

## THE FIDDLER CRABS (OCYPODIDAE: *UCA*) OF DARWIN, NORTHERN TERRITORY, AUSTRALIA

10/11

HEINRICH-OTTO VON HAGEN<sup>1</sup> and DIANA S. JONES<sup>2</sup>

<sup>1</sup>Fachbereich Biologie, Zoologie, Philipps-Universität,  
D-3550 Marburg/Lahn, Federal Republic of Germany.

<sup>2</sup>Department of Crustacea, Western Australian Museum,  
Francis Street, Perth, WA 6000, Australia.

### ABSTRACT

The colour patterns of live fiddler crabs and ontogenetic colour changes were documented in the field and compared with morphological results (particularly the shape of the male gonopods) obtained from a new collection. According to these studies the fiddler crabs of Darwin consist of nine species: *Uca capricornis* Crane, *U. dampieri* Crane, *U. elegans* George and Jones, *U. flammula* Crane, *U. hirsutimanus* George and Jones, *U. mjoebergi* Rathbun, *U. polita* Crane, *U. seismella* Crane, *U. signata* (Hess). The presence of additional *Uca* species, viz. *U. coarctata* (H. Milne Edwards), *U. dussumieri* (H. Milne Edwards) and *U. vomeris* McNeill reported by George and Jones (1982), is not confirmed here. These species appear to be confined to the east coast of Australia. It is also concluded that *U. pavo* George and Jones is a synonym of *U. capricornis* Crane: *U. pavo* represents an adult colour stage which was not adequately described in the original publication of Crane.

KEYWORDS: Brachyura, Ocypodidae, *Uca*, taxonomy, colour pattern, gonopods, Australia, biogeography.

### INTRODUCTION

A study of the waving display and vibration signals of the fiddler crabs of Darwin, undertaken in July 1986 (von Hagen, in prep.) found only nine species of *Uca*, whereas 13 species have been recorded previously from this region (George and Jones 1982). The present contribution re-evaluates the systematics of *Uca* in the Darwin region, as presented in the George and Jones paper, and reduces the number of fiddler crab species known from the region from 13 to 9. The present paper provides a local faunal revision, and may be considered as a supplement to the booklet of George and Jones (1982), which will remain a general source of reference for all future students of Australian *Uca*. For this reason, full descriptions, full synonymies and older references are omitted. A key to the fiddler crabs of Darwin is presented for males and females, along with an annotated list of the nine species. The remarks contained in this list make use of the illustrations (Figs 2-5) that represent the main basis of the proposed corrections. In Figs 2 and 3 we follow the recommendation to give more weight to colour patterns of living individuals

in systematic descriptions of decapods (Bruce 1975; Knowlton 1986). The drawings were prepared from colour slides and are thought to represent typical colour patterns of fiddler crabs from around Darwin, although variation across the ranges of species is not well documented. Scientific names are used in the usual simple binomial (genus, species), ignoring Crane's use of subgeneric names and subspecific ranking (for explanation see von Hagen 1976; Manning and Holthuis 1981; George and Jones 1982).

Material collected in 1986 and described here is lodged in the Zoology Collection of Marburg University (ZCMU). Additional material was provided by the U.S. National Museum, Washington (USNM), the Queensland Museum, Brisbane (QM), the Australian Museum, Sydney (AM) and the Western Australian Museum (WAM). Some of the specimens collected in 1986 are not included in the material listed here. These were left in the Northern Territory Museum, Darwin, as a reference collection. All measurements (given in mm) refer to the width of the carapace.

Abbreviations of species names are used throughout the synopsis of localities (see below) as well as in the legends of Figs 2-5.

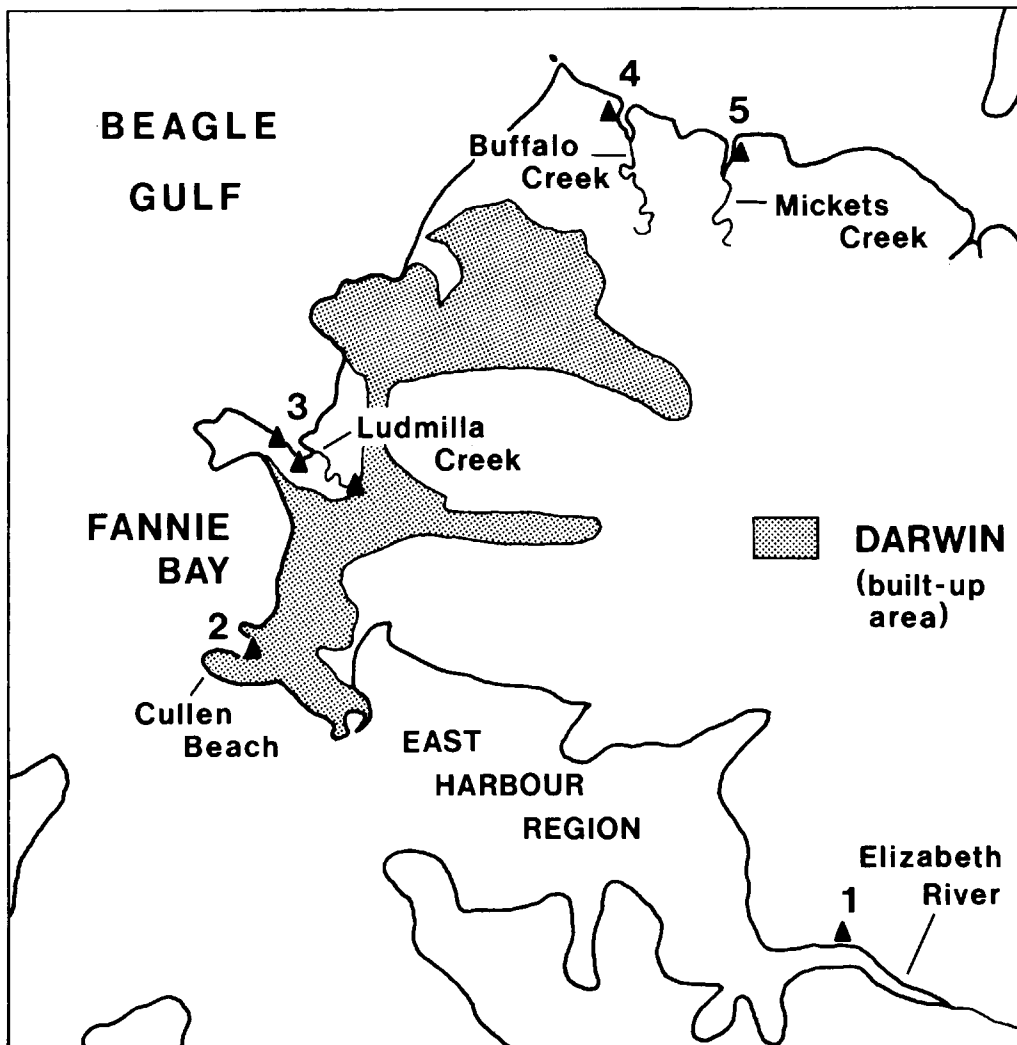


Fig. 1. Study localities in and around Darwin visited in July 1986. See text for explanation of numbers.

The following explanatory list of these abbreviations is supplemented by figures indicating the carapace width of the largest specimens known from Australia (source: George and Jones 1982), which may provide the reader with an impression of the animals' relative sizes.

**Abbreviations referring to species from Darwin:**

cp	<i>U. capricornis</i>	32.3
dp	<i>U. dampieri</i>	26.1
el	<i>U. elegans</i>	26.6
fl	<i>U. flammula</i>	39.6
hs	<i>U. hirsutimanus</i>	18.6
mb	<i>U. mjoebergi</i>	16.4
pl	<i>U. polita</i>	26.2
sg	<i>U. signata</i>	20.0
ss	<i>U. seismella</i>	17.7

**Abbreviations for species from Queensland (used for comparison):**

cc	<i>U. coarctata</i>	37.4
ds	<i>U. dussumieri</i>	39.9
vm	<i>U. vomeris</i>	29.2

Main localities of study (i.e. localities that were especially suitable for the study of each *Uca* species) are listed below. These localities (Fig. 1) were visited from 12 to 29 July 1986, and they are briefly described in the following synopsis. The synopsis also provides a full list of *Uca* species in the order of frequency for each locality (for abbreviations of species names see above).

1. Elizabeth River and Creek H, East Harbour Region - river banks shaded by or covered with mangroves: *fl*, *cp*, *hs*, *ss*; near boat ramp: *fl*, *cp*, *ss*, *hs*, *sg*.

2. Cullen Beach - open stony and muddy sand flats: *ss, mb*; near or among mangroves: *cp, ss, pl*.
3. Ludmilla Creek - Upper Ludmilla Creek, near Dick Ward Drive - among mangroves: *fl, sg, hs, cp, dp*; open loamy salt flats between mangroves and drive: *el*.  
Ludmilla Creek Marina - mangrove clearing around marina: *pl, ss, dp, mb, hs*; open muddy sand flats of the creek's island: *pl, dp, ss*; steep shoulders of creek banks, near and among mangroves: *fl, cp, ss, hs, dp*.  
Mouth of Ludmilla Creek - loamy salt flats with scattered mangrove bushes: *el, mb*.
4. Buffalo Creek - open creek banks near boat ramp: *dp, mb, pl, ss*.
5. Mickets Creek - open creek banks near boat ramp: *hs, fl, pl*; among mangroves: *sg*; open loamy salt flats: *el*.

The fiddler crab fauna of the extensive mangrove creeks of the Harbour Region is relatively depauperate (consisting mainly of *fl, cp, hs, ss*, see locality 1), whereas in the more disturbed urban region, which may offer a variety of different soil types, seven to nine species may occur within relatively short distances (see locality 3).

**Key to the *Uca* species of Darwin.**

**Males.**

1. Front (tongue-like interorbital region) broad; pleonal clasping apparatus (hooking rim of thoracic cavity lodging telson) present.....*mjoebergi*  
Front narrow; pleonal clasping apparatus absent.....2
- 2(1). Outer major dactyl without median groove; outer palm of major chela, at base of pollex, with a large marked triangular depression, often filled with patches of tomentum (pile, woolly hair) .....*dampieri*  
Outer major dactyl with one or two long grooves, the median one always present; no large triangular depression at pollex base.....3
- 3(2). Outer major dactyl with two long grooves running most of its length....4  
Only one long (median) groove present on outer major dactyl.....5
- 4(3). Gonopod distally tapered, with long tubular projection; gape of minor chela with dense, long setae in distal half. Major chela and merus of walking legs slender.....*elegans*

- Gonopod distally rounded, without long tubular projection; gape of minor chela with a few bristles only; major chela and merus of walking legs broad .....*capricornis*
- 5(3). Dorsolateral margin of carapace replaced by a row of widely spaced, blunt tubercles or small groups of tubercles .....*seismella*  
Dorsolateral margin of carapace normal, i.e. a continuous, microscopically beaded line.....6
- 6(5). Long groove of outer major pollex lacking or extremely indistinct; distal tubular projection of gonopod directed sternally.....*polita*  
Long supramarginal groove of major pollex present; distal tubular projection of gonopod directed laterally or sterno-laterally.....7
- 7(6). Supramarginal groove of outer major pollex strongly curving upwards towards centre of pollex base, thus not continuous with supramarginal groove of palm; orbital floor usually without a row of accessory granules behind suborbital crenellations.....*flammula*  
Supramarginal groove of outer major pollex everywhere very close to ventral margin, thus fully or nearly continuous with supramarginal groove of palm; orbital floor always with a row of accessory granules behind suborbital crenellations.....8
- 8(7). Gape of minor chela with a pair of enlarged teeth; major chela frequently with patches of tomentum at least in and around supramarginal groove; distal tubular projection of gonopod directed laterally.....*hirsutimanus*  
Gape of minor chela without a pair of enlarged teeth; major chela without tomentum in and around supramarginal groove; distal tubular projection of gonopod directed sterno-laterally.....  
.....*signata*

**Females.**

1. Front broad.....*mjoebergi*  
Front narrow .....2
- 2(1). Crenellations of suborbital margin distinct throughout, only a few of them fused in pairs; minor chela widely gaping, gape without serrations.....  
.....*dampieri*

- At least some suborbital crenellations (usually inner ones) fused to form a continuous border.....3
- 3(2). Minor chela unusually broad and heavy, prehensile edges with a series of strong triangular teeth, which already start in proximal corner of gape (though highest teeth are located in distal half).....4
- Minor chela slender (of normal appearance); distinct triangular teeth absent from proximal quarter of gape or totally lacking.....6
- 4(3). Dorsolateral margin of carapace disintegrated into a row of widely spaced, blunt tubercles; carpus, propodus and sometimes merus of last walking leg with a patch of tomentum posteriorly.....*seismella*
- Dorsolateral margin of carapace normal, i.e. a continuous, microscopically beaded line; last walking leg without tomentum.....5
- 5(4). Orbital floor with a row of accessory granules behind suborbital crenellations.....*hirsutimanus*
- No accessory granules on orbital floor behind suborbital crenellations.....*polita*
- 6(3). Merus of last walking leg slender (nearly two and a half times as long as broad).....7
- Merus of last walking leg broad (about twice as long as broad).....8
- 7(6). Orbital floor without a row of accessory granules behind suborbital crenellations; gape of minor chela with a series of long setae in distal half.....*elegans*
- Orbital floor with a row of accessory granules behind suborbital crenellations; setae in gape of minor chela less conspicuous.....*signata*
- 8(6). Gonopore with a large protruding tubercle.....*flammula*
- Gonopore without a large protruding tubercle.....*capricornis*

SYSTEMATICS

*Uca capricornis* Crane  
(Figs 2 cp, 4 cp)

*Uca (Deltuca) dussumieri capricornis* Crane, 1975:36 (type locality Broome, W.A.).

*Uca capricornis* - George and Jones 1982:18 (not material from Hitchinbrook Island, Qld.).

*Uca pavo* George and Jones, 1982:25 (type locality Broome).

*Uca dussumieri* - George and Jones 1982:31 (part: material from Darwin and Cape Don, Cobourg Peninsula, N.T.).

**Material.** NORTHERN TERRITORY: Cape Don, Cobourg Peninsula, 1965, AM P16623, 1 male (21.3 mm); Darwin, 1914, QM W3015, part: cf. *U. flammula*, 7 male (13.0 - 23.9 mm), 1 female (18.5 mm), 1978, ex WAM 119-78, 2 male (11.2 - 12.6 mm), 1986, ZCMU 511, 42 male (6.0 - 27.6 mm), 27 female (6.9 - 24.6 mm). WESTERN AUSTRALIA: Broome, 1963, USNM 137675, holotype of *U. dussumieri capricornis*, 1 male (24.0 mm), 1978, WAM 189-78, holotype of *U. pavo*, 1 male (25.6 mm).

**Comparative material of *U. dussumieri* (H. Milne Edwards).** QUEENSLAND: Cairns, 1961, QM W2503, 2 male (29.9 - 32.9 mm); Townsville, 1962, QM W3003, 1 male (34.1 mm), 1 female (34.5 mm). INDONESIA: Kuta (Bali), 1983, ZCMU 351, 16 male (16.1 - 21.7 mm), 5 female (7.3 - 21.3 mm).

**Comparative material of *U. coarctata* (H. Milne Edwards).** QUEENSLAND: Hinchinbrook Island, 1981, WAM 102-81, 5 male (7.0 - 13.5 mm), 2 female (14.6 - 16.3 mm).

**Distribution.** Northwest and north Australia.

**Main localities of study.** Ludmilla Creek Marina, Elizabeth River.

**Remarks.** Apparently, previous confusion concerning *U. capricornis* may have arisen as a consequence of the wide variety of colours of this species and its dramatic ontogenetic colour change (Fig. 2 cp<sub>1,3</sub>).

*U. capricornis* passes a juvenile stage of brilliant blue (Fig. 2 cp<sub>1</sub>) that may temporarily brighten to a pale blue or white of carapace and walking legs, the eyestalks always being yellow and the male's major cheliped pale yellow to light brown. The second colour stage (Fig. 2 cp<sub>2</sub>) is an intermediate one, where the blue colour gradually turns bluish black or black, while some light spots remain on the carapace as well as on the walking legs. These spots are whitish blue or whitish in the male and female, though the latter usually displays yellow patches in addition (in the upper carapace regions). The eyestalks be-

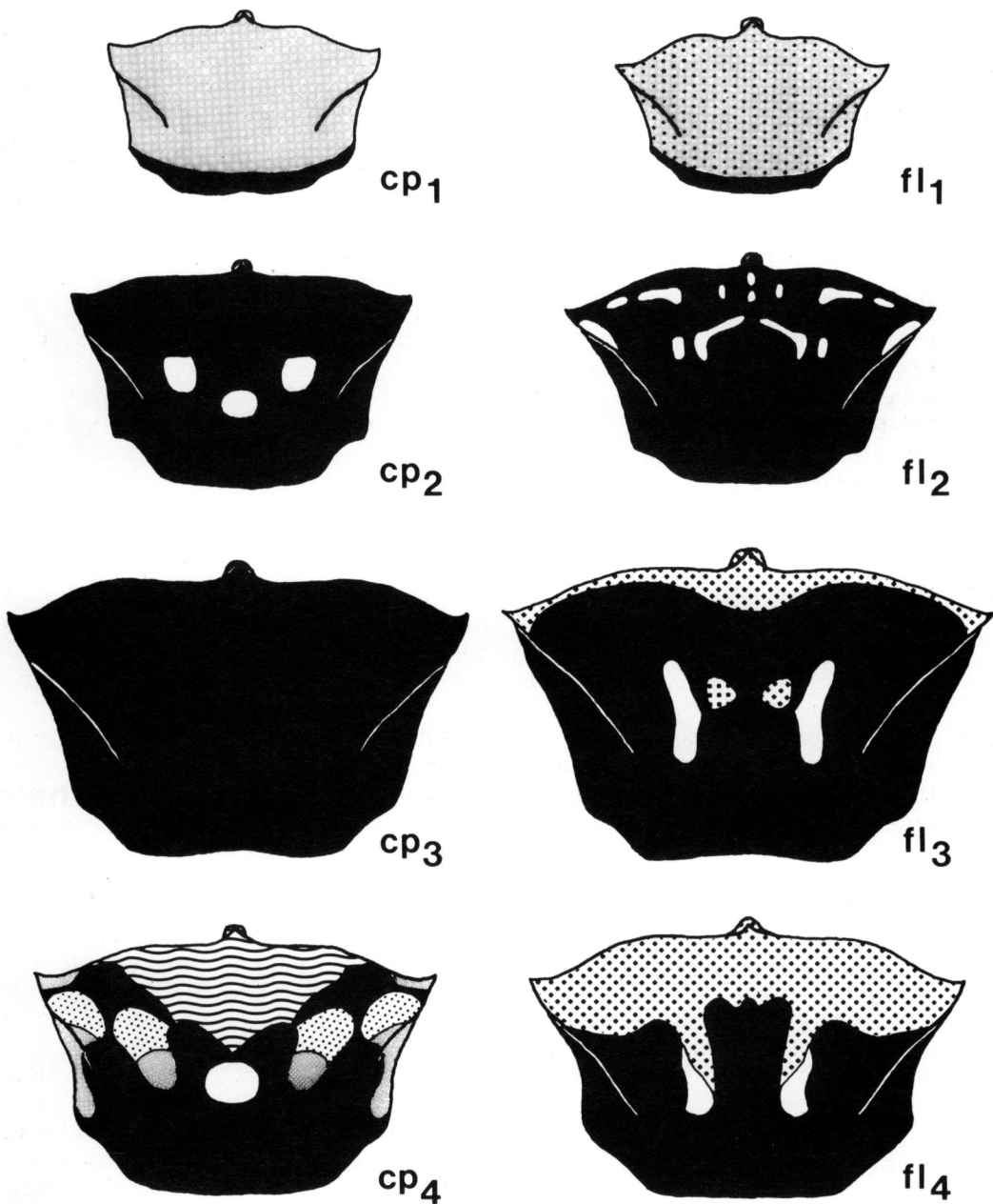
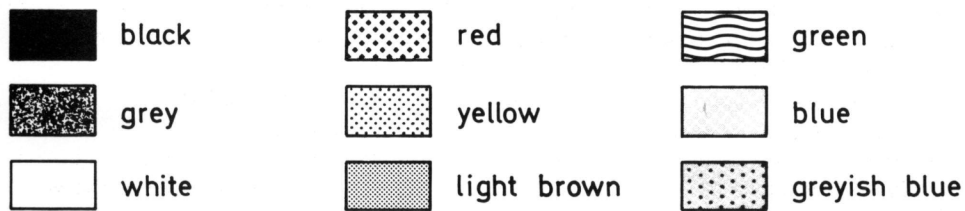
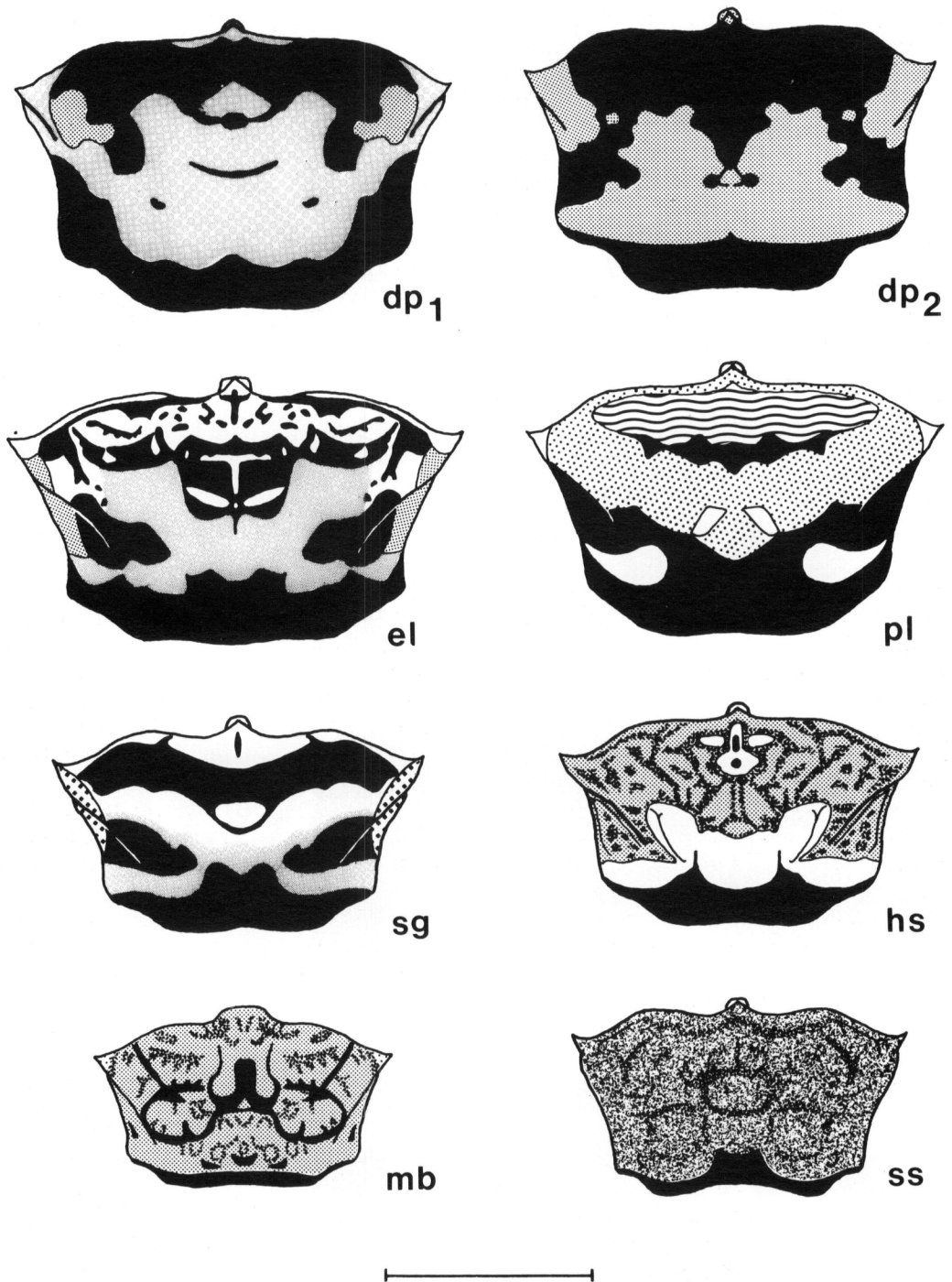


Fig. 2. Typical colour pattern of carapaces in live *Uca* individuals from Darwin (cp<sub>1</sub>, cp<sub>2</sub>, fl<sub>1</sub>, fl<sub>2</sub>, juvenile male; cp<sub>3</sub>, fl<sub>3</sub>, adult male; cp<sub>4</sub>, fl<sub>4</sub>, adult female). Explanation of abbreviations given in text. Scale line (at bottom of Fig. 3) 10 mm.



**Fig. 3.** Typical colour pattern of carapaces in live *Uca* individuals from Darwin (all adult male). Explanation of abbreviations given in text. Scale line 10 mm. Colour key as in Fig. 2.

come greyish green. The major cheliped turns, at least partly, orange or brownish.

The description of *U. capricornis* in George and Jones (1982) mainly refers to small males of the first two colour stages. However, the colour photo of a live *U. capricornis* (*sensu* George and Jones 1982: Fig. 55a) most probably represents a young specimen of *U. flammula* (see this species), because a male *U. capricornis* of this small size would still show yellow eyestalks and blue colours with less grey.

In the third or adult stage ("pavo-appearance") the carapace of both sexes may be male-like blackish (Fig. 2 cp<sub>3</sub>) with a few occasional lighter spots. Normally, however, there is a striking sexual dimorphism, as the female (Fig. 2 cp<sub>4</sub>) retains and refines much of the second colour stage. Most conspicuous is a triangular "scarf-like" field (yellow or green) near the upper margin of the carapace. The sexes frequently have in common a bluish or whitish spot at least on the posterior merus of the fourth walking leg - the last shared remains of their juvenile overall blue colour and the reason for the now-invalid name *U. pavo* (peacock). Perhaps this junior synonym of *U. capricornis* would not have been created, had not Crane (1975:33) explicitly denied this spot for all mature males.

The fact that older material from Darwin and Cobourg Peninsula (see above), previously identified as *U. dussumieri*, now proves to be *U. capricornis* by the shape of its gonopod (Fig. 4 cp<sub>4</sub>) revives the idea of allopatry of the two forms: *U. capricornis* as the Dampierian and *U. dussumieri* as the Solanderian species. Further weight to this idea is added by the result that "*U. capricornis*" from Queensland (*sensu* George and Jones 1982:21) is *U. coarctata* in reality (see comparative material).

### *Uca flammula* Crane

(Figs 2 fl, 4 fl)

*Uca* (*Deltuca*) *coarctata flammula* Crane, 1975:56 (type locality Darwin, N.T.).

*U. flammula* - George and Jones 1982:40.

*Uca coarctata* - George and Jones 1982:37 (part: material from Darwin, N.T.).

**Material.** NORTHERN TERRITORY: Darwin, 1914, QM W3015, part: cf. *U. capricornis*, 2 male (22.1 - 24.9 mm), 1978, ex WAM 105-78, 1 male (15.8 mm), 1978, ex

WAM 107-78, 1 male (15.6 mm), 1986, ZCMU 512, 55 male (7.4 - 31.4 mm), 36 female (11.1 - 25.7 mm).

**Comparative material of *U. coarctata* (H. Milne Edwards).** QUEENSLAND: Brisbane River, 1986, ZCMU 5110, 10 male (15.9 - 27.8 mm), 6 female (14.1 - 21.6 mm).

**Distribution.** Northwest and north Australia, according to Crane (1975) also parts of west New Guinea.

**Main localities of study.** Upper Ludmilla Creek, Ludmilla Creek Marina, Elizabeth River.

**Remarks.** This most conspicuous and biggest of all Darwin fiddler crabs is subject to an ontogenetic colour change that is not less dramatic than the one in *U. capricornis*. Unfortunately, Crane (1975:54) mentions with respect to both subspecies of *U. coarctata* (i.e. including *flammula*) that "males, females, and immature crabs are similarly colored".

Juvenile crabs (Fig. 2 fl<sub>1</sub>) appear uniform light greyish blue, except for the darker eyestalks and the male's pale yellow major cheliped. As these males have no trace of red colour and are already very active in waving display they can easily be mistaken for a species of their own. On the other hand, they can be confused with juvenile *U. capricornis*. These, however, have yellow eyestalks instead of dark blue ones.

During an intermediate colour stage (Fig. 2 fl<sub>2</sub>) the carapace turns black (at least the posterior regions) at first being mottled with a variety of lighter marks, which are usually of more irregular shape than in *U. capricornis*. All appendages gradually become brownish to orange with the male's major cheliped being in advance.

At the final stage (Fig. 2 fl<sub>3</sub>) the appendages (except for the major dactyl of the male) and all underparts of the crab have become bright orange red to scarlet. This colour extends to the orbits and eyestalks and to the anterior eighth (male) to quarter (female) of the otherwise black carapace. The black region can still be interrupted by brighter spots. Typically there are at least two comma-like vertical marks (white or red or a combination as depicted for the female, Fig. 2 fl<sub>4</sub>).

Because of their characteristic colour pattern, living individuals of *U. flammula* are easily separated from *U. coarctata* (which look more like *U. capricornis*). However, the

identification of isolated preserved specimens can be a very difficult task. The male gonopods of the two species are very similar (Fig. 4 fl, cc) and thus not reliable. The subdistal tooth of the major dactyl (large and hook-like in *U. coarctata* only, Crane 1975) is not yet present in young males and a distinct row of granules on the orbital floor (thought to be diagnostic for *U. coarctata*) can also be present in *U. flammula*: it was found in one male out of 55 and seven females out of 36 within the *flammula*-like coloured Darwin material collected in 1986. In addition, six males and no less than 12 females have at least a few orbital granules.

As the Darwin specimens of "*U. coarctata*" of 1978 (*sensu* George and Jones 1982:40) were identified from preserved, mainly immature material, on the base of the accessory granules these specimens cannot serve as a proof for the presence of the species in Darwin. Though we were not able to re-examine the material from Goomadeer River (George and Jones 1982:40), we return to the assumption that *U. coarctata* is a Solanderian species, which does not occur in northwest and north Australia.

#### *Uca dampieri* Crane

(Figs 3 dp, 5 dp)

*Uca (Thalassuca) vocans dampieri* Crane, 1975:91 (type locality Broome, W.A., Crane 1975:597, not Darwin as indicated by Crane 1975:89).

*Uca dampieri* – George and Jones 1982:67.

*Uca vomeris* – George and Jones 1982:70 (part: material from Darwin).

**Material.** NORTHERN TERRITORY: Darwin, 1978, ex WAM 146–78, 2 male (16.2 – 19.8 mm), 1978, ex WAM 274–79, 2 male (14.4 – 15.0 mm), 1 female (17.2 mm), 1986, ZCMU 513, 36 male (7.4 – 24.0 mm), 17 female (12.2 – 20.5 mm). WESTERN AUSTRALIA: Broome, 1963, USNM 137671, holotype of *U. vocans dampieri*, 1 male (19.0 mm).

**Comparative material of *U. vomeris* McNeill.** QUEENSLAND: Sabai Island, Torres Strait, AM P31745, P31758, 17 male (10.0 – 21.3 mm), 13 female (13.4 – 19.5 mm); Yam Island, Torres Strait, 1976, AM P31747, P31759, P31760, P31995, 21 male (9.2 – 22.1 mm), 12 female (9.0 – 17.2 mm); Shorncliffe, 1986, ZCMU 5111, 6 male (11.5

– 21.0 mm), 3 female (8.8 – 15.3 mm); Brisbane, 1981, WAM 120–81, 4 male (23.1 – 29.2 mm), 1 female (21.5 mm).

**Distribution.** Northwest and north Australia.

**Main localities of study.** Ludmilla Creek Marina, Buffalo Creek.

**Remarks.** The male gonopod of *U. dampieri* (Fig. 5 dp) is very dissimilar to that of the closely related *U. vomeris* (Fig. 5 vm) the latter gonopod being strongly twisted anti-clockwise and having the palp (thumb) in a distal instead of a subdistal position (Crane 1975). Any attempts to find other reliable morphological characters for separating the two species (Crane 1975; George and Jones 1982) have failed until now – apparently, because of the variability of the two forms, particularly of *U. dampieri*.

The carapace of *U. dampieri* is greyish brown in juveniles. In adults, it can be either mostly blue (Fig. 3 dp<sub>1</sub>) or mostly light brown to cream (Fig. 3 dp<sub>2</sub>) with various combinations of the two colours and black or dark grey patterns in addition. In the course of colour brightening during low tide, most of the animal, except for the chelae and walking legs, may turn white. This is not confined to males, but also occurs in females (cf. a similar brightening of colours in females of the related eastern Pacific *U. stylifera*, von Hagen 1968:444–445).

The shape of the major cheliped of the male is, likewise, subject to a strong variation, especially with respect to the subdistal triangular projection on the upper margin of the pollex. This tooth can be small (as in the holotype) or even absent in *U. dampieri*, but it can be huge as well.

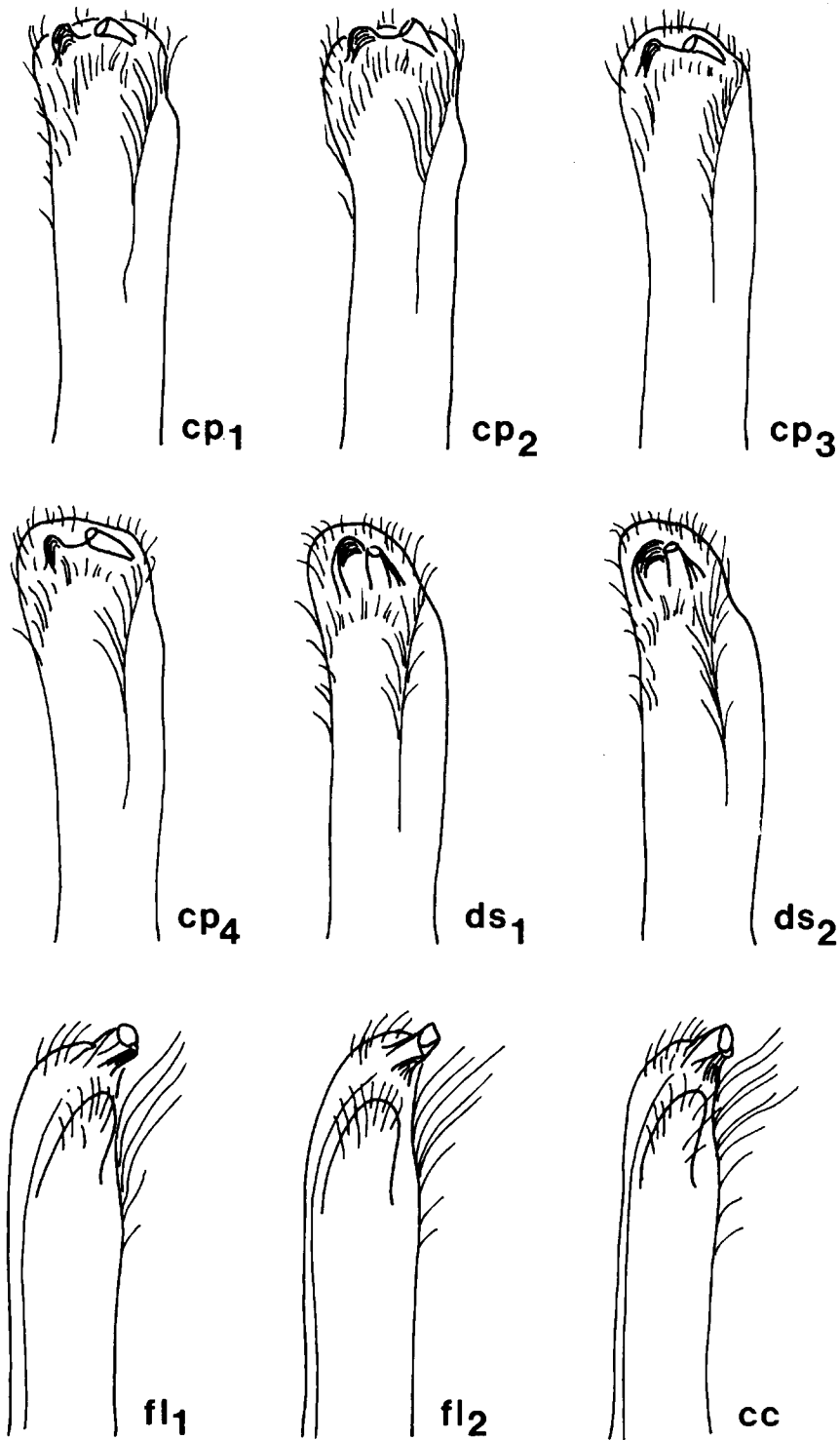
When relying on the shape of the gonopod only, all alleged *U. vomeris* from Darwin turn out to belong to *U. dampieri*. Though we were unable to re-examine the material from Liverpool River (George and Jones 1982:73), we conclude that *U. vomeris* is absent from northwest Australia (as was generally thought prior to the publication of George and Jones 1982). Its presence is, however, confirmed for the islands of Torres Strait mentioned above (see comparative material).

#### *Uca elegans* George and Jones

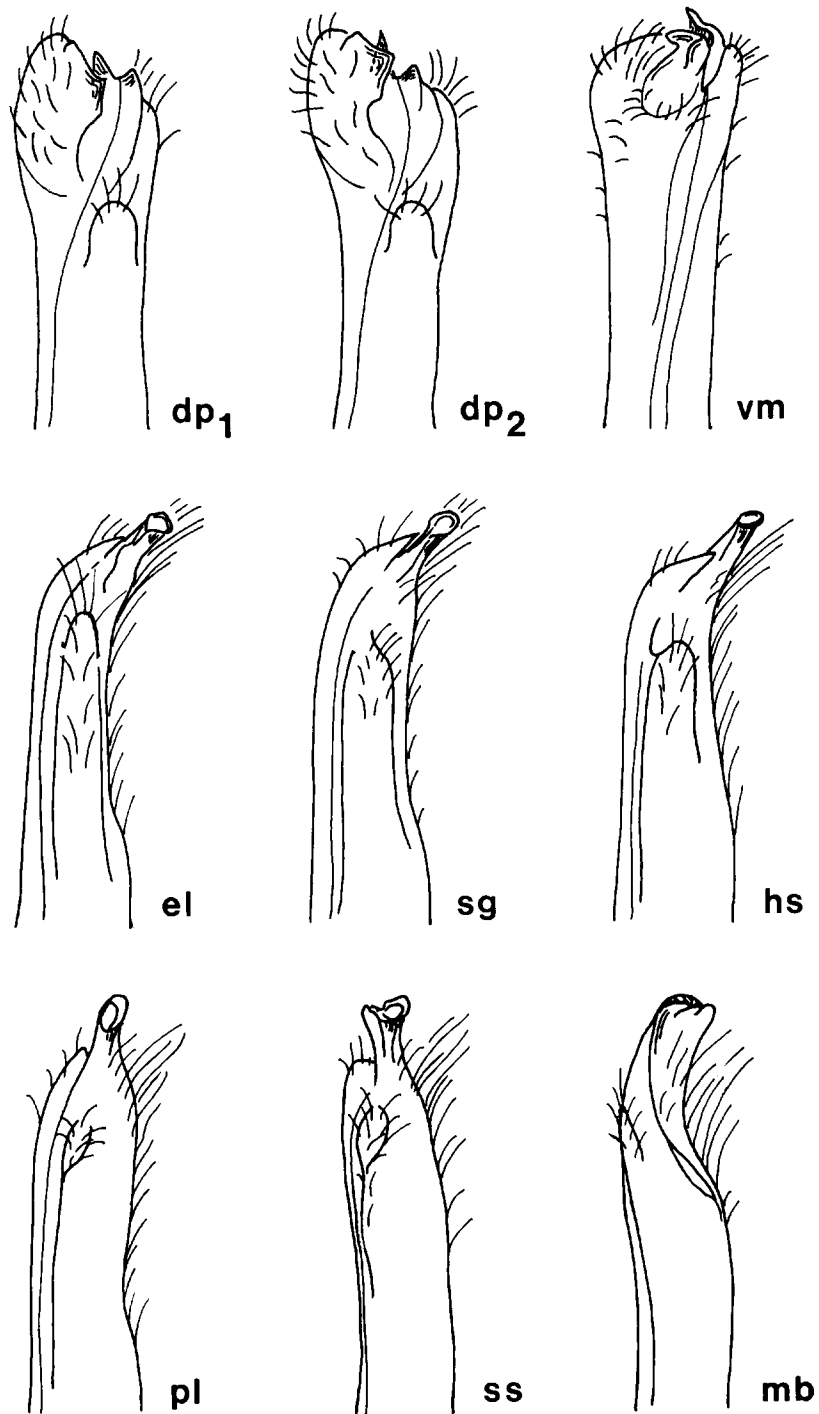
(Figs 3 el, 5 el)

*Uca elegans* George and Jones, 1982:22 (type locality Derby, W.A.).





**Fig. 4.** Terminal portions of male right gonopods (first pleopods) in lateral (outer) view (drawings at top and centre) and sternal (anterior) view (at bottom), respectively. Explanation of abbreviations given in text. Figures (in mm) refer to carapace width. cc 22.2 (Brisbane River 1986); cp<sub>1</sub> 23.0 (Darwin 1986, typical "pavo-appearance"); cp<sub>2</sub> 24.0 (holotype); cp<sub>3</sub> 12.6 (Darwin 1978); cp<sub>4</sub> 20.9 (Darwin 1914, alleged *U. dussumieri*); ds<sub>1</sub> 29.9 (Cairns 1961); ds<sub>2</sub> 21.6 (Kuta, Bali 1983); fl<sub>1</sub> 19.0 (Darwin 1986); fl<sub>2</sub> 15.6 (Darwin 1978, alleged *U. coarctata*).



**Fig. 5.** Terminal portions of male right gonopods in sternal (anterior) view. Explanation of abbreviations given in text. Figures (in mm) refer to carapace width.  $dp_1$  19.8 (Darwin 1978, alleged *U. vomeris*);  $dp_2$  18.9 (holotype); el – ss (Darwin 1986); el 22.0; hs 17.0; mb 14.9; pl 21.3; sg 17.1; ss 17.2; vm 19.6 (Shorncliffe, Qld. 1986).

**Material.** NORTHERN TERRITORY: Darwin, 1986, ZCMU 514, 75 male (10.3 – 24.8 mm), 33 female (10.2 – 20.0 mm).

**Comparative material of *U. australiae* Crane.** WESTERN AUSTRALIA: Broome, 1911, USNM 64250, holotype of *U. demani australiae*, 1 male (about 25.0 mm).

**Distribution.** Northwest and north Australia.

**Main localities of study.** Upper Ludmilla Creek, mouth of Ludmilla Creek, Mickets Creek.

**Remarks.** Judged from the colour pattern of the carapace (Fig. 3 el, cf. with sg), from the waving display (von Hagen, in prep.) and from several morphological characters (including the shape of the gonopod, Fig. 5 el, cf. with sg and hs), *U. elegans* is close to *U. signata* and *U. hirsutimanus* and not a member of the *dussumieri-capricornis* assemblage as was, in view of the two dactyl grooves, originally assumed by George and Jones (1982).

*U. elegans* was compared with the single male (holotype) that exists of *U. australiae* (from Broome, collected by E. Mjöberg in 1911), because in both taxa the gape of the minor cheliped is provided with a conspicuous series of setae distally. For the rest, however, *U. australiae* is unlike *U. elegans*, especially in the shape of its gonopod.

***Uca signata* (Hess)**

(Figs 3 sg, 5 sg)

*Gelasimus signatus* Hess, 1865:146 (type locality Australia).

*Uca (Australuca) bellator signata* – Crane 1975:67.

*Uca (Australuca) bellator minima* Crane, 1975:68 (type locality Darwin; regarded as a synonym of *U. signata* already by George and Jones 1982:44).

*Uca signata* – George and Jones 1982:44.

**Material.** NORTHERN TERRITORY: Darwin, 1956, USNM 137668, holotype of *U. bellator minima*, 1 male (10.0 mm); 1986, ZCMU 515, 78 male (7.9 – 17.7 mm), 42 female (7.9 – 14.7 mm).

**Distribution.** From northwest to northeast Australia.

**Main localities of study.** Upper Ludmilla Creek, Mickets Creek.

**Remarks.** George and Jones (1982) are correct in concluding that Crane's specimens

of *U. bellator minima* are juveniles of *U. signata*. At least one of the other juveniles they used for comparison came from Townsville (George and Jones 1982: Tab. 4) so that *U. minima* was compared also with *U. signata* from the east coast of Australia. However, the problem of possible differences between eastern and northwestern populations of *U. signata* has never been made an explicit research topic of its own. In case essential differences of behaviour or colour will be found in future, one might make use of Crane's subspecific name *minima* for the Dampierian populations.

***Uca hirsutimanus* George and Jones**

(Figs 3 hs, 5 hs)

*Uca hirsutimanus* George and Jones, 1982:49 (type locality Derby, W.A.).

**Material.** NORTHERN TERRITORY: Darwin, 1986, ZCMU 516, 36 male (8.3 – 18.0 mm), 30 female (8.9 – 16.1 mm).

**Distribution.** Northwest and north Australia, Torres Strait.

**Main localities of study.** Mickets Creek, Elizabeth River, Ludmilla Creek.

**Remarks.** Except for the colour (Fig. 3 hs), *U. hirsutimanus* is very much like *U. signata*. The two species live sympatrically west of Cape York only. Interspecific differences were listed by George and Jones (1982: Tab. 5). A supplementary character is the different inclination of the terminal tube of the male gonopod (see key and Fig. 5 hs).

***Uca polita* Crane**

(Figs 3 pl, 5 pl)

*Uca (Australuca) polita* Crane, 1975:72 (type locality Gladstone, Qld.).

*Uca polita* – George and Jones 1982:60.

**Material.** NORTHERN TERRITORY: Darwin, 1986, ZCMU 517, 51 male (9.8 – 23.4 mm), 14 female (13.0 – 21.0 mm). QUEENSLAND: Shorncliffe, 1986, ZCMU 5112, 1 male (16.1 mm).

**Comparative material of *U. longidigitum* (Kingsley).** QUEENSLAND: Brisbane River, 1986, ZCMU 5113, 26 male (8.1 – 19.5 mm), 8 female (7.5 – 14.2 mm).

**Distribution.** From northwest to northeast Australia.

**Main locality of study.** Ludmilla Creek Marina.

**Remarks.** Most characteristic of the colour pattern of *U. polita* are the two large white or cream eye-like spots of the posterior carapace and the frequent occurrence of greenish colours in the anterior carapace regions (Fig. 3 pl). Related colours and patterns can be found in large specimens of the eastern form *U. longidigitum*; (the nomenclatural change to "*longidigita*" by Crane 1975 is an incorrect subsequent spelling, because *longidigitum* is not an adjective). This fact and the common loss of distinct grooves on outer pollex and palm of the major cheliped indicate a close relationship between the two species. The treatment of *U. longidigitum*, like *U. signata*, as a subspecies of *U. bellator* (see Crane 1975) is misleading.

***Uca seismella* Crane**  
(Figs 3 ss, 5 ss)

*Uca (Australuca) seismella* Crane, 1975:70 (type locality Darwin, N.T.).

*Uca seismella* – George and Jones 1982:56.

**Material.** NORTHERN TERRITORY: Darwin, 1986, ZCMU 518, 37 male (3.4 – 17.2 mm), 18 female (5.7 – 12.4 mm).

**Distribution.** From northwest to northeast Australia.

**Main localities of study.** Ludmilla Creek Marina, Cullen Beach.

**Remarks.** This is the smallest and most fragile of Australian narrow fronts. It is also the most cryptic (Fig. 3 ss), although its display is extremely conspicuous. This display was filmed not only in Darwin but also on the banks of the Brisbane River, close to the Botanical Gardens of Brisbane City in August, 1986. Although the crab itself was not collected, this cinematographic sample confirms the extension of the species' geographic range: the previous southernmost record was the Mary River (George and Jones 1982).

In the material from Darwin the terminal tube of the male gonopod (Fig. 5 ss) is provided with a definite flexible mesial keel, which is not mentioned by previous authors.

***Uca mjobergi* Rathbun**  
(Figs 3 mb, 5 mb)

*Uca mjobergi* Rathbun, 1924:9 (type locality Broome, W.A.).

*Uca (Celuca) lactea mjobergi* – Crane 1975:299.

*Uca mjobergi* – George and Jones 1982:80.

**Material.** NORTHERN TERRITORY: Darwin, 1986, ZCMU 519, 39 male (5.4 – 15.0 mm), 37 female (7.7 – 11.7 mm).

**Distribution.** Northwest and north Australia, according to Crane (1975) also northwest New Guinea.

**Main localities of study.** Mouth of Ludmilla Creek, Ludmilla Creek Marina, Buffalo Creek.

**Remarks.** This is the only broad-fronted species that occurs in Darwin (*U. triangularis* is known from Melville Island only, George and Jones 1982). Both the brownish marbled carapace (Fig. 3 mb) and the canary yellow cheliped may be considered cryptic, the former imitating sand, the latter yellow mangrove leaves (cf. a similar colour correspondence in the neotropical *U. thayeri*, von Hagen 1978).

The spelling "*mjobergi*" (Crane 1975) is not in conformity with the International Code of Zoological Nomenclature (1985, Art. 32) and should be replaced by the spelling *mjoebergi*.

## DISCUSSION

The studies of Crane (1975), George and Jones (1982) and the corrections mentioned in the present paper provide the following zoogeographic assumptions:

1. There are 16 species of *Uca* confirmed for the Australian fauna; *U. australiae* Crane and *U. crassipes* (Adams and White)<sup>1</sup> should be omitted until further specimens have been discovered (George and Jones 1982). Although the exact boundaries are not yet known for each species, it seems warranted to suppose that 12 of the 16 species are strictly or mainly confined to one of the two northern biogeographic provinces (Dampierian and Solanderian *sensu* Hedley 1904) as indicated in Table 1, section I. Of these 12 species, six are members of the Dampierian province (northwest and north coasts, west of Torres Strait), six others seem to be confined (now again cf. George and Jones 1982) to the northeast coasts, the Solanderian province, with *U. perplexa* and *U. vomeris* occurring also south of Queensland. Only four species (Tab. 1, section II) are bilat-

1. Note added in proof: *U. crassipes* has since been discovered in Cairns (von Hagen, in prep.)

**Table 1.** Occurrence of the 16 confirmed Australian species of *Uca* in the two tropical zoogeographic provinces.

	Dampierian province	Solanderian province
I. Species occurring in one province		
a) Species forming pairs	<i>U. capricornis</i> <i>U. flammula</i> <i>U. dampieri</i> <i>U. mjoebergi</i>	<i>U. dussumieri</i> <i>U. coarctata</i> <i>U. vomeris</i> <i>U. perplexa</i>
b) Species not forming pairs	<i>U. elegans</i> <i>U. hirsutimanus</i>	<i>U. longidigitum</i> <i>U. tetragonon</i>
II. Species occurring in both provinces	<i>U. polita</i> <i>U. seismella</i> <i>U. signata</i> <i>U. triangularis</i>	

eral, i.e. members of both provinces ("circum-tropical" *sensu* Davie 1985).

- Eight of the 16 species mentioned are endemic to Australia (*U. capricornis*, *U. dampieri*, *U. elegans*, *U. hirsutimanus*, *U. longidigitum*, *U. polita*, *U. seismella*, *U. signata*) and three others are endemic at least to Australasia (*U. flammula*, *U. mjoebergi*, *U. vomeris*, see Crane 1975). Six of these 11 endemic species occur only in the Dampierian province. This fact gave rise to the idea "that northwestern Australia has been a major region of speciation for the genus *Uca* and this region has been efficiently isolated from the east coast" (Davie 1985: 263-264).
- Four of the Darwin species that now appear to be Dampierian endemics have closely related eastern counterparts. The species pairs resulting are illustrated in section I a of Table 1. All these pairs seem to occur in an allopatric pattern of distribution, presumably separated by the Torres Strait region. However, to give these forms only subspecific rank (as Crane 1975 did) would be unwise for the following practical reasons: (a) There might exist at least small zones of overlap, not yet known, within the Cape York region. (b) Even without any local overlap it holds true that all these forms are well defined by different morphological characters including different colour patterns. In the future there may be an urgent need to use the subspecific rank in order to distinguish between less well-defined local forms within some of the eight species mentioned, i.e. within a certain Australian province or within the vast range of the

three non-endemic partners *U. coarctata*, *U. dussumieri* and *U. perplexa*. Use of the subspecific rank may also be desirable when more essential differences are found between western and eastern populations of the bilateral species (Tab. 1, section II). Any differences found within these species are predicted to be of less weight than those within the pairs of species mentioned in Table 1, section Ia.

#### ACKNOWLEDGEMENTS

The practical work underlying this study was supported by the Northern Territory Museum of Arts and Sciences, Darwin, which provided a field vehicle and arranged an excursion by boat. The senior author and his wife wish to thank Dr A.J. Bruce and Mr R. Hanley (both: NT Museum) and Mr P. Davie (Queensland Museum, Brisbane) for their assistance. Dr R.B. Manning (U.S. National Museum, Washington) sent type material of *Uca*. Prof. Dr L.B. Holthuis (Rijksmuseum, Leiden) gave advice on questions of nomenclature, Mrs S. Götzfried (Marburg) made the drawings of the carapace patterns.

#### REFERENCES

- Bruce, A.J. 1975. Coral reef shrimps and their colour patterns. *Endeavour* (Oxford) **34**: 23-27.
- Crane, J. 1975. *Fiddler crabs of the world. Ocypodidae: genus Uca*. Princeton University Press: Princeton.
- Davie, P.J.F. 1985. The biogeography of littoral crabs (Crustacea: Decapoda; Brachyura) associated with tidal wetlands in tropical and subtropical Australia. In: K.N. Bardsley and C.D. Woodroffe (eds) *Coasts and tidal wetlands of the Australian monsoon region*. North Australia Research Unit Mangrove Monograph **1**: 259-275. Australian National University: Canberra.
- George, R.W. and Jones, D.S. 1982. A revision of the fiddler crabs of Australia (Ocypodidae: *Uca*). *Records of the Western Australian Museum Supplement* **14**: 1-99.
- Hagen, H.O. von 1968. Studien an peruanischen Winkerkrabben (*Uca*). *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* **95**: 395-468.
- Hagen, H.O. von 1976. Review of: J. Crane 1975 *Fiddler crabs of the world. Ocypodidae: genus Uca. Crustaceana* **31**: 221-224.
- Hagen, H.O. von 1978. Wo Krabben auf die Bäume steigen. Im Mangrove-Dschungel Trinidads. *Das Tier* **18**: 8-10.

- Hedley, C. 1904. The effect of the Bassian isthmus upon the existing marine fauna: a study in animal geography. *Proceedings of the Linnean Society of New South Wales* **28**: 876-883.
- Hess, W. 1865. Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens. *Archiv für Naturgeschichte* **31**: 127-173.
- International Code of Zoological Nomenclature*. 1985. 3rd ed. International Trust for Zoological Nomenclature, H. Charlesworth and Co., Huddersfield.
- Knowlton, N. 1986. Cryptic and sibling species among the decapod Crustacea. *Journal of Crustacean Biology* **6**: 356-363.
- Manning, R.B. and Holthuis, L.B. 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* **306**: 1-379.
- Rathbun, M.J. 1924. Brachyura, Albuneidae and Porcellanidae. Results from Dr. E. Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. *Arkiv för Zoologi* **16**(23): 1-33.

Accepted 12 April 1989