Breeding experiments to distinguish two sibling species of *Halicarcinus* (Crustacea, Brachyura)

J. S. LUCAS*

Zoology Department, University of Western Australia

(With 4 figures in the text)

Hybridization experiments and various salinities were used in investigating the status of two *Halicarcinus lacustris*-like forms, one of which has no free larval stages (direct-development) and the other of which has normal larval stages (indirect-development).

Hybrids were produced, at least from indirect-development female × direct-development male crosses, but introgression of genetic material was limited to F_1 hybrids from the female parental form. There were no intergrades between the two modes of development in F_1 and F_2 hybrids or as a response to salinity.

These forms are established as sibling species. The name *lacustris* applies to the direct-development form and the other is a new species, *H. paralacustris*, which is described. Hybridization in the field is unlikely due to geographical and reproductive isolating mechanisms. Contrary to a previous view, it seems that *H. lacustris* had a recent origin in Australia and transport by water birds is suggested as the mode of dispersal through south-east Australasia.

Contents

Introduction

The Hymenosomidae (Hymenosomatidae) are a family of small, spider crabs occurring in the Indo-Pacific region. The majority of species are marine, inhabiting a diversity of habitats in the littoral and sublittoral. Of the non-marine species six have been reported from freshwater habitats and five of these have restricted distributions. The other

* Present address: School of Biological Sciences, University College of Townsville, Queensland, Australia.

freshwater species, *Halicarcinus lacustris* (Chilton, 1882), was first collected in Lake Pupuke (also called Takapuna), near Auckland, New Zealand, but it has subsequently been reported from other regions of northern New Zealand and from Norfolk Island, Lord Howe Island, Australia and Tasmania (Fulton & Grant, 1902; Chilton, 1915, 1919; Hale, 1927), always in freshwater habitats.

During a recent field trip in south-east Australia, *H. lacustris*-like specimens were collected from freshwater habitats at localities previously reported for this species in South Australia and Victoria, but also from a new locality near Sydney, New South Wales, in brackish water, 7·4 and 17·2‰ Cl. It was observed that ovigerous females from the brackish habitats carried smaller eggs than ovigerous females from freshwater habitats, and subsequently it was found that larvae emerged from the eggs of brackish females while juvenile crabs emerged from the eggs of freshwater females.

These dissimilar modes of development in different salinity regimes accord with an observed trend of suppression of free larval stages in decapods in low salinities (Gurney, 1942). In a number of families there are genera which include species with normal larval development (indirect-development) and freshwater species with no free larval stages (direct-development). One species, *Palaemonetes varians* (Leach), was generally held to show different degrees of free larval development according to salinity (Gurney, 1942); however, Holthuis (1950) raised the forms with different developments to specific rank in his revision of the Palaemoninae, and they have been shown to be physiologically distinct (Parry, 1957).

It was considered that the different modes of development in *H. lacustris*-like forms may be a phenotypic response to salinity, as earlier claimed for *P. varians*. However, evidence for a genotypic difference was provided by the findings: (i) the female reproductive apparatuses are slightly different; (ii) the two forms have very different geographical distributions, with a small area of sympatry.

The alternatives, a genotypic or phenotypic basis, were investigated in the laboratory by raising juveniles of each form in various salinities, to induce changes in mode of development, if possible, and by attempting crosses between the two forms. With crossing experiments it was hoped to determine the degree of reproductive isolation and hence the status of the two forms. There is no previous record of a series of crossing experiments with crabs and only a few reports of attempts to mate particular crabs in the laboratory, e.g. Cheung (1966).

Hereafter the two forms will be referred to as direct-development and indirect-development forms, abbreviated d.d. and i.d. respectively, until the discussion of their status.

Materials and methods

D.d. males and females were collected from Lake Colac, Victoria, and from Lake Alexandrina, South Australia, i.d. males and females were collected from Cook's River estuary, New South Wales. They were air freighted to Western Australia, and maintained in a laboratory at 20 ± 1 °C. Mature crabs were kept singly in covered glass bowls, 11 cm diameter, containing 150 ml of water and a small piece of nylon gauze for a substrate. Immature crabs were kept similarly, but in groups of 3–11 according to their size. *Artemia salina* nauplii were maintained continually in the water for food and the water was changed at 10 day intervals. Zoeal instars of the i.d. form were kept in groups of 30 in covered glass bowls, 7 cm diameter, with 50 ml of water. They were fed with *A. salina* nauplii and the water was changed daily. Stocks of the required salinities were

prepared by mixing sea-water and conditioned pond water, using a conductivity meter for measurements. Large zooplankters and detritus were removed by filtering the stocks through a 0·2 mm mesh and refiltering immediately before use.

There was little mortality among these laboratory-kept crabs except from cannibalism in groups of immature crabs.

A series of crosses was attempted using the two forms and their hybrids; all the d.d. forms, excepting two females, being from Lake Colac. Females were found to be receptive while soft-shelled immediately after their pubertal moult and all crosses were attempted with a soft-shell, mature female and a hard-shell, mature male. Each female was isolated while immature and after its pubertal moult an appropriate male was added. The male was removed after copulation, or when the female became ovigerous, and the female was kept isolated thereafter.

The occurrence of prepuberty copulations in d.d. females was tested by histological examination of the spermathecae of seven immature females at the instar before maturity, and, for comparison, the spermathecae of one mature female. They were collected from the field, fixed in 10% formalin, then transferred to 70% ethyl alcohol. Both spermathecae were dissected from each female, then mounted in wax, sectioned at 6 μm thickness and stained with haematoxylin and eosin.

Results

Differences in the size, number, and period and mode of embryonic development of the eggs of d.d. and i.d. females are shown in Table I.

TABLE I

Developmental stages of d.d. and i.d. forms

	Direct-development	Indirect-development
(a) Diameter of eggs	0·7 mm	0·35 mm
(b) Number of eggs on ovigerous female of 6 mm carapace width	50 (approx.)	400 (approx.)
(c) Period of embryonic development at 20 ± 1 °C	51–60 days	21–28 days
(d) Free larval instars	Nil	3 zoeal instars
(e) Carapace width of first crab instar	1·05 mm	0·75 mm

Mode of development and salinity

I.d. females

Six females were raised from larvae at 12‰ Cl, two at 6‰ Cl and two at 1·5‰ Cl. On reaching maturity each produced small eggs, approximately 0·35 mm diameter, from which first zoeal instars emerged.

D.d. females

Two females were raised from first crab instar at 12‰ Cl and two at 6‰ Cl. Other immature and mature females, collected from the field, were kept at 1·5, 6 and 12‰ Cl. One female raised at 12‰ Cl failed to mature although reaching mature size, other females

at 12‰ Cl never extruded eggs. At 1·5 and 6‰ Cl, large eggs approximately 0·7 mm diameter were produced and juvenile crabs emerged.

Thus no changes in mode of development were induced by salinity.

Crossing experiments

The results of a series of crosses between the two forms and hybrids are shown in Fig. 1.

The viability of each attempted cross was determined from the fate of the female's first egg mass, which is extruded several days after the pubertal moult regardless of the
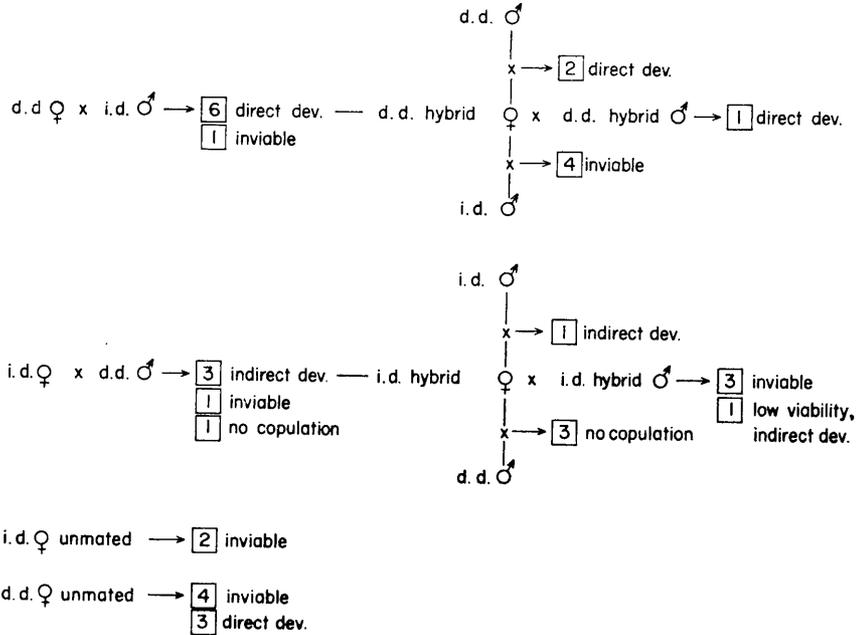

FIG. 1. Results of a series of crosses attempted between d.d. (*H. lacustris*) and i.d. (*H. paralacustris*) forms and their hybrids. The figures enclosed in squares are the number of cases.

time of copulation or its absence. When a female retained at least some of its first egg mass throughout development to hatching, the cross was considered to be viable. In no case did a female retain a totally inviable egg mass for the normal period of embryonic development: the eggs were discarded simultaneously or over several days, generally within ten days of extrusion, and this was taken as the criterion of an inviable cross.

Each mature female produces a series of egg masses in close succession and often all of the egg masses are viable, being fertilized by spermatozoa stored from the postpuberty impregnation. However, when a female discarded its first egg mass all subsequent egg masses were also discarded, confirming that judgments based on the first egg mass are reliable.

There is no intergradation of direct and indirect development in hybrids: hybrid embryos develop in the same way and hybrid females produce the same type of eggs as the original female parental form. For this reason they are hereafter called d.d. hybrids and i.d. hybrids according to their female parental form.

In four cases a d.d. male failed to copulate with an i.d. female or an i.d. hybrid female; the male ignored the female or mutilated her by tearing off legs. This never occurred in crosses between males and females of the same form. Figure 2 is a summary of the behaviour of males in different types of crosses. Most of these data are from the crossing experiments shown in Fig. 1, but the hybrid categories include data for F_1 and F_2 hybrids.

FEMALES

	d.d.	d.d. hybrid	i.d.	i.d. hybrid
d.d.	N a N b	N c N d	NNNN e D f	X c X g D D h D d
d.d. hybrid		N i N j	X k	
i.d.	NNNNN l NN m	NNN l NN n	NNN l NN o N n N p	N l N n N o
i.d. hybrid			X q	NN r NN s N q N t

(MALES — row labels at left)

Fig. 2. The behaviour of males in crosses attempted between d.d. (*H. lacustris*) and i.d. (*H. paralacustris*) forms and their hybrids. Lower case letters, a, b, etc., are the codes of the males and each N, X, or D adjacent to a male code represents a cross attempted using that male. N, Normal copulation; X, no contact with female; D, no copulation, male mutilated the female.

An inconsistency in the crossing experiments was found with controls (females which were not mated after their pubertal moult). Two such i.d. females discarded their egg masses as expected, but of seven d.d. females, four discarded their egg masses while three retained them throughout development and juvenile crabs emerged. An explanation for this result, prepuberty impregnation, is supported by the finding of spermatozoa in four out of seven immature d.d. females from the field. The spermathecae of a mature female in the same sample were larger and contained denser spermatozoa than those of the immature females.

Discussion

Doubtful hybrids

Some large, immature females of *Pachygrapsus traversus* are impregnated (Hartnoll, 1965) and retention of spermatozoa through ecdysis has been shown in a number of Brachyura including another hymenosomid, *Hymenosoma orbiculare* (Broekhuysen, 1955).

Thus it is probable that the source of viability of eggs in "unmated" d.d. females is spermatozoa retained from prepuberty impregnations.

This conclusion renders suspect the nature of some, but not necessarily all, d.d. hybrids. Not all d.d. females are impregnated before their pubertal moult: only 3/7 "unmated" females and 4/7 immature females in which spermathecae were examined were found to be impregnated. A higher observed inviability than 1/7, as found for the d.d.♀×i.d.♂ crosses, would be expected for inviable crosses on the basis of these proportions, i.e. the combined probabilities of this fraction and the more extreme fraction, 0/7 inviable, is 0·14 (Fisher's exact method).
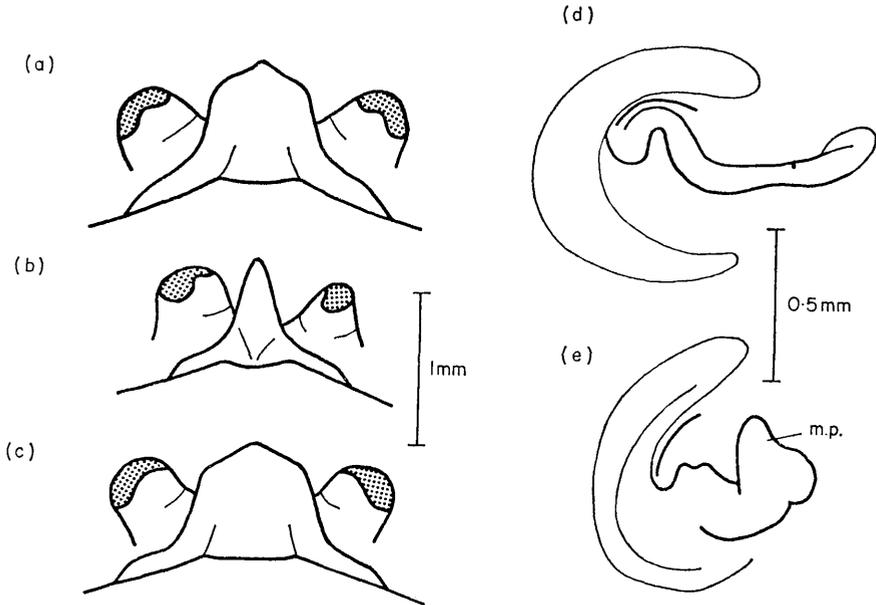

FIG. 3. Rostrum and eyes of: (a) d.d. (*H. lacustris*) female (carapace width 5·8 mm); (b) d.d.♀×i.d.♂ hybrid (?) female (6·1 mm); (c) i.d. (*H. paralacustris*) female (5·9 mm).

Right genital aperture of: (d) *H. lacustris* female (6·1 mm); (e) *H. paralacustris* female (5·4 mm). m.p., Medial prominence.

Even where the d.d. females used in this type of cross were impregnated before puberty, most of their eggs may have been fertilized by i.d. spermatozoa. The d.d.♀×i.d.♂ crosses appeared to be normal and probably resulted in a large predominance of i.d. spermatozoa in spermathecae which already contained some d.d. spermatozoa. Considering the larger size of the spermathecae and greater density of spermatozoa in a mature female, it appears that considerably more spermatozoa are received from postpuberty than prepuberty copulations.

Abnormalities in d.d. hybrid (?) females also suggest that some are hybrids: of 11 d.d. hybrid (?) females which reached maturity, two died soon after puberty without extruding eggs, one had different sized eyes and a very abnormal rostrum, Fig. 3(b) (cf. Figs 3(a),(c)), and another remained immature although growing much larger than the usual size of a mature female.

Irregularities were also found in i.d. hybrids. One i.d. female produced a proportion of

hybrid zoeae with red eyes (normally black) and the red-eyed zoeae failed to moult to second zoeal instars. Two out of 12 i.d. hybrid females which reached maturity showed little ovarian development and did not extrude eggs. Four i.d. hybrid selfed crosses were inviable or poorly viable in contrast to the good viability of an i.d. hybrid ♀×i.d.♂ cross.

It should be noted that the results of the crosses d.d.♀×i.d.♂ and d.d. hybrid (?)♀×i.d.♂ are quite different, the former being generally viable and the latter invariably inviable. The main alternatives are:

(i) the cross d.d.♀×i.d.♂ is at least partially viable and hybrids are produced; the cross d.d. hybrid ♀×i.d.♂ is inviable;

(ii) the cross d.d.♀×i.d.♂ is inviable and F_1 progeny in these experiments were derived from stored spermatozoa; F_1 females in these experiments did not mate with sibling males before their pubertal moult.

The irregularities described above suggest hybrid formation, supporting the first alternative, but a repetition is required with females segregated earlier in their development to preclude prepuberty impregnations.

Status of the two forms

The hybridization experiments and experiments on mode of development and salinity show that the two forms are genetically distinct. There is a degree of genetic compatibility such that hybrids are produced, at least from i.d.♀×d.d.♂ crosses, but there are no intergrades between the two modes of development.

It is not unexpected that F_1 hybrid embryos develop according to the female parental form, since, before fertilization, large or small eggs are produced according to the female form and the amount of yolk will have a strong influence on the mode of embryonic development. However, F_1 and F_2 hybrid females produce eggs which also develop according to the original female parental form.

In these experiments introgression of genetic material was limited to F_1 hybrids from the female parental form. Assuming that there were d.d. hybrid females, then introgression of genetic material was limited by inviability of the d.d. hybrid ♀×i.d.♂ crosses; otherwise there was no introgression in crosses with d.d. females. Introgression of genetic material from i.d.♀×d.d.♂ crosses was limited by failure of d.d. males to copulate with i.a. hybrid females, thus behaviour is also a limiting factor. Data indicating some recognition of form at copulation are presented in Fig. 2.

From these results the two forms are considered to be sibling species. Preserved specimens from Lake Pupuke (the type locality of *H. lacustris*) were examined and found to have large eggs, typical of the d.d. form. Also Chilton (1915) described a female from Lake Pupuke which had only 20 embryos in its abdomino-sternal cavity, "They (embryos) are rather a large size for such a small crab; the abdomen is still folded under the thorax, which is fully 1 mm in length". The name *lacustris* therefore applies to the d.d. form. Specimens from freshwater habitats in Norfolk Island and Tasmania were also found with large eggs and all previous references to *H. lacustris*, although not considering egg size, have always described it as a freshwater inhabitant. The brackish i.d. form is therefore previously unrecorded and is described and named *H. paralacustris* in this paper.

It is probable that there is very little hybridization in the field. In addition to genetic and behavioural isolating mechanisms, they are largely allopatric, Fig. 4, and their salinity preferences isolate them in the area of sympatry. Hovell's Creek, Victoria, is the

only known locality where contact is possible. *H. lacustris* occurs in the upstream portion of Hovell's Creek, near Lara (Walker, 1969), while *H. paralacustris* occurs in the downstream estuarine portion near Corio Lagoon.
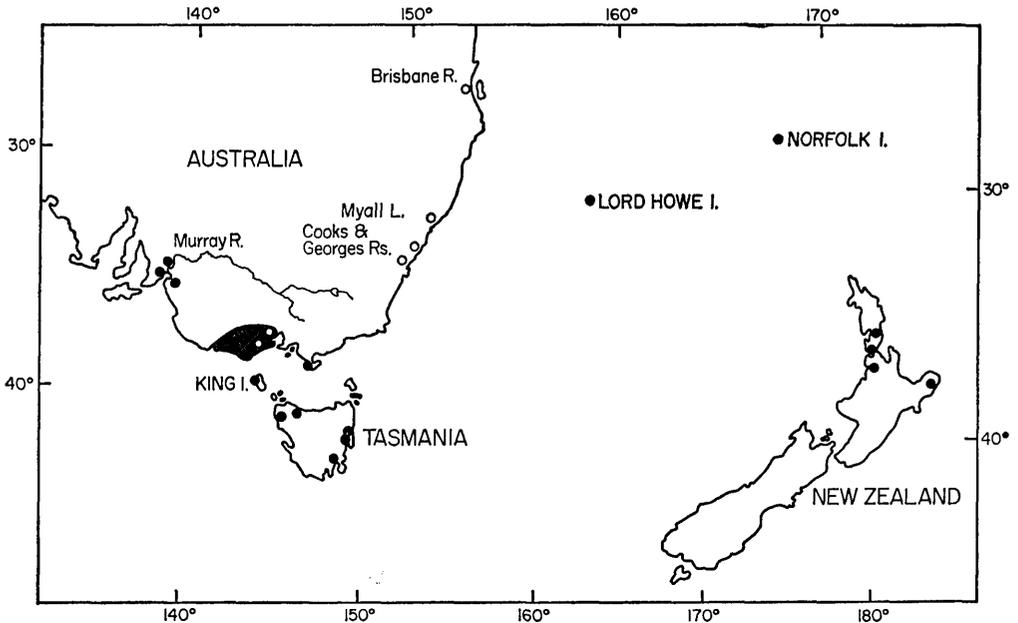

FIG. 4. Map of south-east Australasia showing the distributions of *Halicarcinus lacustris* (direct-development) and *H. paralacustris* (indirect-development). Solid circles and hatching, *H. lacustris*; open circles, *H. paralacustris*.

Origins

The larval instars of *H. paralacustris* are equivalent to those of other *Halicarcinus* species with indirect-development (Lucas, unpubl. data) and it is improbable that this would be the case if *H. paralacustris* evolved from an ancestral form which had no free larval stages. Thus it appears that the ancestor of *H. lacustris* and *H. paralacustris* was an indirect-development form.

Divergence into different salinity regimes is a major factor in the evolution of these sibling species, resulting in great differences in the early developmental stages, but few differences in the morphology of the crab instars. Poor survival of *H. paralacustris* larvae in 1 ‰ Cl and below (Lucas, unpubl. data) suggests that osmoregulatory problems of free larval instars in low salinities were a factor in the suppression of free larval development in *H. lacustris*.

Two findings presented in this paper have implications for the origins of the *H. lacustris* populations on six isolated land masses: (i) since *H. lacustris* has no free larval stages it is very improbable that it dispersed through the ocean; (ii) genetic compatability with a sibling species in Australia and the improbability that *H. lacustris* is ancestral to *H. paralacustris* strongly suggests that *H. lacustris* had a relatively recent origin, probably in Australia, and subsequently dispersed over ocean barriers.

Various modes of passive dispersal of small, aquatic crustaceans are known: (a) as

resistant eggs passing through the intestinal tracts of birds, e.g. Cladocera, Ostracoda and *Artemia salina* (Proctor & Malone, 1965); (b) as resistant eggs transported in the atmosphere e.g. Cladocera, Ostracoda and Copepoda (Maguire, 1963); (c) as adults in the feathers or on the feet of ducks, e.g. Amphipoda (Niethammer, 1953). Modes (a) and (b) are not applicable for *H. lacustris* unless resistant eggs are found. However, it is possible that they are carried by water birds, among feathers or in mud and detritus on the feet. Their small size and clinging habit make this more feasible than for most decapods. It was found that a 6 mm *H. lacustris* female survived in air for more than five days, sufficient time for a trans-Tasman flight as recorded in some water birds common to Australia and New Zealand (D. Purchase, pers. comm.).

This conflicts with Chilton's view that the distribution of *H. lacustris* reflects its antiquity, extending back to periods when there were connections between the land masses now isolated (Chilton, 1915). However paleontological and geological evidence do not support Chilton's view. There is no evidence for land connections between Australia and New Zealand since the Mesozoic era (Fleming, 1957) and, although there are no fossil records for the Hymenosomidae, the other two Oxyrhyncha families evolved much later than the Mesozoic, in Tertiary-Recent times (Glaessner, 1960).

One further alternative is that there are several direct-development, *H. lacustris*-like species which have resulted from at least three cases of parallel evolution in isolation (on either side of the Tasman Sea and on Lord Howe Island) from a ubiquitous ancestor. However there is no evidence of a ubiquitous ancestor: *H. paralacustris* has only been found on the Australian mainland and no similar species has been found on any of the other land masses, although their hymenosomid faunas, particularly the New Zealand hymenosomids, have been well collected and examined. Also, Fulton & Grant (1902) and Chilton (1919) found that collections of *H. lacustris* from the various land masses were so similar that they were not prepared to give them separate taxonomic status.

The times and modes of the origins of the various isolated populations may be elucidated if crossing experiments could be extended to specimens from different land masses and between *H. paralacustris* and *H. lacustris* specimens from beyond Australia. Estimations of percentage viability will probably be necessary in at least some of these crosses and this only seems possible with an *in vitro* technique such as that used in similar studies with Amphibia.

Systematics

Family Hymenosomidae Stimpson, 1858
Genus *Halicarcinus* White, 1846
Kemp, 1917, pp. 245–248; Rathbun, 1925, p. 561

Halicarcinus paralacustris sp. n.

Holotype. Ovigerous female, carapace width 6·5 mm; collected Cook's River, near Campsie, N.S.W., 19.ii.1965, J. S. Lucas, among detritus in littoral zone, salinity 7·4‰ Cl. Lodged in the Australian Museum, Sydney, Reg. No. P.15943.

Paratypes. 36 specimens; collection details as for the holotype. Lodged in the following museums: 4♂♂ (2·7–8·4 mm) 2 ovigerous ♀♀ (4·7, 6·5 mm, eggs and abdomens detached) 7 immature ♀♀ (2·6–5·1 mm) in Australian Museum, Sydney, Reg. No. P.15944 and

P.15945; 4♂♂ (3·5–6·4 mm) 1 ovigerous ♀ (5·6 mm, eggs and abdomen detached) 6 immature ♀♀ (2·2–4·2 mm) in National Museum of Victoria, Melbourne; 3 ♂♂ (4·3–4·8 mm) 1 ovigerous ♀ (5·9 mm, eggs and abdomen detached) 7 immature ♀♀ (2·6–4·2 mm) in Queensland Museum, Brisbane, Reg. No. W.3023; 1 ovigerous ♀ (5·0 mm, eggs and abdomen detached) in Biological Sciences Museum, University College of Townsville.

Other material examined. Victoria, Anglesea, 23.xi.1957, 2 ♂♂ (2·7, 4·0 mm) 2 ovigerous ♀♀ (3·4, 4·5 mm) 1 juvenile (1·6 mm) (in sample including *H. australis*) (Nat. Mus. Vic.). Hovell's Creek, Prince's H'way Bridge, 12.i.1967, K. Walker and J. S. Lucas, 2 ♂♂ (5·5, 6·1 mm) 1 ovigerous ♀ (7·7 mm) 1 immature ♀ (3·7 mm) (Nat. Mus. Vic.). *New South Wales*, George's River, Picnic Point, 21.i.1967, J. S. Lucas, 1 ovigerous ♀ (4·8 mm) in littoral with juvenile *H. australis* (Aust. Mus. Reg. No. P.15942). Cook's River, Undercliffe, 9.ii.1965, J. S. Lucas, 3 ovigerous ♀♀ (5·0–6·9 mm) under rocks in littoral, salinity 17·2‰ Cl (Aust. Mus. Reg. No. P. 15941). Manly Lagoon, xi.1931, I. & B. Iredale, 3 ♂♂ (5·5–8·4 mm) 1 ovigerous ♀ (5·5 mm) (Aust. Mus. Reg. No. P.10116 and P.10117). *Queensland*, Brisbane River, xi.1956, B. Snelling, 1 ♂ (5·8 mm) 1 ovigerous ♀ (6·4 mm) 15 miles up, under stones near low water, labelled *H. australis* (Aust. Mus. Reg. No. P.13145).

Distribution. Eastern Australia, in estuaries along the mainland coast from Anglesea to Brisbane, see Fig. 4.

Description. Carapace subcircular; rostrum simple, strongly deflexed, arising at the level of the dorsal surface of the carapace; anterior lateral angles small and obtuse, posterior lateral angles rarely present; antennal spines (a spine near the base of each antenna) very small; dactylus of each walking leg with one recurved tooth in all crab instars; mature females rarely greater than 8 mm carapace width, neither sex exceeding 11 mm carapace width; ovigerous females with eggs approximately 0·35 mm diameter; female genital apertures with a curved, medial prominence on each; male abdomen constricting slightly at segment one, tapering uniformly from segments two to five; male first pleopods short and stout, slightly curved at the base, ending in a simple, pointed tip; propodus of chela deep and with a crenulated knife edge along the ventral edge in large males; body moderately covered in short setae and coloured dark brown.

Remarks. The only significant morphological differences between the crab instars of *H. paralacustris* and those of *H. lacustris* are in the reproductive apparatuses of mature females. *H. paralacustris* produces eggs which are half the diameter of *H. lacustris* eggs and these species have different female genital apertures (Fig. 3(d),(e)). Other differences in the female reproductive apparatus are: *H. paralacustris* has a curved medial prominence on each genital aperture which is absent in *H. lacustris*; in *H. paralacustris* the length of the sixth abdominal segment is approximately 0·35 of the total length of the abdomen, while in *H. lacustris* it is approximately 0·25; in *H. paralacustris* the inner rami of the pleopods are broader than in *H. lacustris*, the mean values of breadth/length for the four pleopods being approximately 0·40 and 0·25, respectively.

The male reproductive apparatuses of these species are indistinguishable.

One morphological difference between *H. paralacustris* and *H. lacustris* is applicable to both sexes. The tooth on the dactylus of each walking leg becomes proportionally smaller in successive crab instars of both species, but in *H. lacustris* specimens greater than 5 mm carapace width it is generally no longer present, while it is always present in *H. paralacustris*.

Thus, to date, mature females are the only crab instars which can always be identified

as either *H. paralacustris* or *H. lacustris*, although some males and large, immature females are identifiable as *H. lacustris* by absence of teeth on the dactyli of the walking legs. The identity of other crab instars must be inferred from the nature of their environment and associated mature females.

Another brackish-water species, *H. australis*, occurs at all the localities where *H. paralacustris* has been collected. This species has many features in common with *H. paralacustris* and *H. lacustris* and has been confused with them. However mature crabs, i.e. females with an expanded abdomen and males with enlarged chelae, show little overlapping in size; mature specimens of *H. australis* range from 10–22 mm carapace width; mature specimens of *H. paralacustris* and *H. lacustris* rarely exceed 10 mm carapace width. Other features by which these species may be distinguished are shown in Table II.

TABLE II

*Features by which **Halicarcinus australis** may be distinguished from **H. paralacustris** and **H. lacustris***

	H. australis	H. paralacustris and H. lacustris
(a) Antennal spines	Acute and prominent	Obtuse and very small
(b) Tip of first male pleopod	A large blunt lobe and smaller curved lobe	A simple point
(c) Tooth on dactylus of walking legs	Absent except in first few crab instars	Present at least to 5 mm size
(d) Pulvinae* on chelae of mature males	Present	Absent

* A sac arising between the bases of the fingers.

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