

Vibration signals in Australian fiddler crabs - a first inventory

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ABSTRACT

Vibration signals (often called sounds), which are components of the subterranean communication system of fiddler crabs, were recorded in 14 of the 17 confirmed *Uca* species of Australia and analysed by use of oscillograms. Signals of the related crab *Heloecius cordiformis* and two Asian species of *Uca* were used for comparisons. All crabs studied produce "bounces", i.e. burst-pulsed sounds corresponding to laterally directed jerks of the whole animal. All species except *H. cordiformis*, *U. dampieri* and *U. vomeris* also emit "drumwhirls" or "rolls", the familiar rapping sounds of the major cheliped. Parameters of these drumwhirls were compared using aquarium sound recordings of males competing for a burrow. Indications of character displacement were found with regard to western and eastern samples of *U. signata*. The most advanced rapping signals were recorded in *U. signata* and *U. flammula* and in the two Asian species, *U. rosea* and *U. annulipes*; the most simple ones were recorded in *U. longidigitum* and *U. polita*. The two latter appear to have preserved early stages of drumwhirl evolution, contributing to the assumption of an Australian origin of the genus *Uca*.

KEYWORDS. Crustacea, Brachyura, Ocypodidae, *Uca* and *Heloecius*, vibration signals, survey, early stages of evolution, Australian origin of *Uca*.

INTRODUCTION

Crabs inhabiting the semiterrestrial environment—mainly Sesarminae (Grapsidae) and the subfamilies of the Ocypodidae—are well-known examples of communication by vibration signals. Various types of such signals have been reported in literature (see preliminary synopsis in von Hagen 1975), the most important ones being generated by percussion and stridulation. Most research on signal production, transmission and reception has been done in fiddler crabs (*Uca*) and ghost crabs (*Ocypode*) (see Salmon 1983 for a review).

It is not clear to date, how often vibration signalling arose independently in the two crab families mentioned. It is certain, however, that vibration signals are used in both agonistic and courtship situations and occur mostly underground or at least in or near the mouth of the crab's burrow. Being short-range signals, vibrations appear to play a major role in reproductive isolation. At least in two West Indian sympatric and sibling species of *Uca*, vibration signals were found to be much more species-specific than the visual display (von Hagen 1984). As the signals can also have group-specific characters, they allow various phylogenetic inferences (von Hagen 1975, 1984), especially when these inferences are based on quantitative data.

Until now, quantitative studies of *Uca* bioacoustics have mainly dealt with the European fiddler crab *U. tangeri* (von Hagen 1962; Altevoigt 1963, 1970) and American species of both the Atlantic (Salmon 1965, 1983; Salmon and Horch 1972; von Hagen 1984) and Pacific coasts (Altevoigt 1970; Müller 1989). R. Polivka (pers. com.) started a bioacoustic project on fiddler crabs of South East Asia, but did not complete and publish his studies. With respect to Australia, pertinent research seems to be lacking.

In the course of two visits to Australia, the author had the opportunity to record subterranean vibration signals of nearly all Australian species of *Uca* and of the related ocypodid *Heloecius cordiformis*. The recordings were obtained using a special aquarium that allowed direct observation of the crabs during sound production (cf. von Hagen 1970, 1984). The oscillographic analyses published here are meant to serve as a first survey or inventory and thus as a basis for more specific research in future.

With a few exceptions, the vibration signals of Australian fiddlers are simple, especially when compared with the two Asian species included in this study. This result allows certain speculations: that some Australian *Uca* species have preserved an early stage of acoustic communication (early with respect to the whole genus) and that the genus probably originated in Australia.

Table 1. Abbreviations, systematic grouping, scientific names and Australian distribution of the species and origin of the samples studied. Roman group numerals of *Uca* as in George and Jones (1982); in parentheses: subgeneric names from Crane (1975), invalid except *Australuca*. Distribution in Australia: C circum-tropical, E eastern, W western.

Genus <i>Heloecius</i> :			
Hc	<i>H. cordiformis</i> (H. Milne-Edwards)	E	Brisbane
Genus <i>Uca</i> , group IV (" <i>Thalassuca</i> "):			
dp	<i>U. dampieri</i> Crane	W	Darwin
vm	<i>U. vomeris</i> McNeill	E	Bamaga, Brisbane
Genus <i>Uca</i> , group III (<i>Australuca</i>):			
lg	<i>U. longidigitum</i> (Kingsley)	E	Brisbane
pl	<i>U. polita</i> Crane	C	Broome, Cairns, Darwin
hs	<i>U. hirsutimanus</i> George and Jones	W	Broome, Darwin
sg	<i>U. signata</i> (Hess)	C	Cairns, Darwin
el	<i>U. elegans</i> George and Jones	W	Darwin
ss	<i>U. seismella</i> Crane	C	Broome, Darwin
Genus <i>Uca</i> , groups I and II (" <i>Deltuca</i> "):			
cp	<i>U. capricornis</i> Crane	W	Bamaga, Darwin
ds	<i>U. dussumieri</i> (H. Milne-Edwards)	E	Bamaga, Cairns
fl	<i>U. flammula</i> Crane	W	Broome, Darwin
cc	<i>U. coarctata</i> (H. Milne-Edwards)	E	Brisbane
rs	<i>U. rosea</i> (Tweedie)	-	Penang and Malakka (Malaysia)
Genus <i>Uca</i> , group V (" <i>Celuca</i> "):			
mb	<i>U. mjoebergi</i> Rathbun	W	Broome, Darwin
pp	<i>U. perplexa</i> (H. Milne-Edwards)	E	Bamaga, Cairns
an	<i>U. annulipes</i> (H. Milne-Edwards)	-	Bombay (India)

ANIMALS AND METHODS

Species names and localities of the specimens are given in Table 1. The endemic Australian ocyropodid crab *Heloecius cordiformis*, lately placed in a subfamily of its own (Heloeciinae Türkay 1983), was studied in the northern part of its range, which ends at Rockhampton (Davie pers. comm). The present knowledge of the geographic ranges of the Australian *Uca*, as specified in von Hagen and Jones (1989), is also briefly indicated in the Table.

Table 1 lists 14 of the 17 species of *Uca* confirmed for the Australian fauna (only *U. crassipes*, *U. tetragonon* and *U. triangularis* were not studied). As the discussion about the extent and proper naming of the species groups is not yet settled, Table 1 follows the grouping of George and Jones (1982) by Roman numerals; only *U. elegans* is transferred from group I to group III and the order of groups has been altered (see Discussion). In addition the subgeneric names from Crane's monograph (1975) are listed, which are widely in use though mostly (except *Australuca*) invalid because

of Bott (1973). The abbreviations of species names (Table 1) are used also in Figures 1 and 2.

The two Asian species, *U. rosea* and *U. annulipes*, included in the list, were collected by travelling students, and the sounds were recorded in Germany. The Australian species were studied at the places listed in Table 1 during July and August of the years 1986 and 1988. Outdoor recordings of subterranean signals of crabs are useful on certain occasions, but normally do not allow statements on how the sounds are generated (von Hagen 1975). Therefore, the signals were recorded indoors in aquaria (12 l, height 20.5 cm), which, using the technique of von Hagen (1970, 1984), allowed direct observation of subterranean activities of the crabs. Bricks were laid in the centre of the aquaria and only the narrow gap between these bricks and the plastic walls were filled with moist muddy sand from the habitat of the animals. The crabs were forced to dig their burrows within this thin vertical layer of soil and were observed, at very close quarters, through the wall, which had to be kept clean.

Though also called "sounds", the signals recorded act as substrate-borne vibrations; the air-borne

Table 2. Burst-pulsed sounds ("bounces") measured in males of *Heloeius cordiformis* and four Australian *Uca* species (repetition rates calculated from means of preceding column).

Species	One bounce: seconds		Sequences: maximum number of bounces	One bounce plus subsequent silent interval: seconds		Repetition rate: bounces per second	Number of bounces measured (males)
	mean	s.d.		mean	s.d.		
<i>H. cordiformis</i>	0.30	± 0.10	3	0.64	± 0.24	1.56	22 (2)
<i>U. vomeris</i>	0.12	± 0.04	15	0.39	± 0.19	2.56	23 (2)
<i>U. seismella</i>	0.07	± 0.02	43	0.19	± 0.02	5.26	64 (5)
<i>U. coarctata</i>	0.25	± 0.08	4	0.57	± 0.13	1.75	21 (3)
<i>U. mjoebergi</i>	0.20	± 0.06	6	0.69	± 0.14	1.45	64 (5)

components are only by-products. Therefore, a Brüel and Kjaer accelerometer (type 4368) was used as a vibration pick-up system. The accelerometer, screwed to a 6.5 cm probing rod, was placed close to the crab's burrow and was connected to an Uher tape recorder (type 4200 Report Stereo IC) via a small preamplifier designed by the Institute of Applied Physics, Marburg (Dr. K.H. Wittich). The recordings were analysed in Marburg by examination of oscillograms obtained from a Philips oscilloscope PM 3231 in combination with a camera (Tönnies Recordine K-854).

The soil temperature ranged from 23 to 27.5 °C during the recordings (including the ones in Marburg). All crab individuals tested were of medium size when compared with the figures of maximum carapace width for each species (contained in Fig. 2). No special attempts were made to detect signals of females, which tend to be rare and more faint, when present (von Hagen 1984). Thus all data given in this paper refer to males. Mean values of the signals recorded were compared by a version of Student's t-test for heterogeneous variances and unequal sample sizes (L-test, Graf *et al.* 1966; cf. Zöfel 1992).

RESULTS

Main types of sounds. Nearly all of the signals analysed in this paper were recorded in an agonistic context, i.e. the accelerometer was placed close to the mouth of a burrow occupied by a crab ("owner"). A conspecific ("intruder") wandering about in the aquarium either detected the burrow spontaneously or was placed into the mouth of the burrow by the experimenter. In many of these situations one or both crabs emitted vibration signals, sometimes in an antiphonal manner (i.e. duetting with alternation). Sounds were either single ones or sequences of sounds (Fig. 1).

Most of the species tested (though not all) produced the usual percussive or rapping sounds or "rolls" of the

major cheliped, called "drumwhirls" in this paper and also by Salmon and Atsides (1968) and by Crane (1975), who also speaks of "major-manus-drum".

All species emitted signals that are regarded as "additional components" of acoustic behaviour (von Hagen 1984) and are, like respiration noises, normally not specifically searched for by investigators. These signals, called "bounces" in this paper and "leg-flicking" by Salmon and Horsch (1972), are "hoarse" burst-pulsed sounds that correspond to laterally directed jerks of the whole animal during its subterranean approach towards an opponent, often in a "testing" manner. These sounds are produced by the joint jerking motion of the flexed ambulatories and are rather irregularly shaped and spaced (e.g. Fig. 1 vm). By contrast, the drumwhirls of the major cheliped are highly stylized and "elaborate" signals (e.g. Fig. 1 sg) and are used not only in agonistic encounters, but also as courtship display.

"Bounces" (burst-pulsed sounds). Examples of sequences of bounces produced by *H. cordiformis* and *U. vomeris* are given in Figure 1 (Hc, vm; cf. Table 2). Bounces seem to form the only acoustic signals detectable in these two species and *U. dampieri* (not figured), though in *H. cordiformis* the bounces may be superimposed by more evenly shaped short ambulatory "trills", visible in the first and last signal of Figure 1 Hc and probably identical with the "ambulatory tapping" that Griffin (1968) observed in the field.

Bounces were found in all species of *Uca* studied, though not figured in all cases. Bounces (most often a single one) frequently precede drumwhirls (Fig. 1 hs₁, ds₂, fl₂, cc, rs, mb, pp, an), especially in the species of group V ("*Celuca*").

Some species (in addition to *H. cordiformis*, *U. vomeris* and *U. dampieri*) produce bounces in short or long sequences. Such sequences occur at least in *U. seismella*, *U. coarctata*, *U. mjoebergi* and *U. annulipes* (Fig. 1 ss₁, cc₁, mb₁, an₁). Of these, the Australian species

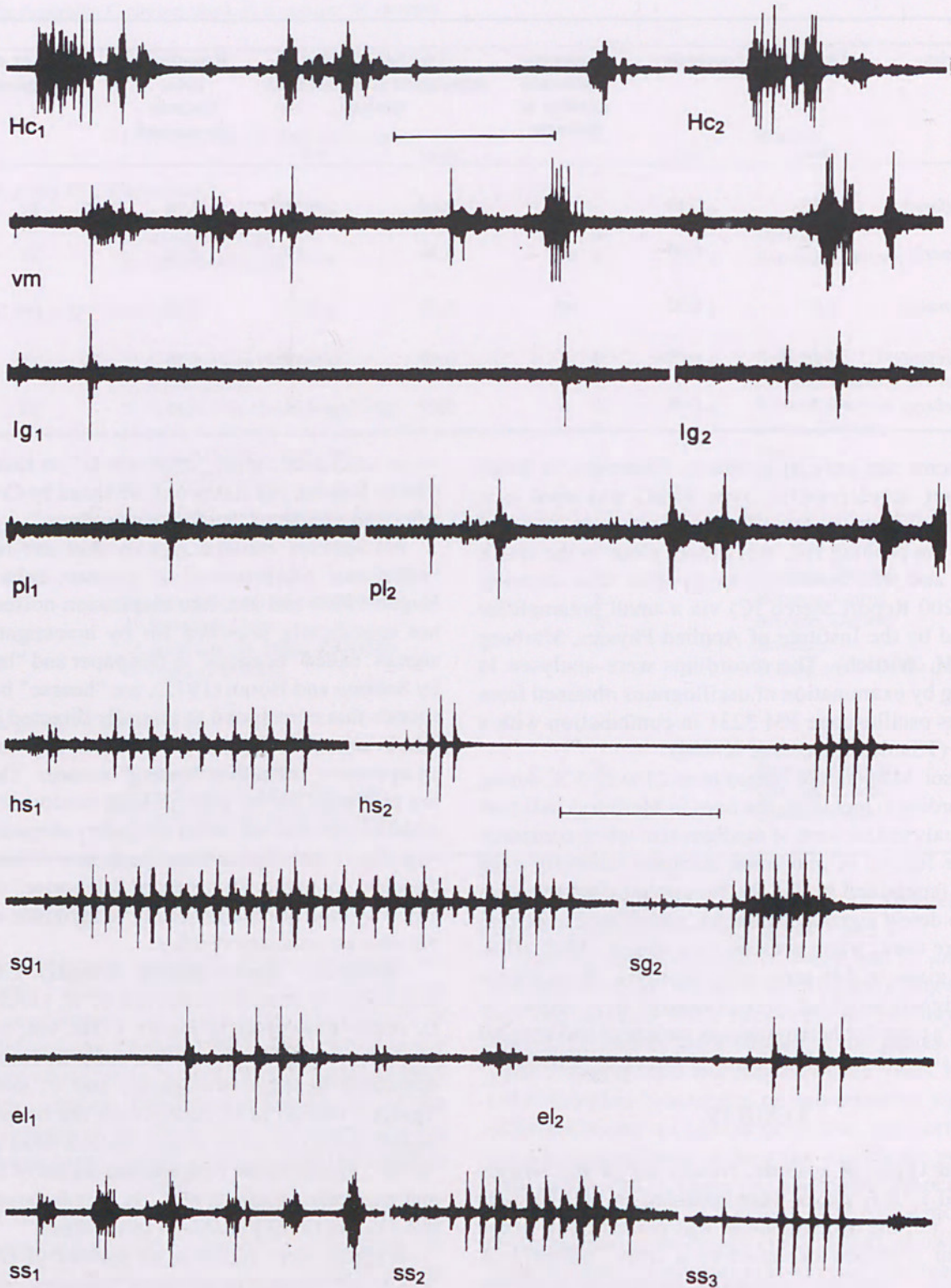


Fig. 1. Oscillographic samples of vibration signals of Australian *Uca* species, two Asian species (*U. rosea*, *U. annulipes*) and *Heloeius cordiformis*. Explanation of species name abbreviations given, in same order, in Table 1. Scale bars 0.5 seconds. Following part of legend lists type and number of signals: B, bounces; D, drumwhirls (with number of strokes in parentheses): *Hc*₁ and *Hc*₂, 4 B, first and last superimposed by ambulatory trills. - *vm*, 8 B. - *lg*₁, 2 D (1 each); *lg*₂, D (2). - *pl*₁, D (1); *pl*₂, 3 D (2 each). - *hs*₁, B + D (15); *hs*₂, 2 D (7 and 8).

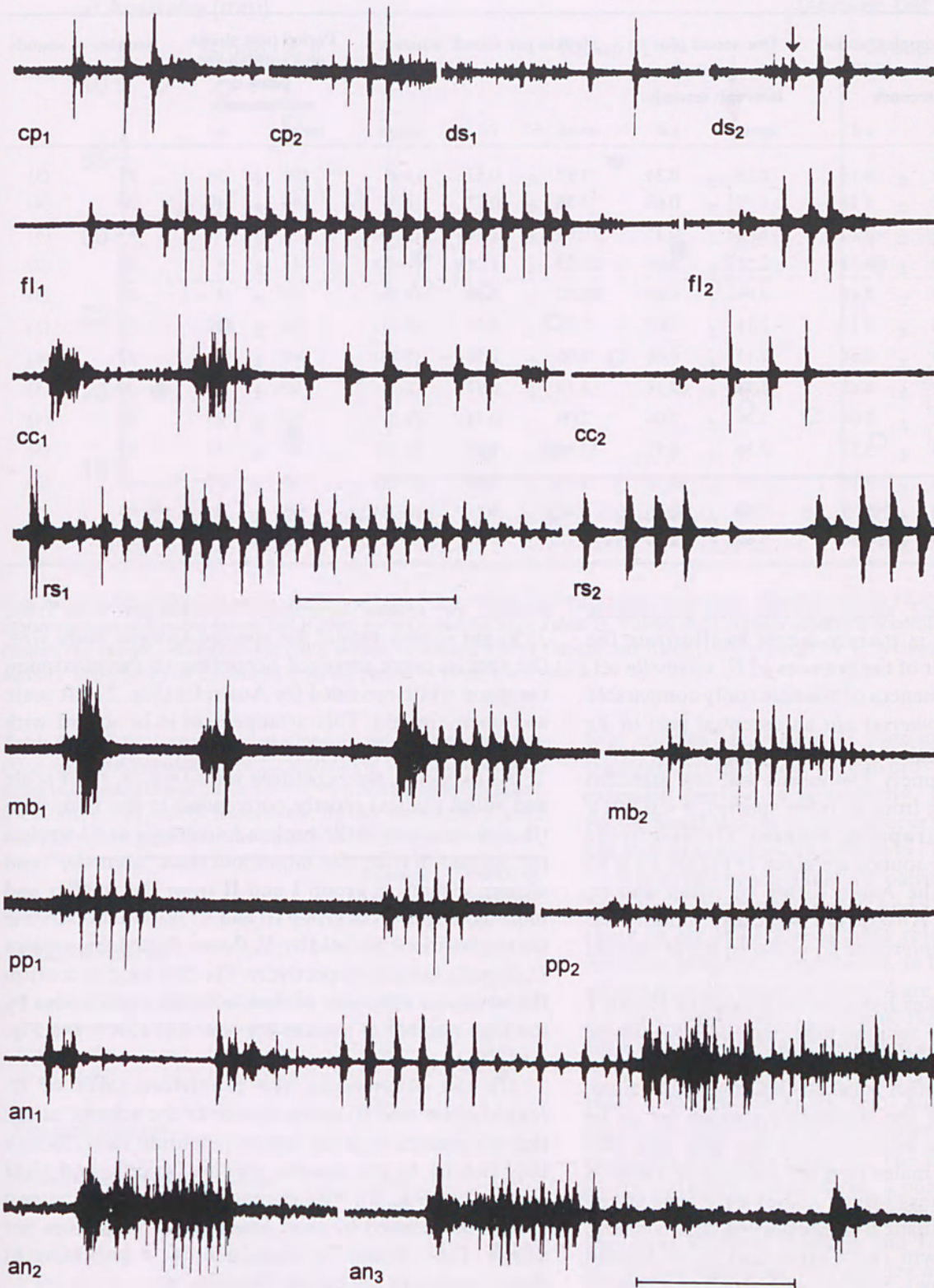


Fig. 1 (cont.): Oscillographic samples of vibration signals. - *sg*₁, D (35); *sg*₂, D (14), (both from Darwin). - *el*₁, D (9); *el*₂, D (6). - *ss*₁, 6 B; *ss*₂, D (12); *ss*₃, D (5). - *cp*₁, D (4); *cp*₂, D (4). - *ds*₁, D (2); *ds*₂, B + D (3), arrow points to first stroke. - *fl*₁, D (21); *fl*₂, B + D (3). - *cc*₁, 2 B + D (6); *cc*₂, B + D (3). - *rs*₁, B + D (26); *rs*₂, D (5) + B + D (3). - *mb*₁, 3 B + D (7); *mb*₂, B + D (16). - *pp*₁, B + D (6) + B + D (5); *pp*₂, B + D (12). - *an*₁, 2 B + D (14) + continuous ambulatory trill; *an*₂, B + D (10); *an*₃, B + D (13) + B.

Table 3. Rapping sounds of Australian male fiddler crabs (results of oscillographic analysis of tape recordings, cf. Fig. 1). W, E: Samples from western and eastern populations, respectively.

Species of <i>Uca</i>	One (complex) sound ("drumwhirl"): seconds		One sound plus subsequent silent interval: seconds		Strokes per sound: number			Period (one stroke plus subsequent pause): milliseconds		Number of sounds measured (males)	
	mean	s.d.	mean	s.d.	mean	s.d.	range	mean	s.d.		
<i>longidigitum</i>	0.18 ± 0.16		1.33 ± 0.34		1.87 ± 0.87		(1-4)	159 ± 34		23	(3)
<i>polita</i>	0.12 ± 0.12		1.39 ± 0.63		1.58 ± 0.77		(1-5)	163 ± 40		36	(4)
<i>hirsutimanus</i>	0.45 ± 0.16		1.86 ± 0.75		10.09 ± 2.78		(5-16)	48 ± 5		43	(4)
<i>signata</i> (W)	0.90 ± 0.52		2.55 ± 0.84		22.03 ± 11.34		(7-45)	41 ± 4		35	(2)
<i>signata</i> (E)	1.03 ± 0.41		2.99 ± 0.63		20.22 ± 7.09		(8-38)	53 ± 4		23	(3)
<i>elegans</i>	0.36 ± 0.17		2.11 ± 1.07		7.30 ± 2.75		(2-11)	54 ± 12		20	(3)
<i>seismella</i>	0.36 ± 0.14		1.17 ± 0.44		8.05 ± 2.58		(5-14)	49 ± 3		37	(4)
<i>capricornis</i>	0.22 ± 0.13		1.71 ± 0.41		3.10 ± 0.97		(2-5)	90 ± 23		20	(3)
<i>dussumieri</i>	0.12 ± 0.04		3.24 ± 1.04		2.06 ± 0.44		(1-3)	98 ± 25		16	(4)
<i>flammula</i>	0.84 ± 0.53		2.36 ± 0.77		13.40 ± 8.89		(2-33)	69 ± 12		57	(5)
<i>coarctata</i>	0.32 ± 0.19		1.91 ± 0.58		3.33 ± 1.88		(1-11)	136 ± 27		27	(3)
<i>mjoebergi</i>	0.49 ± 0.23		2.33 ± 0.80		9.42 ± 3.71		(4-21)	56 ± 6		64	(5)
<i>perplexa</i>	0.38 ± 0.23		1.85 ± 1.00		7.72 ± 3.43		(3-15)	52 ± 7		54	(5)

are included in Table 2, which presents some parameters measured. Table 2 is mainly meant to illustrate the specialized character of the bounces of *U. seismella* (cf. Fig. 1 ss₁). Long sequences of bounces (only comparable with those of *U. vomeris*) are an essential part of its acoustic communication. *U. seismella* is also conspicuous by its extremely low means and low standard deviations (differing from all other species, $p < 0.001$).

"Drumwhirls" (rapping sounds). Oscillographic examples of rapping sounds are given in Figure 1 for 14 species including the Asian forms *U. rosea* and *U. annulipes*. Three Australian species, namely *H. cordiformis*, *U. dampieri* and *U. vomeris*, never emitted rapping sounds.

Numbers of strokes listed in the legend of Figure 1 were verified by the running tape; the sudden extreme decrease of pulse amplitude (e.g. Fig. 1 hs₂, el, mb₂, an₁) is due to reduced contact between chela and substratum.

Time patterns of the Australian species are to be found in Table 3. The means given in this table are partly based on up to five males (see last column of Table 3) and different localities (Table 1). They have been united after testing their statistical compatibility. In *U. signata*, samples from Darwin and Cairns had to be treated separately (see below). Species with small numbers of sounds recorded (Table 3) reflect rarity of sound production (*U. longidigitum*, *U. capricornis*, *U. dussumieri*) or faintness of signals (*U. elegans*). Figure 2 and Table 4 were prepared to facilitate comparisons within Table 3. The results can be summarized as follows:

1) *Relations of body size and repetition rate of strokes.* As the repetition rate of the rapping elements

(strokes per second, calculated from the period in Table 3) might simply reflect the species-specific body size, the species were arranged according to the maximum carapace width recorded for Australia (Fig. 2, left scale and open circles). This arrangement is in accord with the systematic grouping of Table 1.

As expected, the repetition rates (Fig. 2, right scale and filled circles) mostly correspond to the body size (though inversely): the broken line drawn at 17 strokes per second divides the larger and thus "clumsier" and slower species of group I and II from the smaller and more agile species of group III and V. Within this scheme the top positions are held by *U. flammula* and the western *U. signata* sample, respectively. The two species confirm the advanced character of their acoustic signals also by the high number of strokes per sound (Table 3 and Fig. 1 sg₁, fl₁).

On the other hand, the repetition rates of *U. longidigitum* and *U. polita* do not fit the scheme at all: the two species have the lowest repetition rates, though they belong to the smaller species (middle and right sections of Fig. 2). The exceptional status of the two species is stressed by their low number of strokes per sound (Table 3 and Fig. 1 lg, pl). For a weighting of these characters see below (Discussion).

2) *In search of effects of allopatry and sympatry.* Most of the 17 confirmed Australian species of *Uca* are confined to one of the two northern zoogeographic provinces: the Dampierian in the west and the Solanderian in the east, seen from the Torres Strait region (von Hagen and Jones 1989; cf. Table 1 of the present paper). Some of these allopatric species are still similar, i.e. they form inter-provincial pairs or groups of relatives. The

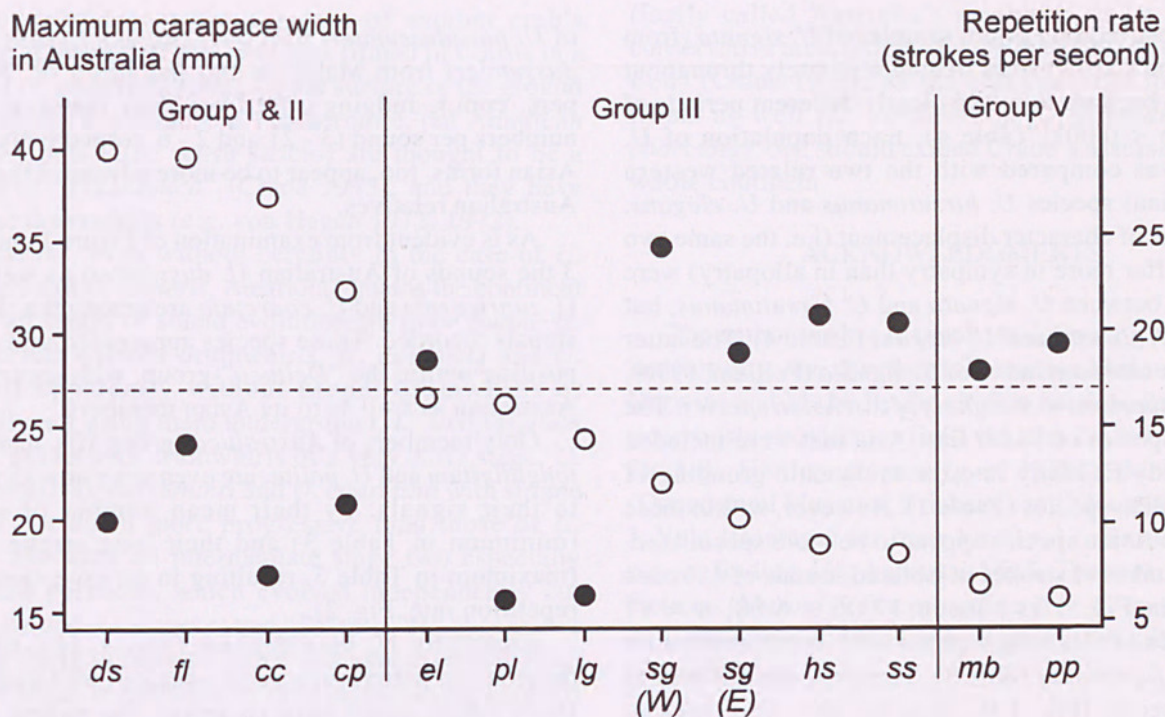


Fig. 2. Body size (left scale, open circles) and repetition rate of rapping strokes (right scale, filled circles) in 12 species of Australian *Uca* (abbreviations of species names and Roman group numerals as in Table 1). Values of *U. signata* separated according to a western (W) and eastern (E) sample. Maximum carapace widths in Australia after George and Jones (1982), except for *U. seismella* (Karumba sample of author). Repetition rate calculated from the period of strokes in Table 3.

Table 4. Statistical comparison of allopatric and sympatric relatives (*Uca* spp.) and populations of *U. signata* (W western, E eastern) using two parameters of Table 3. ***, **, *: differences significant: $p < 0.001$, < 0.01 , < 0.05 , respectively; n.s. not significant (L-test). See Table 1 for geographic distribution of the species mentioned.

		Strokes per sound	Period of strokes
Allopatric relatives:			
<i>U. capricornis</i>	vs. <i>U. dussumieri</i>	***	n.s
<i>U. capricornis</i>	vs. <i>U. coarctata</i>	n.s.	***
<i>U. flammula</i>	vs. <i>U. coarctata</i>	***	***
<i>U. mjoebergi</i>	vs. <i>U. perplexa</i>	*	**
Sympatric relatives:			
<i>U. longidigitum</i>	vs. <i>U. polita</i>	n.s.	n.s.
<i>U. elegans</i>	vs. <i>U. hirsutimanus</i>	***	*
<i>U. seismella</i>	vs. <i>U. polita</i>	***	***
<i>U. capricornis</i>	vs. <i>U. flammula</i>	***	***
<i>U. dussumieri</i>	vs. <i>U. coarctata</i>	**	***
Populations of <i>U. signata</i> :			
<i>U. signata</i> (W)	vs. <i>U. signata</i> (E)	n.s.	***
<i>U. signata</i> (W)	vs. <i>U. hirsutimanus</i>	***	***
<i>U. signata</i> (E)	vs. <i>U. hirsutimanus</i>	***	***
<i>U. signata</i> (W)	vs. <i>U. elegans</i>	***	***
<i>U. signata</i> (E)	vs. <i>U. elegans</i>	***	n.s.

four species (*U. polita*, *U. signata*, *U. seismella*, *U. triangularis*) that occur in both provinces appear to have extended their range secondarily. They are one reason for the fact that close relatives occur not only in allopatric but also in sympatric distribution (Table 4).

It is to be expected that allopatric relatives are rather “careless” of evolving species-specific vibration signals: there is no selection against retaining signals that antedate geographic separation. In fact three of the four allopatric pairs listed in Table 4 are similar (differences n.s. or $p < 0.05$ only) in one of the parameters chosen for comparison (strokes per sound and period of strokes).

Sympatric relatives should reinforce selectivity of their communication system, and the frequency of significant differences in both parameters mainly appears to fit this concept (Table 4). The pair *U. longidigitum* vs. *U. polita* (Table 4) forms a puzzle, as both species are reported from Sandgate and Shorncliffe in Moreton Bay near Brisbane (George and Jones 1982). In 1986 the author found the two species at Shorncliffe on the same mud-flat opposite to the mouth of Nundah Creek, but not a single individual of *U. polita* in the many *longidigitum*-habitats of the Brisbane River itself. Though both are members of the Solanderian province, the two species seem to meet rarely in the field so that their different time pattern of waving display (Pellikan 1990) may be sufficient as a behavioural isolating mechanism.

The western and eastern samples of *U. signata* (from Darwin and Cairns) were treated separately throughout the paper, because they had clearly different periods of strokes ($p < 0.001$, Table 4). Each population of *U. signata* was compared with the two related western (Dampierian) species *U. hirsutimanus* and *U. elegans*. Indications of character displacement (i.e. the same two species differ more in sympatry than in allopatry) were not found between *U. signata* and *U. hirsutimanus*, but between *U. signata* and *U. elegans* (Table 4). The latter may be the closest relative of *U. signata* (Pellikan 1990).

3) *Comparison with signals of two Asian species.* The two *Uca* species of South East Asia that were included in this study fit easily into the systematic grouping of the Australian species (Table 1). However, within these groups the Asian species appear to be more specialized.

The number of strokes in isolated sounds of *U. rosea* (e.g. 26 in Fig. 1 rs_1 ; mean 17.06 ± 6.08 , $n = 17$ drumwhirls of this long type) is only comparable with that of *U. flammula* (Table 3). There are shorter sounds in both species (Fig. 1 fl_2 , rs_2), but only *U. rosea* can "switch" to long sequences of short drumwhirls (up to 12 sounds measured, instead of up to 3 in *U. flammula*).

Likewise, *U. annulipes* is more specialized than the two related Australian species *U. mjoebergi* and *U. perplexa*. The number of strokes per sound is similar to that of *U. mjoebergi* and *U. perplexa*, but the period of strokes is more variable (cf. an_1 , with an_2 and an_3 in Fig. 1). In *U. annulipes* the drumwhirls are often followed (or preceded) by continuous burst-pulsed "trills" (Fig. 1 an_1) of the walking legs, lasting up to about ten seconds. These trills were also recorded in *U. perplexa*, but more rarely, and they appear to be missing in *U. mjoebergi*.

DISCUSSION

In explaining the Figures and Tables in the section on "drumwhirls", a few conclusions were attempted that are more or less well supported. It is clear that body size and repetition rates of strokes are inversely related (with a few striking exceptions), but the second idea that sympatry and allopatry should influence the signals needs to be tested by closer pair-by-pair examinations (cf. von Hagen 1984). A more detailed study of the *U. longidigitum*-*U. polita* pair and of the western and eastern populations of *U. signata* should be especially rewarding. Work on *U. signata* should also include samples from New Guinea, where the species occurs at least around Merauke, Irian Jaya (Leiden Museum, Netherlands: e.g. No. D32522, D33526; von Hagen unpublished).

It is also premature to make general conclusions on the advanced status of the signals of Asian fiddler crabs (see third section). The two species chosen (*U. rosea*, *U. annulipes*) might be specialized species by chance. There exist, however, some additional bioacoustic data:

of *U. paradussumieri* Bott (= *U. spinata* Crane) and *U. dussumieri* from Malaysia and Indonesia (R. Polivka pers. com.). Judging only from their range of stroke numbers per sound (3 - 21 and 2 - 6, respectively) these Asian forms, too, appear to be more advanced than their Australian relatives.

As is evident from examination of Figure 1 and Table 3 the sounds of Australian *U. dussumieri* as well as of *U. capricornis* and *U. coarctata* are among the simplest signals recorded. These species apparently hold a basal position within the "*Deltuca*"-group, with regard to its Australian as well as to its Asian members.

Only members of *Australuca* (group III), namely *U. longidigitum* and *U. polita*, are even simpler with respect to their signals: by their mean number of strokes (minimum in Table 3) and their long stroke period (maximum in Table 3, resulting in an exceptional low repetition rate, Fig. 2).

Especially *U. longidigitum* (Fig. 1, lg), with the distribution pattern of a relict species (see George and Jones 1982), could have preserved the earliest phylogenetic stage of drumwhirl invention in *Uca*, namely rapping as a by-product of waving the major cheliped. Within *Australuca*, *U. longidigitum* is the only species in which the length of one sound plus subsequent interval (1.33 ± 0.34 , $n = 23$, Table 3) is statistically not separable from the length of one waving motion plus subsequent pause (1.22 ± 0.11 , $n = 36$, according to motion pictures taken by the author and analysed by Pellikan 1990). Even in the aquarium *U. longidigitum* tended to switch from waving to rapping (and vice versa), the latter looking like a reduced or weak waving movement.

Vibration components of visual display are well-known in *Uca* (Altevogt 1964), but in *U. tangeri*, a species that also possesses a complete system of drumwhirls. *U. longidigitum* seems to have but one gesture that serves two sensory channels - depending on its intensity or completeness. It is important to note that the nearly all Australian "*Australuca*"-group (which includes *U. longidigitum*) retains, as a whole, some other ancestral traits: above all, minor chelae with large teeth (Crane 1975) and waving display of females (von Hagen 1993).

It is not clear, whether the "*Thalassuca*"-group, which also has waving females (von Hagen 1993), holds a still more ancestral position with regard to sound evolution in *Uca*. The two Australian members, *U. dampieri* and *U. vomeris*, never emitted drumwhirls within the experimental design of the present study, though they should have: Crane (1975) recorded, in the field, underground rapping sounds in the close relatives *U. hesperiae* from East Africa and *U. pacifensis* from Fiji (see her Plate 47 A) and even in *U. vomeris* from New Caledonia; and Salmon (1984) describes a "shuttling" motion of the major chela in *U. vomeris* from Townsville,

used by intruders in the entrance of another crab's burrow. A gesture of this kind was filmed in Cairns in a male of *U. vomeris* fighting on the surface of the ground (von Hagen, unpublished). Furthermore, the American narrow-fronts (*Uca* sensu stricto) are thought to be a branch of "*Thalassuca*" (Crane 1975), and they have genuine drumwhirls (e.g. von Hagen 1971, 1972).

However, even without certainty in the case of *U. dampieri* and *U. vomeris*, Australia remains the continent where all stages of sound evolution are to be found: *H. cordiformis* without drumwhirls, *U. dampieri* and *U. vomeris* apparently without proper drumwhirls or normally not using them underground, *U. longidigitum* and *U. polita* with drumwhirls of a very early stage, *U. capricornis*, *U. dussumieri* and *U. coarctata* with simple sounds not much more progressive than those of *U. polita*, and after an intermediate stage two especially advanced positions, which evolved independently out of *Australuca* (*U. signata*) and "*Deltuca*" (*U. flammula*). Among the intermediate forms (not specified here) two species have, in addition to their drumwhirls, evolved peculiarities: *U. seismella* has specialized in long sequences of "hasty" bounces and *U. perplexa* (like *U. annulipes*) in continuous ambulatory trills.

Housing all stages of sound evolution, especially the early ones, and also the early stages of waving evolution (von Hagen 1993), Australia should be favoured as the continent where the genus *Uca* first evolved.

The author is aware that directional change in behavioural complexity cannot be the only indicator in phylogenetic reasoning. A support at least by morphological studies is necessary (Beinlich and von Hagen in prep.). However, this holds true also for other approaches. Two related papers, which were published some years ago (Levinton *et al.* 1996, Sturmbauer *et al.* 1996), base their phylogenetic trees on certain analyses of 16S rDNA alone. Their inferences, above all an American centre of origin of *Uca*, should be treated with reserve, as they lack a proper morphological background for their discussions, which neglect for example, the most reliable synapomorphy in *Uca* systematics: the unique pleonal clasping apparatus identifying all broad-fronted species as a monophylum (Guinot 1979, Beinlich and von Hagen in prep.).

The assumption that *Uca* first evolved in Australia is, furthermore, supported by an Australian origin of certain mangrove taxa (palynological evidence compiled in Specht 1981). As *Uca* is typically associated with mangroves, it is essential that *Rhizophora*, *Avicennia* and *Sonneratia* first appeared in the late Eocene of West Australia and colonized Indonesia not before Oligocene/Miocene - probably accompanied by fiddler crabs, which made South East Asia not their first, but their second centre of evolution. Crane, who considers "*Deltuca*" the subgenus "least specialized" (Crane 1975) and at first supposed a Malaysian origin of the genus (Crane 1956),

finally called Australia's northwest coast "the most conservative area, judging by the morphology of the local *Uca*" (Crane 1975). As the east coast has its ancestral forms as well (*H. cordiformis*, *U. longidigitum*, *U. coarctata*), one should extend Crane's assessment to the whole continent.

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