. H. Rainford, im. ♀(AM P.5555); High Island Reef, 15.vii.1924, W. E. J. Paradice,♂(AM P.8024); High Island Reef, 1924, W. E. J. Paradice, ov. ♀ (distorted) (AM P.7975); Flinders Island, Princess Charlotte Bay, Sept. 1930, W. L. Wassell, ♀ (AM P.10105); Low Isles, 15.viii.1963, J. Bryan, im. ♀on reef flats (AM P.16585); Low Isles, 27.vi.1973, J. S. Garth, 2♂♂, im.♀, on reef flat under coral rubble (AHF JG-22-73).

ELAMENA ABROLHENSIS Gordon

Figs. 2A, 6C, 8G, 10I

Elamena truncata. — Baker, 1906: 112-3, pl. 2 figs. 2, 2a-c. — Hale, 1927: 119-20, fig. 117.— Montgomery, 1931: 426-7, pl. 27 fig. 2.

Elamena abrolhensis Gordon, 1940: 70-1, figs. 6b, c, 7a-c, 10a.

TYPE LOCALITY AND TYPE: Sandy Island, Abrolhos Islands, Western Australia; HOLOTYPE: ♂ (6.6 mm) (BM 1931.7.24.37).

DISTRIBUTION: South Western Australia and South Australia, as far north as the Abrolhos Islands on the west coast.

DIAGNOSIS: Carapace width greater than length; posterior lateral angles of carapace pointed and obtuse; carapace dorsal surface usually with ridges extending in from angles; rostrum truncated; rostral keel deep and long, continuous with prominent interantennular septum; postocular lobes with small acute spines; terminal spine on carpus much shorter than terminal spine on merus of walking legs; male 1st pleopods S-shaped, with ca. 12 subterminal setae.

DESCRIPTION: The following are additions to the description of *E. abrolhensis* by Gordon (1940): — carapace width to length ratio 1.04-1.18, greatest in large specimens (Fig. 2A); anterior lateral angles not usually as pronounced as in Gordon's fig. 6b; dorsal carapace surface slightly concave or convex, rimmed, often with a gastro-cardiac groove and a median longitudinal ridge; rostrum obscuring all but tips of eyes dorsally; no antennal spines; epistome width to length ratio ca. 1.5; 3rd maxillipeds almost completely enclosing mouth-field, ischium subequal with merus along lateral edge, segment 3 of palp much longer than segments 1 and 2; walking legs ca. 2 X carapace width; chelipeds of large males larger than similar sized females and with a basal tooth on dactylus; telson truncated, longest segment of female abdomen; setation limited to mouthparts, Milne Edwards apertures, dactyli of walking legs, and edge of female abdomen; colour yellow, yellow-green, red-brown, not mottled; largest male 7.7 mm, mature females 6.8-8.4 mm.

MATERIAL EXAMINED: SOUTH AUSTRALIA: Parkside, 22.v.1906, W. H. Baker, ♀, Fulton Collection (NMV); Moonta, Feb. 1937, K. Reed, ♂ (AM P.10838); South Australian coast, undated, 2 ov.♀♀ (dried specimens), labelled *Elamena truncata* (SAM). WESTERN AUSTRALIA: Lucky Bay, east of Esperance, 4.xii.1921, Hull, Grant and Wright, ♂, im.♀ (AM P.5684, P.5679); Hopetown, 9.i.1959, R. W. George, ov.♀, from granite rocks at low tide (WAM); Yanchep, 27.i.1959, R. W. George, ♂, on reef flat (WAM); Cottesloe, near Green Island, 3.x.1960, M. Tyndale-Biscoe, ♂ (WAM); Pt. Peron, 8.ix.1962, W. H. Butler, im.♀ (WAM); Horricks Beach, 11.xii.1964, J.S. Lucas, ♂ (1st pleopod mounted on slide), ♀, under rocks in littoral area of reef (AM P.20169); Radar Reef, Rottnest Island, 13.xii.1964, J.S. Lucas, im.♀, among corals and ascidians on undercut of reef flat (WAM); Armstrong Pt., Rottnest Island, 5.i.1965, B. F. Phillips, ♀, under rock on intertidal platform, ovigerous when collected, larvae from eggs developed in the laboratory (WAM).

ELAMENA GORDONAE Monod

Figs. 2B, 6E

Elamena (Trigonoplax) gordonae Monod, 1956: 469-72, figs. 629-637.

TYPE LOCALITY AND TYPES: West Africa, between Conakry and Monrovia. HOLOTYPE: undated, ov.♀ (2.8 mm) 30-40 m, Debyser collection (MHN); PARATYPE: Sierra Leone coast, 1948, ♀ (3.0 mm, without abdomen) collected by "Maid Honour" (MHN). The specimens were recently examined by Dr. J. Forest (pers. comm.).

DISTRIBUTION: Western Africa and N.E. Australia.

DIAGNOSIS: Dorsal carapace surface convex, sloping up to a medial longitudinal ridge for most of carapace length; rostrum triangular, without keel or spine on ventral surface; postocular lobes undeveloped; one prominent lobe in pterygostominal region; dactyli of walking legs with two subterminal teeth; female abdomen broader than carapace width, conspicuous at posterior of carapace in dorsal view; female pleopods project laterally from abdomen; mature females less than 3 mm carapace width.

DESCRIPTION: The following is additional to the description of Monod (1956) and the Diagnosis. The descriptions are based on four female specimens, no male specimens having been examined:— carapace width to length ratio 0.85-1.00; dorsal carapace surface with a faint gastro-cardiac groove (Australian specimens); lateral carapace wall vertical; rostrum outreaching eyes but not antennules; no antennal spines; ischium of 3rd maxillipeds subequal with merus along lateral edge; cheliped length 1½ X carapace width; female abdomen large compared to body size, segments 1-4 visible dorsally at posterior, segments 1 and 2 short, segments 3, 4, 5 and telson progressively longer, widest at segment 5, possibly some segments fused with sutures remaining; eggs 0.35 mm diameter.

REMARKS: Monod's figures do not show the size of the female abdomen (Monod, 1956): the abdomen is omitted in Fig. 629 and only the small segments 1 and 2 are shown in Fig. 630. Dr. J. Forest (pers. comm.) examined the type specimens and advised that the abdomen of the holotype is as in the Australian specimens; the abdomen is missing in the paratype. See the Remarks on *Halicarcinus hondai* for discussion of female abdomens.

There are only small differences between the west African and Australian specimens: the rostrum has a more rounded apex in the Australian specimens and a faint gastro-cardiac groove is present. Monod (1956) described a "ligne carénée médian gastro-cardiaque", which is perhaps the groove in his specimens, although it isn't figured. Even the faint ridges on the dorsal carapace surface, described by Monod, are present in the Australian specimens and it is considered that they are conspecific. The two regions where *E. gordonae* has been collected are in the tropics, but they are widely separated, i.e. eastern Atlantic versus western Pacific. Also remarkable is that three species to which *E. gordonae* is closely related are Indian species, *E. sindensis, E. cimex* and *E. xavieri,* two of which occur in low salinity habitats.

E. gordonae is smaller than the other "triangular" *Elamena* species, except *E. umerata* n.sp., and it is the only *Elamena* species with an expanded female abdomen. A combination of other features included in the Diagnosis also distinguishes it from the other "triangular" species.

MATERIAL EXAMINED: Queensland: Tyroom Rds, Gt. Sandy Strait, Mar. 1952, J. S. Hynd, 2 ov.♀♀, 10 faths (AM P.12208).

ELAMENA UMERATA n.sp.

Figs 2C, 6F, 9B

TYPE LOCALITY AND TYPES: Darwin, Northern Territory, Australia. HOLOTYPE: Dec. 1923, W. E. J. Paradice, ♀ (2.8 mm; only four legs and one cheliped, all detached, are present), from among marine growths on piles of Rail Pier (AM P.6819); PARATYPE: Tyroom Roads, Great Sandy Strait, Queensland, 6.vi.1946, J. S. Hynd, ♂ (ca. 2.1 mm, the specimen is distorted through drying out at some stage), 10 faths, *Zygometra microdiscus* and spiny alcyonarian also in catch (AM P.12217).

DISTRIBUTION: Northern Australia (two known localities).

DIAGNOSIS: Dorsal carapace surface concave, with lateral carapace margins upturned; anterior lateral carapace angles very prominent, rounded and slightly obtuse; antero-lateral carapace borders at right angles to longitudinal body axis; rostrum equilateral triangular with rounded apex, without keel or spine ventrally; female abdomen with segments 3-5 fused and no sutures evident; male 1st pleopod with thin distal portion curving through two-thirds of a circle, without subterminal setae.

DESCRIPTION: Carapace width to length ratio 0.88 (♀) (Fig. 2C); a faint gastro-cardiac groove present on dorsal carapace; lateral carapace walls sloping slightly out ventrally; posterior lateral angles obtuse and rounded; rostrum laterally concave, pointing slightly upwards, almost concealing eyes and antennules; eyestalks very short; postocular lobes undeveloped; interantennal septum a strong ridge; antennal spines absent; epistome length subequal with breadth; pterygostomial regions with two prominent lobes, one near mouth-field and one near base of cheliped, a further prominent lobe in subhepatic region; ischium of 3rd maxillipeds subequal with merus along lateral edge; male and female chelipeds ca. 2 X and 1.5 X carapace width, respectively, stouter than walking legs, propodus more inflated in male than female, fingers of chelae strongly curved distally; fingers of female chelae without gapes and with fine teeth on cutting edges; fingers of male chelae meet distally, dactylus with two large basal teeth and four teeth distally, propodus finger with one basal tooth, which fits between large teeth on dactylus, and a row of teeth distally; legs moderately slender, longer than 2 X carapace width, a prominent terminal spine on merus, dactylus tapering, strongly curved distally, with two large recurved teeth subterminally (Fig. 6F); a row of setae on ventral surface of dactylus increasing in length distally; female abdomen not broader than carapace width, only segments 1 and 2 visible dorsally, segments 1 and 2 short, telson trapezoidal, ca. ⅓ total length of abdomen, segments 1 and 2 of similar width, abdomen increasing in breadth progressively from segment 3 to junction of segment 5 and telson, pleopods project laterally from abdomen; male abdomen with segments 3 and 4 fused and no suture evident, segments 1 and 2 very short, segments 3-4 longest section of abdomen, segment 5 shorter than telson, telson spade-shaped, segments 1 and 2 of similar width, abdomen expands to maximum width mid-way along segments 3-4 and then narrows to segment 5, segment 5 narrows further towards junction with telson (distorted abdomen, not figured); male 1st pleopod with stout base and thin distal portion strongly curved and twisted, tapering terminally to a long point (Fig. 9B); little setation except for dactyli of walking legs and short setae on lateral borders of rostrum; mature female less than 3 mm carapace width.

REMARKS: *E. umerata* differs from the other "triangular" *Elamena* species in having very pronounced anterior lateral angles. This condition is opposed to the usual "triangular" body form which tends to a triangular or pear-shaped form, with anterior lateral angles very obtuse and rounded and little evident. *E. umerata* also has unusual features of the male and female reproductive morphology. The male 1st pleopod is more uniformly curved than in other *Elamena* species which have been described, so that the thin distal portion curves through two-thirds of a circle. In other *Elamena* species, the male 1st pleopod bends through ca. 90° and then is either relatively straight distally or it bends again to make an approximately S-shape. Also, it is the only species with no subterminal setae on the male 1st pleopod; so that the pleopods are more like those of some *Halicarcinus* species than *Elamena* species. Fusion of segments in the female abdomen is possibly shown by *E. gordonae,* but in *E. umerata* the condition is further advanced because no sutures remain between the fused segments. The abdomen is not expanded as in *E. gordonae*. For further discussion of the abdomens of small females see the Remarks on *Halicarcinus hondai*.

E. umerata is related to the "triangular" *Elamena* species and is most similar to the other very small species, *E. gordonae*. These two species have been collected at the same locality off the Queensland coast.

The name *umerata* (shoulder-possessing; Latin, feminine) refers to the prominent anterior lateral angles of the carapace, giving the appearance of "shoulders".

MATERIAL EXAMINED: Type specimens listed above.

HALICARCINUS White, 1846

Halicarcinus White, 1846:178 (type species, by original designation, *Cancer planatus* Fabricius, 1775).

Liriopea Nicolet, 1849:158 (type species, by subsequent designation of Rathbun (1925), *Hymenosoma leachi* Guérin, 1838 = [?] *Cancer planatus* Fabricius, 1775).

Hymenicus Dana, 1851:253 (type species, by subsequent designation of Kemp (1917), *Hymenicus varius* Dana, 1851).

Hombronia Lucas, 1853:60 (type species, by monotypy, *Hymenosoma ? tridentatum* Jacquinot, 1853 = [?] *Cancer planatus* Fabricius, 1775).

Rhynchoplax Stimpson, 1858:109 (type species, by subsequent designation of Kemp (1917), *Rhynchoplax messor* Stimpson, 1858).

DIAGNOSIS: Carapace subcircular or suboval, laterally or longitudinally elongate; dorsal carapace surface with at least gastro-cardiac, cervical and thoracic grooves well defined; often with an acute spine at either posterior or anterior lateral carapace angles; rostrum separated from dorsal carapace by a ridge or groove or both; rostrum basically trilobate, but varying markedly in degree of fusion of lobes and relative lengths of medial and lateral lobes; epistome short and broad, breadth usually at least 2 X length; pterygostomial regions usually with lobules or spines; 3rd maxillipeds broad, almost completely filling mouth-field; ischium subequal with or shorter than merus along lateral edge; chelipeds stouter than walking legs, especially in large males; walking legs slender to stout, dactyli usually with one or two rows of small teeth and often with one or two large teeth subterminally; female abdomen usually without fused segments; male abdomen without fused segments, except in *H. hondai*; male 1st pleopods either with distal portion thin, strongly curved toward abdomen and with very short setae, or distal portion thin to moderately stout, little curved and with long setae.

SPECIES of *HALICARCINUS:* Based on Sakai (1938), Lucas (1968), Takeda and Miyake (1971b), Melrose (1975) and Takeda and Nunomura (1976).

Species	**Distribution**
H. planatus (Fabricius, 1775)	circum-subantarctic
H. varius (Dana, 1851)	New Zealand
H. ovatus Stimpson, 1858	southern Australia
**H. messor* (Stimpson, 1858)	Japan
**H. setirostris* (Stimpson, 1858)	Japan; China
H. minutus (A. Milne Edwards, 1873)	New Caledonia
H. whitei (Miers, 1876)	New Zealand
H. rostratus (Haswell, 1882a)	southern Australia
H. cookii (Filhol, 1885b)	New Zealand
**H. coralicola* (Rathbun, 1909)	Japan; Taiwan; Singapore
H. bedfordi Montgomery, 1931	northern Australia
H. orientalis Sakai, 1932	Japan
H. innominatus Richardson, 1949b	New Zealand; Tasmania
**H. keijibabai* (Takeda and Miyake, 1971b)	New Caledonia
**H. hondai* (Takeda and Miyake, 1971b)	Ryukyu Is.; Gt Barrier Reef
H. tongi Melrose, 1975	New Zealand
H. afecundus n.sp.	northern Australia

REMARKS: The three species attributed to *Rhynchoplax* Stimpson (1858) by Sakai (1938, 1965) and two further *Rhynchoplax* species described by Takeda and Miyake (1971b) are congeneric with the *Halicarcinus* species. (The five species are marked with an asterisk above.) Sakai (1938) made a review of the confused literature on *Rhynchoplax*, giving a diagnosis of the genus and separating most of the species previously included in *Rhynchoplax* into a new genus, *Neorhynchoplax* Sakai (= *Elamenopsis* A. Milne Edwards, see page 191). Sakai recognised that the *Rhynchoplax* (s.s.) species closely resemble the *Halicarcinus* species and the characters by which he appeared to distinguish them were: *Rhynchoplax* species have a long medial rostral lobe, while *Halicarcinus* species have subequal lobes, and *Rhynchoplax* species have less stout male chelipeds. Stimpson (1858, 1907) also gave long medial rostral lobe as a generic character of *Rhynchoplax*; while most of the other characters that he gave in his diagnosis are applicable to at least some *Halicarcinus* species.

The species included in *Halicarcinus* and *Rhynchoplax* may be ordered according to the relative lengths of the medial and lateral rostral lobes. The series from lateral lobes relatively longest to medial lobe relatively longest is: *afecundus* n.sp., *planatus, tongi, innominatus, cookii, ovatus, orientalis, minutus, varius, whitei, bedfordi, coralicola*, keijibabai*, setirostris*, messor*, rostratus, hondai**. The species towards the end of the series have rostral lobes more fused than those towards the beginning of the series, they also tend to be smaller, more spiny and more slender-legged than those earlier in the series. However, these are only tendencies and there is no basis in these characters for a division into two taxa, e.g. *H. hondai*, the species with relatively longest medial rostral lobe, is also the smallest species, but it has stout legs. Two distinct forms of 1st male pleopod occur among these species: one with a strongly curved, distal portion, e.g. Fig. 9C, and the other which is little curved, e.g. Fig. 9E. The former pleopod occurs in the species from *planatus* to *whitei* in the above series, and in *setirostris, messor* (Fig. 9A) and *hondai*; the latter occurs in *bedfordi, coralicola* and *rostratus*. (*afecundus* n.sp., *minutus* and *keijibabai* are yet to be described.) This is another character showing a tendency, but no clear division, between species early and late in the series. The difference in 1st male pleopods is the most important difference among these species. However, it is not proposed to remove *H. bedfordi, H. coralicola* and *H. rostratus* as they belong in this taxon in all other respects.

There are two hymenosomatid species which may belong in the genus *Halicarcinus* although their trilobate rostra are figured by authors as being continuous with the dorsal carapace surface. Neither of these species has been reported since the original description. The species are:—

1. *Hymenicus krefftii* Hess, 1865, type locality Sydney, Australia. The type specimens were destroyed in the Zoological Museum, Göttingen, Germany, during World War II (P. Kuenzer, pers. comm.). No specimens identified as *H. krefftii* are present in Australian museum collections and no specimens corresponding to Hess' brief description were collected by Lucas (1968). de Man (1887a), examining one of the syntypes, corrected Hess' description and concluded that the specimen appeared to be the same as *Halicarcinus cookii*, a New Zealand species. Sakai (1938) included it in his list of *Neorhynchoplax* species, with a question mark, but there is no evidence that Sakai examined specimens and Hess' description does not include the diagnostic features of *Neorhynchoplax* Sakai. If the type locality is correct, then Hess' specimens were probably *Halicarcinus ovatus*, which he badly described. Since the types are lost and the description is inadequate, the identity of *H. krefftii* remains unresolved.

2. *Elamene filholi* de Man, 1887b, type locality Noordwachter Island, near Djakarta, Java. This is an unusual species in that the eyes are situated well behind the anterior rim of the carapace and thoroughly concealed in dorsal view. The condition is like *Halicarcinides nuytsi*. de Man's description is fairly comprehensive and some important features which he omits are shown in his figures. Fig. 3 clearly shows the rostral lobes continuous with the dorsal carapace surface and Fig. 3a shows broad 3rd maxillipeds, almost meeting medially, with ischium and merus subequal in length. The maxilliped condition precludes inclusion of *Elamene filholi* in *Neorhynchoplax*, as proposed by Sakai (1938). The type specimens were not located.

MATERIAL EXAMINED: (other than Australian localities) *Halicarcinus messor:* Simoda, Japan, Apr. 1934, T. Sakai, ♂ ♂ (one 1st pleopod removed and mounted) and ♀ ♀, labelled *Rhynchoplax messor* (AM P.10497).

HALICARCINUS OVATUS Stimpson

Figs. 3B-E, 6J, 6K, 7E, 9C

Halicarcinus ovatus Stimpson, 1853:109. — Lucas, 1971:475-82, figs. 3I, 4 (larval morphology). — Griffin and Yaldwyn, 1971:45-6. — Griffin, 1972:65. — Melrose, 1975:39-44, figs. 14-15.

For other Synonymy see Melrose (1975).

TYPE LOCALITY AND TYPES: Port Jackson, Australia. No type specimens are extant (see comments on type specimens of *Elamena truncata).*

DISTRIBUTION: Southern Australia, including Tasmania; from Geraldton on the west coast to Port Stephens on the east coast.

DIAGNOSIS: Rostrum arising from level with to distinctly below dorsal carapace surface, rostrum clearly trilobate, medial lobe slightly longer than lateral lobes, rostral lobes projecting forward in same plane, never deflexed, uniting at their bases beneath or slightly anterior to carapace rim; anterior lateral carapace angles obtuse; posterior lateral angles rounded obtuse, with a small acute spine; dactyli of walking legs with two irregular and closely approximated rows of teeth.

DESCRIPTION: Melrose (1975) gave a full description of *H. ovatus* specimens from two Australian localities; but she did not describe the variability of *H. ovatus* due to her limited material. Specimens of *H. ovatus* from different localities, and different habitats at the same locality, show considerable variation in the length and level of the rostrum, shape of the rostral lobes, general setation, fingers of male chelipeds, stoutness of walking legs and size of teeth on the dactyli of the walking legs (Lucas, 1968; Griffin and Yaldwyn, 1971; Griffin, 1972). Some of the variability is shown in Figs. 3B-3E and Figs. 6J and 6K. *H. ovatus* is the most ubiquitous of the Australian marine hymenosomatids, occurring on a range of substrates in the sublittoral, and this may account for the variability. Specimens from hard substrates subject to turbulence tend to have short rostra, arising below the carapace rim, stout legs and little body setation. These specimens resemble *H. planatus* and *H. innominatus,* which also live in this type of habitat. Specimens from soft substrates away from turbulence tend to have long rostra, arising from level with the carapace rim, moderate legs and considerable body setation. Intermediate conditions occur and no discrete divisions could be made on the basis of crab morphology although much material was examined. (*H. ovatus* is well represented in the Australian museum collections.)

Very variable coloration, white, yellow, orange, brown, red, black, often mottled or with patches of colour; females tending more to mottling and inconspicuous coloration; large males rarely exceed 10 mm, mature females 3.7-10 mm, mostly 5-6 mm.

REMARKS: In contrast to apparently continuous variation in crab morphology, three quite different kinds of larvae were produced by ovigerous females collected from different localities in S.W. Australia (Lucas, 1971). One of the larval morphs has distinctive features which it shares with zoeae of *H. planatus* (described by Boschi et al., 1969). On the basis of larval morphology, it is likely that the taxon being considered here is more than one species. It requires a morphometric study of crab morphology and correlation of crab and larval morphology for a range of females to clarify the situation.

H. ovatus has been reported from New Zealand, e.g. Balss (1930), and Melrose (1975) establishes that these reports are erroneous. She provides bases for distinguishing *H. ovatus* from the species in New Zealand and nearby, *H. varius, H. cookii, H. innominatus* and *H. planatus,* with which it has been confused.

MATERIAL EXAMINED: NEW SOUTH WALES: Port Stephens; Port Jackson; Long Reef, Collaroy; Shellharbour; Port Hacking; Jervis Bay; 32♂♂, 21 ov.♀♀,♀, 2 im.♀♀ (AM P.94, AM P.95, AM P.7405, AM P.20178, AM P.20179). VICTORIA: Shoreham; Port Albert; Phillip I.; Rhyll; Flinders; Port Phillip; Beaumaris, Port Phillip; Lorne; Apollo Bay; 25♂♂, 11 ov.♀♀, 4♀♀, 3 im.♀♀, 7 juvs. (NMV 7 lots, AM P. 7486, AM P.11426). TASMANIA: Roches Beach, Frederick Henry Bay; Derwent Channel; D'Entrecasteaux Channel; Pt. Puer, Tasman Peninsula; 13♂♂, ov.♀., 4♀♀, 6 im.♀♀ (TM 14496/G212, TM 15061/G301, TM 19015/G652, TM G1052). SOUTH AUSTRALIA: Robe; The Bluff, Victor Harbour; Port Willunga; Streaky Bay; 11♂♂, 2 im.♀♀, 11 juvs. (SAM C19744, SAM C19745, NMV 1 lot). WESTERN AUSTRALIA: Horricks Beach, Geraldton; Rottnest I., Trigg I.; Blackwell Reach, Swan River; Woodmans Pt.; Cockburn Sound; various localities, Garden I.; Pt. Peron; Oyster Harbour; Dunsborough; Denmark; 24♂♂, 19 ov.♀♀, 4♀♀, 6 im.♀♀, 3 juvs. (WAM 11 lots).

HALICARCINUS ROSTRATUS (Haswell)

Figs. 3F, 6L, 7F, 10H

Hymenosoma rostratum Haswell, 1882a:550; 1882c:116. — Baker, 1906:114, pl. 3 figs. 2, 2a,b.

Halicarcinus rostratus. — Kemp, 1917:247. — Hale, 1927:117-8, fig. 114. — Griffin and Yaldwyn, 1971:46. — Griffin, 1972:65. — Lucas, 1972:475-82, figs. 3H, 5A-5D (larval morphology).

Rhynchoplax rostrata. — Tesch, 1918:17, 18.

Neorhynchoplax rostrata. — Takeda and Miyake, 1971a:4.

TYPE LOCALITY AND TYPES: Griffith's Point, Port Western, Victoria, Australia. There are three specimens in the Australian Museum which, although not labelled as such, are undoubtedly syntypes. They are preserved in the same distinctive manner as the syntypes of *Hymenosoma australe* Haswell. Their details are: Griffith's Point, Victoria, undated, 2 ♂ ♂ (4.9 mm, 5.0 mm; both dried specimens, latter one in poor condition), Haswell Collection No. 213 (the specimens are glued to a glass plate with a red spot and a label cut from Haswell, 1882c) (AM P.15396), ♀ (4.2 mm, dried), Haswell Collection No. 213 (the specimen is glued to another glass plate with a label cut from Haswell, 1882c) (AM P.15397). The smaller male specimen, which is in better condition, is hereby designated lectotype of *Hymenosoma rostratum* Haswell.

DISTRIBUTION: Southern Australia including Tasmania; from Swan River on the S.W. coast to Montague I. on the S.E. coast.

DIAGNOSIS: Rostrum arising from level of dorsal carapace, lateral rostral lobes short, fused with medial lobe and little indicated, medial rostral lobe long and tapering, well outreaching eyes, without long hairs arising from apex; postocular lobes developed into acute teeth, conspicuous dorsally; posterior lateral carapace angles with an acute spine projecting dorsally, especially prominent in large males; three acute spines in pterygostomial regions; male 1st pleopods little curved, stout at base and tapering to a rounded tip, with rows of long setae on distal half.

DESCRIPTION: The following is additional to the descriptions of Haswell (1882a and c) and Baker (1906), which do not include details of females: — females not as spiny as large males, with shorter medial rostral lobe, spines at posterior lateral angles and pterygostomial spines than in large males; female chelipeds shorter than in large males (ca. 1.5 X versus 2 X carapace width), thinner and without spines on merus and carpus, merus elongate, propodus not expanded, no teeth on cutting edges of fingers; female abdomen oval, laterally elongate, with two submedial grooves; variable coloration, white, cream, brown and red, mottled, patched or plain, females more inconspicuously coloured; long setae on gastric and post-branchial regions of carapace surface, dense short setae on sternal surface and abdomen; males rarely exceeding 5.5 mm carapace width, mature females 3.0-5.5 mm carapace width.

MATERIAL EXAMINED: NEW SOUTH WALES: Eden, July, 1922, Livingstone and Fletcher, ♂, 3-4 miles off-shore, 20-30 faths (AM P.5795). VICTORIA: Type material listed above; Mordialloc, Port Phillip Bay, 2.vii.1897, Halliday, ♂ (tip of rostrum lost), 2 ov. ♀♀ (NMV); Beaumaris, Port Phillip Bay, 5.x.1901, ♀, pres. S.W. Fulton, Sept. 1903 (NMV); Western Port Bay, Dec. 1905, C. J. Gabriel and J. H. Gatliffe, ♂, dredged (NMV); Lorne, 1917, A. Kenyon, ♂ (NMV); Western Port, Jan. 1967, K. Walker, 3♂♂, dredged from weedy channel, 10 feet (AM P.20171). TASMANIA: Derwent Channel, July, 1938, ♂, dredged (with *H. ovatus* and *H. innominatus*) (TM 15061/G301); D'Entrecasteaux Channel, 19.x.1964, J. Farnell, ♂, dredged (TM G956). WESTERN AUSTRALIA: Oyster Harbour, 22.viii.1963, B.R. Wilson and G. W. Kendrick, ♂, 2 ov. ♀♀, dredged near Green I. (WAM 2 lots); King George Sound, Dec. 1965, J. S. Lucas, ♂, 2♀♀ (AM P.20172); Emu Pt. Channel, Oyster Harbour, 10/11.vii.1966, J. S. Lucas, 14♂♂, 2 ov. ♀♀, 9♀♀, 5 im. ♀♀ (WAM); Rocky Bay, Swan River, 16.i.1973, P.N. Chalmer, 3♂♂(WAM).

HALICARCINUS BEDFORDI Montgomery

Figs. 3A, 5E, 6N, 7G, 9E, 9F

Hymenosoma sp. — Montgomery, 1921:94-5.
Halicarcinus bedfordi Montgomery, 1931:425-6, pl. 27 figs. 3, 3a, b. — Melrose, 1975:82.

TYPE LOCALITY AND TYPES: Swan River, Western Australia. SYNTYPES: 1931 (presented), S. K. Montgomery, 3 ov. ♀♀ (4.0-4.5 mm, in poor condition) (BM 1931.7.24.35-6). Examined by Dr. R. W. Ingle (pers. comm.).

DISTRIBUTION: Northern and western Australia, as far south as the Swan River on the west coast and Moreton Bay on the east coast.

DIAGNOSIS: Rostrum approximately triangular, narrowing abruptly half-way or further along its length, terminating in a rounded point; eyes reaching to at least 0.4 length of rostrum; without a spine at posterior lateral angle; chelipeds massive and elongate in large males, 3 X or more carapace width; male abdomen almost equilateral triangular; male 1st pleopods with broad base and stout straight distal portion, terminating in a broad rounded point, with tufts of long setae arising subterminally.

DESCRIPTION: The following is additional to the description of Montgomery (1931) and the Diagnosis:— anterior lateral carapace angles hardly indicated, posterior lateral angles obtuse and rounded; rostrum slightly deflexed, concave in cross-section; rostral keel thin, continuous with interantennular septum; postocular lobes acute and prominent; antennal spines acute; two prominences in pterygostomial region, a large lobule or spine near base of cheliped and a smaller lobule or spine more anterior, these may be visible dorsally; ischium of 3rd maxillipeds slightly shorter than merus along lateral edge; chelipeds very enlarged and elongate in large males (Fig. 5E), merus of cheliped of large males with 3 distal spines, carpus with 2 distal spines, propodus progressively expanding towards fingers, fingers with wide gape proximally, distal third of fingers meet with finely serrated cutting edges, dactylus with basal tooth; chelipeds in females and small males less than 1.5 X carapace width, little thicker than walking legs; walking legs ca. 2 X carapace width, dactyli with small teeth along proximal ½-⅔ of length; female abdomen oval, strongly convex, with a medial ridge, segments 1-5 of increasing length and breadth, segments 1 and 2 visible dorsally, telson more than ⅓ total abdomen length, telson trapezoidal; eggs ca. 0.3 mm diameter; telson of male abdomen triangular with rounded apex, segment 5 longest segment in abdomen; colour pale brown; males up to 6.8 mm (Swan River) or 3.7 mm (other localities), mature females 4.0-6.7 mm (Swan River) or 3.2-3.8 mm (other localities).

REMARKS: Montgomery's description and illustration of the rostrum are misleading (Montgomery, 1931). The rostrum is only approximately triangular, it narrows abruptly half-way or futher along its length. The lateral rostral lobes are completly fused with the medial lobe and the point of narrowing is where they terminate. The terminal portion of the rostrum, consisting of medial lobe only, is longer and broader in specimens from Western Australia than from Queensland. The base of the rostrum is continuous with the acute postocular lobes over the bases of the eyestalks. Montgomery considered the postocular lobes to be the lateral rostral lobes.

H. bedfordi is a northern Australian species and the type locality, Swan River, W.A., is the southern-most locality of collection. It is usually rare in the Swan River: during four years of intensive collecting at this locality only one specimen was found (Lucas, 1968). However, in 1973 it was common in the shallows of the Swan River basin (P.N. Chalmer, pers. comm.). This followed several years of unusually mild freshwater discharge in the estuary. Specimens from the Swan River are larger than those from northern localities. Some females greater than 4 mm are immature and some males greater than 5 mm do not show the massive cheliped condition. At other localities the largest mature males and females do not reach these carapace widths.

MATERIAL EXAMINED: QUEENSLAND: Victoria Pt., Stns. 5 and 6, 12.ix.1962, F. C. Vohra, 2♂♂ im.♀, locality codes C96/62, CR 31/62 (QM W. 2350, W. 2355); Victoria Pt., 13.i.1963, F. C. Vohra, ♂ (1st pleopod mounted on slide) (AM P. 20180); Ross River, 8.vii.1970, J. S. Lucas, ov.♀, littoral, muddy substrate (JCU); Weipa, July 1972, W. McCormick, 3♂♂, 7 ov.♀♀ (AM P. 20167 (1♂); QM W. 4064); Moreton Bay, undated, 3♂♂, samples 795, 932, 1037 at locations 31A mud, 22A seagrass and 31C mud, respectively (CSIRO). WESTERN AUSTRALIA: Monkey Mia, Shark Bay, 8.viii.1967, T. D. Meagher, 2♂♂ ov.♀, in trawl net among dead *Posidonia australis* (WAM); Pt. Henry and Pelican Pt., Swan River, 10 and 18.i.1973, P. N. Chalmer, 11♂♂, 11 ov.♀♀, im.♀, 1 juv., on *Halophyla*, ½ m depth (WAM); Salters Pt., Swan River, 10.i.1973, P.N. Chalmer, 8♂♂, 10 ov.♀♀, im.♀ (AM P.20168).

HALICARCINUS INNOMINATUS Richardson

Halicarcinus planatus. — Richardson, 1949a:68, fig. 48 (not *Cancer planatus* Fabricius, 1775).
Halicarcinus innominata Richardson, 1949b:130.
Halicarcinus innominatus. — Melrose, 1968:197, pl. 2 fig. 1; 1975:26-34, figs. 5-11, pl. 1C-F.
See Melrose (1975) for further Synonymy.

TYPE LOCALITY AND TYPE: Wellington Harbour (Melrose, 1975). Richardson (1949b) did not designate type specimens for the new species.

DISTRIBUTION: New Zealand, Chatham Islands, Stewart Island, Tasmania.

DIAGNOSIS: Carapace suboval, broader than long; rostrum arising well below carapace rim, rostral lobes short, subequal, close together, apically rounded, all pointing forward, lateral lobes at level of and not set at an angle to medial lobe; frontal carapace region not projecting; anterior and posterior carapace angles hardly evident, sometimes a small obtuse spine at position of posterior lateral angle; walking legs stout, dactyli with one row of teeth (based on Melrose, 1975).

DESCRIPTION: See Melrose (1975) for a comprehensive description. This is a large *Halicarcinus* species, with males up to 19 mm and mature females 7.5-15.5 mm; colour brown, with green or black tints (Melrose, 1975).

REMARKS: Specimens of *H. innominatus* from New Zealand were attributed to *H. planatus* until Richardson (1949b) recognized that they were another species, differing in features of the rostrum, lateral carapace angles and male chela. Garth (1958) reports Richardson's opinion that *H. planatus* is uncommon in New Zealand and that *H. innominatus* is the common species with which it has been confused. Gordon (1966) made a comprehensive study of the two species, giving further distinguishing features and concluding that *H. planatus* does not occur in New Zealand, but that is occurs south of the Chatham Islands (44°S) (see also Melrose, 1975). Subsequently, Lucas (1968) reported specimens of *H. innominatus* from Tasmania, where it is sympatric with the similar *H. ovatus*.

H. innominatus is unique among the Australasian marine hymenosomatids in having a trans-Tasman distribution. (One freshwater species, *Amarinus lacustris*, also occurs in Australia and New Zealand.) Generally, it appears that the Tasman Sea has acted as an effective geographical barrier between the Australian and New Zealand hymenosomatid faunas. Even the distribution of *H. innominatus* is most likely a recent phenomenon due to man's activities. Melrose (1975) reports that *H. innominatus* is found associated with the mussel *Perna canaliculus* (Martyn). This New Zealand mussel is present in Tasmania together with some other New Zealand marine invertebrates which are considered to have been introduced to Tasmania at various times after 1885 (Dartnall, 1969). The introductions apparently occurred with the importations of a New Zealand oyster, *Ostrea angasi* Sowerby, into Tasmania to bolster the Tasmanian oyster industry. In view of the close association of *H. innominatus* with *P. canaliculus* it is reasonable that they were both introduced to Tasmanian waters, either among the shipments of live oysters or from the keels of ships, which they inhabit (Melrose, 1975). The earliest record of *H. innominatus* from Tasmania is 1926.

MATERIAL EXAMINED: TASMANIA: Hobart Harbour, Derwent R. , Aug. 1926, M. Ward,♂, from wharf piles (AM P.8646); Georges Bay, NE coast, 10.ii.1927, T. T. Flynn, 2♂♂ 3-4.5 faths (AM P.9242); Derwent Channel, July 1938,♂, dredged (with *H. ovatus* and *H. rostratus*) (TM 15061/G301); Roches Beach, Frederick Henry Bay, 26.ii.1964, J. Greenhill, ♂, ov. ♀, midlittoral zone on rocky reef (with *H. ovatus*) (TM 19015/G652).

HALICARCINUS HONDAI (Takeda and Miyake)

Figs. 3H, 6O, 7H, 9K

Rhynchoplax hondai Takeda and Miyake, 1971b:168-70, fig. 3. — Sakai, 1976:149-50.

TYPE LOCALITY AND TYPE: Omonawa, Tukuno-shima I., Ryukyu Is., Japan. HOLOTYPE: 22.viii.1968, K. Honda and M. Takeda, ♀ (1.9 mm) (ZLKU 13088).

DISTRIBUTION: Ryukyu Is., Japan, and Townsville, Australia.

DIAGNOSIS: Medial lobe of rostrum long and narrow, far outreaching eyes, length ¼-⅓ carapace width, with one or more long setae terminally, lateral lobes not evident, completely fused with medial lobes, making broad base of rostrum; eyestalks elongate, with a prominence on medial edge; female abdomen broader than carapace width, conspicuous laterally and posteriorly in dorsal view, segments 3 and 4 fused without suture evident.

DESCRIPTION: The following data supplement the description of Takeda and Miyake (1971b), who only had access to the immature female holotype:— carapace width to length (excluding rostrum) ratio 1.21 (♂) and 1.37 (ov.♀); rostral keel and antennal spines absent; ischium of 3rd maxillipeds subequal to merus along lateral edge; chelipeds of male and female ca. 1½ X carapace width, female chelipeds slightly stouter than walking legs, male chelipeds stouter than female, with a prominent tooth distally on merus and carpus, propodus inflated, fingers 0.4 X total propodus length, dactylus with large basal tooth, fingers with serrations along distal cutting edges; walking legs ca. 2 X carapace width, stout, with large tooth on dorso-distal edge of merus, dactylus curved, without teeth proximally, with a row of teeth increasing in size distally; female abdomen very large, widest at junction of segments 4 and 5, segments 1 and 2 short, fused segments 3 and 4 together longer than segment 5 and shorter than telson, telson trapezoidal; female pleopods projecting laterally from abdomen; eggs 0.23 mm diameter (?) (one only), ovaries appear to extend into abdomen; male abdomen elongate triangular, segments 3 and 4 fused and no suture evident, telson spade-shaped; male 1st pleopod with thinner portion arising at ca. 90° from stout base, bending through ca. 90° again a short distance above base and then slightly curved, tapering to a concave tip distally; colour off-white, pale orange; scattered long setae on dorsal carapace surface and legs; mature individuals less than 3 mm.

REMARKS: The two specimens of *H. hondai* collected from reefs near Townsville, Great Barrier Reef region, show only minor differences from the female holotype and they do not warrant separate taxonomic status without examination of further specimens. The male, but not the female specimen, from the G.B.R. region shows stronger grooves on the dorsal carapace surface than the female holotype; and the rounded prominence on the eyestalk and blunt pterygostomial tooth of the holotype are acute teeth in the G.B.R. specimens. The two widely separated localities where *H. hondai* has been collected suggest that it has a wide geographical distribution in the western Pacific. Because of its very small size it has probably escaped being noticed and collected.

The disproportionate size of the mature female abdomen and projecting pleopods of *H. hondai* are to increase its egg-carrying capacity. This phenomenon also occurs in another minute *Halicarcinus* species, *H. keijibabai*, and in two minute *Elamena* species, *E. gordonae* and *E. umerata*. Fusion of segments in the female abdomen of *H. hondai* may be related to the expansion of the abdomen or lateral projection of the pleopods. This fusion also occurs in *H. afecundus* n.sp., *E. umerata* and possibly in *E. gordonae*, but not in *H. keijibabai* (as figured, but not described, by Takeda and Miyake, 1971b). *H. afecundus* n.sp. does not have an expanded female abdomen, but it has large eggs and the fusion of abdominal segments probably relates to its particular mode of reproduction. These fusions of segments occurring in a few species of *Halicarcinus* and *Elamena*, genera which otherwise show no fusion of female abdominal segments, are considered to be specific adaptations to very small size or a particular mode of reproduction. The condition has arisen independently in each species, i.e. they are analogous conditions, and it is not considered to be of phylogenetic significance.

The single egg on the *H. hondai* female is very small, even by hymenosomatid standards. It may be a prematurely released egg, as the female was in an aquarium for several days before being preserved. If it does represent the normal size of eggs of this species, the zoea emerging must be at, or very near, the end of the scale of small brachyuran zoeae.

It appears that segments 3 and 4 in the male abdomen of *H. hondai* are also fused. In all of these small species with fused abdominal segments it is desirable to have a series of specimens, as it is not easy in some specimens to distinguish sutures from articulations. However, in the sole male specimen of *H. hondai*, not even a suture can be seen between segments 3 and 4 (Fig. 7H), so the condition seems clear. This may be linked with fusion of segments in the female abdomen and it would be interesting to examine males of *H. afecundus* n.sp. to see if they also show fused segments.

MATERIAL EXAMINED: Picnic Bay, Magnetic Island, Queensland, Australia, 8.viii.1972, J. S. Lucas, ♂ (1.93 mm, 1st pleopod detached and mounted on a slide), on coral in intertidal zone (QM W.4068); Townsville, Queensland, Australia, Dec. 1973, J. S. Lucas, ov. ♀ (2.64 mm, carrying only one egg), on coral rubble from patch reef (QM W.4067).

HALICARCINUS AFECUNDUS n.sp.

Figs. 3G, 6M

TYPE LOCALITY AND TYPE: Lindeman Island, Cumberland Island Group, Queensland, Australia. HOLOTYPE: 5.ix.1935, ov. ♀ (5.4 mm) trawled in 10 faths (AM P.12225).

DIAGNOSIS: Rostrum arising slightly below carapace rim, lobes well spaced, lateral lobes distinctly longer and broader than medial lobe, medial lobe slightly deflexed, lateral lobes sloping up; eyes short, little visible dorsally; female abdomen with segments 2-5 fused and sutures inconspicuous; eggs ca. 0.7 mm diameter.

DESCRIPTION: Not including male features:— carapace subcircular, ratio of carapace width to length (including rostrum) ca. 1.08; dorsal carapace surface with a discontinuous medial longitudinal ridge, gastro-cardiac, cervical and thoracic grooves well defined, other grooves faint; lateral carapace walls sloping out ventrally; anterior lateral carapace angles with an obtuse spine, posterior lateral angles obtuse and rounded, a prominent acute spine slightly posterior and below posterior lateral angle; postocular lobes small; interantennular septum well developed; no rostral keel; no antennal spines; pterygostomial regions with an acute spine near base of cheliped, two obtuse lobes anterior to it; ischium of 3rd maxilliped subequal with merus along lateral edge; female chelipeds slightly stouter than walking legs, length 1¼ X carapace width; fingers half total propodus length, fingers with fine serrations, curved distally; walking legs slender, longer than 2X carapace width, dactyli little curved, long and tapering, with two small teeth subterminally; female abdomen oval, convex, telson longest segment, ca. ⅓ total abdomen length; female genital apertures laterally elongate (related to large egg size); eggs few in number, 5.4 mm female carries 24 eggs; female strongly setose around border of abdomen and on legs.

REMARKS: Although no male specimens of *H. afecundus* were seen, the sole female specimen is very distinctive and clearly a new species. It is one of three *Halicarcinus* species in which the lateral rostral lobes are longer than the medial lobe; but, whereas in *H. planatus* and *H. tongi* the lateral lobes are slightly longer, in *H. afecundus* they are twice as long as the medial lobe in the type specimen. *H. afecundus* does not appear to be closely related to *H. planatus* or *H. tongi*. It belongs with the *Halicarcinus* species with well-spaced rostral lobes and most resembles *H. minutus* and some specimens of *H. ovatus*. It is unusual among *Halicarcinus* species in having fused segments in the female abdomen. This character is also shown by *H. hondai*.

The eggs of the *H. afecundus* female are twice the diameter of most other *Halicarcinus* species and it is very probable that this species has suppressed or abbreviated larval development. For comparison: *Amarinus lacustris*, with no free larval stages, carries eggs of 0.7 mm diameter; its sibling species, *A. paralacustris*, with normal larval development, carries eggs of 0.35 mm diameter (Lucas, 1970). The number of eggs in each egg mass is reduced as a consequence of the larger egg size, so that the *H. afecundus* female carries only 24 eggs. Similar sized females of *Halicarcinus ovatus* and *Amarinus paralacustris* (normal larval development) carry ca. 530 and 280 eggs, respectively, while a 5.4 mm female of *A. lacustris* (suppressed larval development) carries ca. 35 eggs (Lucas, 1968, from Fig. 5.13) (see also Table 4). Suppression or abbreviation of free larval development involves a prolongation of embryonic development as well as increased egg size.

Another marine hymenosomatid, *Elamenopsis bovis* (which also occurs in brackish water), is known to have suppressed larval development. The phenomenon is uncommon among marine Brachyura and only known from three other families (see section on Reproductive strategies). An advantage of suppressing or abbreviating larval stages is that it reduces the mortality of the young stages through unfavoural dispersal and exposure to predators of plankton. Disadvantages are reduced dispersal of the offspring and lowered fecundity, because of the need to produce larger eggs supporting longer embryonic development. Other adaptations of hymenosomatid females to compensate for the low fecundity imposed by their small size are considered in the section on Reproductive strategies.

The name *afecundus* (not fecund; Latin, masculine) refers to the small number of eggs carried by the female holotype.

MATERIAL EXAMINED: Holotype.

TRIGONOPLAX H. Milne Edwards, 1853

Trigonoplax H. Milne Edwards, 1853:224 (type species, by monotypy, *Ocypode (Elamene) unguiformis* de Haan, 1839:75-6, pl. 29 fig. 1 and pl. H (called *Inachus (Elamene) unguiformis* in pl. H)).

DIAGNOSIS: Carapace approximately triangular; anterior lateral angles almost absent, antero-lateral borders very long; carapace surface without well defined grooves; rostrum rounded triangular, not defined or poorly defined from carapace surface, concealing antennules, antennae and most of eyes; rostral keel present; epistome very long and bulging; Milne Edwards apertures fused laterally for more than half their length; mouth-field approximately square, completely filled by 3rd maxillipeds; ischium of 3rd maxilliped subequal or longer than merus along lateral edge; chelipeds similar in both sexes, not thicker than walking legs; walking legs long and slender, dactyli with one or two subterminal teeth; female abdomen broad, weakly convex; male abdomen broad, without fused segments; male 1st pleopods curved, bearing a subterminal row of long setae.

SPECIES OF *TRIGONOPLAX*:

Species	**Distribution**
T. unguiformis (de Haan, 1839)	Japan; Singapore; Ternate; G. of Martaban; Andaman Is.; Natal
T. longirostris McCulloch, 1908	southern Australia
T. spathulifera n.sp.	northern Australia

REMARKS: *T. unguiformis* differs markedly from the *Elamena* species with truncate rostra, e.g. *E. mathaei,* in the form of the carapace, rostrum, rostral keel, and epistome — differences which were recognized by early workers. However, with the discovery in India of several species of apparently intermediate form, which were included in the *Trigonoplax* taxon, the differences between *Trigonoplax* and *Elamena* were considered to be trivial and the former at best a subgenus (Alcock, 1900, Kemp, 1917).

Trigonoplax is recognized here as a genus with three similar species which are readily distinguished from all *Elamena* species by their unique partially-fused Milne Edwards apertures (Fig. 5F), almost straight anterior lateral angles, long antero-lateral carapace borders and very long epistome. There are probably at least several other undescribed species, e.g. *T.* species of de Man (1902) and *E. (T.) unguiformis* of Alcock (1900) and Kemp (1917). Specimens from various Indo-West Pacific localities, which have been attributed to *T. unguiformis,* vary in features such as carapace width to length ratio, rostrum, rostral keel, cheliped fingers, size of the terminal spine on the merus and shape of the dactylus of walking legs, and number of segments in the male abdomen (?).

Larval morphology provides further support for the separate generic status of *Trigonoplax* and *Elamena.* As discussed in the Remarks on the genus *Elamena,* larvae of a number of *Elamena* species have been described and they are characterized by unique lateral expansions of the abdomen and very short rostrum, antennae and antennules. The first stage zoea of *T. unguiformis* from Japan, described by Aikawa (1929), has a normal abdomen and moderate-sized rostrum, antennules and antennae.

MATERIAL EXAMINED: (Other than Australian material) *T. unguiformis:* Japan, undated, ♀, Old Collection (stuck to glass plate) (AM P.139); Inland Sea, Japan, undated, ♂ (BM 1907.4.27.5). (Seven dried syntypes of *T. unguiformis* in the Rijksmuseum van Natuurlijke Historie, Leiden, were recently examined by Dr L. B. Holthuis (pers. comm.).)

TRIGONOPLAX LONGIROSTRIS McCulloch
Figs. 5A, B, F, H, 6A, 8A, 9I, J

Elamena (Trigonoplax) unguiformis. — Fulton and Grant, 1906a: 10-11, fig. (not *Ocypode (Elamene) unguiformis* de Haan, 1839).
Trigonoplax unguiformis var. *longirostris* McCulloch, 1908:59, pl. 12 fig. 3 — Kemp, 1917:278.
Trigonoplax unguiformis longirostris.— Tesch, 1918:26.
Elamena (Trigonoplax) unguiformis var. *longirostris.* — Hale, 1924:70-1, fig. 1.
Elamena (Trigonoplax) unguiformis longirostris.— Hale, 1927:120-1, fig. 118.
Trigonoplax unguiformis. — Griffin, 1972:66-7 (not *Ocypode (Elamene) unguiformis* de Haan, 1839).

TYPE LOCALITY AND TYPES: Western Port, Victoria (not Port Phillip, Victoria, given by McCulloch (1908)). SYNTYPES: undated, T. Gabriel, ♂ (9.0 mm), ♀ (15.2 mm), labelled as types of *Trigonoplax unguiformis* var. *longirostris* (AM P.12). The female is the same size as that figured by McCulloch and is hereby designated lectotype of *Trigonoplax unguiformis longirostris* McCulloch, 1908.

DISTRIBUTION: Southern Australia, excluding Tasmania, from Mandurah on the west coast to Western Port on the south-eastern coast.

DIAGNOSIS: Carapace width to length ratio approximately 1.0, less than 1.1; rostrum often deflexed; rostral keel shallow, not nearly reaching tip of rostrum; lateral walls of carapace strongly converging ventrally; fingers of chelae weakly spatulate; dactyli of walking legs distinctly broadest medially.

DESCRIPTION: Carapace width to length ratio 0.97-1.06 (Fig. 5A); carapace surface generally concave, with a slight rim, without grooves; lateral walls of carapace shallow; branchial regions of carapace projecting out over ischia of walking legs 1-3; rostrum elongate triangular with rounded sides and apex, laterally concave in dorsal view, separated from carapace by a slight ridge, level with carapace surface or slightly deflexed (Fig. 5B); rostral keel continuous with prominent interantennal septum; eyes short, eye-stalks very broad and flattened; postocular lobes generally visible dorsally; basal antennular segment with a distal lateral spine; no antennal spines; pterygostomial region simple; length of chelipeds ca. 1¼ X carapace width, fingers with small teeth along most of cutting edges, slightly curved and spatulate, only meeting at tips, 0.4 X propodus length (Fig. 5H); merus of each walking leg with a distal spine; length of walking legs 2½ X carapace width in large specimens, greater in small specimens, each dactylus distinctly broadest medially, about as broad as merus of same leg; 5th segment longest segment of female abdomen; male abdomen broad at segments 1-3, constricting sharply at segment 4; male 1st pleopod strongly curved, not very stout at base, with a subterminal row of 7-10 large setae; setation restricted to borders of Milne Edwards apertures, mouthparts and dactyli of walking legs; colour brown, yellow or yellow-green; largest male 12.7 mm, mature females 12.9-16.8 mm.

REMARKS: McCulloch (1908) considered that *T. u.* var. *longirostris* was probably a species, but since he had only four specimens he preferred to regard it as a variety. This original status of *T.u.* var. *longirostris* is to be regarded as subspecific, according to I.C.Z.N. (1961) Article 45(d) (ii) and (e), and it is here elevated to species. Characters by which McCulloch distinguished *T. u. longirostris* from *T. unguiformis,* carapace width to length ratio approximately 1.0, compared to a ratio of ca. 1.2, and distinct medial broadening of the dactyli of the walking legs, are consistent in all specimens of *Trigonoplax* from southern Australia.

Trigonoplax longirostris McCulloch is invalid if *Trigonoplax* is treated as a subgenus of *Elamena* H. Milne Edwards. *Elamena (Trigonoplax) longirostris* (McCulloch) is a junior secondary homonym of *Elamena longirostris* Filhol 1885a, notwithstanding the fact that the former is in the subgenus *Trigonoplax,* I.C.Z.N. (1961) Article 57(a). *E. unguiformis longirostris* (McCulloch), used by Hale (1927), is also a junior secondary homonym.

MATERIAL EXAMINED: VICTORIA: Syntypes listed above; Shoreham, 10.xi.1902,♂ (NMV); Rhyll, Western Port, May 1906, J. Gabriel, 3♂♂, 2♀♀ (these specimens were examined by Fulton and Grant (1906a) and the largest male specimen was figured) (NMV); Shoreham, undated, S. W. Fulton,♂(NMV). SOUTH AUSTRALIA: Port Vincent, 8.ii.1949, M. Bonnin,♀ (SAM C.3159). WESTERN AUSTRALIA: Emu Point Channel, Albany, 10/11.viii.1966, J. S, Lucas,♀, dredged from sublittoral (WAM); Mandurah, undated, ov.♀, 402/40 (WAM).

TRIGONOPLAX SPATHULIFERA n.sp.

Figs. 5C, D, I, 6B, 8F, 9G

TYPE LOCALITY AND TYPES: Bushy Island, Queensland. HOLOTYPE: im.♀ (7.5 mm, right cheliped detached), collected from a reef at Bushy Island (50 miles east of Mackay, Q.), 1938, F. A. McNeill (AM P.11465). PARATYPES: QUEENSLAND: St. Crispin Reef, off Port Douglas, 1918, A. R. McCulloch, im.♀(the specimen referred to by E. W. Bennett in his 10.xii.1929 letter; walking legs mutilated or absent) (AM P.4307); Nor'West Islet, Capricorn Group, April 1933, F. A. McNeill,♂(1st pleopods detached, one mounted on slide) (AM P.10363); 21°43'S, 152°25'E, NW end of Gillett Cay, Swain Reef Expedition, Stn 1, 1962, Aust. Musuem Party, ♂ (AM P.17011); One Tree Island, Capricorn Group, 25.ix.1965, F. H. Talbot, ov.♀ (AM P.15985); Heron Island, Capricorn Group, undated, A. Cameron, ov. ♀ (AM P.11376). WESTERN AUSTRALIA: Delambre Island, 9.vi.1960, B. R. Wilson, ov.♀, collected from coral reef, under a stone at low tide (WAM); Mary Ann Reef Buoy, Mary Ann Passage, 17.vii.1963, R. J. Hannan, ♀ (WAM); Pt. Hedland, Nov. 1963, G. Beamish, ov.♀, on reef (WAM); 30°00'S 114°28'E, NW of Jurien Bay, 28.i.1964, ov.♀, beam trawl, 70-75 faths, from sponge and bryozoa, DM 1/64 (WAM).

DISTRIBUTION: Northern Australia, from Lancelin Island on the west coast to Gladstone on the east coast.

DIAGNOSIS: Carapace width to length ratio 1.1-1.3; rostrum often strongly upturned; rostral keel deep, extending for full length of rostrum, generally visible dorsally; lateral walls of carapace approximately vertical; fingers of chelae strongly spatulate; dactyli of walking legs varying little in breadth before curved terminal portion.

DESCRIPTION: Carapace surface generally convex, irregular but without distinct grooves, with a distinct rim (Fig. 5C); branchial margins of carapace not overlying ischia of walking legs; posterior lateral angles sometimes with pronounced points; rostrum triangular with rounded sides and apex, varying from level with carapace surface to strongly upturned, laterally concave, flat or convex, not completely concealing antennules dorsally (Fig. 5D); rostral keel usually visible dorsally; postocular lobes small and inconspicuous; basal antennular segment with a small lateral spine distally; epistome shorter than mouth-frame; pterygostomial region with a small ridge; cheliped length ca. 1¼ X carapace width; fingers with fine teeth and some large teeth along most of cutting edges, curved and strongly spatulate, ca. 0.5 X propodus length (Fig. 5I); merus of each walking leg with a prominent distal spine, second walking leg 2½ X carapace width in large specimens, 3 X in holotype and greater in small specimens; telson longest segment of female abdomen; male abdomen broadest at segments 1-3, constricting at segment 4 (see Remarks); setation only on Milne Edwards apertures, mouthparts, dactyli of walking legs and inner surfaces of fingers; largest male 3.6 mm (probably immature), mature females 8.4-14 mm.

REMARKS: The name *spatulifer* was originally suggested by E. L. Bennett. In a letter in the Australian Museum files, dated 10.xii.1929, he proposed a female specimen, AM P.4307, as holotype of a new species, *T. spatulifer,* but never subsequently published a description. This female specimen was one of a number of specimens of an undescribed species from northern Australia examined during this study and as "spatulifer" is an appropriate descriptive name for this species, it is used here. Its correct form is *spathulifera,* flat blade bearer (Latin, feminine), referring to the fingers of the chelae. The specimen proposed as a holotype by Bennett is in poor condition and another holotype is chosen.

It is unusual that only two of nine specimens of *T. spathulifera* in Australian museum collections are males and that these males are much smaller than the smallest female specimen. The males are probably immature, thus the abdomen and 1st pleopod figured (Fig. 8F and 9G) probably represent an immature condition of these structures. They cannot be used for comparison with *T. longirostris.*

MATERIAL EXAMINED: Type material listed above.

ELAMENOPSIS A. Milne Edwards, 1873

Elamenopsis A. Milne Edwards, 1873:324 (type species, by monotypy, *Elamenopsis lineatus* A. Milne Edwards, 1873).

Neorhynchoplax·Sakai, 1938: 194, 200 (type species, by subsequent designation of Holthuis (1968), *Rhynchoplax introversus* Kemp, 1917; this species has precedence over *Rhynchoplax alcocki* Kemp, 1917 designated as "genotype" of *Neorhynchoplax* by Sakai (1976)).

DIAGNOSIS: Carapace approximately circular, octagonal or hexagonal; dorsal carapace surface with well defined grooves, with rim continuous across base of rostrum; rostrum generally tridentate or trilobate; epistome short, breadth exceeding 2 X length; pterygostomial regions plain; 3rd maxillipeds narrow and well separated, ischium shorter than merus along lateral edge; sternal region projecting forward between bases of 3rd maxillipeds; chelipeds stouter than walking legs, especially in large males; dactyli of walking legs often with a subterminal tooth or row of teeth; female abdomen with segments 3-5 fused, without pleopods, with a brood cavity within abdomen and posterior cephalothorax (not described in many species); male abdomen with segments 3-5 or 4-5 fused (or no segments fused?); male 1st pleopods with a stout base and thinner distal portion, curved towards sternum distally, with light setation (not described in many species).

SPECIES OF *ELAMENOPSIS:* Based on A. Milne Edwards (1873), Sakai (1938, 1969), Barnard (1946), Wu et al. (1962) and Takeda and Miyake (1971a).

Species	**Distribution**	**Habitat**
E. lineata A. Milne Edwards, 1873	New Caledonia; Queensland; Philippines	brackish-marine
E. woodmasoni (Alcock, 1900)	Andaman Islands; West Bengal, India; Sri Lanka	marine
E. inachoides (Alcock, 1900)	West Bengal, India	marine
E. alcocki (Kemp, 1917)	West coast, India	brackish
E. octagonalis (Kemp, 1917)	Goa, India; Queensland, Australia	brackish-marine
E. demeloi (Kemp 1917)	Goa, India	brackish
E. exigua (Kemp, 1917)	Thailand	brackish
E. introversa (Kemp 1917)	Kiangsu Prov., China	fresh water
E. nasalis (Kemp 1917)	West Bengal, India	brackish
E. kempi (Chopra and Das, 1930)	Basra, Iraq; Panama Canal	fresh water
E. tuberculata (Chopra and Das 1930)	Cochin, Travancore, India; Sri Lanka	fresh-brackish
E. sinensis (Shen, 1932)	Shantung Pen., China	marine
E. bovis (Barnard, 1946)	South Africa	brackish-marine
**E. species* (Wu et al., 1962)	Shihlin, Taiwan	brackish
E. ariakensis (Sakai, 1969)	Nagasaki Pref., Japan	marine, commensal
E. inermis (Takeda and Miyake, 1971a)	Palau Islands	fresh water
E torrensica n.sp.	Torres Straits, Australia	brackish-marine
E. aspinifera n.sp.	N. Queensland, Australia	brackish-marine

*Not adequately described for identification as a new species or as an already described species.

REMARKS: Sakai (1938) separated a number of the Indian hymenosomatids previously included in *Rhynchoplax* Stimpson, 1858, into a new genus *Neorhynchoplax* Sakai, 1938. He did this on the basis of their slender 3rd maxillipeds and fusion of segments 3-5 in the male abdomen. However, *Elamenopsis lineata* is congeneric with the *Neorhynchoplax* species and *Elamenopsis* is the oldest valid generic name. *E. lineata* is most closely related to the group of *Elamenopsis* species which have short rostra, especially short lateral lobes, and little dentation of the walking leg dactyli, and which tend to have laterally compressed walking legs. These species are *E. demeloi, E. tuberculata, E. ariakensis* and *E. inermis.*

Two species included by Sakai (1938) in *Neorhynchoplax* are excluded from the list of *Elamenopsis* species given here. They are *Hymenicus krefftii* Hess, 1865 and *Elamena filholi* de Man, 1887b. (See Remarks on the genus *Halicarcinus* for discussion of these species.)

In the four *Elamenopsis* species occurring in Australia and in the two Indian species examined at the British Museum the abdominosternal morphology of mature females is most unusual. It is unique among hymenosomatids and possibly among Brachyura. The female abdomen bears no pleopods and the abdominosternal cavity is reduced to a minimum. Instead of being carried on pleopods, eggs are brooded in an internal cavity within the abdomen and the posterior portion of the cephalothorax (Fig. 8H). The fused sternites of the abdomen (Fig. 5J) consist of very thin cuticle which is well separated from the fused tergites. This allows one layer of eggs between the sternites and tergites of the abdomen. The sternite cuticle of the abdomen is connected to the sternum of the cephalothorax from about the level of the 3rd walking legs, behind the genital apertures. If the abdomen is lifted away from the cephalothorax, the abdomen sternite cuticle is torn away from the cephalothorax sternum. In the intact mature female the brood cavity within the abdomen is continuous with a cavity extending into the posterior portion of the cephalothorax. Eggs are visible in this cavity through the dorsal surface of the carapace, at least in preserved ovigerous females. Apparently the eggs are not extruded through the genital apertures but remain within the body. This poses the problems: How are the eggs irrigated for gaseous exchange, etc., during development and how are larvae released? It appears that larvae can only be released by rupturing the thin sternites and cuticle at some point. Two ovigerous females of *E. lineata* and one of *E. aspinifera* n.sp. released larvae while maintained in the laboratory. These were normal first stage zoeae and no abnormalities in the female reproductive structures were suspected at the time.

Most authors have reported ovigerous *Elamenopsis* females without commenting on

Note added in press:

Serene (1971) described a new species, *Neorhynchoplax palawensis,* from the Philippines. Serene's brief description does not include diagnostic features such as 3rd maxillipeds, but it is probably an *Elamenopsis* species. It has laterally compressed walking legs, like *Elamenopsis* species such as *E. demeloi,* unusually elongate lateral rostral lobes and a unique pair of lobes projecting posteriorly from the 1st segment of the male abdomen.

Serene R. 1971. Observations preliminaires sur des Brachyoures nouveaux ou mal connus du Sud-Est Asiatique (Crustacea Decapoda). *Bull. Mus. Hist. nat., Paris* (ser. 2) 42(5): 903-918.

the female reproductive system. However, Shen (1932) figured the female abdomen of *E. sinensis,* from China, showing the characteristic segment fusion and shape, and Wu et al., (1962) noted that the abdomens of both sexes of a species of *Elamenopsis* from Taiwan were composed of four segments. Thus, as the six species examined in detail in this study are representative of the range of *Elamenopsis* species and as fused abdominal segments in females are known for two other species, it is very probable that the unique female reproductive morphology is characteristic of the genus *Elamenopsis.*

In addition to female morphology, *Elamenopsis* is notable for the number of euryhaline species, for three species permanently inhabiting fresh water, and for a commensal species of hymenosomatid, *E. ariakensis,* which is commensal with a holothurian (Sakai, 1969). *Elamenopsis* species differ markedly in morphology from the other group of hymenosomatids in brackish and freshwater habitats, *Amarinus* n. gen. species, in having narrow 3rd maxillipeds, usually tripartite rostra and in fusion of abdominal segments. *Elamenopsis* is mainly a northern hemisphere genus and *Amarinus* n. gen. is mainly in the southern hemisphere, their distributions overlap along the Queensland coast in Australia.

MATERIAL EXAMINED: (other than Australian species) *Elamenopsis alcocki:* Portuguese India, undated (Sept. 1916?), 2 ♂♂, 2 ov. ♀♀, labelled *"Rhynchoplax alcocki* cotypes" (BM 1919.11.1.117-120). *Elamenopsis* species *(demeloi?):* Kuda Kalapu ganga, Randombo, Ceylon, C. H. Fernando, 29.viii.1954, ♂♂ and ♀♀ (BM).

ELAMENOPSIS LINEATA A. Milne Edwards

Figs. 3J, 5J, 8E, 10J

Elamenopsis lineatus A. Milne Edwards, 1873:324-5, pl. 18 fig. 4. — Kemp, 1917:250. — Tesch, 1918:26-8, pl. 1 figs. 5, 5a-c. — Serene and Umali, 1970:58, pl. 5 fig. 11.

TYPE LOCALITY AND TYPE: Dotio, New Caledonia (in brackish water); HOLOTYPE: ovigerous female, not a male as stated by A. Milne Edwards (1873), in Muséum d'Histoire Naturelle, Paris (J. Forest, pers. comm.).

DISTRIBUTION: New Caledonia, northeastern Australia, Philippines.

DIAGNOSIS: Carapace wider than long, approximately hexagonal; rostrum triangular with rounded apex, strongly deflexed and nearly perpendicular; walking legs broad and laterally compressed, dactyli without teeth; male abdomen with segments 4 and 5 fused and suture indistinct or without fused segments (? — see Description).

DESCRIPTION: Tesch (1918) gave a full description of a male specimen of *E. lineata* and generally the Australian material agrees with Tesch's description. In Australian specimens the dorsal carapace surface is slightly concave rather than "perfectly flattened" as in Tesch's specimen and the abdomens of male specimens from Australia have segments 4 and 5 fused (Fig. 8E), while Tesch figures a male abdomen apparently without fused segments. There is still a faint suture evident at the fusion of segment 4 and 5 in some Australian males and it is possible that this is the condition in Tesch's male. The male 1st pleopod, which was not described by Tesch (1918), has a stout base and then tapers to a rounded tip (Fig. 10J). The terminal portion is curved and has a strong ridge on the sternal side. There are scattered short setae near the tip and a few long setae arising just before the curved terminal portion.

Female features are: chelipeds similar to but smaller than those of males, only slightly stouter than legs; abdomen convex, segment 1 widest, segments 2-5 of similar width, telson triangular and much narrower than previous segments (Fig. 5J); sternum distinctly contoured to receive close-fitting abdomen and telson, with two small projections over abdomen at level of segment 5.

Largest male and female 3.3 and 3.8 mm, respectively; coloured dark brown.

REMARKS: There have been three previous reports of *E. lineata,* each involving a single specimen. However, this species is quite common in certain habitats in the Victoria Point-South Dunwich area, south of Brisbane, as evidenced by the number collected and deposited in the Queensland Museum during a survey in 1962. *E. lineata* has been collected on a number of occasions in Ross River, Townsville, by digging in a muddy substrate, and its distinctive larvae are common in plankton samples from Ross River and the Johnstone River, north of Townsville. It has largely escaped notice because its size, coloration and behaviour make it very inconspicuous. With the apparent exception of Tesch's specimen from "on the coral reefs, at Sangir, north of Celebes", "Siboga" Expedition Stn 127 (129?) (Tesch, 1918), the localities where *E. lineata* has been collected are estuaries or coastal localities subject to brackish salinities. "Coral reefs" seem to be an unlikely habitat in view of the other reports.

The zoeae of *E. lineata* are like the zoeae of other hymenosomatids inhabiting brackish water in having well developed carapace spines. The zoeae of *E. lineata* are particularly like those of *Hymenosoma orbiculare,* with elongate rostral and mid-dorsal spines; but these spines in *E. lineata* are extremely elongate, being approximately three times and two times the carapace length, respectively, in the first stage zoea (Lucas, unpublished data). This makes the zoea very distinct among hymenosomatid zoeae and brachyuran zoea generally. Another less conspicuous but distinctive feature of *E. lineata* zoeae is the presence of two setae on the coxal endite of the 2nd maxilla. In other hymenosomatid species in which this larval appendage has been described there is only one seta on the coxal endite.

MATERIAL EXAMINED: QUEENSLAND: Manly, Moreton Bay, 27.vii.1946, J. S. Hynd, ♂, from mud, *Zostera* (AM P.12204); South Dunwich, 15.vii.1962-14.x.1962, J. F. Vohra, 7 ♂♂, 2 ov.♀♀, ♀, 2 im.♀♀, Stns 3, 6 and 7, *Zostera* (QM W.2337, W.2341, W.2342, W.2343, W.2346); Victoria Pt., 12. ix.1962 and 11.x.1962, F. C. Vohra, 3♂♂ Stns 3 and 5 (QM W.2338, W.2353); Ross River, Townsville, Jul. 1969 and 2.x.1970, J. S. Lucas, 2♂♂ 2♀♀(both females released larvae then moulted in laboratory) (JCU); Weipa, Jul. 1972, W. McCormick, im. ♀, benthos off mangroves (AM P.20170); Dunwich, Moreton Bay 4.v.1973, J. S. Garth,♂,♀, sandy mud flats with turnable rocks (with *E. octagonalis)* (AHF JG9-73).

ELAMENOPSIS OCTAGONALIS (Kemp)

Figs. 4A, 6P

Rhynchoplax octagonalis Kemp, 1917:256-8, fig. 5.
Neorhynchoplax octagonalis.— Sakai, 1938:2.

TYPE LOCALITY AND TYPE: Vareeg Islet, Mormugao Bay, Goa, India. HOLOTYPE: ov. ♀(3.9 mm, carapace length) (Indian Museum, Zoological Survey of India No. 9740/10).

DISTRIBUTION: Goa, India; Queensland, Australia.

DIAGNOSIS: Carapace approximately octagonal; lateral carapace walls with a forward directed spine above base of 1st walking leg; rostrum consisting of three separate spine-like lobes, fringed with short setae, lateral lobes well spaced from medial lobe and pointing slightly upward and outward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli with one subterminal tooth; male 1st pleopod terminating in a long thin point.

DESCRIPTION: The following is additional to the description of the female holotype by Kemp (1917) and the Diagnosis: — carapace width to length ratio (excluding rostrum) 0.93-1.07 (Australian specimens) (Fig. 4A); basal antennular segment with strong lateral tooth; no rostral keel; antennal spines small and obtuse; pterygostomial regions with strong ridge dorsally; length of male chelipeds 1½ carapace width, merus with a subterminal tooth ventrally, propodus inflated, particularly expanded ventrally, propodus depth ca. 1.8 mm in 3.4 mm male, fingers each with a row of ca. 7 teeth which fit together when fingers close, fingers curved distally; length of female chelipeds slightly greater than carapace width, stouter than walking legs but much smaller than male chelipeds; telson of female abdomen small, difficult to distinguish from segment 5 and possibly fused to it; male abdomen narrow, segments 3-5 fused without sutures, fused article and telson elongate, similar to *E. demeloi* (see Kemp, 1917, Fig. 9); male 1st pleopod little curved, tapering from stout base to a long thin distal portion (compared to *E. aspinifera* n.sp., Fig. 10G, the thin terminal portion is very much longer); coloured brown-dark brown; males up to 3.4 mm, mature females 2.5-3.0 mm (Australian specimens).

REMARKS: The Australian specimens of *E. octagonalis* are smaller and tend to be more narrow than the holotype, which is the only specimen described from India. Kemp (1917) describes the carapace as slightly broader than long: measuring his figure of the holotype (Fig. 5) the carapace width to length ratio (excluding rostrum) is ca. 1.1. Some Australian specimens approach this ratio, in others the carapace length is greater. One other difference between the Australian specimens and Kemp's description is that the former have a subterminal tooth on the dactyli of the 1st walking legs (Fig. 6P), as well as on legs 2-4. Kemp (1917) states that in the holotype the dactylus of the 1st walking leg is "unarmed". Subterminal teeth on the dactyli of the 1st walking legs are often smaller than those on other legs and no other hymenosomatid is known in which teeth are only present on the dactyli of legs 2-4. It is possible that Kemp overlooked the subterminal teeth among the long setae on the dactyli of the 1st pair of walking legs.

The Australian specimens are considered to be conspecific with the holotype of *E. octagonalis* until examination of further Indian specimens shows a consistent difference in the shape of the carapace.

MATERIAL EXAMINED: QUEENSLAND: Victoria Pt., Moreton Bay, 12.ix.1962 and 11.x.1962, F. C. Vohra, 3 ov.♀♀, 3 im.♀♀, Stns 6 and 7 (QM W.2339, W.2344, W.2352, W.2354); South Dunwich, Moreton Bay, 15.vii.1962 and 12.viii.1962, F. C. Vohra, 3 im.♀♀, Stns 4 and 5 (QM W.2360; AM P.20181); Dunwich, Moreton Bay, 17.iv.1973 and 4.v.1973, J. S. Garth, 4♂♂, ♀, 3 im.♀♀, sandy mud flats with turnable rocks (with *Elamenopsis lineata*) (AHF JG 6-73, JG 9-73).

ELAMENOPSIS TORRENSICA n.sp.

Figs. 4B, 6Q

TYPE LOCALITY AND TYPE: Thursday Island, Torres Strait, Queensland, Australia; HOLOTYPE: undated, ♀ (4.3 mm, all legs and chelipeds detached), Old Collection (AM P.20166).

DIAGNOSIS: Carapace approximately octagonal; lateral carapace walls without spines or crests; rostrum consisting of three rounded lobes which are narrow and separate, without fringing setae, lateral lobes well spaced from medial lobe, pointing slightly upward and curving slightly inward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli with one subterminal tooth.

DESCRIPTION: Not including male features:— carapace width to length ratio 1.07 (Fig. 4B); dorsal carapace surface concave, with gastro-cardiac, cervical and thoracic grooves strongly indicated, carapace walls bulge laterally (not shown in Fig. 4B); anterior lateral carapace angles obtuse, midlateral carapace borders curve slightly in behind anterior lateral angles making them slightly prominent; posterior lateral angles obtuse, without spines; rostrum reaching beyond eyes; eyestalks short, corneas visible dorsally; postocular lobes developed into acute teeth; interantennular septum strong; a slight rostral keel on medial lobe; small acute antennal spines; exopodites of 3rd maxillipeds largely hidden; female chelipeds ca. 1½ X carapace width, fingers with small teeth; walking legs ca. 2 X carapace width, moderately stout, dactylus tapering uniformly, curved distally, with a subterminal tooth and a row of short setae ventrally (Fig. 6Q); female abdomen with segments 1 and 2 visible dorsally, a strong ridge across distal edge of segment 1, segment 5 of fused article (segments 3-5) appears to be very long and broad, constituting most of the abdomen, telson broad triangular; light setation on legs, mouthparts and lateral walls of carapace.

REMARKS: Although only a single female specimen has been found, it is clearly different from other *Elamenopsis* species and may confidently be described as a new species.

E. torrensica, E. octagonalis and *E. aspinifera* n.sp. are related to the *Elamenopsis* species with short tripartite rostra of narrow lobes and with unflattened legs, e.g. *E. woodmasoni, E. alcocki, E. exigua* and *E. introversa*. They differ from all except *E. introversa* in having the lobes unfused at the base, at least in dorsal view. *E. torrensica* is probably most closely related to *E. introversa*; these species may be distinguished by the narrower shape of the anterior of the carapace, very long legs and crests on the lateral carapace walls in *E. introversa*, as well as by less conspicuous features. *E. aspinifera* n.sp. is probably most closely related to *E. octagonalis*; it differs from *E. octagonalis* in carapace shape, male 1st pleopods and in the absence of teeth and spines in the usual places: postocular lobes, antennal spines, lateral carapace walls and dactyli of walking legs.

E. torrensica, E. octagonalis and *E. aspinifera* n.sp. have been collected in Australia from localities where marine salinities prevail, but where salinity is lowered in summer due to freshwater discharge from rivers.

The name *torrensica* (feminine) is based on the type locality of this species, Torres Strait.

MATERIAL EXAMINED: Holotype.

ELAMENOPSIS ASPINIFERA n.sp.

Figs. 3I, 5G, 6R, 8D, 10G

TYPE LOCALITY AND TYPES: Weipa, Queensland, Australia; HOLOTYPE: July, 1972, W. McCormick, ♂ (3.1 mm, 1st pleopod detached and mounted on a slide, only one cheliped and four legs present, all detached), benthos off mangroves (QM W.4069); PARATYPE: Rooney's Bridge, Ross River, Townsville, Queensland, 13.ix.1969, J. S. Lucas, ♀ (3.0 mm, slightly damaged) ovigerous when collected, released larvae in laboratory (JCU).

DIAGNOSIS: Carapace subcircular, lateral carapace walls without spines; rostrum consisting of three separate spine-like lobes, fringed with short setae, lateral lobes well spaced from medial lobe and pointing slightly upward, medial lobe longest and pointing forward; walking legs not laterally compressed, dactyli without subterminal teeth; male 1st pleopod with thin terminal portion short and terminating bluntly.

DESCRIPTION: Carapace width to length ratio 1.00 (♀), 1.03 (♂); dorsal carapace surface concave, with cervical and thoracic grooves not as strongly defined as gastro-cardiac groove; anterior lateral angles very obtuse and hardly evident, posterior lateral angles rounded obtuse; rostrum outreaching eyes; eyestalks short; corneas visible dorsally; postocular lobes undeveloped; basal segment of antennules with a strong lateral tooth; flagellum of antennae very long, much longer than basal portion; interantennular septum strong, continuous with strong rostral keel from medial lobe of rostrum; no antennal spines; palp of 3rd maxillipeds long, about length of merus, exopodite largely concealed; length of male chelipeds ca. 2 X carapace width, merus setose anteriorly, carpus setose anteriorly and dorsally, propodus inflated, particularly expanded ventrally (Fig. 5G), fingers with three large teeth proximally and several smaller teeth distally; length of female chelipeds ca. 1½ X carapace width, with similar but smaller teeth on fingers; walking legs slender, length ca. 2 X carapace width, dactyli tapering to a long thin point, straight proximally, terminal point curving, with a row of short setae and scattered long setae on ventral and dorsal edges (Fig. 6R); female abdomen elongate oval, segments 1 and 2 visible dorsally, segment 2 and fused segments 3 and 4 very short, fused segment 5 elongate, constituting ca. ¾ of abdomen length, segment 5 set at ca. 90° to segments 2-4, abdomen broadest at segment 5, telson very broad triangular; male abdomen with segments 3-5 fused (Fig. 8D), segment 2 shorter than segment 1, fused article constituting ca. ⅔ abdomen length, telson triangular with convex sides, abdomen broadest at segment 1, narrower at segment 2, fused article expanding to equal breadth of segment 1 ca. ¼ along its length, then constricting abruptly to become narrower than segment 2, then tapering down to narrow telson, fused article with an obtuse point on each side at its maximum breadth; male 1st pleopods tapering strongly from stout base into narrow distal portion of uniform thickness (Fig. 10G), distal portion slightly curved toward abdomen, fine terminal portion angled toward sternum, with several rows of short setae distally; setation on legs, mouthparts, lateral walls of carapace and anterior surfaces of chelipeds; mature male and female 3.1 and 3.0 mm, respectively.

REMARKS: *E. aspinifera* is compared with other species of *Elamenopsis* in the Remarks on *E. torrensica*. The name *aspinifera* (not bearing spines; Latin, feminine) refers to the absence of spines on this species.

MATERIAL EXAMINED: Type material listed above.

HYMENICOIDES Kemp, 1917

Hymenicoides Kemp, 1917:267 (type species, by original designation, *Hymenicoides carteri* Kemp, 1917).

DIAGNOSIS: Carapace subcircular, dorsal carapace surface concave, with well defined grooves; rostrum absent; eyes visible dorsally; epistome narrow, breadth ca. 2 X length; pterygostomial region plain; 3rd maxillipeds very narrow, ischium shorter than merus along lateral edge, palp elongate, dactylus especially elongate, reaching to posterior edge of mouth-frame; chelipeds much stouter than walking legs in males and females, very inflated in large males; walking legs moderately stout, length ca. 3 X carapace width, dactyli with a large subterminal tooth and small teeth; female abdomen without fused segments; male abdomen without fused segments, with a trilobate telson; male 1st pleopods strongly bent, with complex apex including long subterminal setae, semicircular lip and denticulate lobe.

SPECIES OF *HYMENICOIDES:* The genus is monospecific. *H. carteri* has been collected from two freshwater-brackish localities in the Gangetic Delta, West Bengal and Bangladesh. No specimens of *H. carteri* have been reported since Kemp (1917).

REMARKS: *H. carteri* occurs in the region of the greatest number of *Elamenopsis* species and in most features described by Kemp (1917) it appears to belong with the *Elamenopsis* species. Kemp did not describe the female reproductive structures and a finding of fused segments in the female abdomen, lack of pleopods, etc., would have confirmed the relationship with *Elamenopsis*. However, during a brief visit to the British Museum (Natural History) in 1975, I examined four cotypes and found that the male and female reproductive morphologies are quite different from the characteristic *Elamenopsis* pattern.

The female abdomen has normal segmentation and four pairs of pleopods. The sternal region is normal and the genital apertures are on small prominences. The female chelipeds are unusually large for a female hymenosomatid, as described by Kemp (1917). The male abdomen is without fused segments. It is unusually broad and contoured as figured by Kemp (1917) (Fig. 21 shows only whole segments 3-5 and telson). The trilobate telson results from contouring of its lateral regions to provide cavities to receive the apices of the 1st pleopods. The 1st pleopods are more complex than those described for any other hymenosomatid. Looking at the pleopods *in situ* against the sternum with the abdomen raised: each pleopod turns inward and down beyond the moderately stout base, then about two-thirds along its length it bends up, projecting away from the sternum so that the apex meets the inner surface of the telson, when it is in place. The inflated apex is complex, with semicircular lips terminally (like Fig. 58G of Melrose, 1975), a row of long subterminal setae on the medial surface and two lobes on the abdominal side, the largest of which is covered in a regular pattern of denticles. The denticulation and complexity of the pleopod apices is suggestive of the pleopods of *Hymenosoma* species.

Reproductive morphology gives no support for the suspected affinity of *H. carteri* with the *Elamenopsis* species and it appears to be rather isolated within the family Hymenosomatidae.

MATERIAL EXAMINED: Hughli R., Sibpur, Calcutta, (S. Kemp, Jan. 1917), 2♂♂, ov.♀, im.♀, cotypes (BM 1919.11.1.121-123).

HALIMENA Melrose, 1975

Halimena Melrose, 1975:106 (type species, by original designation, *Halimena aotearoa* Melrose, 1975).

DIAGNOSIS: Carapace elongate suboval, dorsal carapace surface shallow convex, without well defined grooves, lateral carapace angles obtuse; rostrum spade-shaped, separated from dorsal carapace surface by a ridge, without a keel; epistome breadth almost 2 X depth; pterygostomial regions plain; 3rd maxillipeds broad, almost filling mouth-field, ischium longer than merus along lateral edge; walking legs slender, length ca. 2 X carapace width, dactyli with a single subterminal tooth; male and female abdomens without fused segments.

SPECIES OF *HALIMENA:* The genus is monospecific. *H. aotearoa* occurs in New Zealand.

REMARKS: This genus was established by Melrose (1975) for a rare species represented by four specimens. Only very small males have been seen. Melrose (1975) regards *Halimena* as being closely related to *Elamena* (especially to the "triangular" *Elamena* species), but differing from it in having the rostrum separated from the dorsal carapace surface and in having a short epistome. Details of the male 1st pleopods and larval morphology are desirable.

AMARINUS n.gen.

TYPE SPECIES: *Elamena? lacustris* Chilton, 1882 is hereby nominated as the type species of the new genus. *A. lacustris* is the species of *Amarinus* n.gen. most widely distributed on different land masses, it has been well described and figured in the literature, and an undisputed holotype is extant, although it is an immature female specimen.

DIAGNOSIS: Carapace approximately circular to oval, with width greater than length; dorsal carapace surface flat or slightly concave, with well defined grooves; carapace angles obtuse and rounded, sometimes developed into small spines; rostrum separated from dorsal carapace by a ridge or groove or both, rostrum spade-shaped and deflexed, concave laterally, base of rostrum extending laterally over eyestalks to meet postocular lobes; epistome short, width at least 2 X length; pterygostomial regions usually plain; 3rd maxillipeds broad, slightly separated medially, ischium subequal with or shorter than merus along lateral edge; chelipeds stouter than walking legs, particularly in large males, in which propodus is very deep; walking legs of moderate thickness, dactyli without teeth or with one tooth, dactyli little curved; abdomens on both sexes without fused segments; female abdomen oval; male abdomen narrow triangular, with intercalated plates laterally at base of telson, plates articulated or fused with telson and articulated with segment 5 (not described in *A. woltereck*i); male 1st pleopods stout, curved at base, otherwise with little curvature, terminal portion with fine setae in tufts or scattered, terminating in one or several lobes.

SPECIES OF *AMARINUS:* Based on Holthuis (1968) and Lucas (1970).

Species	**Distribution**	**Habitat**
A pilosus (A. Milne Edwards, 1873)	New Caledonia	freshwater
A. laevis (Targioni Tozzetti, 1877)	southern Australia	brackish
A. lacustris (Chilton, 1882)	S.E. Australasia	freshwater
*A. woltereck*i (Balss, 1934)	Mindanao, Philippines	freshwater
A. angelicus (Holthuis, 1968)	Papua-New Guinea	freshwater
A. paralacustris (Lucas, 1970)	eastern Australia	brackish
A. latinasus n.sp.	N.E. Australia	brackish

REMARKS: The *Amarinus* species have been assigned to various genera and recent authors have included them in the genus *Halicarcinus*. However, Holthuis (1968) questioned whether the four freshwater species were congeneric with *Halicarcinus planatus* (Fabricius), the type species of the genus *Halicarcinus* White; he noted their common features and suggested that they may belong together in another genus. Holthuis had access to insufficent hymenosomatid material to resolve the status of the freshwater species. It has been resolved by this study, and three related brackish water species are included with the four freshwater species in a new genus.

The geographical distributions of the freshwater *Amarinus* species are notable. In addition to the Australian mainland they have been reported from eight different islands scattered over 9,000 km of ocean: Mindanao, Papua-New Guinea, New Caledonia, Norfolk Island, Lord Howe Island, New Zealand, King Island and Tasmania. Their distribution suggests a widespread ancestral species which occurred through the region at times when these islands were variously interconnected by land-bridges. However, the land-bridges between most of these land masses were very ancient, much more ancient than the probable Tertiary – Recent origin of the hymenosomatids. There are no fossil records of the Hymenosomatidae (Glaessner, pers comm.) to illuminate their origins and previous distributions.

The *Amarinus* species form a distinctive homogeneous taxon. They all inhabit low salinity environments, they are all brown to dark brown and pubescent and most species are large relative to the typical hymenosomatid size. With *H. hodgkini* they are unique in having intercalated plates at the articulation of segment 5 and the telson of the male abdomen. Among Brachyura, only Dromiidae are also known to have this character (Holthuis, 1968). Other distinctive features are deflexed spade-shaped rostrum; dactyli of walking legs being relatively straight, without teeth or with a single inconspicuous tooth; and stout male 1st pleopods.

Amarinus is not closely related to the other genus with predominantly brackish and freshwater species, *Elamenopsis* (see Remarks on this genus). They are similar to the *Halicarcinus* species but differ in the basic rostral form (unilobe versus trilobe), type of male 1st pleopods and intercalated plates of the male abdomen. The presence of these plates in one species of *Hymenosoma* suggests an affinity between these genera and there are several other important features in common: basically unilobe rostrum, male 1st pleopods relatively straight and with a complex apex, and no fused abdominal segments. With the exception of the monospecific *Halimena* and *Neohymenicus* n.gen., they are the two genera in which the rostrum is basically a unilobe structure and separate from the dorsal carapace surface.

The name *Amarinus* (not marine; Latin, masculine) refers to the habitats of these species.

MATERIAL EXAMINED (other than Australian species): *Amarinus pilosus:* Oubatche, New Caledonia, Apr. 1898, C. Hedley, im.♀ (AM G.1833).

AMARINUS LAEVIS (Targioni Tozzetti)

Figs. 4C, 7A, 10D

Hymenosoma laeve Targioni Tozzetti, 1877:179-82, pl. 11 figs. 3a-e (fig. 3d is incorrectly labelled 5d). — Tesch, 1918:28 ("species *incertae sedis*"). — Lucas, 1974:142; 1976:268. — Holthuis, 1975:133.

Hymenosoma australe Haswell, 1882b:754; 1882c:115, pl. 3 figs. 2, 2a. — Fulton and Grant, 1906b:19. — Montgomery, 1921:93-5.

Halicarcinus laevis. — Kemp, 1917:247.

Hymenicus australis. — Tesch, 1918:12-13.

Halicarcinus australis. — Hale, 1927:118, fig. 115. — Montgomery, 1931: 423-5, pl. 27 figs. 4, 4a. — Lucas, 1970:277; 1971:475-82, figs. 1-3 (larval morphology); 1974:142-3; 1976:268. — Griffin, 1972:65-6. — Holthuis 1975:133.

TYPE LOCALITY AND TYPES: Melbourne, Australia. The type specimens which were kept in the Museo Zoologico de "La Specola", Firenze, Italy, are not extant; they were lost during World War II (M. Poggesi, pers. comm.). There are two syntypes of *Hymenosoma australe* Haswell in the Australian Museum (see Griffin (1972) and Material Examined section for details; they are ♂ and ♀ specimens, not 2♀♀ as given by Griffin).

DISTRIBUTION: Temperate Australia in estuaries; from Moore River on the west coast to Brisbane River on the east coast. Snelling (1959) describes its distribution in the Brisbane River and Lucas and Hodgkin (1970a, b) describe the distribution of crab instars and larval stages in the Swan River.

DIAGNOSIS: Mature specimens rarely less than 10 mm; males and females up to 22 mm and 18 mm, respectively; antero-lateral carapace margins without a row of teeth or thin spines; antennal spines acute and prominent; male 1st pleopod not tapering at apex, apex complex, with several lobes and tufts of setae; propodus of chela very deep in large males, with knife-edge ventrally and large pulvinus (a sac arising between the bases of the fingers).

DESCRIPTION: The following is additional to the descriptions of Targioni Tozzetti (1877), Haswell (1882b, c) and Montgomery (1931), and details in the Diagnosis above:— posterior lateral carapace angle sometimes with an acute tooth; lateral borders of rostrum raised, terminating in spines which sometimes are very prominent to make apex of rostrum almost trifid; dactyli of walking legs with single tooth in first few crab instars, sometimes persisting in later instars; female abdomen convex and suboval, with two longitudinal grooves near midline, segments 1 and 2 short, of similar width, approximately half carapace width, segments 3-5 successively increasing in length and width, telson arcuate, longer than preceding segments, approximately 0.4 of whole abdomen length; intercalated plates of male abdomen fused with telson with inconspicuous sutures; body and legs covered with short setae, denser on body in mature females than mature males; coloration orange-brown to very dark brown, chelae of large males orange.

Targioni Tozzetti's Figure 3a of the dorsal carapace is misleading in the general shape of the carapace and rostrum, and over-sized eyes. The eyes are shown in normal proportion in Figure 3b (Targioni Tozzetti, 1877).

REMARKS: Between Targioni Tozzetti's description and this study only two authors referred to his name, *Hymenosoma laeve*. Kemp (1917) suggested that *Hymenosoma laeve* belonged in the genus *Halicarcinus* (he may have suspected that *Hymenosoma australe* Haswell was synonymous, because he does not mention *Hymenosoma australe*) and Tesch (1918) included *Hymenosoma laeve* with *Hymenosoma gaudichaudii* Guerin at the end of his hymenosomatid monograph in a section entitled "Species *incertae sedis*". Most authors were unaware of Targioni Tozzetti's description, for a few years later Haswell (1882b, c) described the taxon again and all later authors except Kemp (1917) used Haswell's specific name, often as *Halicarcinus australis*. Thus, although *Hymenosoma laeve* Targioni Tozzetti is the senior synonym for this taxon, it has remained unused in the primary zoological literature for more than fifty years and, according to I.C.Z.N. (1961) Article 23(b), it is to be considered a forgotten name *(nomen oblitum)*. The name *Hymenosoma laeve* Targioni Tozzetti was proposed for suppression under the plenary powers of the International Commission of Zoological Nomenclature (Lucas, 1974) and then withdrawn (Lucas, 1976) when Holthuis (1975) considered the proposal unnecessary.

A. laevis is the largest Australian hymenosomatid and mature specimens can be readily distinguished by their size from other Australian *Amarinus* species, with which it has sometimes been confused. Other features by which *A. laevis* may be readily distinguished from *A. lacustris* and *A. paralacustris* are its prominent and acute antennal spines, untapering 1st male pleopods and the prominent pulvinus which develops on the cheliped propodus of males at their pubertal/terminal moult (Lucas and Hodgkin, 1970a).

Throughout its distribution, *A. laevis* is quite constant in morphology, with minor variation in characters such as the degree of development of the teeth on the posterior lateral angles, degree of trifidness of the rostrum and number of tubercles on the merus of the male chelipeds.

MATERIAL EXAMINED: QUEENSLAND: Brisbane R., Chelmer, 7.x.1940, H. A. Longman, ov.♀ (AM W.1151); Mud Island, Moreton Bay, 27.vi.1941, V. F. Collin,♂ (QM W.1271); Brisbane R., Darra, 19.ii.1942, V. F. Collin, im.♀ (QM W.1473); Brisbane R., 14 miles from mouth, Dec. 1964, I.M.S.,♂, ♀ (JCU). NEW SOUTH WALES: Tweed River, 24.iv.1883, J. Steel, ov.♀, im.♀ (QM Mo.2984); Georges R., Picnic Point, 21.i.1967, J. S. Lucas, ♂, 2♀♀, *A. paralacustris* also collected here (AM P.20175); Budgewoi Lake, 7.ii.1965, J. S. Lucas, ♂ (AM P.20176); Stony Pt., The Broadwater, Myall Lake, 17.ix.1975, ♂, im.♀ (AM). VICTORIA: Williamstown, Port Phillip, Victoria, undated, ♂ (10.5 mm, dried, badly damaged by insects, right walking leg 1 and left walking legs 1 and 2 absent), ♀ (12.2 mm, dried, slightly damaged by insects) Haswell Collection No. 210 (syntypes of *Hymenosoma australe* Haswell; both specimens are glued to a glass plate with a red spot and labels cut from Haswell, 1882c) (AM P.15398). Yarra R., 21.iii.1934, J. E. Dixon, 4♂♂, im.♀ (labelled *Halicarcinus lacustris,* J. Clarke) (NMV); Yarra R., Moonee Ponds, 30.i.1965, J. S. Lucas, 3♂♂, 3im.♀♀(NMV). TASMANIA: Huon, Meredith, Arthur, Pieman and Liven Rivers, Egg Island and Grant's Lagoon, various dates 17.v.1963 — 28.vii.1964, B. C. Mollison, 39♂♂, 8 ov.♀♀, 9♀♀, 2 im.♀♀ (in eight containers) (IFCT); Derwent R., Lime Kilns, 15.ix.1963, 23♂♂, 24 im.♀♀, seven unidentifiable individuals (labelled "from 2½ lb brown trout (DS9 tag)"; most crabs are intact except for some legs missing; the smallest crab is 2.9 mm and the largest male and female are 7.3 mm and 5.7 mm respectively; there is little else in the stomach contents apart from some plant material and fish vertebrae) (IFCT). WESTERN AUSTRALIA: Swan R., Barkers Bridge, 8.i.1964, J. S. Lucas, 4♂♂, ov.♀, 3 im.♀♀ (WAM); Moore R., Nov. 1964, C. Prince, 3♂♂, 3 ov.♀♀ (WAM).

AMARINUS LACUSTRIS (Chilton)

Figs. 4D, 7B, 10E

Elamena ? lacustris Chilton, 1882:172.

Hymenosoma lacustris.— Chilton, 1883:69, pl. 1 fig. 2a-e.— Fulton and Grant, 1902:59-61, pl. 8.— Chilton 1915:316-20, fig. 1; 1919:93-5.

Halicarcinus lacustris.— Kemp, 1917:247.— Holthuis, 1968:111-12.— Walker, 1969:163-5.— Lucas, 1970:267-77, figs. 3a, 3d, 4.— Lucas, 1971:428, fig. 51 (embryo).— Melrose, 1975:84-8, figs. 41, 42.

Hymenicus lacustris.— Tesch, 1918:12.

See Holthuis (1968) and Melrose (1975) for further Synonymy.

TYPE LOCALITY AND TYPES: Lake Pupuke (= Lake Takapuna), Auckland, New Zealand; HOLOTYPE: im.♀ (labelled *Hymenosoma lacustris,* Chilton 1882; no details of collector or date of collection) (Canterbury Museum AQ 3287).

DISTRIBUTION: South-eastern Australasia. Lakes and streams in Victoria, South Australia, Tasmania, King, Norfolk and Lord Howe Islands, and North Island, New Zealand. Found in salinities 0.1-9.6°/oo and most commonly within the range 1-6°/oo in Victoria, Australia (Walker, 1969).

DIAGNOSIS: Rarely exceeding 10 mm carapace width; antero-lateral carapace margins without a row of teeth or thin spines; rostrum not fused with postocular lobes in a broad band; orbits extending dorsally to meet carapace rim; antennal spines obtuse and inconspicuous; female genital apertures 0.6-0.8 mm wide, without a medial prominence; eggs 0.65-0.8 mm diameter; mean value of breadth/length ratios of inner rami of female pleopods ca. 0.25; telson length/total abdomen length ca. 0.25 in mature females; male 1st pleopod very stout, tapering to a simple tip.

DESCRIPTION: Melrose (1975) gave a full description of this species from New Zealand and Norfolk Island specimens. However, she did not describe the female reproductive structures and eggs (see Diagnosis), which are important in distinguishing *A. lacustris* from its sibling species, *A. paralacustris,* in Australia.

Comparing *A. lacustris* specimens from Australia and Tasmania with Melrose's descriptions of New Zealand and Norfolk Island specimens, some minor consistent differences were found (Table 2).

TABLE 2. Minor differences between *Amarinus lacustris* specimens from New Zealand and Norfolk Island (described by Melrose, 1975) and those from Australia and Tasmania.

	New Zealand and Norfolk Island	**Australia and Tasmania**
rostral keel:	absent	a small ridge
large ramus of antennule:	2 segments	3 segments
basal tooth of dactylus of ♂ chela:	rarely present	well developed
dactyli of walking legs:	sometimes remnants of dentition	1 small tooth in specimens less than 5 mm
male abdomen		
(a) telson:	shorter than 3rd segment, semi-circular	equal to 3rd segment, triangular with rounded apex
(b) width 3rd segment/ width 1st segment:	0.55	0.50

REMARKS: The populations of *A. lacustris* on six land masses separated by many hundreds of miles of ocean are genetically isolated, since this species only occurs in inland low salinity waters and has no free larval stages (Lucas, 1970). Morphological differences between specimens from Victoria, Tasmania, New Zealand and Norfolk Island have been described by Fulton and Grant (1902) and Chilton (1919). The differences that they observed relate to: carapace shape, size of teeth on the carapace angles, angle and shape of the rostrum, dentition and tuberculation of the male chelipeds, shapes of male abdominal segments, shape of 3rd maxillipeds, and general body hairiness. These authors acknowledged that there was considerable variation among specimens from one locality and they were not prepared to give separate taxonomic status to the isolated populations. Some of the differences which they observed are in characters which vary with age, e.g. carapace shape, male chelipeds and hairiness, and in other characters there is as much variation between specimens from different Australian-mainland localities as between specimens from Victoria and Tasmania or New Zealand. The only consistent differences found so far between specimens from either side of the Tasman Sea are those shown in Table 2, and it is not proposed to establish specific or subspecific taxa on the basis of these minor differences.

A. lacustris is morphologically very similar to *A. paralacustris,* a brackish water species occurring along the eastern Australian mainland. The only significant differences between crab instars of these species are differences in the female reproductive apparatus which are related to the different sizes and numbers of eggs produced. *A. lacustris* has no free larval stages and ovigerous females carry a small number of large yolky eggs, while *A. paralacustris* has normal larval development and its eggs are half the diameter of those of *A. lacustris* and much more numerous (Lucas, 1970). Thus the female genital apertures are broader in *A. lacustris* and the inner rami of the pleopods (which bear the eggs) are narrower in *A. lacustris* than in *A. paralacustris.* Using morphology, mature females and late instar immature females are the only crabs instars which can always be identified to species. Some large males and immature females from Australian localities can be identified as *A. lacustris* by the absence of teeth on the dactyli of walking legs: the tooth on the dactylus of each walking leg becomes proportionally smaller in larger instars and in *A. lacustris* specimens of greater than 5 mm carapace width it is usually absent, while it is always present in *A. paralacustris.*

The male pleopods of these species are very similar and cannot be reliably distinguished (Figs. 10A, 10E).

In those characters in which there are consistent differences between *A. lacustris* specimens from Australia and New Zealand-Norfolk Island (Table 2), *A. paralacustris* is like the Australian specimens.

The problematical distribution of *A. lacustris* on six isolated land masses, and its degree of genetic compatibility with *A. paralacustris,* which only occurs on the Australian mainland, were discussed by Walker (1969) and Lucas (1970). Both consider that the available evidence is only compatible with a recent origin of *A. lacustris* in Australia and subsequent dispersal to Norfolk and Lord Howe Islands and New Zealand. Walker (1969) suggested rafting on floating debris in the East Australian Current and Lucas (1970) suggested aerial transport among the feathers or on the feet of water fowl, which fly across the Tasman Sea, as the method of dispersal. Whatever the explanation for the origins of these isolated populations, it would seem to be quite unique, as there is no other macroscopic freshwater invertebrate which also occurs on all the above land masses.

MATERIAL EXAMINED: VICTORIA: Lake Colac, 11.i.1967, K. Walker and J. S. Lucas, 20♂♂, 3 ov.♀♀, 3 im.♀♀ (AM P.20173); Skeleton Creek, Apr. 1967, K. Walker, 12♂♂, 2♀♀, 6 im.♀♀ (NMV). TASMANIA: Templestone Lagoon, Orielton Lagoon, Rebecca Lagoon, Old Mines Lagoon, 8.v.—21.x.1963, B. C. Mollison, 14♂♂, 5 ov.♀♀, 15 im.♀♀ (IFCT); King Island, Bass Strait, undated, ♂ (NMV). SOUTH AUSTRALIA: Finnis R., Finnis, 23.i.1965, J. S. Lucas, 5♂♂, 2 ov.♀♀, chlorinity 0.6°/oo (SAM C.19741); Pt. Sturt, Lake Alexandrina, 23. i. 1965, J. S. Lucas, 10♂♂ ov.♀, 9 im.♀♀, 2 juvs., under rocks, 0.4°/oo chlorinity (SAM C. 19743); Eight-mile Creek, Cape Northumberland, undated, ♂ (SAM). Localities not in Australia (only eggs of ovigerous females examined). NEW ZEALAND: Lake Pupuke, Auckland, undated, 2 ov.♀♀ (from Dr C. Chilton collection, presented Fulton and Grant, June 1902) (NMV). LORD HOWE ISLAND: Apr. 1933, A. A. Livingstone, 5 ov.♀♀, freshwater stream (AM P.10344).

AMARINUS PARALACUSTRIS (Lucas)

Figs. 4E, 7C, 10A

Halicarcinus paralacustris Lucas, 1970:275-7, figs. 3c, e; 1971:475-82, figs. 3JK, 5E-H (larval morphology).

TYPE LOCALITY AND TYPES: Cook's River, near Campsie, N.S.W. HOLOTYPE: ov.♀ (6.5 mm) 19.ii.1965, J. S. Lucas, among detritus in littoral zone, 7.4°/oo Cl. (AM P.15943). PARATYPES: 36 specimens, collection details as for the holotype, lodged in the following musems: 4♂♂, 2 ov.♀♀, 7 im.♀♀ (AM P.15944 and P.15945); 4♂♂, ov.♀, 6 im.♀♀ (NMV); 3♂♂, ov.♀, 7 im.♀♀ (QM W.3023); ov.♀ (JCU).

DISTRIBUTION: Eastern Australian mainland, in estuaries along the coast from Anglesea, Victoria, to Russell R., North Queensland.

DIAGNOSIS: Rarely exceeding 10 mm carapace width; antero-lateral carapace margins without a row of teeth or thin spines; rostrum not fused with postocular lobes in a broad band; orbits extending dorsally to meet carapace rim; antennal spines obtuse and inconspicuous; female genital apertures 0.4-0.5 mm wide, generally with a curved medial prominence; eggs less than 0.4 mm diameter; mean value of breadth/length ratios of inner rami of pleopods ca. 0.4; telson length/total abdomen length ca. 0.35 in mature females; male 1st pleopods very stout, tapering to a simple tip.

DESCRIPTION: Lucas (1970) gave a description of this species based on specimens from the southern temperate part of its distribution. However, specimens of *A. paralacustris* from tropical North Queensland differ from the southern specimens in the following features:— thoracic grooves on dorsal carapace surface angled more laterally; with three prominent lobes in pterygostomial region (less developed in small specimens); male 1st pleopods with more elongate pointed apex which projects away from abdomen; female genital apertures without medial prominences; eggs larger, approximating more to 0.4 mm than to 0.35 mm diameter.

REMARKS: This species is morphologically very similar to *A. lacustris* and to an extent genetically compatible with it (see Remarks on *A. lacustris*).

A. laevis occurs at all the temperate localities where *A. paralacustris* has been collected, but these brackish water species may be readily distinguished in their crab instars (see Remarks on *A. laevis*) and larval stages (Lucas, 1971).

On the basis of the temperature tolerances of their larvae, Lucas (1972) predicted that *A. paralacustris* would occur further north than *A. laevis* in the presence of suitable habitats. (At that time, the Brisbane River was the most northern locality reported for both species.) The prediction has been confirmed with the recent collection of *A. paralacustris,* but not *A. laevis,* in North Queensland. However, the North Queensland specimens differ from the southern specimens in several important features, including male 1st pleopod. Development of pterygostomial lobes in the northern specimens is unusual since these lobes are generally insignificant in *Amarinus* species. Further study of crab and larval morphology of specimens from various Queensland localities may indicate some separate taxonomic status for the North Queensland specimens.

MATERIAL EXAMINED: QUEENSLAND: Russell, North Johnstone, South Johnstone and Herbert Rivers, 11.xi.1975 — 28.xi.1976, R. G. Pearson, 12♂♂, 4 ov. ♀♀, 3 im. ♀♀, dredge, net, artificial substrate collector and sand wash samples (JCU). NEW SOUTH WALES: Violet Hill, Myall Lakes, 1975, ♂, 2 ov. ♀♀(AM).

AMARINUS LATINASUS n.sp.

Figs. 4F, 6G, 7D, 10F

TYPE LOCALITY AND TYPES: Johnstone River, Queensland, Australia. HOLOTYPE: 30.xi.1972, M. Draper, ♂ (1.96 mm, with abdomen and 1st pleopod detached and mounted on a slide), among *Elodea* at low salinity (QM W.4066); PARATYPES: collection details as for holotype, 3♂♂(1.52, 1.72, 1.88 mm) (QM W. 4066); Weipa, Queensland, July 1972, W. McCormick, ov. ♀ (4.1 mm, 6 walking legs and left cheliped present, all detached), benthic zone in front of mangroves (QM W.4065).

DISTRIBUTION: Queensland, Australia (two known localities).

DIAGNOSIS: Rostrum broad, only slightly deflexed, abruptly tapering to a point; postocular lobes prominent in dorsal view, extending laterally along antero-lateral carapace borders, forming a shield with rostrum across anterior of carapace; dorsal carapace surface with only gastro-cardiac, cervical and thoracic grooves; dactyli of walking legs with a recurved tooth subterminally; female mature at less than 5 mm.

DESCRIPTION: The four male types are less than half the carapace width of the mature female paratype and their appearance is of immature specimens. Thus the description does not include characters of large males, such as cheliped size:— carapace subcircular (Fig. 4F), carapace width to length ratio 0.88-0.96; dorsal carapace surface flat in branchial regions, with convex cardiac region and less convex gastric region; lateral carapace walls vertical; anterior lateral carapace angles located well forward, rounded and very obtuse, posterior lateral angles not evident, with a small, acute spine below carapace rim in region of posterior lateral angle (not seen in female); eyestalks very short; postocular lobes prominent, continuous with rostrum; interantennal septum well developed; no rostral keel; no antennal spines; epistome width greater than 2 X length; pterygostomial region plain; Milne Edwards apertures oriented well anterior to cheliped bases; mouth-field wider than long; 3rd maxillipeds very broad, meeting medially, ischium shorter than merus along lateral edge, palp arising from inner surface of merus; exopodite hardly visible; female chelipeds slightly longer than carapace width, propodus stouter than walking legs, fingers slightly less than half total propodus length, cutting edges plain; walking legs ca. 1½ X carapace width, moderate thickness, dactyli little curved, with long setae along ventral edge; female abdomen oval, segments 1-5 progressively longer and broader, telson triangular with rounded apex, telson ca. ⅓ total abdomen length; eggs 0.3 mm diameter; male abdomen elongate triangular (Fig 7D), segments 1-5 subequal in length, segments 2-5 becoming progressively narrower, telson spade-shaped with broad apex; male 1st pleopod stout and straight (Fig. 10F), tapering slightly along its length, then tapering more abruptly to a pointed lobe terminally, with tufts of setae subterminally; coloured dark brown; scattered setae on legs and carapace walls, setae lining Milne Edwards apertures and dactyli of walking legs.

REMARKS: *A. latinasus* is the smallest of the *Amarinus* species. It is also distinguished from other *Amarinus* species by the large development of postocular lobes. There is some fusion between the rostrum and postocular lobes, but this is not as great as in *A. angelicus*; and while the fusion of rostrum and postocular lobes is in the horizontal plane in *A. latinasus,* it is in the vertical plane in *A. angelicus* and not visible in dorsal view.

In other characters in which the *Amarinus* species vary, e.g. carapace grooves, dactyli of walking legs, antennal spines, breadth of carapace and male 1st pleopods, *A. latinasus* is most like *A. lacustris* and *A. paralacustris.* The male 1st pleopod is similar to that of *A. angelicus,* but it is of the same form, i.e. terminating in a single lobe, as those of *A. lacustris* and *A. paralacustris.* The male 1st pleopd figured (Fig. 10F) is probably an immature form; the mature pleopod will show the same basic structure, but be more elongate.

The two localities where *A. latinasus* has been collected are at the opposite extremes of estuarine systems: in prevailing marine salinities at Weipa and in prevailing freshwater salinities at Johnstone River. Thus it is presumed to be a euryhaline brackish-water species. There are two other brackish-water *Amarinus* species, *A. laevis* and *A. paralacustris,* which occur in southern and eastern Australia, respectively. Thus, since it is probable that *A. latinasus* has a wider distribution in northern Australia than represented here (the region is very poorly collected), there may be at least one *Amarinus* species in most Australian estuaries.

The name *latinasus* (wide nose; Latin, masculine) refers to the broad rostrum of this species.

MATERIAL EXAMINED: Type material listed above.

HALICARCINIDES n.gen.

TYPE SPECIES: *Halicarcinus nuytsi* Hale, 1927 is hereby nominated as type species of the new genus.

DIAGNOSIS: Carapace subcircular, dorsal carapace surface with sharply defined grooves; rostrum absent; eyes completely concealed in dorsal view by carapace; epistome broad, but breadth less than 2 X length; 3rd maxilliped broad, almost filling mouth-field, ischium shorter than merus along lateral edge, palp reaching only to junction of ischium and merus; walking legs ca. 2 X carapace width, dactyli without a row of teeth; chelipeds stouter than walking legs, especially in large males; female abdomen without fused segments; male abdomen narrow, with segments 3 and 4 fused (?); male 1st pleopods strongly curved, with stout base and thin distal portion.

SPECIES OF *HALICARCINIDES*: The genus is monospecific. *H. nuytsi* occurs in southern Australia.

REMARKS: This new genus is established for *H. nuytsi,* an unusual and rare species which was previously included in the genus *Halicarcinus* by Hale (1927, 1928). *Halicarcinides* is most closely related to *Halicarcinus,* but *H. nuytsi* differs conspicuously from the *Halicarcinus* species in having no rostrum and having the anterior carapace completely concealing the eyes in dorsal view. Some other differences from most *Halicarcinus* species are:— the epistome is longer, there are no rows of teeth on the dactyli of walking legs and, possibly, there are fused segments in the male abdomen. The uncertainty of this last character is because only one small male was examined during this study. Although it appeared to show segments 3 and 4 fused with a suture evident, Hale (1928), who examined a small series of both sexes, specifically stated that *H. nuytsi* has no fused segments in the male abdomen. Abdominal segments and sutures are sometimes inconspicuous in small male specimens and more specimens are needed to clarify the condition.

Another hymenosomatid species has no rostrum. This is *Hymenicoides carteri* Kemp, which has few other important characters in common with *Halicarcinides nuytsi,* and they are not closely related.

The name *Halicarcinides* (Greek, feminine) refers to the affinity with *Halicarcinus.*

HALICARCINIDES NUYTSI (Hale)

Figs. 2F, 6I, 8C, 9D

Halicarcinus nuytsi Hale, 1927:118, fig. 116; 1928:98-9, fig. 22.

TYPE LOCALITY AND TYPE: St. Francis Island, South Australia; HOLOTYPE: undated, J. Verco, ov. ♀ (5.8 mm, dried specimen, some legs detached and damaged) dredged (SAM C1497).

DISTRIBUTION: Southeastern Australian mainland (3 localities).

DIAGNOSIS: Dorsal carapace rim lined with tubercles extending back to posterior lateral angles, tubercles most prominent near eyes.

DESCRIPTION: The following is additional to the descriptions of Hale (1927, 1928) and the Diagnosis:— portion of carapace over-reaching eyes with three short longitudinal ridges, one ridge above each eye and a slight medial ridge; postocular lobes and antennal spines absent; interantennular septum thin and elongate; dactyli of walking legs with a small sub-terminal tooth (Fig. 6I); female abdomen ovoid, segments 1-5 progressively longer and broader, telson arcuate, longer than preceding segments, approximately ⅓ total length of abdomen; eggs ca. 0.33 mm diameter; male abdomen widest at segments 3 and 4, suture (?) between segments 3 and 4, segment 5 with concave sides, telson triangular (Fig. 8C); male 1st pleopod bent at ca. 90° above base, distal portion relatively straight, terminal portion tapering to a point (Fig. 9D); largest male ca. 7 mm, mature females 4.9-5.8 mm.

REMARKS: It is most unusual that no specimens of *H. nuytsi* have been collected since 1930. In addition to the holotype from South Australia, a few specimens were collected from under rocks in the littoral zone at Long Reef, Collaroy, and Bottle and Glass Rocks, Port Jackson, N.S.W., all except one by Mr Melbourne Ward. Some of Ward's specimens were forwarded to Hale at the South Australian Museum (described by Hale, 1928) and have been lost, and four specimens are in the Australian Museum. The two localities in New South Wales were visited in 1965 to try to find more specimens, but only *Halicarcinus ovatus* was collected.

MATERIAL EXAMINED: NEW SOUTH WALES: Bottle and Glass Rocks, Port Jackson, 25.v.1926, M. Ward, ♀, between tide marks (AM P.9227); Long Reef, Collaroy, Mar. 1928 and Mar. 1929, M. Ward, ♂, ov. ♀ (AM P.9364 and P.9074); Long Reef, Collaroy, Jan. 1930, F. A. McNeill, im. ♀ (AM P.9432). SOUTH AUSTRALIA: Holotype.

NEOHYMENICUS n.gen.

TYPE SPECIES: *Hymenicus pubescens* Dana, 1851 is hereby designated type species of the new genus.

DIAGNOSIS: Carapace subcircular, dorsal carapace surface with well defined grooves, lateral carapace angles obscure; rostrum triangular, deflexed, separated from dorsal carapace surface by a groove; epistome short, breadth ca. 2 X depth; pterygostomial region plain; mouth-field almost completely filled by 3rd maxillipeds, ischium subequal in length with merus along lateral edge; chelipeds stouter than walking legs, especially in large males, but not greatly inflated; walking legs moderately stout, dactyli with a subterminal tooth; male and female abdomens without fused segments; male 1st pleopods sickle-shaped, with stout base and thinner, strongly-curved distal portion, with a row of long setae subterminally.

SPECIES OF *NEOHYMENICUS:* The genus is monospecific. *N. pubescens* occurs in New Zealand.

REMARKS: Dana (1852) distinguished *Hymenicus* from *Halicarcinus* on the basis of the rostrum which is a "simple rounded or trilobate prominence", compared to "three teeth of *Halicarcinus*" and the walking legs which are "much longer and more slender than in any of the species of *Halicarcinus*". The new genus included four species: *Hymenicus pubescens, H. varius, H. novi-zealandiae* (synonymous with *H. varius* Dana, 1851 (Melrose, 1975)) and *Hymenosoma depressum* (excluded from the genus by later authors).

Hymenicus varius Dana should clearly be included in the genus *Halicarcinus*. Its rostral condition is variable and terminally trilobate in some specimens. It is very similar to *Halicarcinus cookii* and *H. ovatus* with which it has been confused (Melrose, 1975). *Hymenicus pubescens* Dana does not as readily belong in the genus *Halicarcinus*. Its rostrum is similar to that of *Halicarcinus bedfordi* and may be interpreted as fused trilobate, but it is also similar to the unilobe rostrum of *Hymenosoma* species. The arrangement of grooves on the dorsal carapace surface is unusual: in addition to the gastro-cardiac groove, the cervical and other anterior grooves are well defined, strongly outlining the gastric region (Melrose, 1975, Fig. 36), while the cardiac region of the carapace is hardly indicated. The dactyli of the walking legs have a single tooth and the male 1st pleopod has a subterminal row of long setae and is like that of an *Elamena* species. In fact, *Hymenicus pubescens* could equally well be a *Amarinus* species as a *Halicarcinus* species. It generally conforms with the diagnostic features of *Amarinus,* only the rostrum is more triangular than spade-shaped, the dorsal carapace grooves and male 1st pleopod are unlike *Amarinus* species (and unlike *Halicarcinus* species) and it has no intercalated plates in the male abdomen.

Larval morphology provides the most conclusive evidence that *Hymenicus pubescens* does not belong in the genus *Halicarcinus* or *Amarinus*. The zoeal stages show the lateral expansions of the 5th abdominal segment characteristic of *Elamena* zoeae. But, unlike the globular zoeae of *Elamena* species, the zoeae of *H. pubescens* have well developed dorsal and lateral spines (Wear, 1968). In crab and larval morphology, *Hymenicus pubescens* shows affinities with *Elamena, Halicarcinus* and *Amarinus,* but it belongs in a separate genus.

This conclusion regarding *Hymenicus pubescens* differs from Melrose (1975), who included it in the genus *Halicarcinus,* with *Hymenicus varius;* although recognising the unusual features of *H. pubescens.* Melrose's conclusion is at least partly explained by the fact that she included species now removed to *Amarinus* in the genus *Halicarcinus*, which was thus a more heterogeneous taxon.

With the inclusion of *Hymenicus varius*, type species of *Hymenicus* Dana by subsequent designation of Kemp (1917:246), in the genus *Halicarcinus* White, *Hymenicus* Dana becomes a junior synonym of *Halicarcinus* White and a new generic name is created for *Hymenicus pubescens* in this study.

Hymenicus pubescens Dana, 1851 should not be confused with *Halicarcinus pubescens* Dana, 1851, which is regarded as a probable synonym of *Halicarcinus planatus* (Rathbun, 1925; Garth, 1958). Melrose (1975) resolved the state of homonymy between the two species when *Hymenicus pubescens* was included in the genus *Halicarcinus* by rejecting the name *pubescens* Dana 1851, as published in combination with *Halicarcinus pubescens*, and proposing a replacement name *Halicarcinus patagoniensis* Melrose, 1975.

MATERIAL EXAMINED: NEW ZEALAND: 17 and 18.i.1964, J. S. Garth, 9♂♂, 12 ov.♀♀,♀, 2 juvs. (AHF); Parekura Bay, Bay of Islands, North Island, 10-12.ii.1973, J. S. Garth, 5 im. ♀♀, rocky outcrops on either side of gravel beach (AHF JG2-73).

PART B, REVIEW OF BIOLOGICAL DATA

LIFE CYCLES AND GROWTH

The hymenosomatids with free larval stages hatch from eggs 0.25-0.45 mm diameter and pass through three planktonic zoeal stages. The third zoeal stage moults to the first crab instar which settles from the plankton; there is no transitional megalopa larva. The first instar crab is small: carapace widths of *Hymenosoma orbiculare, Amarinus paralacustris, A. laevis* and *Halicarcinus planatus* are 0.9, 0.75, 1.0 and 0.95 mm respectively (Broekhuysen, 1955; Lucas, 1968; Boschi et al., 1969). There follows a series of crab instars which are not markedly different except in size and in relative proportions of features which show allometric growth, such as carapace width to length ratio. Differentiation of secondary sex characters occurs at an early stage and sex may be distinguished by abdomen shape at about the fourth crab instar. At an earlier stage than this, in *Halicarcinus planatus*, appropriate pleopods are present in males at the second crab instar (Richer de Forges, 1977).

After a series of immature crab instars there is a pubertal moult which is distinguished by morphological changes that are generally characteristic of Brachyura at this moult (Hartnoll, 1974). The female abdomen expands laterally and anteriorly and becomes more convex; the pleopods broaden and become more setaceous. The genital apertures and branchiosternal canals enlarge, but these are essentially in the mature form in late prepubertal instars. The change in abdomen size from immature to mature condition is particularly pronounced in hymenosomatid females. In *Amarinus laevis* and *Halicarcinus planatus*, the only hymenosomatids subjected to morphometric studies, the female chelae decrease slightly at the pubertal moult relative to body size (Lucas and Hodgkin, 1970a; fig. 8; Richer de Forges, 1977; fig. 10). At the pubertal moult in males the chelae increase in relative size (*Trigonoplax* species may be exceptional). In *A. laevis* males the chelae also develop a prominent sac (pulvinus) between the fingers. There may also be relative increases in cheliped length, rostrum size, body spine sizes and general setation in males at their pubertal moult; but the abdomen and male pleopods show little relative change, being essentially in their mature form in late prepubertal instars.

In crabs reared from eggs in the laboratory, Lucas (1968) found eight prepubertal crab instars for females of *Amarinus lacustris* and 10 to 12 or 13 for *A. paralacustris*. Size after the pubertal moult was 4.9-5.9 mm and 4.2-5.9 mm, respectively. Based on crabs maintained in an aquarium after collection in the field, Richer de Forges (1977) estimated that there were 11 prepubertal crab instars in the development of *Halicarcinus planatus* which reached approximately 14 mm at its pubertal moult. These are large numbers of instars considering the small mature sizes of these crabs. For comparison, *Scylla serrata* Forskål (Portunidae) reared in captivity reached 45.0-57.3 mm at its twelfth crab instar (Ong, 1966) and Hiatt (1948) estimated that *Pachygrapsus crassipes* Randall (Grapsidae) was 22 mm at its twelfth crab instar. Part of this size difference results from proportionally smaller growth increments in hymenosomatids; part is due to the smallness of first crab instars of hymenosomatids, a consequence of their small eggs and few larval stages. First instar crabs of *S. serrata* and *P. crassipes* are approximately 3.4 mm carapace width, which is larger than the adults of some hymenosomatid species.

In hymenosomatids, as in other Brachyura, intermoult periods increase as the crabs get older and larger. At the same time, percentage increments in carapace width, or other linear dimensions, decrease through the series of ecdyses. These trends have been shown for *Hymenosoma orbiculare* (cf. Broekhuysen, 1955), *Amarinus lacustris* and *A. paralacustris* (cf. Lucas, 1968), and *Halicarcinus planatus* (cf. Richer de Forges, 1977) in groups of crabs kept in the laboratory. *A. lacustris* and *A. paralacustris* took a minimum of 177 and 121 days, respectively, from hatching to pubertal moult when reared at 20 ± 1°C (Lucas, 1968). In field populations of *A. laevis* in the Swan River estuary, Western Australia, recruits which hatched in November-December reached 10-12 mm carapace width about five months later in April; at which time some females underwent their pubertal moult (Lucas and Hodgkin, 1970a). Water temperature was 21-27°C during this period. In contrast, the subantarctic hymenosomatid, *Halicarcinus planatus,* living in water temperature 1.5-8°C at Kerguelen Island, was estimated to take more than two years from hatching to its pubertal moult (Richer de Forges, 1977; fig. 17b). *H. planatus* occurs in atypically cold water; all other hymenosomatids are temperate or tropical, and the periods of immaturity of the *Amarinus* species are probably more typical.

There is a major division of hymenosomatid life cycles according to whether the pubertal moult is also the terminal moult. Crabs of the genera *Amarinus* and *Halicarcinus* have a common pubertal/terminal moult. Mature specimens of *A. lacustris* and *A. paralacustris* were kept for more than a year and mature specimens of *A. laevis, H. ovatus* and *H. rostratus* for some months without moulting. Indirect evidence from the field (suggested by Hartnoll, 1965) supports this laboratory observation: in these species there is no limb bud formation in mature crabs where pereiopods are lost. Richer de Forges (1977) also found a pubertal/terminal moult in *Halicarcinus planatus*. In contrast to these species of *Amarinus* and *Halicarcinus, Hymenosoma orbiculare* and *Elamenopsis lineata* females continue moulting after their pubertal moult (Broekhuysen, 1955; Lucas, unpubl. data).

There are no precise data for longevity of hymenosomatids in the field. In the laboratory some individuals of *Amarinus lacustris* and *A. paralacustris* survived for more than two years from hatching (Lucas, 1968), but this does not necessarily reflect longevity in the field. In population studies of three hymenosomatid species in non-marine habitats, *Hymenosoma orbiculare, Amarinus lacustris* and *A. laevis,* there was basically a one-year life cycle (Broekhuysen, 1955; Walker, 1969; Lucas and Hodgkin, 1970a). In size-frequency plots the mode of mature crabs virtually disappeared after the annual period of highest proportions of mature females, and predominantly small immature crabs remained. For *A. laevis* in the Swan estuary, Western Australia, the adult mortality occurred in mid-summer; but a few mature crabs survived to a second summer, as evidenced by a small proportion of individuals with very encrusted carapaces among the newly mature crabs in early summer. (Because these crabs do not moult after their pubertal moult, their cuticles become progressively encrusted with epiflora and epifauna.) Because of its long period of immaturity, *Halicarcinus planatus* lives longer than the species discussed above. Richer de Forges (1977) estimated the duration of its final instar as approximately 10 months, giving a total life-span of more than three years in Kerguelen Island populations.

REPRODUCTION

Ovary development before the pubertal moult has been found in some hymenosomatid females. This was observed through the translucent carapaces of laboratory-reared *Amarinus lacustris* and *A. paralacustris* and confirmed by extrusion of an egg mass within two days of their pubertal moult (Lucas, 1968). *Halicarcinus ovatus* females also extrude eggs within two days of their pubertal moult (Lucas, 1968). Broekhuysen (1955) found well developed ovaries in an immature female of *Hymenosoma orbiculare*. Some hymenosomatid females may copulate before their pubertal moult: this was observed in laboratory populations of *Halicarcinus planatus* (Richer de Forges, 1977). Also, four of seven immature females of *Amarinus lacustris,* collected from the field, had spermatozoa in their spermathecae (Lucas, 1970). Copulation of immature females is physically possible because their genital apertures are essentially in the mature condition. However, among Brachyura it is exceptional for females to copulate prior to their pubertal moult (Hartnoll, 1969); parasitic pinnotherids are the only general exception to this pattern described so far.

The pubertal moult in male hymenosomatids is equivalent to the pubertal moult in females in terms of abrupt acquisition of mature features and it is appropriate to apply this name to the distinctive moult in the male. However, males of at least some species are sexually mature before their pubertal moult. Laboratory-reared males of *Amarinus lacustris* and *A. paralacustris* up to three instars before their pubertal moult successfully impregnated females (Lucas, 1968). Copulating pairs of *A. laevis* collected in the field included large prepubertal males (Lucas and Hodgkin, 1970a). Richer de Forges (1977) observed copulation by prepubertal males of *Halicarcinus planatus*. Successful copulation by late prepubertal males is possible because their intromittent organs, the 1st and 2nd pleopods, are in an essentially mature condition.

After its onset, several instars before the pubertal moult, spermatogenesis may continue for long periods. Individual males of *Amarinus lacustris* and *A. paralacustris* were used for a number of successful impregnations over periods of months (Lucas, 1968). One male of the latter species was used for twelve impregnations over a period of 16 months. Broekhuysen (1955) found apparent seasonallity in testis size in a *Hymenosoma orbiculare* population, but this may be related to the annual cycle of recruitment in the Sand Vlei estuary, South Africa.

Copulation in Brachyura always involves a hard-shelled male and Hartnoll (1969) distinguished two patterns of copulation according to shell condition of the female. In one pattern the female is soft-shelled and copulation is usually preceded by lengthy premoult courtship; in the other pattern the female is hard-shelled and there is relatively brief courtship. Both patterns have been reported for hymenosomatids (Table 3) and they may both occur in one species, e.g. *Halicarcinus ovatus.* The requirement for females to be soft-shelled for copulation severely limits the period available for copulation. This is not so critical for *Hymenosoma orbiculare,* females of which continue to moult after their

TABLE 3. Shell condition of female in copulation. F — observed in field. L — observed in laboratory.

	Female		
Species	**Soft-shelled**	**Hard-shelled**	**Source**
Amarinus lacustris	L	L*	Lucas (1968)
A. paralacustris	L	L*	Lucas (1968)
A. laevis	F		Lucas and Hodgkin (1970a)
Halicarcinus ovatus	L	L	Lucas (1968)
H. rostratus	L		Lucas (1968)
H. cookii		L	Melrose (1975)
H. planatus		L	Richer de Forges (1977)
Hymenosoma orbiculare	L		Broekhuysen (1955)

* This only was observed at times when a male was introduced into a small container with a solitary female; the females were apparently not successfully impregnated since they produced inviable egg masses.

pubertal moult giving opportunities for impregnation or re-impregnation. However, in species of *Amarinus* and *Halicarcinus,* which have a pubertal/terminal moult and which may only copulate while the female is soft-shelled, the period immediately following the pubertal moult is critical as the last opportunity for impregnation.

Hymenosomatid females may extrude eggs within a day or two after their pubertal moult and after release of larvae from the previous egg mass. As a result of this pattern of egg masses in close succession, females may be ovigerous for most of their reproductive life and high proportions of mature females in hymenosomatid populations may be ovigerous. In the Material Examined for *Halicarcinus ovatus,* representing a number of collections from different Australian localities, there are 52 ovigerous females of a total of 64 mature females. All 33 mature females of *H. bedfordi* examined during this study were ovigerous. Where Melrose (1975) examined a large number of specimens of a *Halicarcinus* or *Elamena* species from New Zealand, these included a high proportion of ovigerous females among mature females. Almost all mature females of *Halicarcinus planatus* were ovigerous throughout the autumn to spring breeding season at Kerguelen Island (Richer de Forges, 1977). More than 70% of females, mature or immature, of *Hymenosoma orbiculare* were ovigerous from July to October in the Sand Vlei estuary, South Africa (Broekhuysen, 1955). Most mature females of *Amarinus laevis* are ovigerous during the summer breeding season in the Swan estuary, Western Australia (Lucas and Hodgkin, 1970a), but, if females reach maturity before summer, they delay extrusion of eggs for several months.

Amarinus paralacustris females reared in the laboratory first extruded eggs within 36 hours of their pubertal moult, whether copulation occurred or not (Lucas, 1968). They then extruded successive egg masses within 24 hours of release of larvae from the previous egg mass until the female died or her ovarian cycle ceased. In seven females the number of successive egg masses produced was four to 14, with a mean of eight (Lucas, 1968). There was no seasonal suppression of the ovarian cycle in these laboratory animals. Ovulation appeared to be total, with the ovaries (visible through the translucent carapace in laboratory animals) being very small after ovulation and egg extrusion. The ovaries increased in size progressively during the period of embryonic development of the concurrent egg mass in the abdominosternal cavity. They reached maximum size shortly before larval release. Since ovulation and extrusion of eggs occur so soon after larval release, the stimulus for ovulation and extrusion of eggs must be related to the events of larval release to achieve this synchronisation.

Amarinus lacustris females reared in the laboratory also extruded eggs soon after their pubertal moult (Lucas, 1968). Thereafter ovulations and extrusions of eggs generally followed release of juveniles from the previous egg mass. The ovarian cycle is similar to *A. paralacustris* except the period of embryonic development is much longer in *A. lacustris* and the ovarian cycle is correspondingly longer. The number of successive egg masses produced per female ranged from one to four with a mean of 2.6 for 10 females. In three females the ovarian cycle lapsed and recommenced, resulting in periods of more than 100 days between successive ovulations.

Because of the pattern of successive egg masses during the mature life of females, there is usually a prolonged breeding season in hymenosomatid populations. Ovigerous females have been collected throughout the year from *Halicarcinus ovatus* populations near Perth, Western Australia (Lucas, 1968), and in the following New Zealand species which are well represented in collections: *Halicarcinus cookii, H. varius, H. whitei, H. planatus* (subantarctic), *Neohymenicus pubescens* and *Elamena producta* (Melrose, 1975). Although these species do not have discrete breeding seasons, reproductive effort may be more intense in one part of the year. The abundance of *H. ovatus* larvae in the plankton of Cockburn Sound, Western Australia, was greatest in summer (Lucas, 1975). The proportions of ovigerous females in populations of *H. cookii* at Leigh and Coromandel, New Zealand, were highest in summer, January-February (Melrose, 1975). The proportion of mature females which were ovigerous was highest in winter, April-August, in *H. planatus* populations at Kerguelen Island (Richer de Forges, 1977). Even in the estuarine species, *Hymenosoma orbiculare* and *Amarinus laevis,* ovigerous females occur through most of the year, despite marked seasonal variation in salinity (Broekhuysen, 1955; Lucas and Hodgkin, 1970a). In populations of a freshwater species, *Amarinus lacustris,* at Skeleton Creek, Victoria, there were ovigerous females from July to February (Walker, 1969).

Broekhuysen (1955:324) and Lucas (1968: Table 5.4) described the embryonic development of *Hymenosoma orbiculare* and *A. laevis,* respectively, which follows the pattern of other brachyuran embryos, e.g. Hiatt (1948). Mean periods of embryonic development at 20 ± 1°C are 29, 29, 25.5 and 54.5 days for *Halicarcinus ovatus, Amarinus laevis, A. paralacustris* and *A. lacustris,* respectively (Lucas, 1968). The much longer period of embryonic development in *A. lacustris* results from suppression of free larval stages. Embryonic development of *Hymenosoma orbiculare* takes approximately 43 days at 13°C (Broekhuysen, 1955).

The morphology of the female reproductive system of *Elamenopsis* species is unique (see Remarks on this genus) and they are excluded from the following paragraph discussing ventilation of egg masses. The mechanisms of ovulation, egg ventilation and larval release need to be elucidated in the *Elamenopsis* species.

Ovigerous hymenosomatid females carry their eggs on the endopodites of their four pairs of pleopods. The egg mass in usually competely enclosed between the abdomen and thoracic sternites (some very small *Halicarcinus* and *Elamena* species are exceptional). The female may bend her abdomen away from the sternum to expose the egg mass for inspection and larval release, but most of the time the egg mass is totally enclosed within the abdominosternal (brood) cavity. Branchiosternal canals connect the brood cavity to the branchial chambers in these females. A branchiosternal canal leads from each of two sternal apertures at the junction of the last thoracic sternite and first abdominal sternite. Pericardial sacs extend along the canals and water currents flowing through the canals were demonstrated using dye in mature females of three *Amarinus* species and *Halicarcinus ovatus* (Lucas, 1968). The current flows from the brood cavity to the branchial chambers and its function must be to irrigate the egg mass (Lucas, 1968). Branchiosternal canals are present in females of other brachyuran families (Lucas, unpubl. data), but they appear to have been described in only one other family, the Leucosiidae (Drach, 1955). Drach found a water current flowing through the canals from the branchial chambers to the brood cavity in leucosiid females, due to piston-like pumping of the elongate pericardial sacs. The direction of flow in leucosiids is opposite to that in hymenosomatids, but Drach (1955) also proposed that it ventilates the egg mass in ovigerous females. It is necessary in leucosiids, as in hymenosomatids, because the abdomen is held against the sternum, restricting water change between the environment and the egg mass.

Spermatozoa storage has been conclusively shown in some hymenosomatids. Females of *Amarinus lacustris, A. paralacustris* and hybrids from them produced series of fertile egg masses without further impregnation after one post-puberty impregnation (Lucas, 1968). One hybrid female produced fifteen viable egg masses in succession after one impregnation. Among these females there was a trend of declining numbers of larvae from successive egg masses, apparently due to decreasing proportions of fertilized eggs, until the female began rejecting all eggs from each ovulation. *A. laevis* and *Halicarcinus* *ovatus* also produced viable egg masses in the laboratory without re-impregnation. Broekhuysen (1955) showed spermatozoa storage, including trans-moult retention of spermatozoa, in *Hymenosoma orbiculare* in the laboratory. As in other female Brachyura, spermatozoa are stored in the spermatheca which is an enlarged region of the genital duct between the vagina and the oviduct (Hartnoll, 1968). The spermatozoa are densely scattered in a noncellular matrix that fills the lumen of the spermatheca in *Amarinus lacustris* and *A. laevis* (Lucas, 1968). The spermatozoa of these species are spherical to ovoid, 2.2-3.3 μm in size; they are densely basophilic and have little cytoplasm. Eggs are fertilized between ovulation and extrusion in the lumen of the ovary or in the oviduct (Cheung, 1966b). Hartnoll (1966) briefly considers the female genital ducts of *Halicarcinus planatus* in relation to general patterns in Brachyura with sternal apertures.

REPRODUCTIVE STRATEGIES

The family Hymenosomatidae includes some of the smallest, if not the smallest, species of Brachuyra. There has obviously been selection pressure for smallness; but, whatever the advantages of small size in this family, there is one potential disadvantage. Small size means small amounts of energy and material available for reproduction. Also, in these crabs fecundity is futher limited by the necessity to produce relatively large eggs, which support extensive embryonic development, and by the necessity to retain extruded eggs until they hatch. Brachyuran eggs give rise to large advanced larvae or juvenile crabs; the eggs require ventilation and maternal care to survive the long period of embryonic development and thus they are attached to the body of the female. It would be a very radical change for hymenosomatids to deviate from this pattern to increase fecundity, e.g. to revert to nauplius larvae hatching from small planktonic eggs, as in penaeid decapods. The hymenosomatids do not show radical modifications of the brachyuran pattern of reproduction and development, but they show several reproductive strategies to increase fecundity and to promote survival of their early developmental stages.

Adaptions of hymenosomatids to increase fecundity are:—

(i) **Reduced egg size:** Reducing egg size results in more eggs per unit expenditure of energy and material. However, there is a lower limit to the size of an egg which gives rise to a functional zoea larva. Many hymenosomatids may be close to the limit: their eggs and their larvae are among the smallest in the Brachyura. The *Elamenopsis* species and smaller *Halicarcinus* and *Elamena* species have eggs less than 0.3 mm diameter; the smallest egg reported is 0.23 mm for *Halicarcinus hondai.*

(ii) **Increased volume of the brood cavity:** This allows more eggs to be carried and, as a corequisite, the female must be able to increase the volume of eggs produced per ovulation.

In most female hymenosomatids the edge of the abdomen fits closely to the thoracic sternum to make an enclosed brood cavity. However, in the very small species, *Halicarcinus hondai, H. keijibabai, Elamena gordonae* and *E. umerata,* the abdomen is wider than the cephalothorax and/or the pleopods project laterally beyond the abdomen, giving a greater volume for egg bearing. The condition of the abdomen is similar to that in symbiotic pinnotherid females. (It would be interesting to know more of the habitats and habits of these hymenosomatid species, because their very large abdomens must restrict locomotion.) In *H. hondai,* at least, the ovaries appear to extend into the abdomen to increase the volume of eggs produced per ovulation.

In two *Hymenosoma* species the female abdomen projects posteriorly, increasing the volume of the brood cavity without interfering with the walking legs. In *Elamenopsis* species a brood cavity extending from within the abdomen to within the cephalothorax completely replaces the abdominosternal cavity, apparently to increase the volume for bearing eggs (Fig. 8H).

(iii) **Many egg masses:** A characteristic of hymenosomatid populations, discussed in the Reproduction section, is the high proportion of mature females which are ovigerous through much of the year. This results from successive extrusions of egg masses, often within a day or two of liberation of larvae from the previous egg mass. Thus females may be ovigerous for most of their mature lives. The common pubertal/terminal moult in at least *Amarinus* and *Halicarcinus* species is an advantage for egg mass production because the ovarian cycle can continue without interruption by moulting cycles, see Cheung (1966a).

Although hymenosomatids show adaptions to increase fecundity, this is within the constraints of their small size. Data on numbers of eggs carried per egg mass by females are presented in Table 4. The range for hymenosomatid species with larval development is from less than 100 eggs per egg mass to unit thousands per egg mass. By comparison, a moderate sized grapsid, *Pachygrapsus crassipes,* 36.5 mm carapace width, carries 48,600 eggs (Hiatt, 1948) and a large portunid, *Scylla serrata,* 131 mm carapace width, carries 2,012,000 eggs per egg mass (Arriola, 1949). Even allowing that hymenosomatids may produce more egg masses per female, or per unit time, than most Brachyura their total fecundity must be in the lower range for the Brachyura. In fact their fecundity is at the lower extreme of the range of average numbers of eggs spawned by benthic marine invertebrates with planktotrophic larvae. Thorson (1950) gave values of 1.1×10^3 to 5×10^8 eggs per female for this range, but the smaller hymenosomatids fall below 1.1×10^3 eggs. Thus hymenosomatids must achieve much higher rates of larval survival and higher rates of recruitment from pelagic to benthic populations than most benthic marine invertebrates with planktotrophic larvae.

TABLE 4. Approximate numbers of eggs per egg mass in ovigerous hymenosomatid females from marine and brackish environments.

Species	Carapace width (mm)	Number of eggs	Source
Amarinus laevis	16.0	3,200	Lucas (1968)
Halicarcinus planatus	13.7	1,400	Richer de Forges (1977)
Halicarcinus ovatus	6.5	850	Lucas (1975)
Amarinus paralacustris	6.0	400	Lucas (1970)
Halicarcinus rostratus	4.0	250	Lucas (1975)
Elamenopsis lineata	3.7	130	Lucas (unpubl.)
Elamenopsis aspinifera	3.0	77	Lucas (unpubl.)
Elamenopsis bovis	5.5	30*	Barnard (1950)
Halicarcinus afecundus	5.4	24**	this study

* direct development

** direct development suspected

Adaptations by hymenosomatids to promote survival of their larvae are:—

(i) **Abbreviated larval development:** Reducing the period of planktonic larval development reduces mortality from plankton predators, unfavourable dispersal and other sources of larval mortality (reviewed by Thorson, 1950). Conversely, the advantages of planktotrophic development, dispersal and exploitation of an alternative food source, are reduced.

The larval development of hymenosomatids is abbreviated compared to other Brachyura and most other decapod Crustacea, consisting of only three zoeal stages and no megalopa stage. Duration of larval development has only been studied in a few species and it is relatively brief, with the exception of the subantarctic *Halicarcinus planatus* (Lucas, 1972; Richer de Forges, 1977).

The extreme case of abbreviated larval development is direct development, i.e. retention of all larval stages within the egg or within the brood cavity of the female. Direct development or near direct development occurs only rarely in marine Brachyura. It has been recorded only from Australian and New Zealand Brachyura in some species of Dromiidae, Majidae and Xanthidae (Wear, 1967). Direct development offers the advantage of omitting the high mortality of planktonic life; although it is at the price of reduced fecundity, because larger yolkier eggs must be produced, and at the price of reduced dispersal. In the balance of advantages and disadvantages of direct development, it would be surprising to find that no hymenosomatids have adapted direct development, since they must achieve particularly high rates of survival through early development. Yet among marine and brackish water hymenosomatids, only one species is known to have direct development: a female of *Elamenopsis bovis* had juveniles in its brood cavity (Barnard, 1950). Another species, *Halicarcinus afecundus* is suspected of direct development from the number and size of eggs on the female holotype (see Remarks on this species and Table 4).

(ii) **Restricted dispersal:** Wide dispersal of planktonic larvae is advantageous for finding new habitats and exploiting all suitable habitats in a region. The disadvantage of wide dispersal is large wastage of larvae through dispersal to unfavourable regions (Thorson, 1950). Species with low fecundity may not be able to afford wide dispersal of their larvae and it would be advantageous if most larvae remain in, or return to, the vicinity of the adult populations from where they were released. Efford (1970) suggested four types of field situation where this would occur.

Most hymenosomatids occur in shallow coastal waters. Although they may occur on exposed coasts, they tend to be most abundant in sheltered coastal localities, in bays, inlets, sounds and estuaries. These semi-enclosed water masses provide protected habitats for the crab populations. But another feature of these localities is that water exchange with the adjacent ocean may be limited by the geomorphology, and dispersal of larvae reduced.

Lucas (1975) investigated the dispersal of larvae of *Halicarcinus ovatus* and *H. rostratus* in Cockburn Sound, Western Australia, which is typical of the type of semi-enclosed locality where these species are most abundant. There were very high rates of retention of larvae within the Sound: overall ratios of numbers of third stage zoeae to first stage zoeae were 0.4:1 and 0.59:1 in plankton samples throughout a year. All three zoeal stages were obtained in the vicinity of crab populations at several other localities where these species are abundant. Lucas (1975) concluded that a major factor in the abundance of *H. ovatus* and *H. rostratus* in semi-enclosed localities is that these localities restrict dispersal of larvae away from the adult habitat. At these localities the small crabs can compensate for their low fecundity with relatively high rates of recruitment. These localities act as "nursery areas", one of the suggested field situations of Efford (1970).

The conclusions for *Halicarcinus ovatus* and *H. rostratus* may be relevant to many other hymenosomatids which are most abundant in protected coastal localities and estuaries. In fact, the absence of a megalopa stage in the development of hymenosomatids may reflect a general strategy of retaining larvae in the vicinity of crab populations. Where the phase of planktonic development is completed in the vicinity of the benthic crab populations the transition from plankton to benthos is rapid. There is no need for a transitionary larval stage, the megalopa, to locate the adult habitat.

BEHAVIOUR

The major source of data on the behaviour of hymenosomatids is Melrose (1975). Melrose gave detailed observations on various aspects of the behaviour of some New Zealand species, *Halicarcinus innominatus, H. cookii, H. whitei, H. varius, Neohymenicus pubescens* and *Elamena producta*. Lucas (1968) included some data on the behaviour of *Amarinus* species and there are several other brief descriptions of hymenosomatid behaviour. There are, unfortunately, no observations on the behaviour of any species of the largest genus, *Elamenopsis*.

Locomotion: Hymenosomatids tend to walk forward, but they are not restricted to this direction. Some species, such as *Halicarcinus cookii,* walk rapidly for short periods; others, such as *Neohymenicus pubescens,* walk slowly and this is more typical of hymenosomatid species. Where males have very large chelipeds these may regularly contact the ground and be used in walking. Melrose (1975) studied the sequence of leg movements during forward walking in the slow-moving *Neohymenicus pubescens.* There was a general pattern of walking leg movements R1, L1, R3 and L3 alternating with R2, L2, R4, L4. Each pair of legs was almost in phase on both sides of the body, both being propulsive together, but no two legs appeared to be exactly in phase. Also, the pattern would alter at random.

Hymenosomatids may also swim, an activity involving much more rapid movements than walking. In swimming the chelipeds are held forward and bent; the walking legs are held laterally and they beat vigorously out of phase in a vertical or slightly backward plane. There are rows of ventrolateral setae on the walking legs and these fold together on the upward recovery stroke and spread on the downward power stroke (Hartnoll, 1971). The crab moves upward or upward and forward, usually with the body in a normal horizontal plane, but sometimes tumbling "head-over-tail" in small crabs. Swimming is most prevalent in early crab instars, especially the first crab instar where it may assist in substrate selection (Lucas, 1968). Some adult hymenosomatids with long setae on their walking legs are well adapted for swimming and often swim for locomotion. These are *Hymenosoma depressum, H. orbiculare* and *Halicarcinus whitei* (Graham, 1938; Barnard, 1950; Melrose, 1975). Other adult hymenosomatids, *Amarinus laevis, A. lacustris, Halicarcinus ovatus, H. varius, H. cookii* and *Neohymenicus pubescens,* swim only as an escape reaction when disturbed or when in unfavourable conditions such as near-lethal water temperature or deoxygenated water (Hartnoll, 1971). Others, *Halicarcinus innominatus* and *Elamena producta,* have not been seen swimming (Melrose, 1975).

Thigmotaxis: Hymenosomatids are strongly thigmotactic beginning at the first crab instar. If a group of first instar crabs is kept in a glass vessel without any object for attachment they form a tight bundle of bodies as they cling to each other (Lucas, 1968). Adult crabs will similarly cling to each other if there is no substrate to hold with their walking legs or to burrow into (Melrose, 1975). They may show selection for the type of substrate which they hold: *Halicarcinus cookii* is highly selective for finely divided algae when given a choice of substrates (Melrose, 1975).

Burrowing: *Hymenosoma orbiculare, Halicarcinus varius, H. whitei* and *Elamena producta* are known to burrow in sandy to muddy substrates (Barnard, 1950; Melrose, 1975). No permanent burrows are constructed. The crab burrows by digging the posterior of the cephalothorax into the substrate with thrusting movements of the walking legs. It is a gradual process and not a flurry of digging (Melrose, 1975).

Alarm: If repeatedly prodded or lifted from the substrate, hymenosomatids become immobile. *Halicarcinus whitei* "freezes" in a normal posture; *H. innominatus, H. cookii, Neohymenicus pubescens* and *Amarinus laevis* "freeze" with their walking legs tightly folded under their cephalothorax; and *Elamena producta* and *E. abrolhensis* "freeze" with their chelipeds and walking legs projecting out laterally (Melrose, 1975; Lucas, unpubl. data).

Display: Large males of some hymenosomatid species are more conspicuously patterned than females, suggesting visual display. Large males of most species have relatively large chelipeds and in some species the males have been observed using their chelipeds in threatening displays. The male usually postures with the anterior of the body raised and with its chelipeds held high and wavering or with its chelipeds spread laterally and fingers gaping (Melrose, 1975). Males of two species which use the spread chelipeds display, *Halicarcinus varius* and *H. whitei,* engage in intraspecific agonistic display, facing each other with chelipeds spread and with the anterior surfaces of the palms touching those of the other male (Melrose, 1975). Males of *H. innominatus,* which use the waving cheliped threat display, grip each other's chelae in some agonistic displays. *Neohymenicus pubescens* and *Elamena producta* show no reaction to other males (Melrose, 1975).

In these limited data on display there is considerable variation among related species.

Courtship: In hymenosomatids, copulations may involve hard-shell or soft-shell females (Table 3) and several patterns of courtship and post-copulatory behaviour have been reported. As in other Brachyura, only hard-shell males are involved in mating behaviour.

In copulation with a hard-shell female of *Halicarcinus cookii* there was no evidence of courtship; the male climbed onto the female, moved beneath her and clasped her above himself (Melrose, 1975). The crabs separated immediately after copulation. In *Hymenosoma orbiculare* only soft-shell females were involved in mating (Broekhuysen, 1955). Copulation was preceded by the male carrying the female beneath him for some time before she moulted. After copulation the male returned to holding the female beneath him for up to a day or longer. These observations accord with the two basic patterns of crab courtship behaviour described by Hartnoll (1969): lengthy pre-moult courtship before mating with soft-shell females and brief courtship before mating with hard-shell females.

No courtship was observed in males of *Amarinus lacustris* and *A. paralacustris* which mated with soft-shell females (Lucas, 1970). However, in most of the observed copulations the male was only given access to the female immediately after her pubertal moult. In this circumstance, the male often gripped the female and manoeuvred her into copulation position at first contact. The copulation position was consistently female-over-male; when on top of their substrate the female gripped it with her walking legs, when on the undersurface of the substrate the male gripped it with several walking legs (Lucas, 1968). The copulation position was held for 10-30 minutes, and then the male manoeuvred the female without releasing her until he was holding her beneath him, both being upright and facing the same direction. This post-copulatory behaviour is the same as in *Hymenosoma orbiculare* and it lasted for several hours to five days in *A. lacustris* and *A. paralacustris*.

Post-copulatory pairing has been reported in some other Brachyura, always in cases of soft-shell female mating (Hartnoll, 1969). Presumably it protects the female (from other males?) until her integument hardens.

Species recognition: Lucas (1970) attempted a series of interspecific crosses between *Amarinus lacustris* and *A. paralacustris* using soft-shell females immediately after their pubertal moult. These are very similar species which cannot be distinguished on male morphology. In six out of ten cases where an *A. lacustris* male was introduced to an *A. paralacustris* female or to a hybrid *(A. paralacustris* ♀ x *A. lacustris* ♂) female no copulation occurred; the male either ignored the female or mutilated her by tearing off legs after she resisted being manoeuvred. In a cross attempted with a mature soft-shell female of *H. rostratus* and a male of *H. ovatus* no copulation occurred and the male tore legs off the female (Lucas, 1968). Thus there is some species isolation at copulation, either from the male failing to recognise the female as a mating partner or from the female resisting the male. In attempted interspecific crosses where the male mutilated the female, it appeared that initially the male attempted copulation, but the female thwarted him.

Opposed to the data suggesting precise recognition at copulation are various observations of males of *A. lacustris* and *A. paralacustris* which showed no recognition of sex or shell condition. In the laboratory, males attempted copulation and showed post-copulatory pairing with other males, with immature hard-shell females, with exuviae and with ovigerous females (Lucas, 1968). Lack of discrimination was most common in males which had been isolated from females.

ECOLOGY

Broekhuysen (1955), Lucas and Hodgkin (1970a), Melrose (1975) and Richer de Forges (1977) made population studies of hymenosomatids in marine and estuarine habitats. The most comprehensive of these studies, Lucas and Hodgkin (1970a and b), related the annual cycle of recruitment and growth in *Amarinus laevis* populations in the Swan River estuary to larval survival and seasonal variations in temperature and salinity. Other ecological data on hymenosomatids are scattered through the literature, with Walker (1969), Melrose (1975) and Richer de Forges (1977) being major sources of data on *Amarinus lacustris*, New Zealand hymenosomatids and *Halicarcinus planatus*, respectively. Ecological data for the larval stages of hymenosomatids are contained in Lucas and Hodgkin (1970b) and Lucas (1975).

Habitats: The occurrence of hymenosomatid species in freshwater, brackish and marine habitats is summarised in Table 5. As evident from the table, most marine hymenosomatids occur in shallow coastal waters, in the littoral zone or sublittoral to 20m. The deepest record for a hymenosomatid is 494 m for *Halicarcinus tongi* off Mayor Island, New Zealand (see Melrose, 1975:91). *H. tongi* appears to be the only deep water species and the shallowest depth of its collection is 55-73 m. Other hymenosomatids collected from below 100 m depth, *Halicarcinus planatus* (270 m; Garth, 1958), *H. setirostris* (110 m; Takeda 1973), *Elamena longirostris* (90-116 m; Takeda and Miyake, 1969), and *Trigonoplax spathulifera* (128-137 m, this study), also occur in the littoral zone or at less than 30 m depth. Although many hymenosomatid species occur in the littoral zone, none

TABLE 5. Occurrence of hymenosomatid species in freshwater, brackish and marine habitats.

GENERA	Freshwater	Brackish	Littoral	Marine Sublittoral			Total Species
				to 20 m	20-100 m	>100 m	
Trigonoplax			1	3	2	1	3
Elamena		2	6	8	2	1	12 + 2*
Halicarcinus		1	12	8	5	3	15 + 1*
Halimena			1	1	1		1
Halicarcinides			1	1			1
Neohymenicus			1	1			1
Hymenosoma	1	1	3	3	1		3
Elamenopsis	3	8	6	1	1		16 + 1*
Hymenicoides		1					1
Amarinus	4	3					7
TOTAL SPECIES	8	16	31	26	12	5	64

* Insufficient habitat data to include in table

are active out of water. They do not tolerate desiccating conditions for long (Melrose, 1975: Table 3) and they either move out with the tide or conceal themselves in non-desiccating conditions at low tide.

Marine hymenosomatids not only occur most frequently in shallow coastal waters, they tend to be most abundant in protected localities, in bays, sounds and inlets. This is partly because, with the exception of several stout-legged species, e.g. *Halicarcinus planatus* and *H. innominatus,* they avoid conditions of strong wave action. But also it is postulated that these semi-enclosed water masses restrict larval dispersal, permitting high rates of recruitment (see Reproductive strategies section). Because many marine hymenosomatids occur in protected coastal localities they are in the promixity of estuaries and may be exposed to lowered salinity at times of strong freshwater discharge from the land. Thus it is not surprising to find that some hymenosomatids have become brackish water inhabitants (Table 5). The invasion of low salinity environments is considered in the next section.

Concealment substrates: A major need of hymenosomatid crabs is an appropriate substrate in which to conceal themselves: they are such small, thin-shelled crabs that they can only avoid large predators by being inconspicuous and inaccessible. Hymenosomatids hide in a great range of aquatic substrates: in filamentous and coralline algae, among algal holdfasts, in mussel beds between empty valves or among byssal threads, among ascidians, sponges and bryozoans, among marine angiosperm roots and branches, under rocks, in coral rubble, in plant debris and buried in mud, silt and fine sand. Each species occurs on particular substrates and certain morphological features can be related to the type of substrate inhabited by the crab. Species occurring on soft substrates tend to have slender legs, while those occurring on hard substrates, and in turbulent conditions, tend to have stouter legs. Species occurring on filamentous algae tend to have well developed spines on the body and well developed teeth on the dactyli of their walking legs. Species occurring on silty and muddy substrates tend to have a shield-like rostrum, they tend to be hairy and they have few teeth on the dactyli of their walking legs. Species which inhabit algae and brightly coloured substrates tend to have brighter and more varied pigmentation than species in silty and muddy habitats. The latter species tend to be uniformly brown.

Hairiness of the body surface leads to accumulation of fine particles which helps to camouflage the crab in muddy and silty habitats. Patterns of chromatophores on the body surface assist in camouflage and light/dark adaptation of chromatophores has been shown in *Halicarcinus cookii* (Melrose, 1975).

Density: Although the hymenosomatid crabs are never conspicuous members of benthic communities, careful collecting may reveal that they are quite abundant. Density data on hymenosomatid crabs in various habitats are presented in Table 6. Cassie and Michael (1968) found a community on an intertidal mud flat which was characterised by *Halicarcinus cookii* and a tubiculous polychaete. Obviously *H. cookii* was abundant, but Cassie and Michael do not give density data.

The abundance of hymenosomatid larvae in Cockburn Sound, Western Australia, is a further example of their density at favourable localities. In plankton samples over a year at two inshore stations there were as many hymenosomatid larvae as all other brachyuran larvae combined (Lucas, 1975).

Food: Analyses of the gut contents of some hymenosomatid crabs show that they are omnivores. A major component of their gut contents is debris, mainly plant material, which has been masticated by the mouthparts and gastric mill. In addition to debris,

TABLE 6. Densities of hymenosomatid species in various habitats.

Species	**No./0.1m^2**	**Substrate**	**Source**
Halicarcinus cookii	2-4	*Corallina* turf	Melrose (1975)
H. innominatus	10-15	mussel beds	Melrose (1975)
H. innominatus	3-4	littoral pools	Melrose (1975)
H. whitei	0.8	sand	Melrose (1975)
H. varius	4-6	*Sargassum*	Melrose (1975)
H. varius	4	sheltered beach	Wood (1968)
H. varius	12	*Zostera* flat	Wood (1968)
H. planatus	2.3-13.5	mussel beds	Richer de Forges (1977)
H. rostratus	1-16	*Heterozostera*	Littlejohn (unpubl.)
H. ovatus	1-11	*Heterozostera*	Littlejohn (unpubl.)
Hymenosoma orbiculare	0.2	lake bottom	Boltt (1969)
Neohymenicus pubescens	2-6	reef platform	Melrose (1975)

Lucas (1968) found crustacean remains, including amphipods, in *Amarinus laevis, A. lacustris* and *Halicarcinus ovatus*; Walker (1969) found amphipod remains, algal strands and root fibres in *Amarinus lacustris;* and Richer de Forges (1977) found sand particles, shell fragments, remnants of algae, diatoms, polychaete setae, and fragments of copepods and isopods in gut contents of *Halicarcinus planatus*. The animal remains may result from capture of live prey. *Amarinus lacustris, A. paralacustris,* small *A. laevis* and *Halicarcinus* ovatus captured live *Artemia salina* nauplii in the laboratory and the first two species and hybrids were reared through successive generations with *Artemia* nauplii as sole food source (Lucas, 1968). Melrose (1975) found that *Halicarcinus cookii, H. varius, H. whitei* and *E. producta* captured live amphipods and polychaetes in aquaria. Some *H. cookii* and *E. producta* required moving prey to initiate their capture behaviour. Prey were captured as the crab waited in an alert posture and then seized the prey in its chelae as the prey passed in front of the crab (Melrose, 1975); or, for feeding on *Artemia* nauplii, as the prey swam into contract with the inner surfaces of the walking legs (Lucas, unpubl. data). In the former case the crabs responded to visual perception, in the latter to tactile perception.

Halicarcinus cookii, H. varius and *H. whitei* ate algae or *Zostera* when deprived of prey (Melrose, 1975) and several other food sources and modes of feeding have been described for hymenosomatids. *H. whitei* scooped sand into its mouthparts, apparently extracting organic material, as well as being predatory and eating macroscopic plant material; *H. innominatus* preferred dead animal flesh and entered the valves of decaying mussels; *Neohymenicus pubescens* ate sponge and appeared to filter feed with its hairy mouthparts (Melrose, 1975). *Hymenosoma orbiculare* was observed feeding by probing sandy substrates with its chelipeds and it was presumed to feed on interstitial crustaceans (Boltt, 1969).

Symbioses: No hymenosomatids are known to deliberately mask their bodies with biological material, but their cuticles tend to collect epizooites. These are most common in mature crabs after their terminal moult because of the long period without moulting. Epizooites reported from hymenosomatids are sessile Protozoa, sponges, small anemones, nematodes, serpulids, cirripeds and Bryozoa (Lucas, 1968; Melrose, 1975; Richer de Forges, 1977). Garth et al. (1967) and Richer de Forges (1977) report specimens of *Halicarcinus planatus* with rhizocephalan parasites. Lucas (1968) found bivalved organisms in the abdominosternal region and penetrating the body cavity of *Amarinus lacustris* males.

As well as the above cases of symbioses where the crabs act as hosts, three hymenosomatid species possibly use larger invertebrates as hosts in symbiotic relationships. The hosts in each case are echinoderms. *Elamenopsis ariakensis* is commensal with the holothurian, *Protankyra bidentata* (Woodward and Barrett) on mud flats at Shimabara, Nagasaki Prefecture, Japan (Sakai, 1969). Unfortunately, Sakai does not explain the nature of the commensalism and, as only a few specimens have been reported, it is not clear that the crab is invariably associated with the holothurian. Shen (1932) notes that *Elamenopsis sinensis* is found under stones and "sometimes attached on sea urchins". This may be a casual relationship with the crab using the echinoid as nothing more than one of its concealment substrates, just as other hymenosomatids conceal themselves among sessile invertebrates. Takeda et al. (1976) found *Halicarcinus orientalis* associated with an ophiuroid, *Ophiocoma brevipes* Peters at Hachijs Island, southern Japan. The crabs clung to the oral surface of the ophiuroid in the vicinity of the disc. Usually one, but sometimes two, crabs occurred on one ophiuroid; and, at two shallow localities, one in three and one in ten ophiuroids had crabs on them. The crabs remained in place as the ophiuroid moved. Considering their position, it is possible that the crabs obtained food from their host through its feeding or defaecation. *H. orientalis* is known from other localities as a free-living species occurring under rocks and among algae in the littoral and shallow sublittoral zones (Sakai, 1938, 1965).

Predators: Analyses of gut content of New Zealand fish show that many fish prey on hymenosomatid crabs and that hymenosomatids are an important component of the diets of fish feeding on the benthos. Of 52 species of elasmobranch and teleost fish which fed on crabs, 26 species contained hymenosomatids in their gut contents (Graham, 1938; Godfriaux, 1969). One hymenosomatid species, *Hymenosoma depressum,* occurred in gut contents of 23 fish species. In terms of number of fish species for which it served as food, *H. depressum* was the second most important species of Brachyura in New Zealand (Graham, 1938). (The abundance of *H. depressum* in fish gut contents is in contrast to the low numbers in Museum collections, see Melrose (1975).) In snapper, *Chrysophrys auratus* (Block and Schneider), specimens of *H. depressum* were most common in fish from shallow muddy habitats near estuaries and more abundant in gut contents of female fish than in male fish (Godfriaux, 1969).

Hymenosoma orbiculare is heavily preyed on by fish, in particular *Clarias gariepennis,* in Lake Sibayi, South Africa (Boltt, 1969). All teleost fish feeding on the benthos at Kerguelen Island prey on *Halicarcinus planatus* at least occasionally and some fish have *H. planatus* as a major component of their diet (Richer de Forges, 1977). Rays, *Raja* spp., also prey on *H. planatus.* Probably the largest number of hymenosomatids recorded from a fish's gut contents is 54 specimens of *Amarinus laevis* recorded from a brown trout, *Salmo trutta,* in the Derwent River, Tasmania (see Material Examined for *A. laevis*).

Sea birds which feed in the littoral zone may also prey on hymenosomatids (Richer de Forges, 1977).

Richer de Forges (1977) concluded from his study at Kerguelen Island that *Halicarcinus planatus* plays a fairly important role in food webs. Considering the reported densities of hymenosomatid crabs in some habitats and their frequent occurrence in fish gut contents from some localities, it is probable that hymenosomatids play a significant role in food webs in marine, brackish and freshwater habitats at other localities, at least in New Zealand, southern Australia and southern Africa.

INVASION OF LOW SALINITY HABITATS

Previous authors have remarked on the occurrence of hymenosomatids in low salinity habitats, e.g. Kemp (1917), Chopra and Das (1930), Balss (1934) and Holthuis (1968). But only after tabulation of the distribution of hymenosomatid species in various habitats (Table 5) has the high proportion of species in low salinity habitats become evident. Eight species occur in permanent fresh water: *Hymenosoma orbiculare* (Lake Sibayi population), *Elamenopsis introversus, E. kempi, E. inermis, Amarinus lacustris, A. wolterecki, A. pilosus* and *A. angelicus.* Twenty three of the 64 hymenosomatid species, i.e. 36% of the species, inhabit low salinity waters, either fresh water or brackish water that may vary between fresh and marine salinity. Six genera, including all the multispecific genera except *Trigonoplax,* contain species inhabiting low salinity waters, suggesting that there has been a number of independent invasions of non-marine habitats. This assumes that the hymenosomatids are primarily marine, which is a very reasonable assumption considering the habitats of related Brachyura, i.e. other Oxyrhyncha or the Pinnotheridae and Leucosiidae, which have also been suggested as relatives of the hymenosomatids. There is no fossil record of the Hymenosomatidae (Glaessner, pers. comm.) to illuminate their ancestry. The family apparently originated in Tertiary-Recent times and the process of evolution into low salinity habitats may still be proceeding. Two species, *Amarinus lacustris* and *Hymenosoma orbiculare,* have recently invaded freshwater habitats (Allanson, et al., 1966; Lucas, 1970). Five or six hymenosomatid species have populations occurring permanently in brackish water, while other populations occur in essentially marine conditions; the different populations may be physiological races (cf. Dorgelo, 1976).

As described in the previous section on Ecology, marine hymenosomatids tend to occur in protected coastal localities where they may experience lowered salinity at times of strong freshwater discharge from the land. Thus, Melrose (1975) recorded habitat salinities down to 30.5, 27.3 and 24°/oo for the marine species *Neohymenicus pubescens, Halicarcinus varius* and *H. innominatus,* respectively. Salinity tolerance experiments provide further evidence of euryhalinity in some marine hymenosomatids. Specimens of *H. cookii* survived indefinitely in 50% seawater; specimens of *H. varius* from two localities survived for mean periods of 6 hours and 6 days in fresh water (the specimens which survived much longer were from a locality where they were normally subject to lowered salinity); specimens of *H. whitei,* which extends into estuaries, survived for a mean period of 10 days in fresh water (Melrose, 1975). Adult crabs of *H. ovatus* survived for more than a week at 27°/oo Sal. without mortality (Lucas, 1968) and first stage zoeae of this species survived for 4-5 days at 21.1°/oo Sal. with little mortality (Lucas, 1972).

In the classification of Crustacea according to their salt tolerance, proposed by Dorgelo (1976), it is likely that the majority of marine hymenosomatids are type II, "more or less euryhaline inhabitants of hyperhaline, marine, intertidal and estuarine environments". The only type I, "polystenohaline, true oceanic", species may be *Halicarcinus tongi* and *Elamena longirostris.* Thus it is not surprising that from this large group of "more or less euryhaline" marine species there has been evolution into habitats of progressively lower and variable salinity.

Osmoregulation has been studied in only one hymenosomatid, *Hymenosoma orbiculare* (Forbes and Hill, 1969). Crabs of this species from an estuarine locality showed the pattern of hyperosmotic regulation in low salinity and hyposmotic regulation in salinities near seawater and more saline, which is typical of euryhaline decapod Crustacea. Lucas (1972) studied physiological adaptations to brackish water in the larval stages of two *Amarinus* species. The periods of larval development of *A. laevis* and *A. paralacustris* were about 9 days shorter than the periods of larval development of two *Halicarcinus* species at the same temperature. This abbreviation of the period of larval development is advantageous in the estuarine habitats of the *Amarinus* species: prolonged larval development is unnecessary for dispersal and it increases the probability of larvae being lost from the estuary or encountering adverse conditions in these characteristically heterogeneous habitats. Further adaptations of *A. laevis* and *A. paralacustris* larvae to brackish conditions are relatively broad salinity and temperature tolerances and tolerance of abrupt salinity changes (Lucas, 1972).

The mode of early development is known for only three of the hymenosomatid species which occur in fresh water. Two of these, *Amarinus lacustris* and *A. angelicus,* have no free larval stages (Lucas, 1971; J. C. Yaldwyn, pers. comm.). Another species, *Elamenopsis kempi,* probably has no free larval stages as it has large eggs, 0.52-0.6 mm diameter (Abele, 1972). This mode of development accords with the trend of suppression of free larval stages among freshwater decapod Crustacea (Gurney, 1942). Lucas (1971, 1972) discusses how suppression of free larval development is related to limited dispersal required in small freshwater habitats, to unsuitability of planktonic stages in running fresh water and to osmoregulatory problems of small larval stages. *Hymenosoma orbiculare,* the other hymenosomatid for which early development is known, has free larval stages in 0.25°/oo Sal. in Lake Sibayi (Allanson et al., 1966; Forbes and Hill, 1969).

TABLE 7. Numbers of species of each hymenosomatid genus in various geographical regions. The numbers in brackets are numbers of species which are endemic to that region; species indicated with an asterisk are probably recent introductions by man. The regions are listed from most northern to southern; they are explained further in the text.

	GENERA										
Region ›	*Hymenosoma*	*Elamena*	*Halicarcinus*	*Trigonoplax*	*Elamenopsis*	*Hymenicoides*	*Halimena*	*Amarinus*	*Halicarcinides*	*Neohymenicus*	Total Species
Japan		1	4(2)	1	2(2)						8(4)
Red Sea		1			1(1)						2(1)
India		6(4)		1	7(6)	1(1)					15(11)
Micronesia					1(1)						1(1)
Indo-Malaya		1	3	1	4(2)			1(1)			10(3)
Cen. America					1*						1*
W. Africa		1									1
S.E. Africa	1	2									3
N. Australia		3(1)	5(3)	1(1)	4(2)			4(3)			17(10)
S. Australia	1(1)	1(1)	3+1*(2)	1(1)				3(1)	1(1)		10+1*(7)
S. Africa	1			1	1(1)						3(1)
New Zealand	1(1)	3(3)	5(5)				1(1)	1		1(1)	12(11)
Subantartica			1(1)								1(1)
TOTAL SPECIES	3	13	17	3	17	1	1	7	1	1	64

These larvae warrant further study as there are unusual data relating to them: larvae of *H. orbiculare* from an estuarine locality could not be acclimated to low salinity near that of Lake Sibayi (Forbes and Hill, 1969); *H. orbiculare* larvae in another low salinity lake were collected in grab samples of the benthos at various stations (Boltt, 1975).

ZOOGEOGRAPHY

Zoogeographical considerations of the family Hymenosomatidae are complicated by the presence of marine, estuarine and freshwater species. Many zoogeographical studies treat marine fauna and fauna of inland waters independently, as different dispersal mechanisms and barriers are involved. However, most of the freshwater hymenosomatid species are closely related to marine species and probably evolved from them quite recently (see previous discussion on invasion of low salinity habitats). For this reason, and for convenience, all species of Hymenosomatidae will be treated together in this brief discussion of their zoogeography.

The distribution of hymenosomatid species is summarised in Table 7. The geographical regions listed in this Table are:

Japan — Japan and northern (temperate) China.
Red Sea — Red Sea and S. W. Asia.
India — India, Pakistan, Bangladesh, Burma and Sri Lanka.
Micronesia.
Indo-Malaya — Indo-Malayan Region defined by Ekman (1967), extending from Ryukyu Islands and southern China through S. E. Asia and the Indo-Malayan archipelago to Kei Islands.
Central America.
Western Africa — tropical coast.
Eastern Africa — tropical coast including Madagascar.
Northern Australia — tropical Australia, Papua-New Guinea and New Caledonia.
Southern Australia — temperate Australia and Lord Howe Island.
Southern Africa — temperate Africa.
New Zealand — New Zealand, adjacent islands and Norfolk Island.
Subantarctica — circum-polar, subantarctic islands and subantarctic region of South America (Magellan Province).

The majority of hymenosomatid species occur in the tropical and sub-tropical shelf waters of the Indo-West Pacific Region and adjacent inland waters. This Region is characterised by a general great diversity of species, even compared to the other shallow-water, tropical Regions of the world, the Eastern Pacific, Western Atlantic and Eastern Atlantic Regions. It is also characterised by a large number of endemic families (Briggs, 1974). The hymenosomatids, although they may well have arisen in the Indo-West Pacific Region, are not endemic to it: a substantial number of species, in eight genera, occur in the temperate and cold-temperate regions to the south.

The hymenosomatids have not dispersed eastward across the Pacific Ocean. In fact, the marine species have not even reached the Central Pacific Islands. This is probably because their brief larval development and low fecundity are unsuited to dispersal over long distances. One exceptional species, *Halicarcinus planatus,* has prolonged larval development because of low environmental temperatures (Boschi et al., 1969; Richer de Forges, 1977) and it has achieved a circum-polar distribution in the Southern and Atlantic Oceans on widely separate land masses. *H. planatus* is one of three hymenosomatid species occurring in the Atlantic Ocean. The other species, *Hymenosoma orbiculare* and *Elamena gordonae,* occur on the west coast of Africa.

Four geographical regions listed in Table 7 have seven or more endemic species. They are India, northern Australia, southern Australia, and New Zealand. The endemic Indian species are mainly species of *Elamena* and *Elamenopsis* in brackish and freshwater habitats, reflecting speciation in non-marine habitats. The hymenosomatid faunas of southern Australia and New Zealand are restricted to one or the other region except for a freshwater species, *Amarinus lacustris,* and a marine species, *Halicarcinus innominatus,* which may have been introduced to Tasmania by man (see Remarks on this species). The Tasman Sea is a very effective isolating mechanism between Australia and New Zealand for the hymenosomatids. There is also an abrupt change in hymenosomatid fauna from southern temperate to northern tropical Australia; only two species, *Amarinus paralacustris* and *Halicarcinus bedfordi,* are common to both regions. Various zoogeographical regions have been proposed for Australia (Ekman, 1967; Briggs, 1974) with a common concept of divisions into northern and southern regions. The poorly-known distributions of marine hymenosomatids in northern Australia correspond approximately to a combination of the Dampierian and Solandarian Regions; the distributions of marine hymenosomatids in southern Australia, which are better known, correspond to a combination of the Peronian and Flindersian Regions.

In contrast to the gererally limited dispersal of marine hymenosomatids across ocean barriers, the freshwater species have been surprisingly successful in crossing these barriers. A freshwater species, *Amarinus lacustris,* occurs in Australia and New Zealand and also on Lord Howe Island and Norfolk Island. It is the only macroscopic, freshwater invertebrate known to occur on all these land masses. Its dispersal to these islands appears to be a recent event since it is genetically compatible with a sibling estuarine species in Australia (see Remarks on *A. lacustris).* Other *Amarinus* species occur in fresh water on isolated land masses: *A. pilosus* in New Caledonia, *A. woltereckí* in Mindanao and *A. angelicus* in the highlands of Papua-New Guinea. A freshwater *Elamenopsis* species, *E. inermis,* is the only hymenosomatid known from Micronesia. None of these freshwater hymenosomatids has related brackish or marine species occurring on the same land mass from which it may have evolved. Their origins and mode of dispersal are problematical considering that they do not have the resistant eggs of some other small freshwater crustaceans (see Remarks on *Amarinus*). There is another extreme case of dispersal of a freshwater hymenosomatid over an ocean barrier: *Elamenopsis kempi* occurs at Basra, Iraq, and in the Panama Canal, Central America, and must have crossed either the Atlantic or the Pacific Ocean. However, its presence in the Panama Canal has been explained as a recent introduction by man (Abele, 1972). *E. kempi* was not collected in the Panama Canal in surveys before 1939. Since then the water plant *Hydrilla* was introduced into the Canal and, as *Hydrilla* occurs in the habitat of *E. kempi* in S.W. Asia, it is possible that they were introduced to the Panama Canal at the same time.

Another unusual distribution of hymenosomatids involves three marine species, each found in northeastern Australia and also at one other locality or region far from Australia. These species are *Elamena gordonae, Halicarcinus hondai* and *Elamenopsis octagonalis,* which are known from western Africa, Ryukyu Island (Japan) and Goa (India), respectively, as well as from northeastern Australia. In each species there are only minor morphological differences between the overseas and Australian specimens and they have not been given subspecific status in view of the small numbers of specimens collected. These may be species which previoulsy had wide geographical distributions, or they may still be widely distributed species for which the two localities or regions of collection are only small parts of their ranges. The three species, like many hymenosomatids, are inconspicuous in size and habit and it is quite probable that they have not yet been collected over most of their geographical ranges.

Almost a quarter of the hymenosomatid species are known only from their type locality; forty per cent of the species are known from three or fewer localities. Of the thirteen geographical regions listed in Table 7, in only three, Japan, southern Australia and New Zealand, have reasonably representative collections been made of the hymenosomatid fauna. In the other regions, with the exception of Central America and Subantarctica, there are likely to be new records and some new species with more adequate collecting. The Indo-Malayan Region, which is central to the geographical distribution of the Hymenosomatidae, is particularly poorly collected.

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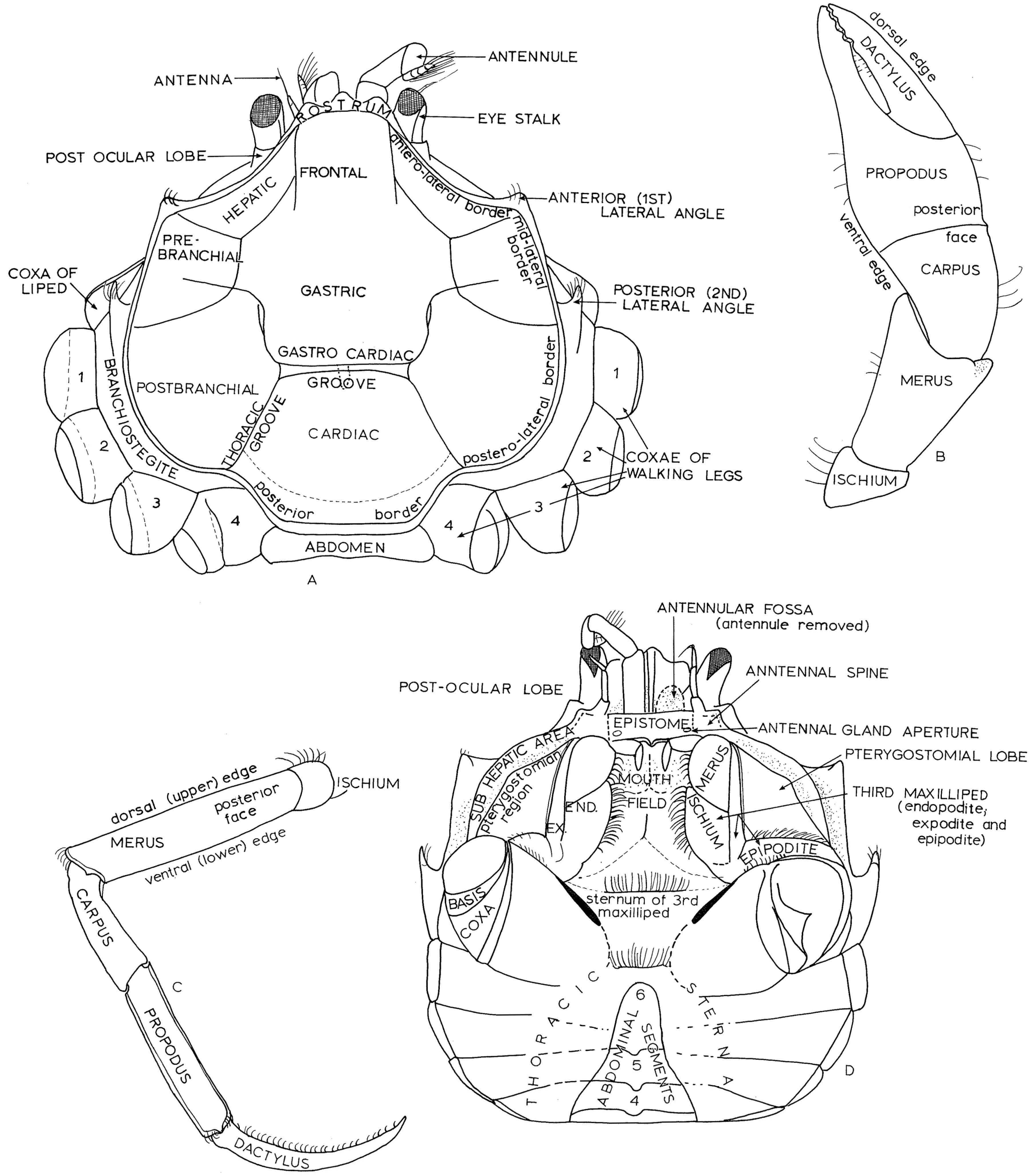

Fig. 1. Generalised hymenosomatid ♂, showing the terms used in descriptions: (A) dorsal view of carapace and leg bases; (B) posterior view of left cheliped; (C) posterior view of 3rd walking leg; (D) ventral view of carapace and leg bases. (From Melrose (1975, Fig. 1) used with permission.)

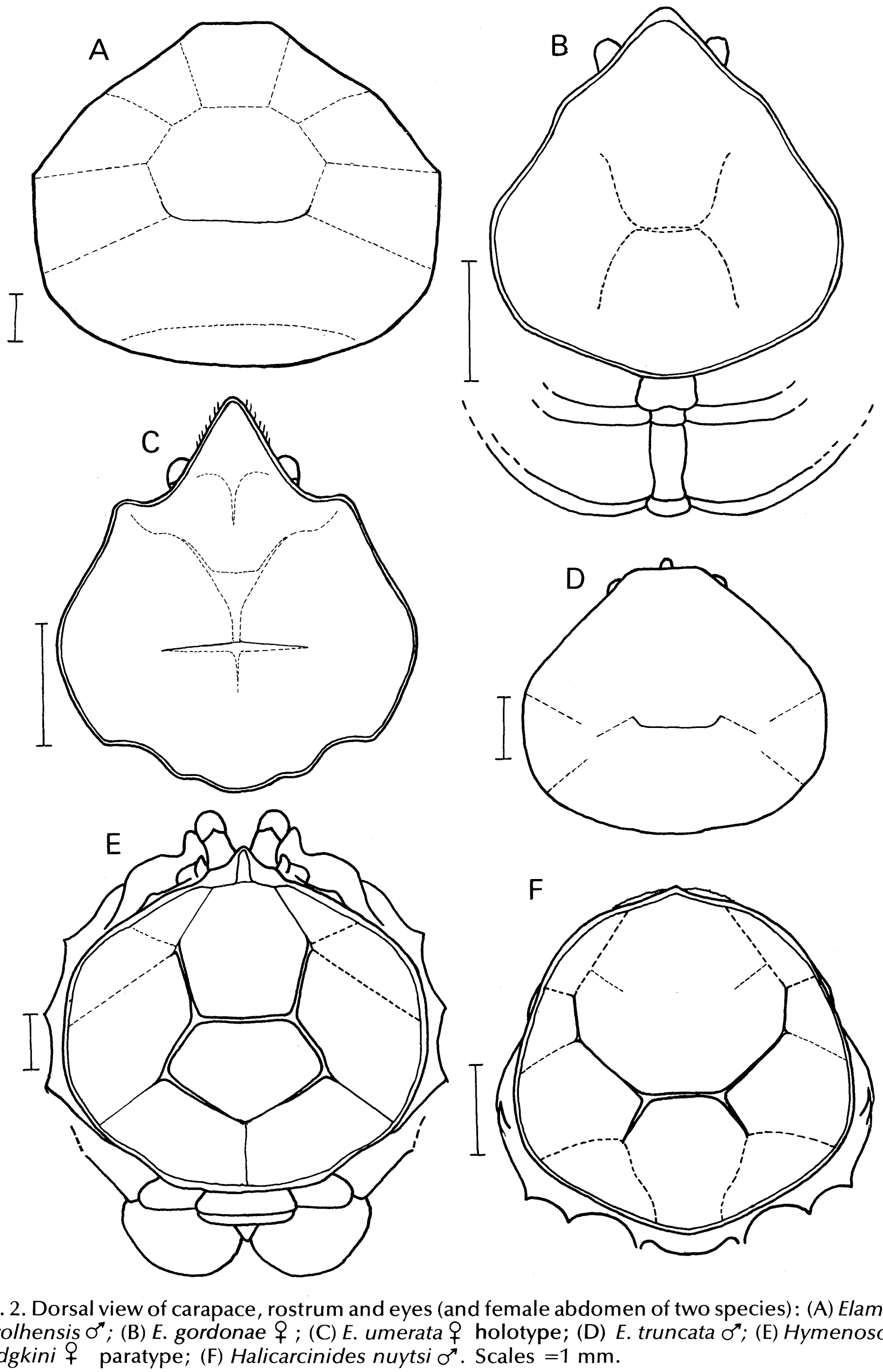

Fig. 2. Dorsal view of carapace, rostrum and eyes (and female abdomen of two species): (A) *Elamena abrolhensis* ♂; (B) *E. gordonae* ♀; (C) *E. umerata* ♀ holotype; (D) *E. truncata* ♂; (E) *Hymenosoma hodgkini* ♀ paratype; (F) *Halicarcinides nuytsi* ♂. Scales =1 mm.

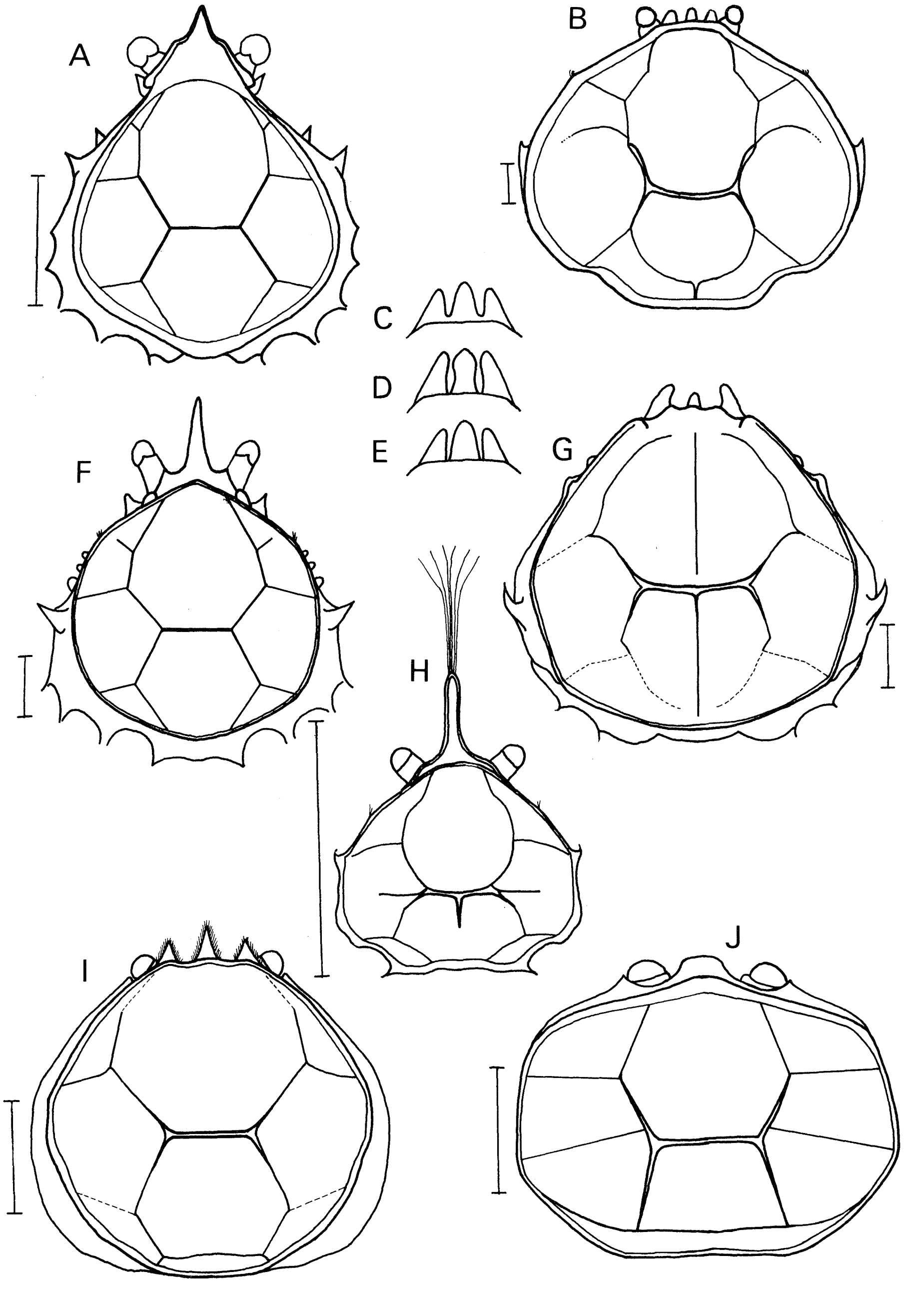

Fig. 3. Dorsal view of carapace, rostrum and eyes: (A) *Halicarcinus bedfordi* ♂; (B) *H. ovatus* ♂; (F) *H. rostratus* ♂; (G) *H. afecundus* ♀ holotype; (H) *H. hondai* ♂; (I) *Elamenopsis aspinifera* ♂ holotype; (J) *E. lineata* ♂. Variation in rostra of *Halicarcinus ovatus:* (C), (D), (E). Scales = 1 mm.

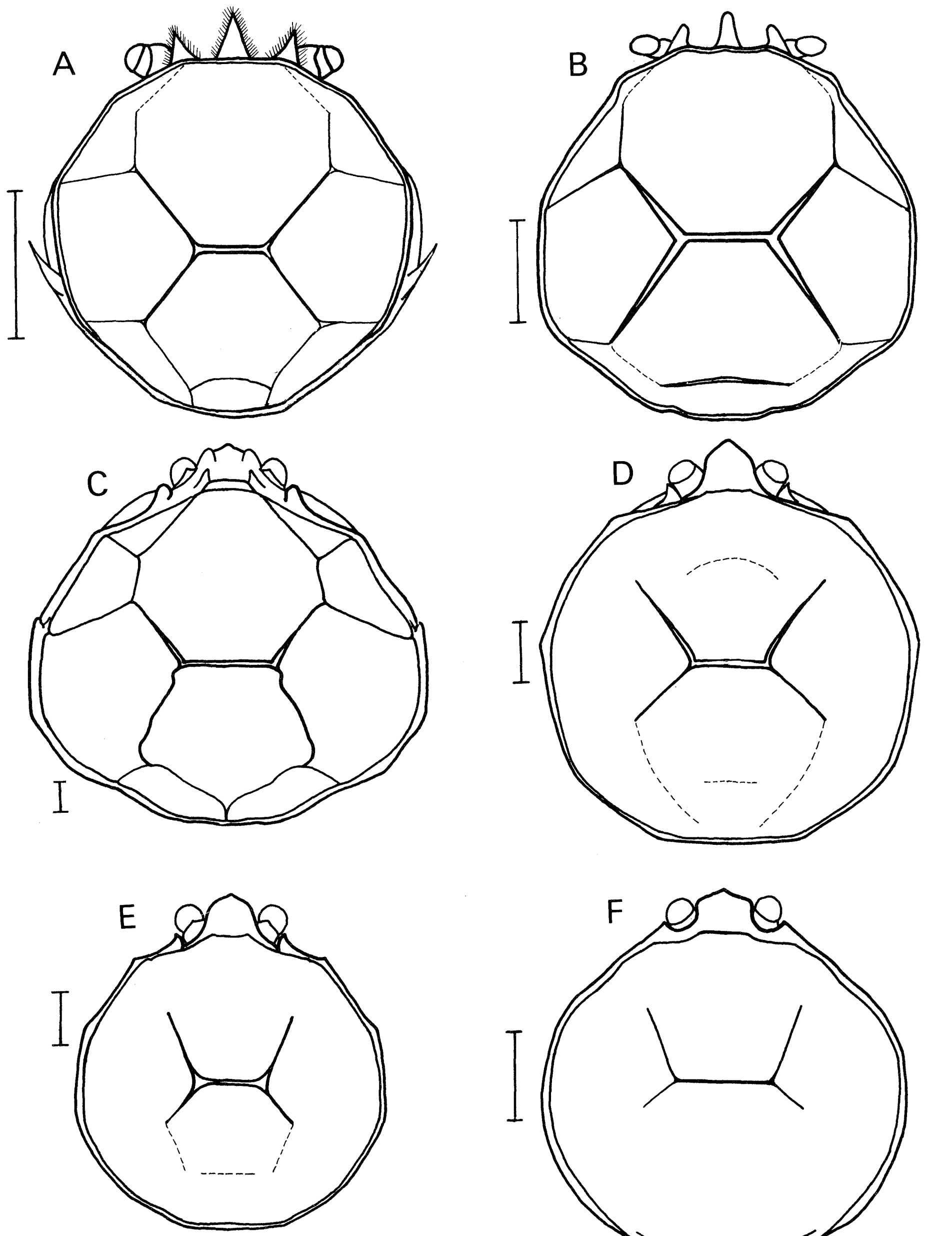

Fig. 4. Dorsal view of carapace, rostrum and eyes: (A) *Elamenopsis octagonalis* ♀ ; (B) *E. torrensica* ♀ holotype; (C) *Amarinus laevis* ♂; (D) *A. lacustris* ♀ ; (E) *A. paralacustris* ♀ ; (F) *A. latinasus* ♀ paratype. Scales = 1 mm.

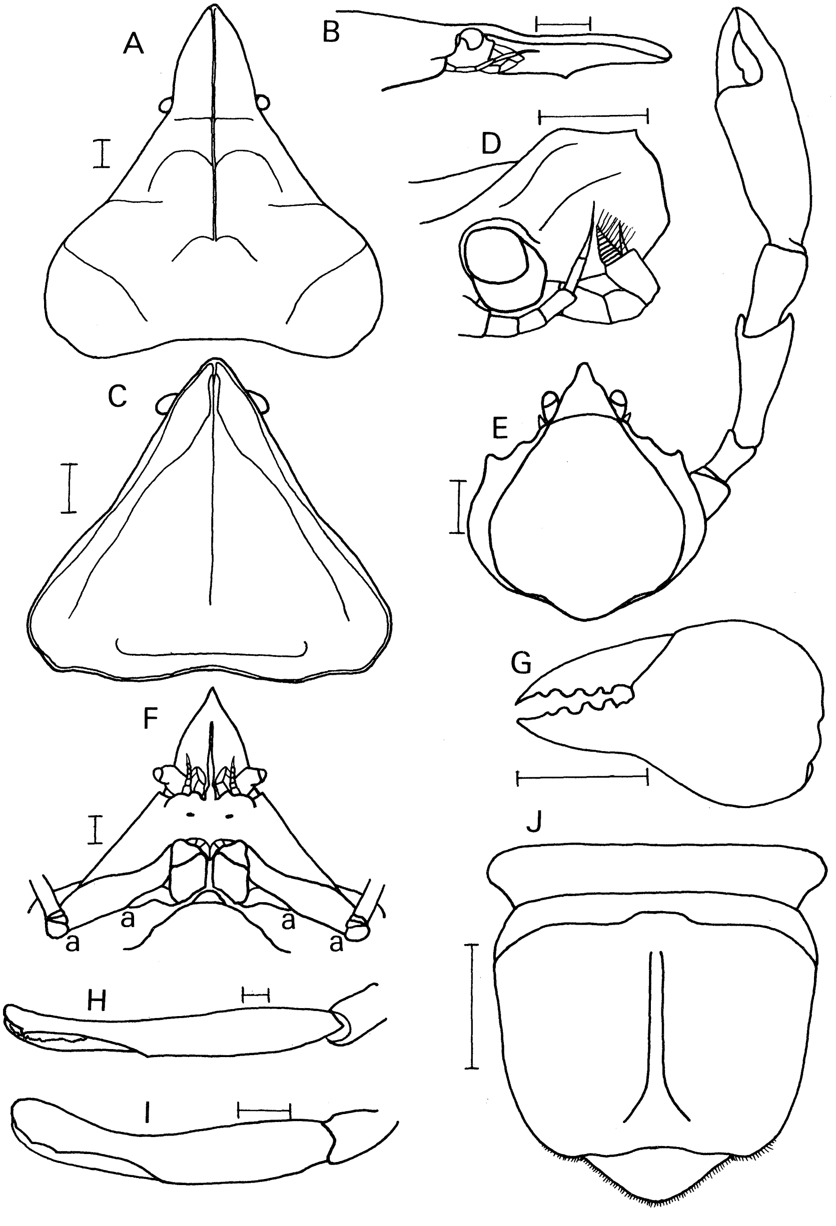

Fig. 5. *Trigonoplax longirostris*♂: (A) dorsal carapace and eyes; (B) lateral view of rostrum; (F) ventral view of front to show fusion of Milne Edwards apertures (a—a); (H) ventral view of right chela. *T. spathulifera* ♀ holotype: (C) dorsal carapace and eyes; (D) lateral view of rostrum; (I) ventral view of right chela. *Halicarcinus bedfordi* ♂: (E) carapace and right cheliped of large ♂. *Elamenopsis aspinifera* ♂ holotype: (G) lateral view of left chela. *Elamenopsis lineata* ♀ : (J) abdomen. Scales = 1 mm.

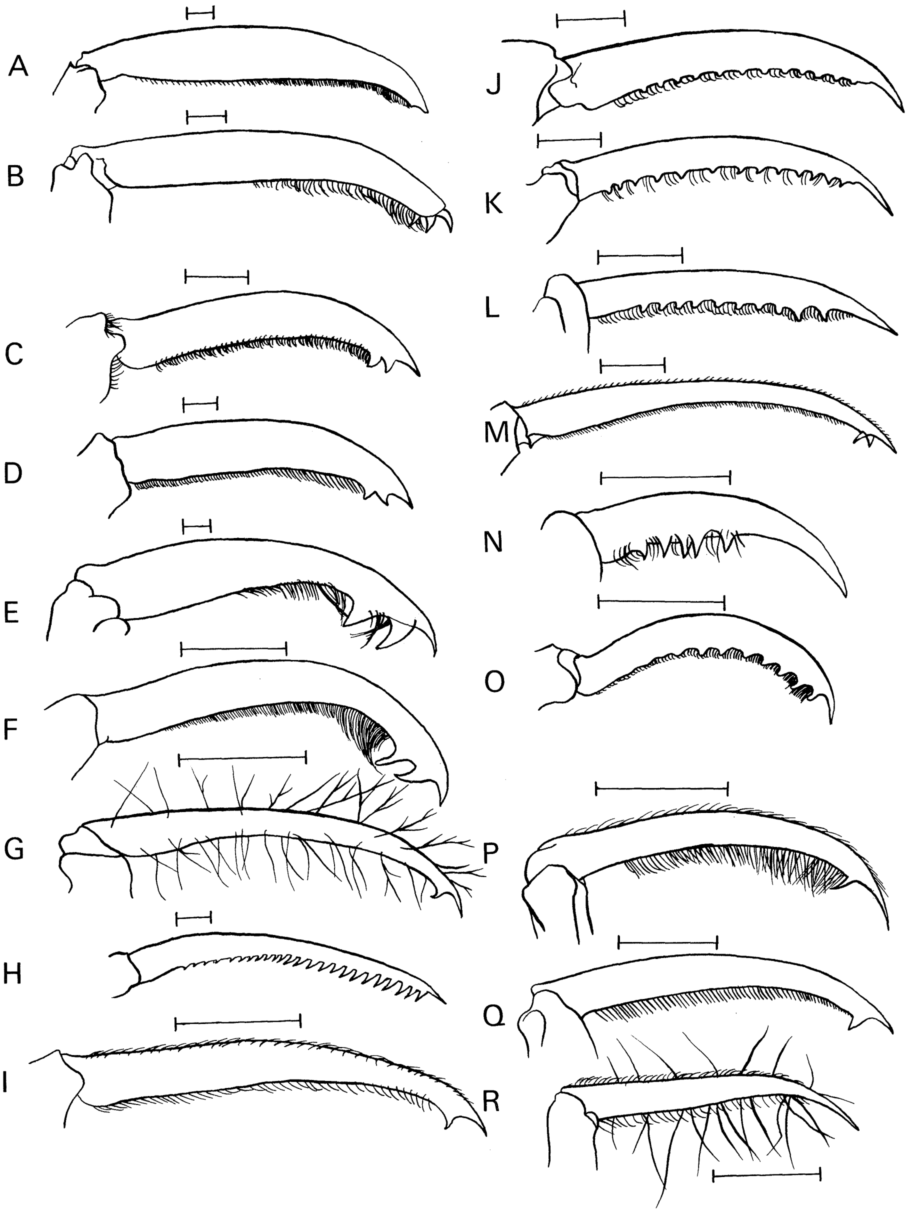

Fig. 6. Dactylus of walking leg: (A) *Trigonoplax longirostris* ♂; (B) *T. spathulifera* ♀ holotype; (C) *Elamena abrolhensis* ♂; (D) *E. truncata* ♂; (E) *E. gordonae* ♀ ; (F) *E. umerata* ♀ holotype; (G) *Amarinus latinasus* ♀ paratype; (H) *Hymenosoma hodgkini* ♂ paratype; (I) *Halicarcinides nuytsi* ♂; (J) *Halicarcinus ovatus* ♂ (Cockburn Sound); (K) *H. ovatus* ♂ (Port Hacking); (L) *H. rostratus* ♂; (M) *H. afecundus* ♀ holotype; (N) *H. bedfordi* ♂; (O) *H. hondai* ♂; (P) *Elamenopsis octagonalis* ♀; (Q) *E. torrensica* ♀ holotype; (R) *E. aspinifera* ♂ holotype. Scales = 0.5 mm.

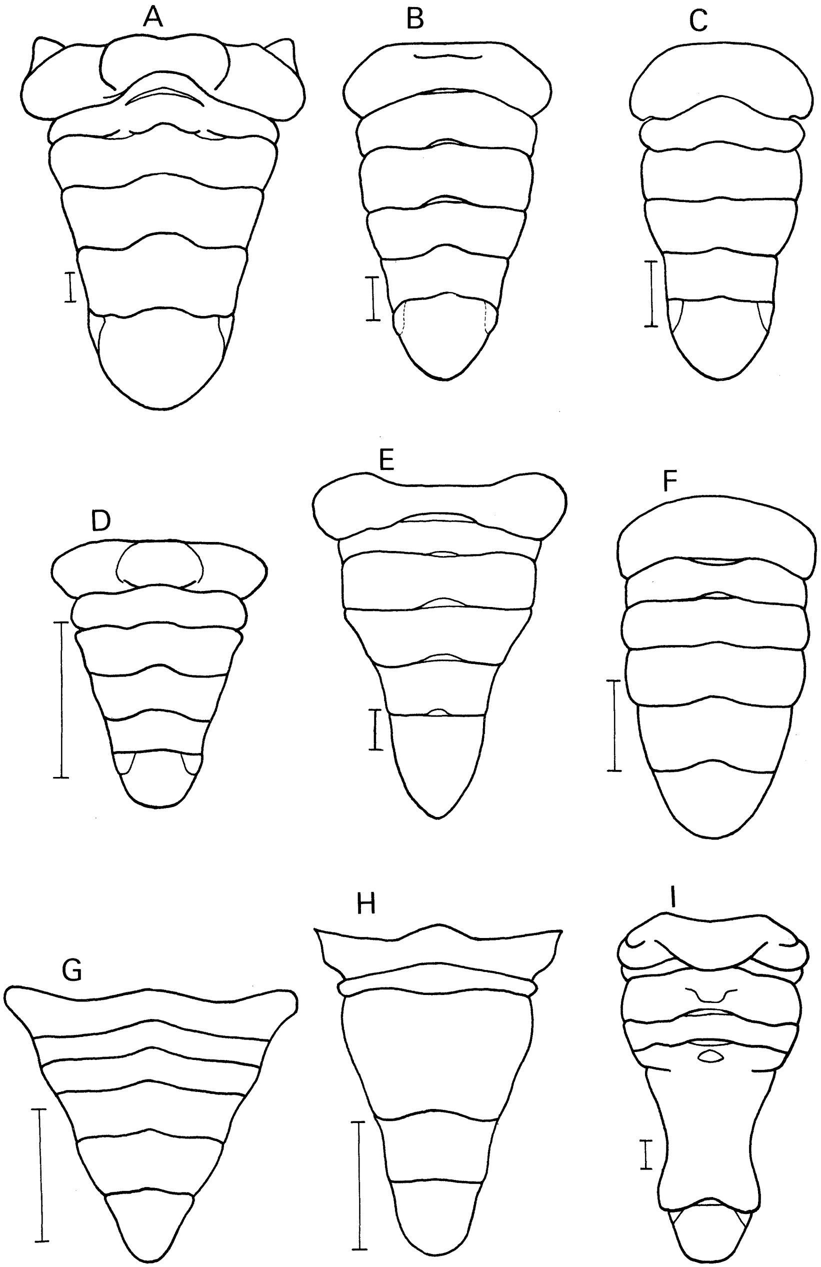

Fig. 7. Male abdomen: (A) *Amarinus laevis; (B) A. lacustris;* (C) *A. paralacustris;* (D) *A. latinasus* holotype; (E) *Halicarcinus ovatus;* (F) *H. rostratus;* (G) *H. bedfordi;* (H) *H. hondai;* (I) *Hymenosoma hodgkini* paratype. Scales = 0.5 mm.

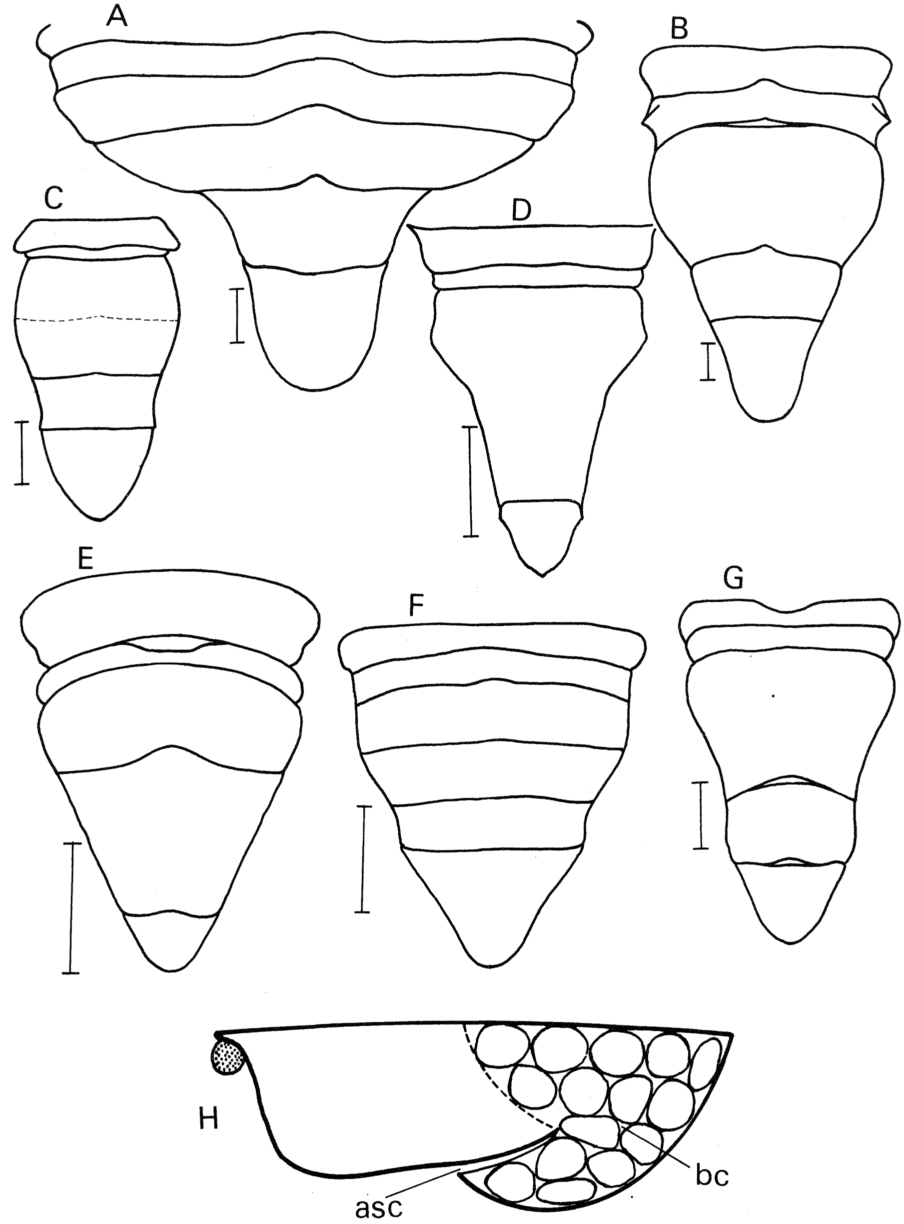

Fig. 8. Male abdomen: (A) *Trigonoplax longirostris;* (B) *Elamena truncata;* (C) *Halicarcinides nuytsi;* (D) *Elamenopsis aspinifera* holotype; (E) *E. lineata;* (F) *Trigonoplax spathulifera* paratype; (G) *Elamena abrolhensis.* Scales = 0.5 mm.

Elamenopsis ovigerous ♀: (H) diagrammatic longitudinal section showing the brood cavity and eggs within the cephalothorax and abdomen. asc: abdominosternal cavity (reduced); bc: brood cavity.

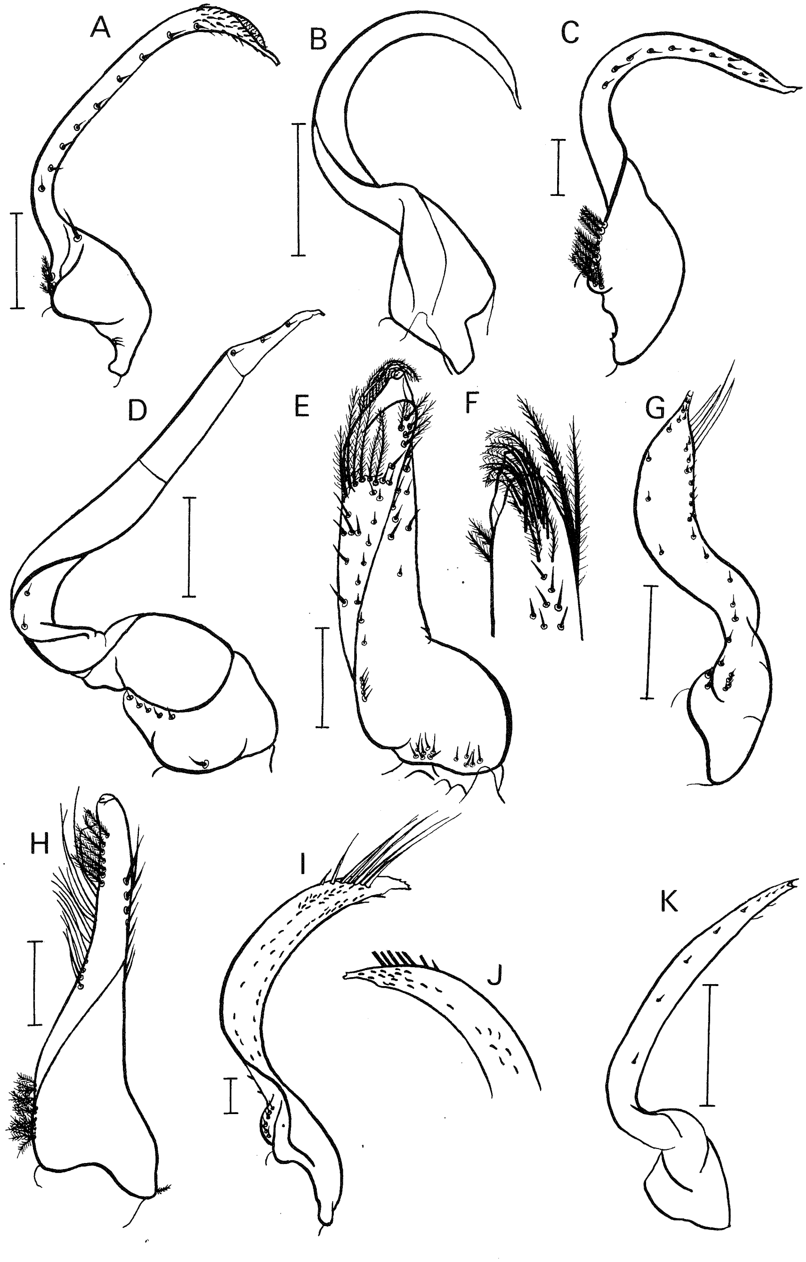

Fig. 9. Male 1st pleopod (lateral view of right side of right pleopod and, for two species, lateral view of left side of apex of right pleopod): (A) *Halicarcinus messor* (Japan); (B) *Elamena umerata* paratype; (C) *Halicarcinus ovatus;* (D) *Halicarcinides nuytsi;* (E) (F) *Halicarcinus bedfordi;* (G) *Trigonoplax spathulifera* paratype; (H) *Halicarcinus rostratus;* (I) (J) *Trigonoplax longirostris;* (K) *Halicarcinus hondai.* Scales = 0.25 mm.

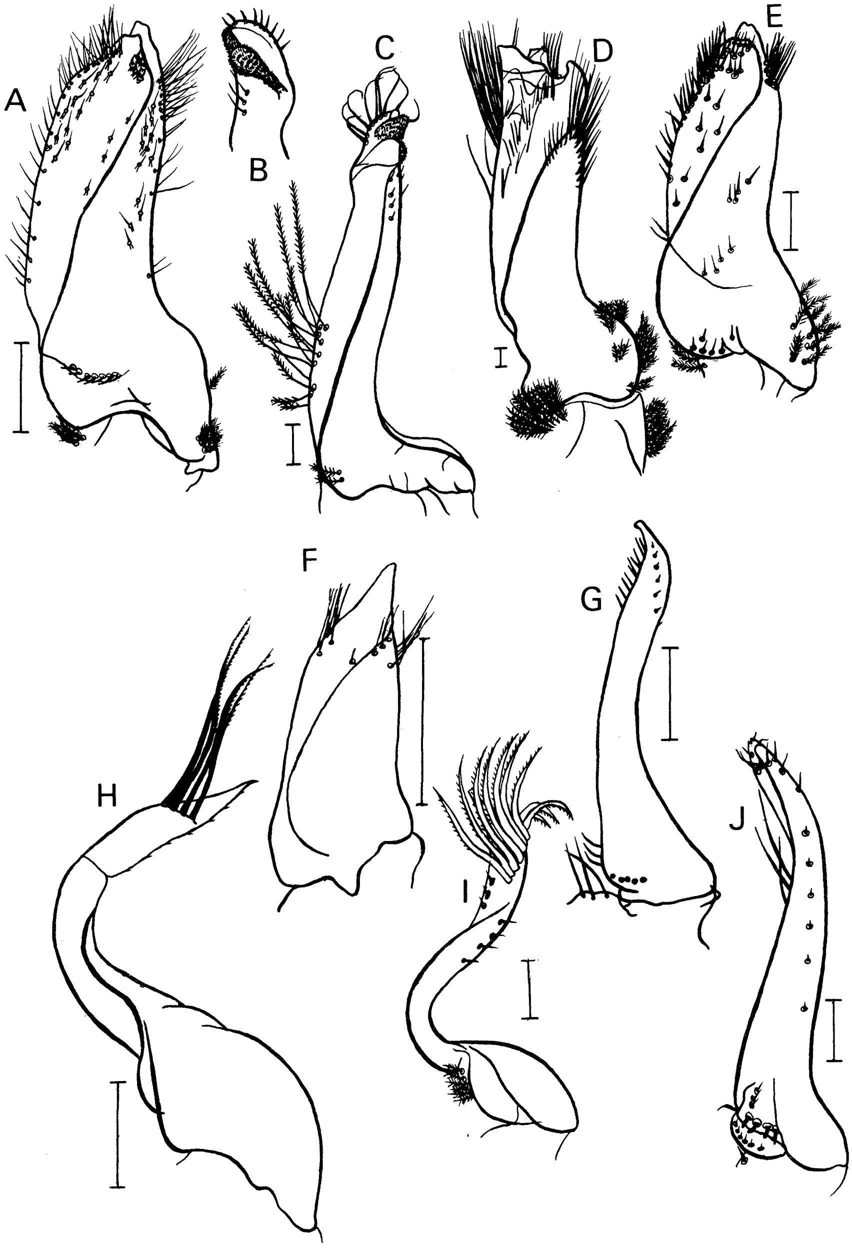

Fig. 10. Male 1st pleopod (lateral view of right side of right pleopod and, for *Hymenosoma hodgkini*, lateral view of left side of apex of right pleopod): (A) *Amarinus paralacustris;* (B) (C) *Hymenosoma hodgkini* paratype; (D) *Amarinus laevis;* (E) *A. lacustris;* (F) *A. latinasus* holotype; (G) *Elamenopsis aspinifera* holotype; (H) *Elamena truncata;* (I) *E. abrolhensis;* (J) *Elamenopsis lineata.* Scales = 0.25 mm.

[This erratum was published in Volume 33, Number 10 in May, 1981, Editor]

ERRATUM

Records of The Australian Museum Vol. 33 No. 4, p.148.

Owing to a printer's error a line was misprinted in the summary of the paper by J. S. Lucas, 'Spider crabs of the family Hymenosomatidae (Crustacea: Brachyura) with particular reference to the Australian species: Systematics and biology'.
Line 15 of the summary should read:

fecundity. Brief larval development and restricted dispersal compensate for low

not

shallow coastal waters and there has been a number of independent invasions of low

We apologise to the author for any inconvenience caused by this mistake.