TABLE 13 (*Continued*)
Organization of 84 Structures on *UCA* Claws and Their Relation to Ritualized Combat

Area (*Figs.* 42, 43, 44)	*Structure No.*	*Structure Name*	*Type of Variation*	*Range of Variation*	*Combat Components Using Structure* (*cf. Table 14*)	*Structure No.*
PALM						
A. Upper, predistal area (= between upper distal part of carpal cavity, dorsal margin, & dactyl base)	25	General form	a. Relative size b. Shape	Small to large Narrow to broad	Unknown	25
	26	Distal extension of carpal cavity into predistal area	a. Occurrence b. Shape	Present or absent Tapering; narrow to broad	↓	26
	27	Downward extension of carpal cavity's beaded, dorsal edge	a. Occurrence b. Separation of cavity from predistal area	None, slight or extensive None, partial or total	↓	27
	28	Other separations between cavity & predistal area	a. Grouped tubercles b. Tubercles continued up from apex c. Higher predistal plane	Present or absent Present or absent Present or absent	↓	28
	29	Separation by tubercles, differences of lower part of predactyl area from upper palm	Occurrence	Present or absent	↓	29
	30	Depression in middle of area	Occurrence	Present or absent	↓	30
	31	Armature of area	a. Occurrence b. Tubercles unpatterned c. Tubercles in row d. Tubercles in reticulations e. Rugosities	Range as in #23, a–e	↓	31
B. Predactyl area (= upper distal palm, beside dactyl base)	32	Proximal row of tubercles (continued as inner row along pollex gape)	a. Occurrence b. Extent upward c. Tubercle characteristics	Present, few or absent Full length or ventral part only In row regular, irregular or multiple; small to large	Interlace	32
	33	Distal row of tubercles	a. Occurrence b. Tubercle characteristics c. Series stronger than proximal	Present, few, obsolescent, or absent In row single or multiple; minute to small (1 species): Tubercles larger and row longer	Interlace	33
	34	Intervening groove	Occurrence	Well-marked, indistinct or absent	Unknown (partial interlace)	34
C. Central palm	35	Convexity	Occurrence	Direction(s) of slope; degree	Pregape-rub	35
	36	Small depression near gape	Occurrence	Present or absent	Unknown	36
	37	Oblique depression, dorsal to oblique ridge	Occurrence	Present or absent	Unknown	37
	38	Tubercles	Occurrence	Varying local distributions & sizes	Pregape-rub	38
D. Oblique, tuberculate ridge	39	Ridge form between carpal cavity and lower palm at pollex base	a. General height b. Edge thickness c. Steepness of sides d. Extent distally	High to obsolescent Thick to thin Steep to very gentle Almost or entirely to pollex base	Heel-&-ridge	39
	40	Apex, at lower, distal end of carpal cavity	Height, cf'd. ridge	Higher, equal or lower	Heel-&-ridge	40
	41	Tuberculation, ridge, and apex	a. Occurrence of linear tubercles b. Location of largest c. Degree of irregularity	Present or absent On apex or more distally Slight to great	Heel-&-ridge	41
	42	Tuberculation continued from apex, upward around distal end of carpal cavity	a. Occurrence b. Extent c. Irregularity	Present or absent Slightly, moderately or merging with downturned dorsal margin Slight to great	Heel-&-ridge	42

E. Carpal cavity	43	Distal slope	Degree	Gradual to steep	Heel-&-ridge	43
	44	Lower edge	a. Height b. Thickness c. Tuberculation	Low to moderate Thick to thin Present or absent	Unknown (in *triangularis* prob. heel-&-ridge)	44
F. Lower, proximal triangle	45	Armature	a. Tubercles: occurrence b. Tubercles: general size c. Tubercles: location of largest d. Tubercles: where regionally absent e. Tubercles: in rows f. Tubercles: in reticulations g. Rugosities h. Oblique row of parallel striae: occurrence	Present or absent Minute to moderate Proximal end ventral to dorsal or distal Rarely from distal half, dorsal half or entire triangle except near oblique ridge Present or absent-location variable Present or absent-location variable Present or absent-location variable Present or absent	Unknown (excluding use in autostridulation with 1st ambulatory)	45
G. Depression at pollex base	46	Form	a. Extent b. Shape	Large or small Shallow with boundaries indistinct or relatively deep, subtriangular	Heel-&-hollow	46
	47	Tuberculation	a. Occurrence b. Size	Present or absent Same as on adjacent palm or different	Heel-&-hollow	47
POLLEX						
Entire	48	Length, cf'd. manus	Range	Longer or clearly shorter	Heel-&ridge when long	48
	49	Shape	Range	Approximately straight & slender; lower margin clearly convex, or straight with tip turned up; broad; or triangular	Heel-&-ridge when straight (?)	49
Ventral Margin	1	Tubercles (see under *MANUS*)	–	–	See Structure 1	1
	2	Outer furrow (see under *MANUS*)	–	–	See Structure 2	2
Outer Surface	6	Keel (see under *MANUS*)	–	–	See Structure 6	6
A. Lower part	50	Groove above keel	Occurrence	Present or absent	Pollex-rub Dactyl-along-pollex-groove	50
B. Outer surface as a whole	5	Distal end of depression at pollex base (see under *MANUS*)	–	–	See Structure 5	5
	51	Tuberculation	a. Occurrence b. Extent	Present or absent General or near ventral margin and/or near prehensile edge	Manus-rub Pollex-rub	51
Dorsal Margin (= prehensile edge)						
A. Entire Margin	52	Curvature	a. Degree b. Location of concavity	Straight to strongly concave General or subdistal only	(Unknown)	52

TABLE 13 (*Continued*)
Organization of 84 Structures on *UCA* Claws and Their Relation to Ritualized Combat

Area (*Figs.* 42, 43, 44)	*Structure No.*	*Structure Name*	*Type of Variation*	*Range of Variation*	*Combat Components Using Structure* (*cf. Table 14*)	*Structure No.*
B. Proximal part	53	Tubercles: outer row	Occurrence	Present, weak or absent	1 or more of these rows in components: Pollex-under-&-over-slide Interlace	53
	54	Tubercles: median row	Occurrence	Present, weak or absent		54
	55	Tubercles: inner row	Occurrence	Present, weak or absent		55
	56	Space between outer and median rows	Breadth	Narrow or wide	Interlace	56
	57	Space between median and inner rows	Breadth	Narrow or wide	Interlace	57
C. Median & distal parts	58	Tubercles: outer row	Occurrence & extent	Present, weak or absent, extended to tip or not	1 or more of these rows in components: Pollex-under-&-over-slide Subdactyl-&-subpollex slide Pollex-base-rub Upper-&-lower-manus-rub Pregape-rub Heel-&-hollow Heel-&-ridge Subdactyl-&-suprapollex-saw	58
	59	Tubercles: median row	Occurrence & extent	Present, weak or absent, extended to tip or not		59
	60	Tubercles: inner row	Occurrence & extent	Present, weak or absent, extended to tip or not		60
	61	Large, tuberculate tooth	a. Occurrence b. Location c. Row(s) of origin	Present or absent Submedian or subdistal Median and/or outer	Unknown	61
	62	Keel: tip of median row	a. Occurrence b. Tubercles	Present or absent Present or absent	Unknown	62
	63	Keel: tip of inner row	a. Occurrence b. Tubercles	Present or absent Present or absent	Unknown	63
	64	Pollex tip appearing bifid or trifid	Occurrence	Present or absent	Unknown	64
Inner Surface	46	Distal end of depression inside pollex base (see under *MANUS*)	-	-	See Structure 46	46
	65	Tuberculation	a. Occurrence b. Extent	Present or absent General, proximal only, or near prehensile edge only	Unknown	65
DACTYL						
Entire	66	Length compared with manus	Range	Shorter to much longer	Heel-&-hollow Heel-&-ridge	66
	67	General shape	Range	Slender to broad; central portion broader or narrower than corresponding part of pollex	Heel-&-hollow Heel-&-ridge	67
Ventral Margin (= prehensile edge)						
A. Entire margin	68	Curvature	Range	Arched throughout or distally only	Heel-&-hollow Heel-&-ridge	68
B. Proximal part	69	Tubercles: outer row	Occurrence	Present, weak or absent	1 or more of these rows in components: Interlace Dactyl-submanus-slide	69
	70	Tubercles: median row	Occurrence	Present, weak or absent		70
	71	Tubercles: inner row	Occurrence	Present, weak or absent		71

C. Median & distal parts	72	Tubercles: outer row	Occurrence & extent	Present, weak or absent	1 or more of these rows in components: Dactyl-slide Upper-&-lower-manus-rub Heel-&-hollow Heel-&-ridge Supraheel-rub (vertical) Dactyl-along-pollex-groove Subdactyl-&-suprapollex-saw	72
	73	Tubercles: median row	Occurrence & extent	Present, weak or absent		73
	74	Tubercles: inner row	Occurrence & extent	Present, weak or absent		74
	75	Large tuberculate tooth	a. Occurrence b. Location	Present or absent Proximal, median or distal	Unknown	75
	76	Keel: tip of median row	a. Occurrence b. Tubercles	Present or absent Present or absent	Unknown	76
	77	Keel: tip of inner row	a. Occurrence b. Tubercles	Present or absent Present or absent	Unknown	77
Outer Surface	78	Tuberculation	a. Occurrence b. Extent	Present or absent General or near dorsal margin, and/or near prehensile edge	Manus-rub	78
	79	Lateral Groove	a. Occurrence b. Extent	Present or absent Proximal only or extending beyond the middle	Unknown	79
	80	Proximal subdorsal groove	a. Occurrence b. Extent	Present, weak or absent Extremely short to moderately long	Heel-&-ridge (Guide to heel)	80
Dorsal Margin	81	Tuberculation	a. Density b. Extent	Close-set, sometimes continuing in subdorsal groove, to very sparse Above and below subdorsal groove only, to continuing dorsally nearly to dactyl tip	Dactyl-slide Upper-&-lower-manus-rub	81
Inner Surface	82	Tuberculation	a. Occurrence b. Extent	Present or absent General, proximal only or near prehensile edge only	Unknown	82
	83	Lateral groove or depression	a. Occurrence b. Extent	Present or absent Proximal only or extending almost to tip	Unknown	83
GAPE	84	Breadth	Range	Middle part much narrower than to much broader than adjacent pollex (exclusive of any tuberculate tooth)	(when wide): Heel-&-ridge	84

TABLE 14*
Ritualized Combat in *UCA:* Distribution of Components

Component	*Actor*		*Inactor*	
	Instruments	*Structure Nos.*	*Contact Areas*	*Structure Nos.*
1. Manus-rub	Outer manus Outer pollex Outer dactyl	3 51 78	Outer manus, almost always ventral half Outer pollex Outer dactyl	3 51 78, 79
2. Pollex-rub	Lower, outer pollex	6, 50, 51	Lower outer pollex	6, 50, 51
3. Pollex-under-&-over-slide	a. Pollex: prehensile edge, median	58, 59, 60	aa. Pollex: ventral margin.	1, 2
	b. Pollex: ventral margin	1, 2	bb. Pollex: prehensile edge, median & proximal rows.	53, 54, 55 58, 59, 60
4. Subdactyl-&-sub-pollex-slide	Dactyl: proximal half dorsal margin	81	Dactyl: prehensile edge, median part	72, 73, 74
	Pollex: prehensile edge, median part	58, 59, 60	Pollex: proximal part ventral margin	1, 2
5. Pollex-base-rub	Pollex: prehensile edge, median	58, 59, 60	Outer manus: flat area at pollex base	5, 6
6. Dactyl-slide	Dactyl: prehensile edge, median	72, 73, 74	Dactyl: upper margin	81
7. Upper-&-lower manus-rub	Dactyl: prehensile edge, median and distal part	72, 73, 74	Dactyl: proximal dorsal margin. Outer manus: upper third, submarginal area & dorsal margin	81 11–24 incl. (some or all)
	Pollex: prehensile edge, distal part	58, 59, 60	& lower margin	1
8. Dactyl-submanus-slide	Dactyl: prehensile edge, median part	72, 73, 74	Manus: ventral margin	1, 2
9. Interlace	Dactyl: prehensile edge, proximal parts, inner, median and/or outer rows	69, 70, 71	*When actor engages from outer side:* Palm: predactyl area Pollex: prehensile edge. inner row, extreme proximal part	 32, 33, 55
	Pollex: prehensile edge, proximal parts, inner, median &/or outer rows plus enlarged space between rows	53, 54, 55, 56, 57	*When actor engages from inner side:* Outer manus: cuff Outer manus: central, distal portion Pollex: prehensile edge, outer &/or median rows, extreme proximal parts	 53, 54
10. Pregape-rub (longitudinal)	Dactyl: prehensile edge, median part	72, 73, 74	Outer manus: central, distal area	10
	Pollex: prehensile edge, median part	58, 59, 60	Palm: central distal area	35, 38
11. Heel-&-hollow	a. Dactyl: prehensile edge, distal part; length, shape, curvature	72, 73, 74 66, 67, 68	aa. Outer manus: heel area	3, 4
	b. Pollex: prehensile edge, distal part	58, 59, 60	bb. Palm: Depression at pollex base	46, 47
12. Heel-&-ridge	a. Dactyl: prehensile edge, distal part; length, shape, curvature	72, 73, 74 ?76, ?77, 66, 67, 68	aa. Outer manus: heel area	3, 4
	b. Pollex: prehensile edge, median & distal parts; length & shape	59, 60 ?62, ?63, ?64 48, 49	bb. Oblique ridge inside palm & its upward extension Ventral edge, carpal cavity	39–43 incl. 44
	Indirect instrument gape: breadth	84		
			Guides to heel: Dactyl: subdorsal groove Upper manus: submarginal groove	 80 17
13. Supraheel-rub (vertical)	Dactyl: prehensile edge, median & distal parts	72, 73, 74	Outer Manus: subdorsal proximal area	3, 13
14. Dactyl-along-pollex-groove	Dactyl: prehensile edge, distal part	72, 73, 74	Proximal outer pollex	50
15. Subdactyl-&-suprapollex-saw	Dactyl: prehensile edge, median-&-distal part	72, 73, 74	Pollex: prehensile edge, median part	58, 59, 60

*See also Table 13 and Figs. 42, 43, and 44.
**Plus a different component related to the numbered one listed; data being analyzed.

TABLE 14 (*Continued*)
Ritualized Combat in *UCA:* Distribution of Components

Known Occurrence of Component in Genus Uca						
Deltuca	*Thalassuca*	*Amphiuca*	*Afruca*	*Uca*	*Minuca*	*Celuca*
dussumieri *coarctata* *urvillei*	*vocans*	*chlorophthalmus* *inversa*	*tangeri*	*maracoani*	*rapax* *pugnax*	*pugilator* *cumulanta* *inaequalis* *stenodactylus* *lactea***
					rapax	*pugilator* *lactea***
						pugilator *lactea*
					rapax *pugnax*	*lactea*
						pugilator
dussumieri *urvillei*					*rapax* *pugnax*	*pugilator* *cumulanta* *lactea*** *deichmanni*
					rapax *pugnax*	*pugilator* *lactea***
						pugilator
	vocans		*tangeri*		*rapax* *pugnax*	*pugilator* *cumulanta* *lactea*
						pugilator
urvillei	*tetragonon* *vocans*					*lactea*
					rapax *pugnax*	*cumulanta* *lactea***
		chlorophthalmus *inversa*				*pugilator*
	vocans	*inversa*				
	vocans					

TABLE 15*

UCA RAPAX. Composition of 154 Combats Observed at Cocorite, Trinidad, October 13–17 and November 26–29, 1966

NOTE: Combats are listed only if observation is believed to have included the first component

	Combats Between an Aggressive Wanderer and a Burrow Holder		*Combats Between Two Burrow Holders*		
Sequences of Components	*Homo-clawed*	*Hetero-clawed*	*Homo-clawed*	*Hetero-clawed*	*Total*
Manus-push only	1	–	1	1	3
Manus-push + manus-rub	–	–	2	2	4
Manus-rub only	19	10	18	10	57
Manus-rub + dactyl-slide	1	13	3	6	23
Dactyl-slide only	1	3	1	1	6
Manus-rub + dactyl-slide + heel-&-ridge	1	1**	1	–	3
Manus-push + manus-rub + heel-&-ridge	–	–	1	–	1
Manus-rub + heel-&-ridge	9†‡	4**	4	2	19
Dactyl-slide + heel-&-ridge	1	–	1	1**	3
Heel-&-ridge only	5**‡	–	5†	1	11
Manus-rub + interlace	–	5†	–	–	5
Heel-&-right + interlace	–	4	–	–	4
Interlace only	–	2‡	–	2	4
Manus-rub + heel-&-ridge + interlace	1	–	–	–	1
Dactyl-slide + heel-&-ridge + interlace	–	1‡	–	–	1
Manus-rub + dactyl-slide + heel-&-ridge + interlace	–	3‡	–	1	4
Manus-rub + dactyl-slide + interlace	–	2	–	1	3
Dactyl-slide + interlace	1	1	–	–	2
Total	40	49	37	28	154

*From Crane, 1967: 56, Table II.
**1 heel-&-ridge component not followed by tapping
†2 heel-&-ridge components not followed by tapping.
‡1 combat with forceful ending included.

TABLE 16*

UCA RAPAX. Relative Frequency of Components in 154 Combats (From data in Table 15)

	Frequency (%)	
Component	*In 77 Homoclawed Combats*	*In 77 Heteroclawed Combats*
Manus-push	6	4
Manus-rub	78	77
Dactyl-slide	14	44
Heel-&-ridge	38	23
Interlace	3	29

*From Crane, 1967: 56, Table III.

TABLE 17*

U. RAPAX. Divisions of 104 Combats of Known Duration

	Duration Less than 20 secs.		Duration More than 60 secs.		
Intensity	*With Force*	*Fully Ritualized*	*With Force*	*Fully Ritualized*	*Total*
Low	10	35	0	0	45
High	4	46	4	5	59
Total	14	81	4	5	104

*From Crane, 1967: 66, Table VII.

TABLE 18*

UCA RAPAX. Behavior of Opponents. Following 148 Combats

KEY: AW—Aggressive wanderer larger than opponent
aw —Aggressive wanderer smaller than opponent
BH —Burrow-holder larger than opponent
bh —Burrow-holder smaller than opponent
M —Mutual component(s) clearly present
† —Burrow-holders dispossessed; waving resumption delayed more than 2 minutes

Result	***Combat Class***	***General Combat Composition***						***Subtotal***	***Total***
		Low intensity only		*High intensity*					
				With forceful end		*No forceful end*			
		With push	*No push apparent*	*No taps*	*With taps*	*No taps*	*With taps*		
Subsequent behavior apparently unchanged	AW & bh	1	5 (1M)	–	–	1	3 (1M)	10	
	aw & BH	–	15 (2M)	5 (1M)	–	23 (6M)	13 (10M)	56	
	BH & bh (BH = trespasser)	4 (1M)	7	–	–	7 (3M)	3 (2M)	21	
	BH & bh (bh = trespasser)	1	5 (3M)	1	–	4 (1M)	5	16	
	BH & bh (on boundary)	–	6 (2M)	–	–	3	–	9	
	Subtotals	6	38	6	–	38	24	112	112
Resumption of waving by burrow-holder delayed (less than 2 minutes except as noted)	AW & bh	–	4	–	2 (1M)†	3	2	11	
	aw & BH	–	2	–	–	1	–	3	
	BH & bh (BH = trespasser)	2	3	–	–	2	2 (1M)	9	
	BH & bh (bh = trespasser)	–	–	–	–	–	–	–	
	BH & bh (on boundary)	–	–	–	–	1 (1M)	2 (1M)	3	
	Subtotals	2	9	–	2	7	6	26	26
Wanderer's aggressiveness reduced	AW & bh	–	–	2	1 (M)	–	1 (M)	4	
	aw & BH	–	4	–	2	–	–	6	
	Subtotals	–	4	2	3	–	1	10	10
	Totals	8	51	8	5	45	31	148	148

*From Crane, 1967: 67, Table VIII.

TABLE 19

Waving Display in *UCA*: Counts and Timing Data from Film Analysis

NOTE: Characteristics of low-intensity waves excluded. See also p. 498.

KEY: V Vertical; L Lateral; V/L Semi-lateral; - No data; * Pause at apex of wave; † Secondary waves present, included in durations; = C No. of high-intensity courtship waves

Name	Locality	Chief Wave Form	Counts: Jerks Up	Counts: Jerks Down	Duration (sec.) Entire Wave: Moderate Intensity	Entire Wave: High-intensity Courtship	Up-strokes Only: Moderate Intensity	Up-strokes Only: High-intensity Courtship	Down-strokes Only: Moderate Intensity	Down-strokes Only: High-intensity Courtship	Pause between Waves (in Same Series)	Material Analyzed: No. of Waves	Material Analyzed: No. of Crabs
DELTUCA													
acuta rhizophorae	Singapore	V	None	None	0.15–0.25	0.25–0.3	0.08–0.11	0.11–0.17	0.08–0.11	0.08–0.11	0.08–0.11	29 (9 = C)	2
rosea	Malaysia: Penang	V	5–6	3	3.71–4.12	–	3.32–3.58	–	0.50–0.54	–	–	2	1
dussumieri capricornis	Australia: Broome	V	None	None	0.12–0.38	0.16–0.38	0.13–0.25	0.18–0.21	0.18–0.21	0.18–0.21	0.08–0.25	46 (13 = C)	8
dussumieri dussumieri	Philippines: Madaum	V	1 or 0	None	0.38–0.50	–	0.29–0.46	–	0.08–0.13	–	0.29–0.58	8	1
dussumieri dussumieri	Philippines: Sasa	V	2–3	None	0.54–1.58	–	0.38–1.46	–	0.08–0.21	–	0.42–0.88	12	4
dussumieri dussumieri	Philippines: Zamboanga	V	2–3	None	0.71–2.04	0.80–1.08	0.58–1.84	0.58–0.88	0.13–0.25	0.08–0.42	0.08–1.34	39 (11 = C)	6
demani	Philippines: Malalag	V	None	None	0.58–0.92	–	0.46–0.75	–	0.16–0.21	–	0.88–9.08	6	1
forcipata	Singapore	V†	None	None	0.21–0.25	–	0.13–0.17	–	0.08	–	0.08–0.13	5	1
coarctata coarctata	Fiji Is.	V†*	2–4	None	0.84–1.25	0.84–1.08	0.46–0.96	0.42–0.63	0.29–0.54	0.34–0.54	0.50–1.54	10 (5 = C)	3
coarctata coarctata	Philippines: Iling	V†*	0–4	None	1.71–3.38	0.96–1.29	Inapplicable	0.71–1.08	Inapplicable	0.21–0.34	0.08–0.75	14 (3 = C)	2
coarctata flammula	Australia: Darwin	V†	3–5	None	1.63–2.58	1.69–2.58	0.92–1.8	0.96–1.42	0.38–0.96	0.63–0.80	0.08–0.29	12 (4 = C)	2
urvillei	E. Africa: Pemba	V	None	None	1.00–1.21	0.75–0.88	0.42–0.63	0.38–0.67	0.38–0.80	0.21–0.38	0.04–0.75	7 (4 = C)	2
AUSTRALUCA													
bellator bellator	Philippines: Manila	V	None	None	0.75–1.42	0.50–1.08	0.50–1.21	0.24–0.80	0.17–0.38	0.21–0.29	0.46–0.92	22 (6 = C)	4
bellator bellator	Philippines: Iling	V	None	None	0.71–1.63	0.67–1.42	–	–	–	–	0.21–0.87	59 (19 = C)	7
bellator bellator	Java: Semarang	V	None	None	0.71–0.96	0.58–1.42	–	–	–	–	0.21–0.54	40 (32 = C)	6
bellator signata	Australia: Gladstone	V	None	None	0.63–2.50	–	–	–	–	–	0.67–2.50	20	8
bellator minima	Australia: Darwin	V	None	None	0.67–1.25	–	–	–	–	–	0.46–1.13	22	3
seismella	Australia: Darwin	V	None	None	0.08–0.20	–	0.04–0.12	–	0.04–0.12	–	0.04–0.08	16	1
THALASSUCA													
tetragonon	Ethiopia: Massawa	V	None	None	0.20–0.50	–	0.08–0.27	–	0.08–0.20	–	0.21–0.54	25	3
vocans borealis	Hong Kong	V	None	None	0.38–1.39	–	0.21–1.00	–	0.17–0.38	–	–	5	5
vocans pacificensis	Fiji Is.	V	None	None	0.38–2.25	–	0.17–2.00	–	0.17–0.54	–	0.21–2.54	43	6
vocans dampieri	Australia: Broome	V	None	None	0.21–0.75	–	0.13–0.46	–	0.13–0.42	–	0.04–0.96	51	3
vocans dampieri	Australia: Darwin	V	None	None	0.38–1.84	0.46–1.25	0.21–1.58	0.29–1.08	0.17–0.34	0.13–0.17	0.08–0.71	38 (18 = C)	3
vocans hesperiae	E. Africa: Zanzibar	V	None	None	0.50–1.71	–	–	–	–	–	0.08–2.04	25	5
vocans vocans	Philippines: Madaum	V	None	None	1.04–1.17	1.34–1.88	0.88–0.92	0.92–1.50	0.13–0.25	0.21–0.42	2.67–> 3	13 (8 = C)	1
vocans vocans	Philippines: Sasa	V	None	None	0.58–1.97	–	–	–	–	–	0.50–4.00	19	5
vocans vocans	Philippines: Puerto Princessa	V	None	None	–	1.29–1.67	–	0.96–1.00	–	0.25–0.42	1.6–4.8	6 (6 = C)	2
AMPHIUCA													
chlorophthalmus crassipes	Philippines: Zamboanga	V/L	None	None	0.54–0.75	–	–	–	–	–	0.50–0.63	11	2
chlorophthalmus crassipes	Tahiti	V/L	None	None	0.38–0.88	–	0.25–0.58	–	0.08–0.17	–	0.29–0.80	45	6
chlorophthalmus chlorophthalmus	E. Africa: Pemba	V/L	None	None	0.42–0.96	–	0.29–0.63	–	0.08–0.25	–	0.04–0.80	37	3
inversa inversa	E. Africa: Zanzibar	V/L	None	None	0.46–1.54	–	–	–	–	–	0.75–2.29	32	3
inversa sindensis	Pakistan: Karachi	V/L	None	None	0.63–0.92	–	0.46–0.80	–	0.13–0.21	–	0.21–0.25	10	1

BOBORUCA *thayeri thayeri*	West Indies: Trinidad	V/L	2–3	None	1.29–2.4	–	0.63–1.50	–	0.54–0.92	–	3.13–7.0	6	2
thayeri thayeri	Brazil	V/L	2–3	None	1.17–1.84	–	0.80–1.42	–	0.34–0.42	–	–	3	1
AFRUCA *tangeri*	Portugal: Faro	L	None	None	–	0.75–1.00	–	0.54–0.80	–	0.20–0.25	0.34–1.80	12 (12 = C)	1
tangeri	W. Africa: Angola	L	None	None	–	1.08–1.66	–	0.71–1.16	–	0.33–0.66	0.25–1.50	12 (12 = C)	1
UCA *heteropleura*	Panama	L	None	None	0.71–1.20	0.42–1.04	0.54–0.87	0.25–0.79	0.25–0.29	0.16–0.25	1.17–5.1	19 (9 = C)	2
maracoani maracoani	West Indies: Trinidad	L	None	None	1.41–3.54	1.04–1.54	1.00–1.58	0.63–0.92	0.34–1.96	0.34–0.42	0.58–1.88	37 (22 = C)	4
ornata	Panama	L	None	None	0.50–1.66	1.08–1.83	–	–	–	–	0.67–4.34	19 (6 = C)	2
MINUCA *galapagensis herradurensis*	Costa Rica: Golfito	L*	5–7+1	3–4	1.21–2.67	–	← Not relevant—Double peaks →				(Single wave)	5	2
rapax rapax	Florida: Miami (Tahiti B.)	L	12–20	2–4	6.20–6.54	4.04–5.87	5.0 –5.29	3.29–5.20	1.20–1.25	0.54–1.42	0.08–0.50	9 (5 = C)	3
rapax rapax	Florida: Miami	L	5–16	1–6	2.12–5.08	–	1.62–3.70	–	0.25–1.91	–	0.08–0.80	19	5
rapax rapax	Puerto Rico: San Juan	L	8–29	1–5	3.91–12.00	–	2.04–9.75	–	0.29–2.25	–	0.04–0.80	9	3
rapax rapax	West Indies: Trinidad	L	13–18	3	4.87–7.33	–	4.0 –6.12	–	0.87–1.20	–	0.58–1.71	5	2
rapax rapax	Venezuela: Pedernales	L	14–15	4–7	5.98–7.29	–	4.29–4.88	–	1.17–2.42	–	1.08–1.17	3	1
rapax rapax	Brazil: São Luiz	L	8–22	2–5	3.67–10.37	–	3.00–8.70	–	0.67–2.58	–	1.25–2.71	6	4
rapax rapax	Brazil: Recife	L	11–17	2–7	4.70–8.79	3.75	3.62–6.08	3.62	0.91–2.70	0.12	0.13–0.17	10 (1 = C)	5
rapax rapax	Brazil: Rio de Janeiro	L	8–34	1–8	5.2 –12.87	4.2 –5.6	3.67–11.70	–	0.91–4.04	–	0.17–0.96	50	15
pugnax pugnax	New York: Long Island	L	3–14	1–7	0.87–5.0	–	0.5 –3.25	–	0.25–1.83	–	0.08–0.34	8	2
zacae	Costa Rica: Golfito	L*	2	None	3.66–5.16	–	0.16–0.29	–	0.20–0.33	–	–	3	2
CELUCA *pugilator*	Florida: St. Augustine	L*	None	None	0.79–0.91	–	0.29–0.46	–	0.33–0.42	–	0.96–2.34	4	1
pugilator	Florida: Miami	L	2–3	None	0.92–1.80	0.63–1.08	0.38–1.25	0.25–0.71	0.29–0.50	0.17–0.54	0.38–0.75	18 (8 = C)	3
speciosa speciosa	Florida: Miami	L	None	None	0.38–0.50	–	0.21–0.42	–	0.13–0.17	–	1.29–2.29	8	1
cumulanta	West Indies: Trindad	L	None	None	1.00–3.4	–	0.58–2.21	–	0.46–1.46	–	0.80–3.00	17	3
batuenta	Panama	L*	None	None	0.34–0.58	–	0.08–0.34	–	0.08–0.17	–	0.42–1.34	25	4
saltitanta	Panama	L	None	None	0.29–0.89	–	0.16–0.54	–	0.08–0.38	–	0.50–1.58	21	2
oerstedi	Panama	L	None	None	1.12–2.84	–	0.91–2.00	–	0.20–1.29	–	0.75–2.17	29	5
festae	ex-Buenaventura, Colombia (crabbery)	L	None	None	2.63–4.71	–	2.21–3.83	–	0.42–0.88	–	0.88–3.17	16	2
beebei	Panama	L	None	None	0.29–0.46	0.29–0.50	0.16–0.33	0.20–0.37	0.08–0.20	0.08–0.13	0.13–0.96	27 (17 = C)	2
stenodactylus	Panama	L	None	None	1.37–2.79	–	0.75–1.42	–	0.25–0.62	–	(1 only = 1.21)	4	3
lactea annulipes	E. Africa: Pemba	L	None	None	0.42–1.17	0.58–0.88	0.29–0.58	0.67–1.00	0.34–0.58	0.25–0.42	0.98–3.63	47 (9 = C)	10
lactea mjobergi	Australia: Broome	L†	None	None	0.6–1.25	0.3 –2.3	–	–	–	–	0.80–0.96	35(15-C)	8
lactea lactea	Taiwan: Tamsui	L	None	None	0.58–1.46	–	0.50–1.34	0.04–0.13	0.17–0.50	0.04–0.08	0.25–2.08	41 (16 = C)	5
lactea lactea	Hong Kong	L	None	None	1.04–1.63	–	0.75–1.46	–	0.17–0.34	–	0.67–2.38	5	1
lactea perplexa-form	Singapore	L	None	None	0.54–0.71	0.17–0.34	0.38–0.54	0.08–0.17	0.17–0.29	0.08–0.13	0.17–3.58	14 (9 = C)	1
lactea perplexa	Fiji	L	None	None	0.42–1.00	0.13–0.25	0.38–0.71	0.04–0.13	0.13–0.25	0.08–0.17	0.04–3.5	94	12
lactea perplexa	Philippines: Madaum	L	None	None	0.38–1.04	–	–	–	–	–	1.25–5.5	62 (31 = C)	14
leptodactyla	Brazil: Recife	L	None	None	0.87–1.42	0.67–1.00	0.54–1.00	0.46–0.83	0.29–0.62	0.16–0.46	0.50–2.46	21	3
limicola	Panama	L	2	None	1.62–2.46	–	1.04–1.87	–	0.37–0.75	–	2.38–4.41	5	1
deichmanni	Panama	L*	None	None	0.50–1.29	0.46–1.34	–	0.08–0.17	0.08–0.38	0.08–0.13	0.13–2.75	28 (5 = C)	4
latimanus	Costa Rica: Golfito	L*	None	None	0.92–2.79	1.71–1.75	0.58–1.16	0.62–1.13	0.20–0.75	0.25–0.33	0.92–2.20	12 (3 = C)	2

TABLE 20
Waving Display in *UCA;* Distribution of Components

KEY: + Component present.
× Component present but weak.
? Presence of component questionable (field observation or film record dubious).

Subgenus	Species	Wave Forms								Other Components						Timing Elements Résumé				
		1. Vertical	2. Jerking-vertical	3. Semi-unflexed	4. Lateral-straight	5. Lateral-circular	6. Jerking-oblique	7. Reversed-circular	8. Overhead-circling	9. Minor-wave	10. Leg-stretch	11. Prolonged-leg-stretch	12. Leg-wave	13. Curtsy	14. Herding	Pause at Peak	Usual Wave Duration (Moderate to High Intensity) < 1 Sec.	1-2 Sec.	> 2 Sec.	(Drumming Incorporated, Sometimes Ritualized)
Deltuca	*acuta*	+															+			
	rosea	+	+																+	
	dussumieri	+	+								×						+			
	demani	+		+							+	+					+			
	arcuata	+		×							+						+	+		
	forcipata	+	+									+					+	+		
	coarctata	+	+	×							×						+	+		
	urvillei	+															+	+		
Australuca	*bellator*	+		+	+					+	+				+		+	+		
	seismella	+		+													+			
	polita			+	+					?	?						+			
Thalassuca	*tetragonon*	+		+						+	+						+			
	vocans	+		+						+	+				+		+	+		
Amphiuca	*chlorophthalmus*			+	+					+							+			
	inversa	+		+	+					+	×		+		+		+	+		
Boboruca	*thayeri*		+	+						+								+		
Afruca	*tangeri*				+	+				?		+		+			+	+		
Uca	*princeps*				+	+				+	+	+			+		+	+		
	heteropleura				+	+				+	+						+	+		
	major			+	+	+				+	+								+	
	stylifera			+	+					+		+							+	
	maracoani				+				+	+		+	+					+	+	
	ornata				+				+	?		+	+				+	+		
Minuca	*panamensis*				+													+		
	vocator				+	+	+				+					+			+	
	burgersi					+	+			+		+	+						+	
	mordax					+	+			+		+	+						+	
	minax					+	+			+		+	+						+	
	galapagensis					+	+			+		+	+			+		+	+	
	rapax				+	+	+			+		+	+	+	+	+			+	
	pugnax					+	+			+		+	+	+	+	+			+	
	zacae				+		+					+	+						+	

TABLE 20 (*continued*)

Subgenus	***Species***	***Wave Forms***								***Other Components***						***Timing Elements Résumé***				
																	Usual Wave Duration (Moderate to High Intensity)			
		1. Vertical	*2. Jerking-vertical*	*3. Semi-unflexed*	*4. Lateral-straight*	*5. Lateral-circular*	*6. Jerking-oblique*	*7. Reversed-circular*	*8. Overhead-circling*	*9. Minor-wave*	*10. Leg-stretch*	*11. Prolonged-leg-stretch*	*12. Leg-wave*	*13. Curtsy*	*14. Herding*	*Pause at Peak*	*< 1 Sec.*	*1–2 Sec.*	*> 2 Sec.*	*(Drumming Incorporated, Sometimes Ritualized)*
Celuca	*pugilator*				+		+	+		+	+					+	+	+		
	uruguayensis					+														
	crenulata				+												+			
	speciosa				+	+				+		+					+	+		
	cumulanta				+	+				+	+							+	+	
	batuenta					+				+	+					+	+	+		+
	saltitanta				+	+				+	+						+	+		+
	oerstedi				+	+				+		+						+	+	
	inaequalis				+	+				+	+							+		+
	tenuipedis				+	+				+	+					+	+			+
	tomentosa					+				+	+		+			+		+		
	festae				+	+				+		+			+	+	+	+	+	
	dorotheae				+	+				+	+		+		×	+		+		
	beebei				+	+				+		+	+				+			
	stenodactylus				+					+		+			+			+	+	
	triangularis	+		+		+								×			+	+		
	lactea	+			+	+				+	+	+	+	+	+		+	+		
	leptodactyla				+	+				+	+						+	+		
	limicola					+	+			+	+							+	+	
	deichmanni				+						+					+	+	+		+
	musica					+				+		+	?				+			
	latimanus				+	+	+					+			×	+	+	+	+	

TABLE 21
Reference List of Components in Four Categories of Social Behavior in *UCA*
(For explanation see text)

Ritualized Combat (*pp. 488–491; Table 14, p. 652*)	*Waving Display* (*pp. 494–496; Table 20. p. 658*)	*Agonistic Postures and Associated Motions* (*pp. 479–480; no table*)	*Sound Components* (*pp 482–484; Table 12, p. 644*)
1. Manus-rub	1. Vertical-wave	1. Raised-carpus	1. Major-merus-rub
2. Pollex-rub	2. Jerking-vertical-wave	2. Down-point	2. Minor-merus-rub
3. Pollex-under-&-over-slide	3. Semi-unflexed-wave	3. Frontal-arc	3. Minor-claw-rub
4. Subdactyl-&-subpollex-slide	4. Lateral-straight-wave	4. Forward-point	4. Palm-leg-rub
5. Pollex-base-rub	5. Lateral-circular-wave	5. Lunge	5. Leg-wag
6. Dactyl-slide	6. Jerking-oblique-wave	6. After-lunge	6. Leg-side-rub
7. Upper-&-lower-manus-rub	7. Reversed-circular-wave	7. Carpus-out	7. Major-merus-drum
8. Dactyl-submanus-slide	8. Overhead-circling	8. Flat-claw	8. Minor-merus-drum
9. Interlace	9. Minor-wave	9. Chela-out	9. Major-manus-drum
10. Pregape-rub	10. Leg-stretch	10. Lateral-stretch	10. Minor-chela-tap
11. Heel-&-hollow	11. Prolonged-leg-stretch	11. Creep	11. Leg-stamp
12. Heel-&-ridge	12. Leg-wave	12. Prance	12. Bubbling
13. Supraheel-rub	13. Curtsy	13. High-rise	13. Membrane-vibration
14. Dactyl-along-pollex-groove	14. Herding	14. Legs-out	14. Claw-rub
15. Subdactyl-&-suprapollex-saw	(Duration components omitted)		15. Claw-tap
			16. Interdigitated-leg-wag

TABLE 22
Coincident populations of subspecies in *UCA*

NOTE: Specimens from localities marked with asterisk were collected personally; the others were examined in museum collections. Sources in Appendix A, pp. 597f. and 611ff. Discussion in text, pp. 87, 294. See also maps 20, 21.

Area	*Subspecies of U. VOCANS*	*Locality*	*Subspecies of U. LACTEA*	*Locality*
New Guinea	*pacificensis, vomeris:*	Port Moresby	–	–
	pacificensis, vomeris:	Madang*	–	–
Philippines				
Sulu	*pacificensis, vocans:*	Joló*	*perplexa, annulipes:*	Tawi Tawi*
Mindanao	*pacificensis, vocans:*	Zamboanga*	–	–
G. of Davao	*pacificensis, vocans:*	near Davao*	*perplexa, annulipes:*	Malalag*
G. of Davao	*pacificensis, vocans:*	Madaum*	*perplexa, annulipes:*	Sasa*
Panay	–	–	*perplexa, annulipes:*	Iloilo
Indonesia				
Celebes	–	–	*perpexa, annulipes:*	Makassar, Para Pare
Java	–	–	*perplexa, annulipes:*	Madera, Besoeki, Djakarta
Borneo	–	–	*perplexa, annulipes:*	Pontianak
Malaysia				
Singapore	*hesperiae, vocans:*	Bedok*	*perplexa, annulipes:*	Kallong*
Malaya	–	–	*perplexa, annulipes:*	Port Dickson
India	–	–	*perplexa, annulipes:*	Pondicherry

TABLE 23
Comparisons of High Intensity Courtship Display Between Two Series of Allopatric Forms: A Possible Factor in Sympatric Coexistence (See p. 529)

Area	*Allopatric Group*	*Display*		*Allopatric Group*	*Display*	
	UCA DUSSUMIERI	*Jerks During Primary Wave*	*Secondary Waves*	*UCA, superspecies* COARCTATA	*Jerks During Primary Wave*	*Secondary Waves*
Fiji Is.	[absent]	–	–	*c. coarctata*	Present	Weak
Philippine Is.	*d. dussumieri*	Present	Absent	*c. coarctata*	Present	Strong
N. W. Australia	*d. capricornis*	Absent	Absent	*c. flammula*	Present	Weak
Malaysia	*d. spinata*	Absent	Absent	*forcipata*	Present	Weak
E. Africa	[absent]	–	–	*urvillei*	Absent	Absent

TABLE 24
Sites of Field Work on *UCA* 1953–1970*

Region	*Locality*	*No. of Visits*	*Duration of Stay (Number of Day-time Low Tides)* 1 to 2	3 to 7	More than 10
Eastern Atlantic					
Portugal:	The Algarve: Vila Real de Sto. Antonio to Sagres	1			+
Nigeria:	Lagos	1		+	
Angola:	Luanda	1		+	+
Indo-Pacific					
Ethiopia:	Massawa	2			+
Tanzania:	Pemba	1		+	
	Zanzibar	1			+**
	Dar-es-Salaam	1	+		
Mozambique:	Inhaca I.	1		+	
Aden		1	+		
Pakistan:	Karachi	2	+		
India:	Bombay	1	+		
	Ernakulam	1		+	
Ceylon:	Negombo	2			+
Malaysia:	Penang	1	+		
	Negri Sembilan: near Sungei Dua	1	+		
	Malacca	1	+		
	Sarawak: Santobong	1	+		
Singapore		1			+**
Indonesia:	Java: Semarang	1		+	
	Surabaja	1		+	
Australia:	Broome	1		+	
	Darwin	1		+	
	Gladstone	1		+	
	Shorncliffe: near Brisbane	1	+		
New Caledonia:	near Nouméa	1		+	
N. E. New Guinea:	near Madang	1			+**
Philippines:	Sulu: Tawi-Tawi	1	+		
	Jolô	1	+		
	Mindanao: Zamboanga	1			+
	near Davao	1		+	
	Palawan: Puerto Princesa	1	+		
	Basilan R.	1	+		
	Luzon: near Manila	1	+		
Hong Kong:	Kowloon	1		+	
Taiwan:	Tamsui	1		+	
Japan:	Kyushu: Ariadne Bay	1		+	
Fiji:	Viti Levu	3			+
Tahiti		1			+
Bora Bora		1	+		

TABLE 24 (*Continued*)

Region	*Locality*	*No. of Visits*	*Duration of Stay (Number Day-time Low Tides)* 1 to 2	3 to 7	More than 10
Eastern Pacific					
Costa Rica:	Golfito	1		+	
Panama:	Panama City	2		+	
Western Atlantic					
U.S.A.:	Massachusetts: Cotuit	1			+**
	Florida: St. Augustine	2		+	
	Miami	2		+	
	Puerto Rico	3		+	
	St. Thomas	3		+	
Guatemala:	Puerto Barrios	1		+	
Guadeloupe		2		+	
Martinique		1	+		
Barbados		1	+		
Trinidad-Tobago		Many			+†
Guyana	Georgetown	2	+		
Surinam:	Paramaribo	2		+	
Brazil:	Belém	1	+		
	São Luiz	1		+	
	Fortaleza	1	+		
	Recife	1	+		
	São Salvador	1	+		
	Rio de Janeiro	1			+

*Before 1953 work was also done on *Uca*, without cinematography, on the coast of Venezuela and, in the eastern Pacific, from southern California to the Gulf of Guayaquil.

**Between one and two months.

†Sporadic work on *Uca*, including the use of crabberies, carried out at the William Beebe Tropical Research Station, Simla, Trinidad, West Indies, especially during 1957, 1958, and 1962–1966.

Appendix D. Field Methods and the Maintenance of Fiddler Crabs in Captivity

CONTENTS

INTRODUCTION

As in every other branch of zoology, each worker who begins to study fiddler crabs quickly develops his own methods of work. Accordingly the paragraphs below will be most helpful to newcomers. Little will be said of particular instruments, since those available on the market change rapidly, often with improvements useful to a biologist in the field, while the disadvantages of any model may be soon corrected.

On the other hand it seems worthwhile to include a number of suggestions for elementary aids to success. Many will seem obvious to a worker experienced in dealing with the minor crises that often loom when living animals, both delicate and strange, are the subjects of his study. Yet the simple solutions may not occur to him in time to avert a disaster to his efforts—whether these are attempts to fly a hundred healthy crabs across an ocean or merely to keep some fiddlers in a pail from kicking off their legs.

TIMING OF FIELD TRIPS

Many species in the tropics are socially active throughout the year, so that seasons may be disregarded in the making of plans. This attitude is reasonably safe when the trip includes territory in the equatorial zone, extending from about lat. 10° N to lat. 10° S. Even here local peculiarities of climate are to be expected, when drought or excessive rain may immobilize the crabs. It follows that the only reliable course is to learn as much as possible about the seasons of the area before selecting dates for the trip. In out-of-the-way places letters to the government meteorological service, to the nearest museum, or to a school of agriculture should be sent, preferably months ahead, in order to allow time for follow-up correspondence. The enquiry should stress that average rainfall at the capital city or the average number of days on which rain falls during each month will not give the information desired; instead, detailed rainfall tables should be requested for the coastal zone over a period of years. In parts of the tropics which have long had stable governments, such as Singapore, there is of course no problem; in many other areas time and persistence are necessary.

In the tropics outside of the equatorial zone, a single dry season usually contrasts strongly with a single rainy season and here information on the seasons and their variations becomes essential. The species that occur farthest from the open sea are subject to desiccation during the dry season and these populations accordingly aestivate as need arises. Even when they do not do so, they show little or no social activity until after the start of the rains; on the other hand even species that breed throughout the year may show a peak of social behavior near the beginning of the rainy season, always in accordance with a characteristic lunar or semi-lunar cycle. For example, in the West Indies social behavior studies of the subgenus *Minuca* should be avoided from about the middle of January until May or June. Even though meteorological information is easily available in this region, annual variations in the arrival of the rains are sometimes striking and always unpredictable; if time or funds are short, it may prove helpful to ask a local field biologist to keep watch and cable when the crabs start waving; if such a correspondent does not exist, it would be almost equally helpful for an acquaintance or official to cable as soon as the first strong downpour—not the first shower—occurs.

In the subtropics temperature becomes a factor and, as in the temperate zone, most social activity is confined to the local spring and summer. The length of the season depends in general on the latitude, but adequate information has not yet been gathered.

An essential tool in the planning of any field work is the volume of tide tables appropriate to the area. A complete set is published annually in English by both the United States Department of Commerce and by the British Admiralty. The tables permit the selection for almost any suitable locality of appropriate periods for the visit; when only a short stay on a tropical shore is possible, such planning is fully as important as a knowledge of the seasons. If both the locality itself and the activity rhythms of the desired species are unfamiliar, it is best to arrive at least two days before the occurrence of a low tide around 0800; often this tide occurs several days after new or full moon. If time is limited to a week or so, optimal populations can be located during the first two days of the stay when most species—with the tide low around 0600 to 0700—are not socially at their most active. Then, if the work period can extend through the week to include the day on which low tide occurs about 1300, the chances are good that the major part of the social activity cycle will have been observed. At least in tropical species, when the tide is low during the afternoon the populations show minimal social activity even when heat is not excessive. In a few species waving display, but not combat, is resumed when the tide is sufficiently low between 1700 and dusk. In several species the most active periods of all fall between 1700 and 1800 as well as in the morning between 0700 and 0900. Nocturnal social activity when present apparently takes place chiefly during periods of low tide before midnight, corresponding to the high activity of corresponding morning lows; many further observations are needed on appropriate species, however, during parts of the cycle when low tide takes place between midnight and dawn.

Coasts having very irregular tides underline the need for special comparative studies of fiddler crab activity rhythms. Here during parts of the year the tide ebbs conspicuously only once every 24 hours and only during daylight or, as the tide tables put it, "low tide largely diurnal." At these times the diurnal highs and nocturnal lows are usually barely perceptible in the tables as very slight, brief reversals of flow direction that are virtually undetectable in the real world of a mud flat. A normal set of tides may or may not abruptly appear for a few days at or near the change of the moon; very often even these periods do not provide a diurnal low during the hours elsewhere found to be optimal for social activity in a particular species. Sometimes the tides are reversed, being low only at night for long periods. Good examples of these and other irregularities appear on the Gulf coast of the United States, the north coast of Java, and the north central coast of New Guinea. All these conditions provide challenges to the investigator and also, it would seem, to the crabs. A short-term visitor can only aim for a morning or midday low occurring reasonably near full moon or new moon, and hope for the best.

Selection and Use of Sites

A vital factor in selecting for field work a particular stretch of shore is its history of pollution. Unfortunately, clean-looking small bays, margined ideally with mangroves or northern marshes, often turn out to be contaminated by runoffs from the inland use of agricultural pesticides, chemical fertilizers, and processing plants. Sometimes the health and behavior of the crabs appear to be unaffected. I found one happy example in Barbados, where a population of *burgersi* behaved characteristically, although the crabs shared a stream mouth with a sugar refinery; this plant was probably responsible for the vivid red that entirely suffused every individual in the population, a situation never found elsewhere. As we learn more of the effects on behavior and reproduction of pollution in other animals, however, the need for care in the investigation of local conditions becomes always more apparent. This is especially true before work on species in which the criteria and ranges of "normal behavior" are as yet unknown, or when the forms to be expected are unfamiliar in life to the investigator.

The importance of this factor in certain studies cannot be exaggerated. It becomes crucial, for instance, in comparative investigations of different populations of the same species. Another example will illustrate the uncertainties that can arise. Several summers ago on Cape Cod, Massachusetts, I concentrated on observing the social behavior of an apparently typical population of *pugilator*. The site appeared ideal and reliable sources reported that no aerial spraying against mosquitoes had taken place over the small cove for three years; in contrast to this certainty, the runoff patterns from tilled fields and cranberry bogs, prevalent inland, were unknown; the collection of shellfish for food from the cove and adjoining bay was permitted by the authorities, although areas a few miles away were blocked off as contaminated.

The purpose of the study was to compare the social behavior of the population here near the northern boundary of the species' range with that of populations in more southern localities. Individual components of waving behavior, courtship, threat, and combat proved to be entirely comparable to those previously observed in Connecticut and Florida; the crabs appeared to feed as energetically as usual in the genus; finally, that particular summer included a proportion of warm and sunny weather that was normal for the locality. Yet the amount of social activity of the crabs was far below that of more southern populations. In particular, bouts of waving and combat were rare and the periods devoted to these activities exceedingly short. I ended the season uncertain as to whether I had been watching an interesting effect of climate, or whether pollutants were after all at work, or both. Data accumulated on gonads and egg production have not yet been analyzed.

Fiddler workers will keep in mind a sharp division between artificial pollution and the presence of natural sewage, which gives one of the best guarantees of a rich and varied fauna of *Uca.* Such a favorable location is often easily spotted from the air in the tropics, as the plane circles for a landing, since it characteristically includes thatched huts, preferably on stilts, along the edge of a cove partly fringed with mangroves and flanking the mouth of the usual stream. Small fishing boats drawn up on such a shore almost insure good crabbing, except close to the frequent turmoil at the landing place itself.

In selecting such sites, it is useful automatically to remember three points. First, a close association often occurs here of species that are not usually sympatric; accordingly the assembly is in that particular atypical. Second, in future studies of the effects of crowding we shall very likely find that even conspecific members of such populations behave differently in some ways from aggregations with more space among the burrows. Finally, no able-bodied observer of fiddlers should avoid wading into the mud as usual and getting down to his customary crab's eye point of view.

Work in tropical mud deserves amplification. Aesthetically the experience practically never proves displeasing; regardless of their unsavoury reputation, mangrove swamps and flats frequented by thriving fiddlers smell only of good, flourishing vegetation and the fresh odor of tide-washed mud and salt air. We counteract the slight risk of infection after working near houses by scrubbing when back at the field base with soap and water to which we add a liquid disinfectant; the local pharmacy always carries some appropriate and usually familiar brand. As a further precaution we apply additional solution after washing to any area of skin that came in contact with the mud and allow it to dry there. Since modern workers take whatever prophylactic measures against disease that have been professionally recommended, most health risks are small. In the mud, especially, these include the danger of infection of small cuts, which should be well protected. Otherwise, nowadays most indispositions are fortunately quickly curable, although they can be exasperating wasters of time and opportunity. In brief, only the local prevalence of a serious epidemic should keep a healthy worker out of the mud.

When a newcomer to a region is unfamiliar with the appearance of the local species in the field, he may not be able to recognize them in spite of preliminary work on preserved specimens. This difficulty may be partly because in each species the individuals show great variation in proportions due to allometric growth and to contrasts among males that are strongly leptochelous or brachychelous; almost all populations also show a striking range of color differences. Biologists who are not systematists sometimes feel understandably reluctant to become familiar with the morphological features of gonopods, preferring to concentrate on characters that do not need a lens, much less a microscope. Yet if a worker takes time before the trip briefly to investigate gonopods of expected species, he can catch sample males in the field and usually identify them in the hand with a pocket lens; when time in the locality is limited, this rapid certainty proves rewarding.

Finally, as will be amplified below, in work with unfamiliar species it seems best not to cut down on observation time in favor of operating cameras and other demanding instruments. Human eyes, binoculars, and patience give the best foundations.

Equipment and Its Uses

The selection of instruments and supplies, and the divisions of time for their use, depends of course on the primary interests of the investigator, not to mention the size of his budget. The following remarks therefore provide rough guidelines only.

Binoculars. In my experience this important instrument's most desirable characteristics, aside from good optical quality, are light weight to aid prolonged use without shifting position, and adjustment to permit short-range focusing, preferably to less than 2 meters. The ideal magnification for me is $\times 7$. Unlike its effect in bird glasses, a narrow field is not a disadvantage.

Motion Picture Photography. For all serious motion picture work on fiddler crabs a 16 mm camera of professional caliber is essential. Lesser instruments at present do not seem sufficiently flexible for the demands of the work and in particular are inadequate for photographing in sufficient detail for ethological analysis many of the significant motions of individuals. The most useful lenses, all telephotos, have proved to be 63, 135, and 150 mm in focal length, respectively. The 63 mm lens gives the greatest magnification and good depth of field for small crabs that allow a close approach, since in the particular model used the lens can be racked out without removing it from the camera; extension tubes, which under field conditions are at the least inconvenient, become unnecessary. The 150 mm lens makes possible usable films of excessively shy populations. When air travel, combined with the need for taking other heavy equipment, makes it desirable to carry minimal cine gear, I take only the camera, two magazines, and the 135 mm lens along with its adapter; a camera case is omitted, since everything can be safely padded with clothing in a suitcase during travel; in the field plastic bags and an umbrella protect the instruments and film from mud and the weather. Styrotex picnic boxes are efficient insulators against heat and can usually be bought locally; otherwise the ubiquitous plastic pail serves well.

Exposure at 24 frames per second proves better than at 16 frames, not only because a sound track can then be added later if desired but because, since more frames cover a given action, inspection of fine details in projection or under a microscope is facilitated.

Color film, in spite of its relative slowness and the extra expense, is far better than black-and-white for observing and analyzing the motions of waving display, combat, and sound production, whether during ordinary projection or special analyses; on black-and-white film the crabs tend to merge with their backgrounds so that their morphological details can be frustratingly indistinct during attempts to distinguish, for example, their methods of stridulation. Since I have always used color film, I did not appreciate its advantages during analyses until good quality black-and-white prints were made to save the original from wear caused by repeated projections; the experiment was not a success, when judged even from the limited viewpoint of eyestrain alone. With care, projection does not hurt the original and, with specially important footages, an investment in color duplicates can and should be made.

No matter how limited the budget, ample film should be carried on a trip if at all possible; it should be exposed in quantity even if conditions are not optimal; many important insights into fiddler behavior, and suggestions for future work, were obtained through rerunning films made months and years later from film exposed for quite different reasons and often in bad weather.

For any behavioral study it is unsatisfactory to include many individuals in one frame in the hope of being able to analyze display and details of social interchanges in this way of an entire group. Details are invariably disappointing, and the use of long shots is, for serious film analysis, strictly limited. An exception that has not yet been tried will probably prove to be wide-angle photography directed vertically down on a population to record the progress of aggressive wanderers and of wandering females, or to determine the division of waving and non-waving time in individual burrow-holders. Because of the shortness of reels and the expense of film this project, when instruments improve in resolution, will probably be found to be a very suitable use for a television camera.

During film analysis, the duration of components and their parts are determined by counting the individual frames, either manually through a microscope or by means of the counter on a projector for time-motion studies. Accordingly, after every season in the field and more often after rugged use, the camera's motor should be checked to ensure the accuracy of its indicated speed.

Video Equipment. At this writing videotape is not yet available in color in portable television equipment. Since black-and-white videotape is not nearly equivalent in definition to color motion picture film, and because of other shortcomings, videotape images do not replace motion picture close-ups for ethological analysis. Nevertheless video equipment proves invaluable as a means of inexpensively recording large numbers of repetitions of the gross characteristics of waving displays; these sequences can determine reliably ranges in variation in such categories as duration of individual waves, height, and angle of the major cheliped, and elevations of the ambulatories during display. The equipment also serves excellently as a monitor close to the mouths of one or more individual burrows, since it can operate unattended for long periods. Finally video work is the only technique now available for proving that certain motions result in sound, the synchrony of sound and image being perfect. Related comments will be found in the following paragraphs.

Microphones, Tape-recorders, and Batteries. As far as is known, fiddlers do not make high-frequency sounds; accordingly the range in a good microphone for general use proves adequate. Future work may well show that certain kinds of stridulation produce high-frequency, airborne sounds, comparable to those of some orthopterans; if so, special equipment will of course be needed.

Tough, small, contact microphones, when pressed into the substrate close to the crab, are at present the most useful instruments for receiving fiddler sounds transmitted through the substrate. A variety of inexpensive hearing aids and guitar amplifiers have been used with success by others and by me.

Microphones capable of picking up airborne sounds produced by such components as leg-twiddling are expensive. I have had no success with any except a strongly directional instrument. Even the best must be used very close to the performing crab;

they are far more delicate than contact microphones and must be protected from direct contact with both substrate and moisture. For these microphones a small windscreen is essential and its size is important; although a large one may be more efficient, it may then constitute for the crabs a strange object of such importance that they need more than a few minutes to become habituated; sometimes a selected individual will not again during that particular low tide ever become active, or even reemerge from his burrow sufficiently close to the microphone for its operation.

Tests with two models of hydrophones were failures, since each instrument picked up subsurface sounds from, apparently, a number of neighboring fiddlers; not enough is yet known of fiddler sounds for the observer confidently to disregard all except a particular sound, much less to attribute each correctly to sex, phase, and species, or even usually to be certain that the producing animal is a fiddler. As soon as sufficient knowledge is accumulated, hydrophones, because of this very sensitivity, will certainly prove invaluable. For example they should serve well to detect social situations underground, to determine the presence and distribution of males and perhaps females when producing sounds deep in their burrows, and to detect antiphonies and choruses.

Tape-recorders of sufficient toughness for travel and for hard use in the tropics are now fortunately prevalent. In my experience their weak points remain their batteries. If rechargeable types are carried, along with a range of adapters for foreign electrical outlets, the problem is only partly solved. The best of them soon become weakened and hold their charges inadequately, even when they are fully recharged after each use. The trouble sometimes results from weak voltage in the local current; in this case charging for long periods—for example for 24 consecutive hours—sometimes will yield several needed hours of current in the field. More often the only reliable solution is to rent or buy a car storage battery. If power is needed daily at the same site for a week or more, and if the chosen spot is either sufficiently guarded, fenced, or isolated, the battery may be wrapped after use in a piece of plastic and left on a board above the level of high tide. Unfortunately, in perhaps most parts of the world likely to be visited by a short-term field worker the object would prove to be such a temptation to pilferers that its weight would be no deterrent. Nevertheless its dependable power is worth a large sum in car-hire money, perhaps not otherwise needed, to take it to and from the base.

Still Photography. The general methods and equipment employed in macrophotography of small living animals are altogether applicable to fiddler crabs, although the uses of such photographs are limited. Because of the fast and complex movements of socially active individuals, still photographs are almost always less useful for ethological study than in many other groups of animals. One needs to be able, for reconstruction of memories after field work and for comparative analyses, to review action patterns rather than simple postures. Obvious exceptions exist, such as various threat positions, the highest point a cheliped attains in waving display, the form of a structure beside a burrow, and the position held during a surface copulation; nevertheless these useful pieces of patterns are few. Again, color photographs show limitations in recording color changes. For scientific use, at least, a well-exposed sequence on color motion picture film, made at a suitably close distance, is worth much more than a series of stills in illustrating any aspect of fiddler behavior, and requires far less precious field time. The relatively poor quality of single frames for reproduction is counterbalanced by the wide choice of the moment to be illustrated.

Tripods. In most sequences it is extremely important to photograph the crabs close to ground level, as near as feasible to a crab's eye view. When taken from other angles the films may not show details vital to ethological analysis and correct interpretation. For example, a display sequence shot obliquely from above often cannot settle whether the major cheliped touches the ground in a drumming component, whether ritualized drumming occurs instead, or whether, in contrast, the major merus is vibrating against the suborbital region. On the other hand, occasional long shots and wide-angle views require normal heights for the camera.

A necessity therefore is a tripod with adjustable legs which when fully contracted measure less than 10 inches long. Such lengths are readily available in "table-top" tripods; unfortunately none of these models has the requisite strength to support the heavy, tilting, tripod head that must be added, plus the weight of a professional 16 mm motion picture camera, or of a television unit. If a light tripod is used, the film shows the effects of vibration, while a weak and unversatile head both fails to hold the camera at an angle and cannot cope with some of the work's demands. Finally, the design of the tripod's legs is important, since in spite of a large diameter they must be quickly sinkable, with the aid of strong distal points and a trowel, into firm substrates for further height reduction, while the locks on the joints must work easily for rapid extension at need. Frequent cleaning and oiling help avoid lost opportunities; as any photographer knows, few frustrations except a stuck camera are worse in a crisis than a balky tripod.

Although at least one adequate model used to be available, it is no longer manufactured; at present a machinist must generally be asked to alter a heavy duty tripod to the desired specifications. While it is always possible to use a standard model sunk deep in a pit, the digging wastes time, proves impracticable in underlayers of coral or rock, slows position shifts, and, most important, messes up the habitat. It is far better to travel with a suitable instrument.

Collecting Tools. The best all-around tool for catching fiddlers is a gardening trowel. This implement is unknown in many parts of Asia and no substitute proves as useful, with the occasional exception of the human hand. Accordingly it is advisable to carry a heavy model of stainless steel; the handle and scoop should be forged in one piece; lighter designs will probably not last out the trip.

When crabs are wanted merely as preserved specimens, members of small species with shallow burrows can often be dug up efficiently by wielding the trowel as fast as possible and dropping the crabs into pails variously supplied with liquid, as described in a later section. Difficulties arise when the crabs are larger and live in deep burrows, when they are aestivating or hibernating in hard ground, when the substrate is laced with roots or rhizophorae, when stones are prevalent, or when the burrows extend into coral or creviced limestone. Under any of these conditions the collector must simply take whatever measures suggest themselves, from depending on difficult digging by hand, through the use of a shovel, to changing his activities to more cooperative terrain.

When large general collections are needed and no selection of individuals is required, the fastest method is to borrow a shovel and persuade a cooperative adult to wield it at a distance from the site of ethological observations; troops of enthusiastic small boys should be provided with jars or pails and rewarded for staying far away.

When particular individual crabs must be caught, whether as records following observations, after filming, or for transport alive to crabberies, a trowel still proves to be the most convenient tool. This procedure can never be hurried. The direction of the passage that slants downward inside the burrow mouth must first be determined. When the crab is in its burrow, the collector moves, with as little vibration of the substrate as possible, to a position on one side of the hole so that the trowel can be held vertically, close above the ground under which the passage lies and several inches from the hole itself. As the crab starts to emerge and before it becomes aware of strange objects close by, the blade thrusts swiftly into the ground, scooping underneath the crab and blocking its retreat. Although the subsequent capture and handling will shock the crab it recovers quickly. When the individual is destined for a crabbery it should be placed at once in a dish by itself, as described in the section on crabberies. If a trowel is not available, individual crabs may be similarly cut off from their burrows with any broad blade; butcher knives, machetes, and even a Malay kris have all worked.

One method seems most effective for seizing male fiddlers so that their appendages remain in place and their claws do not pinch human fingers. The system works even when a large male is sitting at arm's length in the bottom of a burrow. It consists of grasping the crab by placing your thumb firmly against the posterior part of his carapace and then using your fingers, with the first one bent above his major dactyl, to push his claw into the flexed rest position in front of his mouth region and to hold it there. If the crab is in a high intensity threat position above ground, with the claw "open," you must meanwhile force his major dactyl slowly down against his pollex with help from your other hand. Even females should be grasped similarly to prevent their losing some legs.

Marking Paint. Several opaque, fast-drying lacquers are available in artists' supply stores and hobby shops that are suitable for marking crabs. The brands selected by behavioral entomologists for use on bees and other insects are often appropriate. Providing the carapace and outer major manus of individual crabs are cleaned and dried before marking, and the marked crab kept in a dry pail for several minutes before releasing, the paint needs renewal in outdoor crabberies only about every four weeks, unless of course an individual molts.

I have not yet had success in marking crabs either in the field or in crabberies with spray paint. Out-of-doors air currents blow the spray even on calm days so that it either misses the target crab or gets in its eyes or soft areas connecting segments. When this happens the fiddler interrupts its activities to rub eyes or legs with other appendages; sometimes paralysis of an appendage occurs and sometimes captive crabs have soon died after showing one or more symptoms. I have watched similar effects on salticid spiders and butterflies when the paint by accident flowed over sensitive areas. An array of brands should be systematically tested in the home laboratory and perhaps a suitable formula concocted.

Sometimes particular crabs in the field can be touched with a brush fastened to the end of a dark-colored, slender, flexible rod of bamboo or other material. My chief difficulty in limited attempts has been that when lacquer dries fast enough to stick on the crab's next abrasive trip underground it also dries before the target crab can be touched, as I wait with the rod poised above its burrow. No matter how habituated it has become to an observer, it retreats almost inevitably before the paint-filled brush can be eased down to touch it; therefore the actual dab must await its emergence. Nevertheless some variation of this technique should be made eventually to work.

Color of Clothing and Equipment. Like birds and many other animals, fiddler crabs—easily startled by strange objects and abrupt motions—are keenly sensitive to moving objects that contrast with the substrate. Accordingly, in order to encourage their rapid habituation to a nearby human being, experienced observers avoid fast or sudden motions, white or pastel clothing, and large expanses of untanned European skin. Tennis hats can be tinted in coffee or tea, while a felt-tipped pen or crab-marking enamel will blacken the shine on a camera's chrome trim.

Field Data

In the study of *Uca* it seems more important than in many groups that all notes, films, and recordings be accompanied by plentiful data on both meteorology and ecology. This necessity is caused by the importance of weather, circadian and other rhythms, and even microhabitats in the behavior of the crabs. The data include ideally the following information: exact geographical location, including any local names in dialect that might simplify the location of the study area by a later worker; date; time; weather during the period, as well as any special events, such as a typhoon in the recent past; temperature both at the surface and within a burrow; substrate; proximity and type of vegetation; associated species of *Uca* and other animals; size and degree of crowding of the population; relative numbers of displaying and non-displaying males; evidence of partial isolation of displaying males in a lek-like formation; prevalence of aggressive wanderers; number of wandering females; proportion of ovigerous to non-ovigerous females; presence and proportion of young; color phases and their distribution; information related to possible pollution. It is convenient when reviewing notes to find at the beginning of each day's data a note beside the date giving the time of low tide and the phase of the moon, such as "low 0850; 3rd day after full," even though this information, unlike the rest, is readily retrievable at home.

Especially important are records of precise display circumstances surrounding the observation or filming of particular episodes. All of these written details, particularly of short film sequences made on poorly known species, prove exceedingly useful when analysis is under way, months and sometimes years later. For example, helpful notes will include whether the filmed display appeared to be of high or low intensity, and whether the behavioral fragment was apparently elicited by the presence of a female beyond range of the lens or by another male making some particular motion.

When either a species, a locality, or the behavior on which I intended to concentrate was unfamiliar, it seemed essential to devote time for as long as possible—whether the first low-tide period or, in a long stay, a week or more—to observations and note-taking only, with photography and recording saved for later sessions. When this course was followed, the non-observational chores could all be planned and carried out far more intelligently. For me attempts to combine in a single session the use of camera and recorder with observation resulted in poor work in both areas. Odd notes scribbled inconspicuously, while waiting between instrument set-ups and their operation, sometimes of course prove invaluable, but they probably should be viewed as unexpected dividends; because of the division of attention, they may prove unreliable. As described in the preceding paragraph, exceptions are the descriptions of circumstances surrounding an episode, which should be written immediately after filming or recording.

A final exception to the postponement of the use of equipment seems to me to exist when, in a far-off place, a concatenation occurs that consists of very brief field time, uncertain weather, and rare or unexpected species; then it usually proves wise to photograph a few representative waving displays as rapidly as possible and so, in the photographer's phrase, "get some film under your belt."

Data for Allometric Studies

The growth characteristics of series of individual fiddlers were investigated in different populations of a number of species. In previous studies of the changing proportions of the major cheliped to the body, as in Huxley, 1924, the investigator selected the relation of the weight of the major cheliped to that of the total weight of the crab.

In the present study this procedure proved unsatisfactory and linear proportions were substituted. The relation of the carapace length to that of the propodus (major manus plux pollex) appeared to be the most useful and convenient. Efficiency in the use of the material required that at least these two measurements be made at the field base rather than at the home laboratory, since in spite of care some claws become detached during travel. In detailed growth studies of large collections all needed additional measurements should of course be made at the same time, to keep the measurements of individuals of the same length distinct. Since caliper measurements cannot be accurately made at less than about 10 mm, and because of the usual dearth of microscopes with micrometer scales at field bases, it is often necessary to take the time gently to flex the major cheliped against the front of the body of each small crab and tie it in place before packing for travel. Every measurement can then be taken with confidence at home.

This use of meristic relationships does not share several disadvantages characteristic of weight proportions, even when only ratios of major claw to body are investigated. First, preserved individuals do not lend themselves to any technique of weighing that makes the results acceptably comparable, in the absence of information on the effects of chemicals on the organs. Different kinds, strengths, and sequences of preservatives must, it seems, affect the weight of the material differently. Again, no formula has been devised to regulate the time to be given for draining off the liquid which would make the weights of crabs of different sizes fully comparable. Even if all specimens are thoroughly dried before weighing, the values obtained are probably undesirably artificial. Second, even if in contrast living specimens are weighed, each comparably dried and drained of water from the branchial chambers, the weighing must be done on a sensitive balance. Yet in most of the places where I made collections it was impossible to bring an adequate instrument and living crabs together. On tests in Trinidad, where we had a suitable balance, the total weight of a crab changed as much as 20 percent in either direction between weighing within two hours after capture and weighing again after one week in the crabberies. Significant variations in weight presumably occur also in crabs living under natural conditions. For example, when crabs in the dry season have not been feeding regularly, the general body weight may be expected to be less with respect to the major claw, the weight of which consists largely of the integument. It is obvious that linear proportions do not share these disadvantages.

Preservation of Specimens

In preserving specimens of *Uca* for general study in the laboratory the following system has been adopted. It forms a compromise among several methods favored by various investigators. Its advantages for the needs of the present kind of study are the following: a minimum number of specimens lose their chelipeds; the internal organs are well preserved; the joints of the appendages are eventually left flexible enough for convenient manipulation. Although these intersegmental areas remain somewhat stiffer than in specimens placed sooner or solely in alcohol, the improved condition of the internal organs appears to give more than adequate compensation.

Jars or plastic pails are partly filled with 4 percent formalin made with fresh water in which crustaceans have already died. This solution, carried daily to the collecting site, is used repeatedly and becomes increasingly effective. The animals in a well "ripened" solution succumb quickly with practically no struggle or autotomy, while the formalin prevents the internal decomposition which so often begins in the heat of a mud flat.

In the field base, whether laboratory or hotel room, the specimens are drained, rinsed gently in tap water, and covered to twice their depth with 4 percent formalin, previously unused, to which borax has been added in the proportion of one tablespoon per gallon. After seven days the crabs are changed to 70 percent grain alcohol and this, after another week, is changed once more. Crabs may be left longer than one week in formalin, but should be transferred to alcohol at the first opportunity. In many foreign countries pure ethyl alcohol (C_2H_5OH) is both prohibitively expensive and difficult to obtain. Here ethyl alcohol that has been slightly adulterated under government control, to make it unfit for drinking, is often both usable for crab preservation and readily available. Methyl (wood) alcohol (CH_3OH), however, should never be used except as a temporary last resort.

Sufficient full strength formaldehyde, with its bottle tightly sealed, padded and packed in a taped plastic pail, can safely be carried by air as checked baggage in sufficient quantity to last throughout a long field trip. In its place, emergency supplies can almost always be obtained in small tropical towns from the local undertaker, if not from a pharmacy; the only difficulty is the prevalence of holidays.

In an extreme emergency full-strength rum, whisky, arrack, or other hard liquor may be used full strength, but it should be replaced with a conventional preservative as soon as possible, since the specimens soften while the appendages gradually drop off. If a high-proof grade is available, it should of course be selected.

If formalin is not carried from the field base onto the mud flat and the crabs are alive on the return to headquarters, they may be placed in a refrigerator freezer for an hour, then well covered with 4 percent formalin and returned to the refrigerator overnight; at this time they should not be stored in the freezer compartment. After that washing and change of solutions continues as before. Or, on being brought from the field and in the absence of refrigeration they may be killed by covering to twice their depth with 10 to 15 percent formalin for 20 minutes. Washing, 4 percent formalin, and subsequent steps then continue as usual. The disadvantage to the latter technique is that while it prevents autotomy and struggle it leaves the legs permanently less flexible than any of the other methods. However in my opinion it is still preferable to the sole use of alcohol on either living or dead crabs, if both intact legs and well-preserved internal organs are desired.

Tweedie's suggestion (1950.2) for placing tropical grapsoids as soon as caught into wide-mouth thermos jars of ice water with floating ice is, as he recommends, unexcelled for small, delicate crabs, particularly of certain Indo-Malayan genera. The containers are, nevertheless, unwieldy and unnecessary for most *Uca*. A modern compromise is provided by styrofoam picnic boxes, in which ice can be heaped around plastic containers each holding a little ice water, in which the crabs can be dropped upon capture.

Well-preserved crabs travel successfully by air, when both the expense of weight and regulations against the transport of alcohol are factors, if the specimens are packed in plastic pails with only a small amount of preserving liquid and a layer of cotton or cloth soaked in weak formalin or water on top. Labeled packets of groups or individuals to be kept separate may be wrapped in porous material, such as cheesecloth, and tied with string. The pail's cover is sealed on with freezer tape. Needless to say, the crabs should be unpacked promptly on arrival and immersed in suitable preservative.

Transportation of Living Crabs

For ethological work in crabberies the only feasible system of transportation has proved to be the following. Individual crabs are selected in the field, collected as described above (p. 669), washed off by submersion in a clean plastic pail that has never been used for chemicals and is filled with seawater, and then placed at once, while the collector is still at the site, in a plastic refrigerator dish large enough to allow the crab ample space to move about. A small amount of the local seawater is added, not sufficient even fully to cover the bottom of the dish. The lid is taped on, preferably with freezer tape, since its adhesion is unaffected by water. Each dish is placed in the nearest patch of shade until time to return to the field base; it is never moved abruptly. If at any stage the journey involves transportation by car over a rough road, the dishes are protected by padding from both shock and engine heat; if styrofoam picnic boxes are available, they provide additional insulation for groups of the dishes; the car is driven slowly. The captures are preferably made one to two days before departure from the field base for the home laboratory. Local seawater, preferably taken at high tide from the shore where the crabs were captured, is brought to the local base in plastic pails that, as usual, have not been used for chemically preserved specimens. Each crab is submerged in a tumblerful of the water and allowed to move about freely at least once before traveling, while its dish is cleaned with more of the seawater, thus removing mud and faeces. After each cleaning the crab is replaced in its dish with seawater only a few millimeters deep; the amount depends on the size of the crab and should be only enough to enable it to moisten its gills through the afferent apertures when it settles on the bottom. If the air is tropically humid, even less moisture is used in the final servicing before travel, since the moisture will condense at lower temperatures during flight, or during a cold-weather arrival in the north. For reasons still unknown, a fiddler's chance of survival is decreased when more than minimal water is provided; it may be that waste matter dissolved in the water acts as a poison. The boxes are sealed as usual with freezer tape. No food should be provided; fiddlers have been carried for seven days with no food and even without a change of water, providing they have been prepared for travel as just described. Ideally, as in a trip across the Pacific, a long voyage should be broken at, for example, Honolulu, and the containers cleaned, with the water replenished by freshly dipped, fully marine, unpolluted seawater, taken preferably at high tide and always in an uncontaminated plastic pail; no attempt should be made in the middle of a trip either to feed the crabs or to provide them with water from a local mud flat. When transporting crabs on long trips by sea the water may of course be provided from mid-ocean; even the crew on large liners seem to enjoy this kind of request, but must be warned to dip the water after leaving a polluted harbor and not to take it from near one of the ship's waste outlets. The crabs feed well on a trip of this kind on ordinary food for marine fish or for turtles; a few pellets should be provided once a day after cleaning, and removed within one hour. The dish should then be cleaned again and fresh seawater provided.

In the more usual trip by air, every attempt should be made to carry the crabs into the cabin and not ship them either as checked baggage or as air freight. In order to carry more than a small box or flight bag of specimens in the cabin, requests should be made well ahead to the local airline representative; in out-of-the-way places impressive letters of identification help, especially when stamped with institutional seals; in addition, polite persistence is usually essential. Sometimes the agent refers the matter to the pilot.

In case all persuasion fails and the crabs must be checked in the baggage compartment, the individual dishes should be packed in styrofoam boxes, which provide some degree of insulation, and marked clearly that the contents are live animals to be kept upright and away from heat and cold. An airline should not only be selected that is known to maintain the baggage compartments at cabin temperature and pressure, but the point should be rechecked locally before departure. "Approximately cabin temperature" sometimes turns out to be less than 15° C, which can kill a tropical crab. We do not yet know the effects of moderate but swift changes in pressure. I have had few occasions to carry crabs in small, unpressurized planes; the flights were always short and at low altitudes; no ill-effects were apparent.

If it is absolutely necessary to send crabs by air freight, they should be completely routed ahead of time, with space reserved for each leg of the voyage; day flights with stops at tropical airports should be avoided even when no transshipment is needed, since baggage compartments often heat up rapidly when the plane is on the ground; a transfer between airlines should also be avoided, unless it can be handled personally by an acquaintance, since in spite of the labels boxes can easily be left out-of-doors in freezing or torrid weather long enough to kill the entire contents; such shipments are always a gamble and the worst must be expected.

Two examples will emphasize the varied fortunes to be encountered during transportation. I have carried 92 living specimens of *Uca arcuata*, including adults and young of both sexes, from Japan to Trinidad without a single death; water was changed once, during an overnight stop in Honolulu; the entire trip took six days. On the other hand, another trans-Pacific collection of about 100 specimens of several species, including *arcuata*, was lost; I assembled, packed, and routed it in Hong Kong, with every safeguard dictated by experience, sending it by air freight; although the booking was followed in detail as shown by the papers delivered with the shipment, and although the trip only lasted three days, every crab was dead on arrival. More success has, fortunately, been achieved with other, shorter shipments of air freight, although nothing replaces the advantage of carrying the crabs by hand.

If a change of water is indicated en route at a point where no freshly collected seawater is available, a sufficient amount, taken at high tide as close to the open ocean as possible, should be brought with the traveler; modern plastic jugs with screw tops make the transport easy. The water may be safely checked in the baggage compartment; the point is that water from or close to the site where the crabs were collected should not be used except when absolutely necessary, and then taken at or close before high tide, because of the abundant animal and plant matter that may soon pollute the stored water. The transport of seawater for a change in mid-journey worked, for example, at a stopover in Paris on a trip from Ceylon to New York; the entire, hand-carried collection of 96 examples of *Uca lactea annulipes* came through alive and the great majority lived in excellent condition for several months in the crabberies at the New York Zoological Park; at that point the work was terminated—but the crabs were still showing every sign of good health and going through cycles of social activity.

A common practice of commercial collectors in Florida and elsewhere is to ship local fiddlers by the hundred to laboratories, crowding the living specimens into cartons in a tangle of legs. Such a procedure does not work when specimens are wanted for behavior study, since the crabs' subsequent activity is affected; in any case it is suitable only for such relatively hardy forms as *pugilator*. Another system that does not work with *Uca* is the shipment of crabs in plastic bags filled with water and pumped-in air, in the method used so successfully in carrying and shipping small fishes.

Crabberies

For ethological work on fiddler crabs in captivity, only a few principles will be given. The details of successful construction and maintenance, and the suitability of various subjects for research, can vary within wide limits.

The essential points that need attention are provision for space suitable for the species to be kept; artificial tides; water appropriate for the species; a bank of substrate that, again, must be composed of material within the toleration of the species; an efficient filter system; and sunlight, whether real or an artificial facsimile. Almost equally important is care in the capture and transportation of specimens, as described above, and the provision of a population density resembling, at least initially, that found at the source of supply.

Regardless of the small size of the species under observation the smallest tank I have found useful measures 3 ft. by 5 ft. As has long been known, specimens of some *Uca* will live and even breed in fingerbowls, but for ethological work this sort of maintenance is virtually worthless. At the other extreme of size out-of-door crabberies 10 ft. by 15 ft. or more in dimensions are practicable and convenient, at least in the tropics. The minimum advisable depth of any crabbery seems to be with substrate, exclusive of filter, about 7 inches deep at its deepest part; more is of course preferable. Sometimes the tops of open-air crabberies need screening against predators, especially kingfishers; in the mountains of Trinidad these birds quickly learned of the new source of food. At the same station we had to fence the crabberies with wire netting to a height of about 8 inches even in installations so close to the house that the kingfishers did not trouble them; the reason was the attraction of crabbery water for marine toads (*Bufo marinus*) during the dry season; although they apparently did not seize the crabs, the amphibians jumped in and waddled about over the mud bank, knocking down burrow markers and generally disturbing the fiddlers.

The simplest method of simulating tides is to pour a few pails of seawater into the tank at the time of high tide and siphon it slowly out again, starting several hours after its introduction. Out-of-doors in their natural climate, all the tropical species of *Uca* kept in captivity, totaling about 28, responded with apparent health and appropriate behavior when provided with a single low tide in each 24-hour period, with the low arranged to occur at the same hour every morning. The caveats given at the end of this section on crabberies must be particularly heeded in the conduction of any ethological work under such an entirely artificial tidal regimen. Its great advantage is its convenience for indefinite maintenance of a population when minimum facilities and help are available.

In contrast, at the Zoological Park in New York three pairs of fiberglass tanks were maintained with success, seawater being pumped back and forth between the members of each pair with the time controlled automatically by a clockwork mechanism. The dials could be set so that the water flow would reverse any desired number of minutes later at each tide, in accordance with the schedule being followed. While this regimen provided a useful approximation to reality for several days, such as on holiday weekends, it became too quickly out of synchrony with the normal semi-lunar tidal periods to be used for longer periods under the only conditions when such precise schedules were needed. These occurred during particular observations when the crabs' activities had to be carried out under conditions as nearly approaching those in the field as possible. Accordingly, in the usual type of operation the clocks were set once a day during the regular maintenance period in strict accord with the tide table being followed, unless the tanks were under a simple maintenance regimen. At those times a morning or midday low tide was given, the choice depending on the natural period of highest activity for the species; since the clockwork mechanism was available, a low was also set to occur 12 hours later, at night. Just as in out-of-door tanks, the indoor population stayed in good shape indefinitely on this artificial schedule.

Between the extremes of the pail-and-siphon system and the clockwork controls in simulating tides, a number of intermediate systems have been used with success. For example, the two largest Trinidad crabberies were built on a slope, with a storage tank below each. To bring about low tide the tanks were slowly drained by gravity into the storage tanks. From these the water was pumped up again with regulated speed, in time to cover the bank of substrate at the appropriate hour. In this system only one inexpensive pump was needed for each tank; although it had to be started manually, it stopped automatically when the storage tank was almost empty. Whatever the system, just as with apparatus for any saltwater aquarium, the parts of the pumps and fittings that came into contact with the water had to be corrosion-proof and free of copper.

Whether indoors or outdoors it proved possible to use the same seawater for several months or more. Out-of-doors in the rainy season natural showers and downpours maintained the seawater in a naturally variable brackish state, the crabs being adaptable, in the species kept, to a wide range of salinity. In the dry season evaporation was so rapid that liberal additions of fresh water were needed daily from the garden hose; this water had not yet been chemically treated and so could be used from the tap. In the crabberies as in the field the salts in the water that stood in the crab holes during low tide were persistent, giving higher salinity in the burrows; these levels doubtless went far to counteract the wide swings in salinity we provided in the crabberies.

In the indoor crabberies in New York evaporation had also to be carefully watched, since the strong electric lights had an effect on the small tanks similar to that of the sun and wind out-of-doors. Again the daily addition of fresh water, along with frequent checks with a hydrometer, kept the salinity within optimal ranges. Care was taken to dechlorinate all tap water used with a material obtainable from any aquarium supply house; the plastic pails of treated water were allowed to stand at least 12 hours before use in the crabberies, as a safeguard, even though the directions sometimes state that the water is fit for use in ordinary aquaria at once. It was also important that the tap water reach a temperature comparable to that of the circulating "tides"; the fresh water was added to the storage tanks, or at least to the crabbery water at the time of the incoming flow, rather than poured suddenly onto the exposed bank itself. An exception which may, perhaps, be important was the daily simulation at the time of the diurnal low tide of a brief shower of rain, through dribbling dechlorinated water through a perforated plastic dish over the substrate. This procedure seemed to stimulate the crabs to a higher level of activity, just as does a true shower in the field in the middle of a hot and sunny day. Care was taken for some of the fresh water to get into the burrows from time to time, so that the salinity level did not build up excessively. Standing water from the burrows, either indoors or outdoors, was drawn out now and then by syringe and tested with a hydrometer, to be sure that the concentration had not risen above about 40°/00, the highest figure I have found in burrows in the field in Trinidad and the Philippines.

Crabs from special localities, such as the shores of the Red Sea, tolerate considerably higher peaks under their normal conditions of life, and probably should be maintained in captivity at similar levels.

Artificial seawater can always be used for short periods in crabberies, but it should probably not be used indefinitely, any more than such reliance is generally recommended for ordinary aquaria.

The substrate selected should be of the general kind in which the species to be kept most often occurs. For example, it obviously would not be wise to provide a mud-living crab such as *coarctata* or *maracoani* with a relatively sandy substrate that would be entirely suitable for *pugilator*. Nevertheless three of the most pleasant surprises resulting from the crabbery work were connected with substrate provisions, and emerged in New York. I had expected that it would be necessary to transport portions of their own substrate along with foreign crabs; this would have entailed great expense, moderate inconvenience, and an almost certain impasse at customs unless the soil were sterilized. Even if foreign crabs proved adaptable to local substrates, no doubt with the provision of appropriate (and unknown) kinds and quantities of added food, I foresaw that the artificial bank would have to be replaced at frequent intervals which, in temperate latitudes, would be difficult in the winter when microorganisms on local shores are largely inactive.

These apprehensions fortunately proved needless. Substrate from nearby Long Island was used without replenishment for periods lasting up to 6 months, and supported a variety of species from the same locality, from the West Indies and from Ceylon. We took great care to collect the substrate from a shore which had not been subjected as far as we could learn to chemical pollution and which remained the continuing habitat of large and apparently healthy populations of *Uca*. We were also careful to bring back to the laboratory only the top layer of substrate on which the crabs normally fed, and to layer the sections carefully in chemically uncontaminated plastic pails. Finally, we did not collect the material during the winter, November 1 of a mild autumn being the latest we gathered a load; there had been as yet no frost. We always included small tussocks of swamp weed which, although they died back during the winter, doubtless continued to provide organic richness and resprouted in the spring. Most surprising was the fact that substrate of this kind without replenishment and without provision to the crabs of supplementary food kept the captive populations in vigorous health. After our success the first winter—a full period of 6 months—we brought additional substrate from the same locality, but kept half of the original material to "season" the new sandy mud, and managed the addition with minimal upset to the crabs.

We feel sure that a most important part of the success indoors in New York was our provision for a filter system far more extensive than I can find is recommended for any home aquaria, either freshwater or marine. The systems used by marine biological stations and exhibition aquaria are not really comparable, because of the availability to them of circulating seawater and their lack of need for natural substrate for their specimens. The system that worked in New York I devised in consultation with experienced aquarists and a search of the literature. The result uses parts of several arrangements, as well as screens to prevent disruption of the filters by digging crabs, and, finally, the addition of the thick layer of substrate on top. The system includes a total of six different layers. It may prove in the future feasible to reduce or omit one or more of the ingredients, thus cutting down on their considerable cost; in the course of the work to date there has been no time to experiment along these lines.

The filter and substrate arrangement in each tank is as follows, with the layers listed from the bottom up. (1) Sheets of plastic, manufactured commercially for the purpose, their surfaces covered with parallel slits and their edges turned down so that each surface is raised slightly above the tank's bottom; several sizes fit against one another so that one side and a part of each end of a tank is covered, about one-third of the bottom being left bare; the siphons provided with the apparatus are discarded. (2) A layer of coarse, white, quartz gravel, at least two inches thick. (3) A similar layer of fine, coral sand. (4) A layer of powdered carbon. (5) A layer of fine, aluminum screening, to prevent the crabs from digging into the filter layers. (6) The substrate, arranged to form a gently sloping bank with its top extending along the tank's long dimension. Like the substrate the entire filter system can be reused with little replenishment when a tank is reorganized. An investigator familiar with aquaria will be reassured to find, on examining all levels of the filter, that they remain sweet, even though small crabs occasionally die in their burrows and dissolve without being found.

In both indoor and outdoor crabberies two additional safeguards are needed. First, the open, fourth side of the filter layers, adjoining the uncovered third of the tank bottom, are held approximately in place by a vertical strip of aluminum screening. This not only prevents sliding of the layers and digging by the crabs but also minimizes loss of material from the layers during drainage. Second, since most *Uca* are good climbers and since it is always desirable to have the top of the bank heaped as high as possible close to the lip of the tank, to provide maximum depth for the burrows, overlapping rectangles of window glass are thrust into the substrate all around the tank against its sides, except on the side bare of substrate; there it is not necessary provided the tank sides are very smooth and kept clean. The glass itself should be polished often. Once the crabs have settled down in the new quarters they normally do not attempt at all to climb out except during the wandering and aggressive wandering phases; then they literally climb the walls if measures have not been taken. The glass should project at least 5 inches above the substrate.

In outdoor tropical aquaria we have had success with only a thin layer of coarse sand as a filter, covering the portion of the tank beneath the substrate to a depth of several inches at most; we have also used instead a single, similar layer of coarse charcoal, such as is used in local stoves. In Trinidad, however, it was always possible to bring up frequent truckloads of mangrove mud and seawater from the shore, and because of this we changed the mud, seawater, or both on the average of once every 6 weeks during seasons when we were working seriously with the installations and not keeping them on a purely maintenance level. Again, the substrate remained completely sweet, even though the usual deaths sometimes occurred without our being aware of them, so that we failed to remove the casualties.

In New York the question of illumination gave us the most difficulty in design because of the need for an intensity sufficient to simulate sunlight. This strength seems to be of importance because in the field a population attains its highest levels of social activity when the sun is shining, even though at the peak of a display phase individuals often wave vigorously in dull weather and although some acoustic behavior is prevalent at night. At the end of our attempts we finally managed to achieve an intensity level approaching for short periods that of tropical sunlight, although overheating of the substrate remained a limiting factor and further improvement is needed.

Our first care was to select a group of 12 fluorescent lamps for suspension over each crabbery tank. Each storage tank also had its own group, so that the seawater would be exposed to light during a daytime period in that container; we hoped that the water's consequent exposure to a full quota of illumination daily would help to keep it in acceptably wholesome condition. Additionally, we sometimes used the storage tanks, on an alternate tidal schedule, to maintain crabs temporarily when we had more specimens than could be properly housed in the fully fitted crabberies, or when they housed large specimens being saved for physiological work in which maintenance conditions were not, it seemed, so demanding.

Each group of fluorescent lamps was composed of four kinds of tubes of known emission spectra, selected to resemble as a group the spectral composition of sunlight. Because of the limitations of their spectra, an exact reproduction could not of course be made. Fortunately, the crabs did well under this illumination alone. Nevertheless it seemed unsatisfactory that the level of intensity of the light reflected from the substrate, as measured in foot candles, was only equivalent to that reflected from a comparable substrate in the tropics on a cloudy day with imminent rain. The quality of the light furnished by the lamps was of course in some ways nearer to that of sunlight than was that of a tropical overcast, but the situation still called for improvement. Supplementary photofloods and similar lamps were unsatisfactory because of their short lives and high heat. We finally secured quartz halogen lamps and fitted them with heat absorbing glass filters that cut down the intensity only moderately. Limited tests with this setup indicate that their use during particular periods when observations, photographs, or experiments were under way did indeed stimulate the crabs to somewhat greater activity. The area struck by the beam had to be checked frequently for overheating; usually the crabs themselves gave the first warning, as they do on hot afternoons in the field, by dropping down their burrows and staying there—a response an investigator hopes fervently to avoid.

The large banks of fluorescent tubes were controlled automatically, as part of the clockwork system operating the pumps. When tropical species were kept, the lights were set to go on and off at 0600 and 1800 respectively, corresponding roughly to the times of sunrise and sunset in the tropics. Local hours were kept for temperate zone crabs. Since the laboratory admitted some daylight through a skylight, no attempt was made to keep crabs from overseas on their original circadian schedule; this particular biological clock in *Uca* is easily shifted without apparent effects on the behavior patterns to be investigated. The rhythm, as well as the tidal rhythm, had of course already been interrupted and upset by a long journey.

In conclusion, although fiddler crabs can be kept in health in captivity, and although surprising degrees and varieties of activities can be elicited, the use of crabberies for reliable ethological study is very strictly limited. I firmly believe that no descriptions of waving displays or combat behavior, for example, should be derived from observations made wholly in crabberies, whether indoors or out. A single example will illustrate the dangers. The usual waving rate of *festae* in the field is half again as fast as that shown by several individuals that lived for months in apparent health in a Trinidad crabbery out-of-doors and that went through the expected behavioral phases. Such a difference between a component in the field and in captivity is unusual, but it can serve as a warning. Nevertheless, to verify fine details of displays or of combat techniques, or to learn the kind of behavior that may yield specially interesting observations on future field trips, crabbery work is unexcelled.

The tanks also give excellent opportunities for certain kinds of photography and for sound recordings, including television work. Again, an appropriately designed crabbery is certainly the place where observations of crabs inside their burrows can best be made. Finally, various experiments, based safely on a foundation of familiarity in the field with the behavior of the species, can be done as well in crabberies, and some of them doubtless only under those conditions; the sensible possibilities for future work seem in fact to be unlimited. It seems very clear, nevertheless, that any observations or experiments that depend on quantitative aspects of the data obtained should be undertaken only with the greatest care; in particular they should rest on a solid basis of preliminary field work, accomplished on the particular subspecies, and preferably on members of the same population, from which the transplanted crabs are afterwards derived.

Appendix E. Conventions, Abbreviations, and Glossary

CONVENTIONS

! The specimens listed have been examined by the author of the present contribution. This convention is used in the systematic section under the headings Type Material and References and Synonymy.

( ) 1. A scientific name or initial enclosed in parentheses is that of a subgenus. *Examples. Uca (Deltuca) dussumieri, U. (D.) dussumieri*, or simply, in a list of species in the text, *(Deltuca) dussumieri.*

2. An author's name and date enclosed in parentheses after the name of a species indicate that when he described the species he placed it in a genus with a different name. *Example. Uca (Deltuca) dussumieri* (Milne-Edwards, 1852).

When no parentheses surround the author's name, his original description of the species placed it in the same genus in which it appears in the present study. *Example. Uca (Deltuca) demani* Ortmann, 1897.

[ ] A scientific name or initial enclosed in brackets is that of a superspecies. *Examples. Uca (Deltuca) [acuta] acuta* (Stimpson, 1858); *U. (D.) [a.] acuta rhizophorae* Tweedie, 1950.

Note. For general treatments of taxonomic practice, see Blackwelder, 1967, and Mayr, 1969. For technical details, see also the "International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology," published for the International Commission on Zoological Nomenclature by the International Trust for Zoological Nomenclature; London, 1961. References to specific bulletins published by the International Trust are given in the present text.

Throughout this volume "Milne-Edwards," without an initial, refers to H. (Henri) Milne-Edwards; "A. Milne-Edwards" to his son, Alphonse. The hyphen between the two parts of the surname has often been employed in the past; its use is revived here as a possible aid to non-carcinologists who may only occasionally need to use the bibliography.

ABBREVIATIONS

AMNH—American Museum of Natural History; Central Park West at 79th St., New York, New York 10024, U.S.A.

Amsterdam—Zoölogisch Museum; Plantage Middenlaan 53, Amsterdam C, Netherlands.

Bishop—Bernice Pauahi Bishop Museum; Honolulu, Hawaii 96818, U.S.A.

BM—British Museum (Natural History); London, S.W.7, England.

Copenhagen—Universitetets Zoologiske Museum; København K, Denmark.

Frankfurt—Natur-Museum und Forschungs-Institut "Senckenberg"; Senckenberg-Anlage 25, Frankfurt am Main, Germany.

Göttingen—Zoologisch Institut der Universität; Göttingen, Germany.

Hancock—Allan Hancock Foundation; University of Southern California, University Park, Los Angeles, California 90007, U.S.A.

Leiden—Rijksmuseum van Natuurlijke Historie; Raamsteeg 2, Leiden, Netherlands.

MCZ—Museum of Comparative Zoology; Harvard University, Cambridge, Massachusetts 02138, U.S.A.

NYZS—New York Zoological Society; Bronx, New York 10460, U.S.A. (*Note.* Collections of *Uca* have been transferred to USNM; see p. 591.)

Paris—Muséum National d'Histoire Naturelle; Paris Ve, France. Address for correspondence on Crustacea: Laboratoire de Zoologie, 61 Rue de Buffon, Paris Ve.

Philadelphia—The Academy of Natural Sciences at Philadelphia; 19th St. and the Parkway, Philadelphia, Pennsylvania 19103, U.S.A.

Raffles—Raffles Museum, Singapore.

Torino—Istituto e Museo di Zoologia della Università di Torino; Via Accademia Albertina, 17, Torino (204), Italy.

UPNG—Department of Biology, University of Papua and New Guinea; Boroko, Territory of Papua and New Guinea.

USNM—Division of Marine Invertebrates, National Museum of Natural History; Smithsonian Institution, Washington, D.C. 20525, U.S.A.

Yale—Peabody Museum of Natural History; Yale University, New Haven, Connecticut 06520, U.S.A.

Yokohama—Faculty of Liberal Arts and Education; Yokohama National University, Yokohama, Kamakura, Japan.

GLOSSARY

Introduction

This glossary consists of terms that may be divided roughly into three categories. First are words used here in a restricted sense; many morphological terms are included for this reason. The second group comprises coined words and phrases, most of which are names for behavioral components in *Uca* or for structures on the gonopod. The final category includes terms that are widely used in particular fields of biology. Each appears in the glossary because the term may not be familiar to a worker outside the discipline it serves. When complex and sometimes controversial concepts are involved, recent definitions are quoted directly and references given to discussion by the authorities cited; in some cases an annotation comments on the term's use in the present study.

Abdomen. The segmented part of the body that is folded underneath the carapace, fitting into a depression in the sternum. It is narrow in males (Fig. 2) and broad in females. (P. 463.)

Actor. In combat, the individual at any particular moment performing the motions of a component. (P. 487.)

After-lunge. A feint by a burrow-holder directed toward a departing opponent. This activity is often associated with combat. (Agonistic component no. 6, p. 479.)

Agonistic. See *Behavior, agonistic.*

Alliance. A group of closely related species consisting both of allopatric forms and of one or more other species living sympatrically with one or more of the allopatric forms. This usage corresponds approximately to the definition given by Mayr (1969: 412) of superspecies used in the broader sense: ". . . entirely or *largely* allopatric species. . . ." (Italics mine.) The introduction of *alliance*, in an apparently new, informal usage of the word, provides a brief term to cover this wider situation, the term *superspecies* being reserved for a series of allopatric forms. Cf. *Superspecies.*

Allies. Members of an alliance. See above.

Allometry. "The study of proportion changes correlated with variation in size of either the total organism or the part under consideration. . . . The variates may be morphological, physiological or chemical . . ." (Gould, 1966: 629.) Also: "1. growth of a part of an organism in relation to the growth of the whole organism or some part of it." (Random House Dictionary of the English Language, 1966.) (P. 449.)

Allopatry. The distribution of distinct populations of a species or of closely related species so that they occupy areas that with marginal exceptions are mutually exclusive. Adj.: *Allopatric.* In this study *allopatric* is used also as a n. (cf. patronymic, in accepted use as both adj. and n.). See also *Superspecies*; *Alliance*; cf. *Sympatry.* Discussions on pp. 432 and 527ff.

Ambulatory. One of the eight walking legs; arranged in four pairs, they are inserted behind the chelipeds. They correspond to the second to fifth pairs of legs or periopods of authors who count the chelipeds as the first pair of legs. The latter designation is of course phylogenetically exact, but in *Uca* the use of *chelipeds* and *ambulatories* is preferred for clarity and convenience. Where *leg* is used in this study, it is always for the sake of brevity in an unambiguous situation and refers only to ambulatories, as in a coined name for a behavioral component, such as *leg-wave.* (Figs. 1, 2.)

Angle, antero-lateral. The angle formed by the meeting of the anterior and side (antero-lateral) margins of the carapace. (Fig. 3.)

Antenna, pl. *antennae.* On the lower, anterior surface of the body, one of the outer pair of very short, flagellate appendages lying between the edge of the front and the buccal cavity. (Figs. 2, 28.)

Antennule. On the lower, anterior surface of the body, one of the inner pair of very short appendages lying between the edge of the front and the buccal cavity; it lies folded inconspicuously in a cavity. (Figs. 2, 28.)

Aperture, afferent branchial. The opening between the bases of the second and third ambulatories through which water is drawn into the branchial chambers.

Aperture, efferent branchial. The opening between the outer anterior margin of the buccal cavity and the outer anterior edge of the flexed palp of the third maxilliped. Through it water and bubbles are expelled from the branchial cavity.

Area, friction. In combat, a part of the inactor's claw correlated with one or more structures on the actor's claw during the performance of a component. See Table 14, "contact area."

Armature. Specializations of the integument consisting principally of ridges, tubercles, and grooves. Occurring on the carapace, chelipeds, and ambulatories, they are used in sound production or, when on the major claw, almost altogether in intermale combat.

Armed. Equipped with armature.

Autotomy. The casting off, by reflex action, of a cheliped or ambulatory that has been strongly stimulated, as when seized by a predator. The break is always cleanly made between the basis and ischium. The lost appendage is regenerated more or less perfectly, the process requiring a number of molts.

Basis, pl. *bases*. The second segment from the proximal end of a cheliped or an ambulatory. (Fig. 2.)

Beading. A row of similar, rounded tubercles, contiguous or nearly so and usually very small. See *Edge, beaded.*

Behavior, acoustic. Production of sound, along with associated activities.

Behavior, agonistic. Postures and motions indicating aggression, defense, submission, withdrawal, or flight; often ambivalent.

Behavior, conflict. Postures and motions indicating the simultaneous or alternate activation of two drives, such as combat and flight.

Behavior, displacement. Activities, inappropriate to the circumstances, which partially or wholly replace suitable behavior, such as the occurrence of feeding during conflict between drives to court a female and to threaten another male.

Behavior, post-combat. Activities, such as the afterlunge, that occur immediately following combat.

Behavior, precopulatory. Final stages of courtship immediately preceding copulation on the surface or presumed copulation underground. Characterized by behavior not found either in earlier stages of courtship or in agonistic behavior.

Behavior, social. Postures and motions that ordinarily serve as mutual stimulation among members of the same species.

Behavior, submissive. Postures and motions indicating unreadiness to engage in or to continue aggressive behavior. Cf. *Creep.*

Behavior, territorial. Postures and motions indicating readiness to defend from intruders the mouth of a burrow, or the mouth and its immediate vicinity; the behavior exhibited consists of waving display, threat components, and combat.

Belt, hybrid. "A zone of interbreeding betwen two species, subspecies, or other unlike populations; zone of secondary intergradation." (Mayr, 1969; 405.)

Biotope. A habitat characteristic of a group of animals, whether of a formal taxon, such as a species, or of a local population. Cf. *Niche.* (See also p. 445.)

Book. One of the contiguous layers of tissue in a gill. All lie perpendicular to each side of the gill's long axis. (Figs. 78, 81.)

Brachyura; adj. *brachyuran.* The order of Crustacea consisting of the true crabs, including *Uca.* In adults the abdomen is always relatively small and folds underneath the body, while the abdominal appendages are not used in locomotion.

Brachychelous. Individuals or species having the fingers of the major chela relatively short and broad in comparison with those of other members of the group. Cf. *Leptochelous.*

Bubbling. Emission of foam from the efferent branchial openings. Composed of air bubbles and moisture from the branchial regions, it apparently serves several functions, as a cleansing agent, heat regulator, aerator of eggs, and sound-producing mechanism. In its latter role it is described as component no. 12, p. 484. (General account on p. 472.)

Burrow-holder. A male in the display phase, centering his activities around a particular burrow, and defending its vicinity from intrusion by conspecific males through threat postures, combat, or both. (P. 487.)

Carapace. The crab's "shell," covering the dorsal and lateral parts of the body above the chelipeds and legs; anteriorly it includes the orbits and pterygostomian regions. The carapace is posteriorly truncate, the abdomen being bent underneath the body. (Figs. 1, 2, 3.)

Carpus. The fifth segment from the proximal end of a cheliped or an ambulatory. (Figs. 1, 2.)

Carpus-out. An agonistic posture in which a male, having descended his burrow, leaves the carpus of his flexed major cheliped projecting above the surface. (Agonistic component no. 7, p. 479.)

Cavity, buccal. The mouth area, lying between the antennae and antennules anteriorly and the chelipeds posteriorly. Covered, when not in use, by the third maxillipeds. (Fig. 2.)

Cavity, carpal. On a major cheliped, the depression in the proximal part of the palm. When the cheliped is flexed, bent into rest position, the carpus fits into the cavity. (Fig. 44.)

Chela. The grasping, distal portion of the claw on either of the two chelipeds. Each chela is formed by a distal extension of the sixth segment, the manus, and the opposing distal seventh segment, termed the dactyl. The two parts of the chela are referred to together as fingers; the lower, immovable finger as the pollex; and the pollex along with the rest of the manus as the propodus. (Figs. 1, 2, 42, 44.)

Chela-out. An agonistic posture in which a crab, otherwise completely withdrawn into his burrow, leaves his major chela's tip projecting. (Component 9, p. 479.)

Cheliped. One of the two appendages that end in a chela. Morphologically these appendages form the first pair of periopods. Each is bounded anteriorly by the suborbital region, externally by the vertical lateral margin, and posteriorly both by the sternum and by the coxa of the first ambulatory.

Cheliped, major. The large cheliped; confined to males. (Fig. 1.)

Cheliped, minor. The small cheliped in a male. (Fig. 1.)

Cheliped, small. Either of the two chelipeds in a female, or, when used plurally in simultaneous reference to both sexes, the chelipeds excluding the major.

Chimney. A wall made of substrate erected by an individual around its burrow. (P. 500.)

Chromatophore. A pigment-bearing body in the integment that influences the individual's color through its expansion and contraction.

Claw. The sixth and seventh segments of a cheliped, formed of the propodus (the specialized manus) and the dactyl. An informal term, but conveniently brief. See *Chela.*

Claw-rub. A general term for sound produced by rubbing of the claws of two males against each other during combat. (Sound component no. 14, p. 484.)

Claw-tap. A general term for sound produced by tapping or vibration of the claws of two males against each other during combat. (Sound component no. 15, p. 484.)

Cline. "A gradual and nearly continuous change of a character in a series of contiguous populations; a character gradient (cf. *Subspecies*)." (Mayr, 1969: 400.)

Clock, biological. See ***Rhythm, endogenous.***

Close-set (adj.). Applied to tubercles in the same series which, while not widely spaced, are not continuous and hence cannot be termed beading.

Combat. A general term for any behavior between males in which the claws of the chelipeds come into contact. Because of the usually high degree of ritualization, it might be preferable to substitute the word *encounter*, thus avoiding the "loaded" words *combat* and *fight.* Since the behavior discussed undoubtedly has an aggressive base, frequently shows overtly forceful components, and probably often includes pushing elements effectively masked by ritualizations, it seems permissible to use all three terms. In this contribution, therefore, *combat* is selected for general use; *encounter* appears occasionally in the discussion of fully ritualized combats; and *fight* is restricted to combats with overtly forceful components.

Combat, heteroclawed. In one opponent the claw on the right side is enlarged, in the other on the left.

Combat, high-intensity. Part of the claw of each opponent comes between the dactyl and pollex of the other, in other words enters into the gape. In forceful endings the claw tips may grip the opponent's claw; in fully ritualized encounters they do not do so.

Combat, homoclawed. Both opponents have the claw of the same side enlarged, whether right or left.

Combat, low-intensity. Contact between opponents is confined to the outer surfaces of mani and chelae.

Combat, mutual. In many ritualized combats both crabs perform one or more of the components, either in sequence or alternately. They can perform simultaneously only during manus-rubs.

Combat, ritualized. Encounters consisting of ritualized components and lacking the ingredient of irregular force.

Component. An activity that is a characteristic part of some aspect of social behavior and appears to the observer to be distinct from adjacent actions.

The most clear-cut examples are so distinct and so stereotyped that they may confidently be termed fixed-action patterns, in the sense developed by Lorenz and Tinbergen and now often used in ethological studies. These examples are characterized not only by distinctive motor patterns but in ritualized combat by the juxtaposition of specialized morphological structures.

Other activities, however, show considerable variability connected neither with intensity nor with transition to other components. All of these, instead, often appear instantly adaptable to the changing circumstances of an agonistic situation or a courtship. In combat, for example, the sequence of components used in a particular kind of encounter in a certain species is only moderately predictable, while force may be suddenly interjected in the midst of an otherwise ritualized combat at any time. Any or all of the components in the various classes of social behavior may need subdivision or other modification. Only further study with emphasis on comparative work within the genus can resolve the uncertainties.

Therefore it seems that the use of *fixed action pattern* would be at present a semantic disservice. The more general word *component* is adopted instead, in the same spirit shown by morphological taxonomists when they feel it premature to use a definite term such as *subgenus* and compromise on the noncommittal *group.*

Component, forceful. In low-intensity combat, manus-pushes; in high-intensity combat, grips, flings, and upsets. All are highly variable and irregular, and hence are here considered to be unritualized, since the cheliped is wielded variously and unpredictably in pushing, grasping, and lifting. Most or all ritualized components at times also are interrupted by the use of overt force which sometimes develops almost insensibly during the performance of the ritualized component, in the form of visible pressure. Exceptions to the above definition of forceful components are now being studied in *Uca lactea*, in which overt force itself is sometimes ritualized. (P. 494.)

Component, mutual. In combat, the same component is performed by both crabs, either in sequence or alternately. Only the manus-rub can be performed by both crabs simultaneously.

Component, ritualized. In combat, a component in which no pushing, grasping, or lifting motions are ordinarily included and which is distinguished by its predictability of form, and sometimes sequence, and by its association with a particular series of structures. See also *Component, forceful* and *Ritualization.*

Conglomerate. An assembly of stones, sessile marine organisms, or both, fastened together by natural deposits or secretions; the organisms often include corals, dead or alive, mollusks or their shells, and tube worms. Sometimes the conglomerate is in the form of lumps, large or small; sometimes it forms in itself a local substrate.

Cornea. See *Eye.*

Courtship. Behavior patterns in both sexes that, when fully elicited, are followed by copulation. They usually include high-intensity waving display, along with following of the female or her attraction to the male's burrow. Special display motions and sound production also sometimes are part of a species-specific pattern. See also *Behavior, precopulatory.*

Coxa, pl. *coxae.* The first segment of a cheliped or ambulatory, always short (Figs. 1, 2).

Creep. Method of locomotion adopted by nonaggressive individuals under certain conditions, the body being held close to the ground. Cf. *Behavior, submissive.* (Agonistic posture no. 11, p. 479; Fig. 84*C*.)

Crenellations. Tubercles along the suborbital margins of the orbit, often separated and truncate. (Figs. 2, 3, 26, 27.)

Crest. On a cheliped or walking leg, a thin ridge, often relatively high, with the edge either entire or tuberculate. Cf. *Ridge.*

Curtsy. In waving display and in high-intensity courtship, the crab's body rapidly lowers through bending the legs and is raised again. A bob. (Component no. 13, p. 496.)

Dactyl. The most distal segment, the seventh, of a cheliped or ambulatory. On a cheliped also termed the movable finger.

Dactyl-along-pollex-groove. In high-intensity combat the actor slides the tip of his dactyl along the narrow, longitudinal furrow on the inactor's outer pollex. (Ritualized component no. 14, p. 491.)

Dactyl-slide. In high-intensity combat the prehensile edge of one dactyl slides along the upper edge of the opponent's dactyl. (Ritualized component no. 6, p. 489.)

Dactyl-submanus-slide. In high-intensity combat the actor rubs his dactyl's prehensile edge along the lower margin of the inactor's manus, both claws being appropriately tilted. (Ritualized component no. 8, p. 489.)

Deme. "A local population of a species; the community of potentially interbreeding individuals at a given locality." (Mayr, 1969: 401.)

Dendrogram. A diagram, more or less in the form of a tree, designed to indicate apparent degrees of relationship.

Depression. An indentation on the integument, usually shallow and irregularly shaped.

Depression, H-form. On the carapace the design formed by the meetings of the furrows dividing the cardiac, intestinal, and branchial regions from one another. Often this roughly H-shaped result includes the only distinctly marked regional boundaries in a species of *Uca*, where the regions are in general weakly indicated. (Fig. 1.)

Display, visual. A general term that includes agonistic postures, their associated motions, and waving display.

Display, waving. A rhythmic motion of the major cheliped, along with any associated movements of other appendages. Used interchangeably with *waving.*

Display, waving: high-intensity. Waving characterized in general by the maximum tempo, precision of motions, amplitude of wave, brevity of pauses between waves, and sometimes additional motions or elision of motions characteristic of a species.

Display, waving, low-intensity. The wave is relatively slow, and often variable in tempo and amplitude, with the series widely spaced and pauses between waves often longer than at high intensity; feeding during and between waves is prevalent; characteristics may be present that are absent at high intensities, or the converse may be true. Sharp boundaries between the two intensities are rare, gradual change being the rule.

Down-point. A threat posture of high-intensity often leading to combat. Two opponents face each other, their major claws pointed straight downward. (Component no. 2, p. 479.)

Down-push. One crab is pushed down his own burrow by his opponent. An activity associated with combat. (P. 491.)

Drove. An aggregation of individuals, moving more or less in unison. (P. 478.)

Drumming. Sound production through repeated tapping of the major or minor merus against the carapace, or of the major manus against the ground. (Sound components 7, 8, and 9, p. 483.)

Duration. The length of a combat timed from the moment at which the two chelipeds come into contact to their separation immediately preceding the departure of one of the crabs. Associated activities, ranging from preliminary threat behavior to after-lunges, are not included. See also Duration, p. 493.

Ecology. The study of organisms in relation to their environment.

Edge, beaded. A structure sometimes present on the upper, major palm, between the dorsal margin and the carpal cavity. (Fig. 44.)

Edge, prehensile. On a cheliped, the dorsal margin of the pollex or the ventral margin of the dactyl.

Encounter. A fully ritualized combat. See also *Combat.*

Estuary. A tidal waterway in the delta region of a stream or river, usually running through mangrove or other kinds of swampland. See also *Lagoon.*

Ethology. "The science of the comparative study of animal behavior." (Mayr, 1969: 402.) In a wider sense, "the biological study of animal behavior." (Eibl-Eibesfeldt, 1970.)

Eye. The faceted structure at the tip of the eyestalk; the cornea.

Eyebrow. An elongate area along the dorsal margin of the orbits, varying in length, breadth and inclination; bounded by raised edges that are sometimes beaded or granulate.

Eyestalk. The peduncle supporting the eye.

Fight. A combat including components that are at once forceful, irregular in form, and unpredictable. See also *Combat.*

Finger. On a cheliped, either of the two distal elements forming the chela or pincer. Usually used in the plural, to designate in one word both dactyl and pollex.

Finger, fixed. The pollex.

Finger, movable. The dactyl of a cheliped.

Flagellum, pl. *flagella.* On each of the two antennae, the slender, tapering, distal portion composed of many segments. (Fig. 28.)

Flange. On the gonopod, a calcified wing near the tip, normally extending anteriorly or posteriorly but sometimes differently oriented because of torsion. (Fig. 58.)

Flat-claw. An agonistic posture in which a crab, having descended his burrow, leaves his major claw projecting and bent so that it lies flat on the surface. (Component no. 8, p. 479.)

Fling. In combat, a variable, unritualized component at the close of a forceful ending. One opponent is pushed backward in a skid or is partly overturned. (Forceful component no. 2, part, p. 488.)

Forward-point. A threat posture of moderate intensity. The major claw is directed forward, the fingers held apart. (Agonistic component no. 4, p. 479.)

Front. On the anterior part of the carapace, the middle section that projects forward and down between the orbits. (Figs. 1, 2.)

Frontal-arc. A threat pattern of low intensity; the major chela parallels the ground, fingers open, and moves forward and back. (Agonistic component no. 3, p. 479.)

Furrow. See *Groove.*

Gape. On a claw, the space between the dactyl and pollex when their distal portions are in contact or, in other words, when the claw is "closed."

Gills. Organs responsible for the extraction of oxygen from the water. Five principal ones, all elongate, distally tapering and divided into sections (*books*), are located in the posterior part of the branchial region; single gills, small to vestigial and variously shaped, are located proximally on the 2nd and 3rd maxillipeds. (Figs. 81, 82, 83.)

Gonopod. In males, one of the pair of anterior abdominal appendages, situated on the ventral, proximal part of the abdomen. When not in use, these slender, stiff appendages are bent forward, parallel to the similarly bent abdomen, fitting into an indentation in the sternum. Spermatophores are introduced into the female gonopores through the specialized tips. (Fig. 58.)

Gonopore. In females, one of the pair of genital openings. They are located on the third sternal segment near the midline. The term has often been applied also to the genital opening of the male; in this study the word *pore* is used for the male opening in order to avoid confusion.

Granule. An imprecise term for a tubercle that is considered by the observer to be particularly small in relation to other tubercles on the same individual.

Grip. In combat, the prehensile edges of one claw seize the claw of the opponent. (Forceful component no. 2, part, p. 488.)

Groove. A narrow depression or furrow in the integument.

Group. "A neutral term for a number of related taxa, especially an assemblage of closely related species within a genus." (Mayr, 1969: 404.)

Growth, allometric. Development in which one part of an organism grows at a different rate than another; heterogony. (P. 449.)

Habitat. The general kind of environment in which a species usually lives. (P. 440.) (Cf. *Biotope*; *Niche.*

Heel. The proximal ventral portion of the major manus. (Fig. 42.)

Heel-and-hollow. In high-intensity combat, the pollex tip rubs or taps the depression on the palm lying at the base of the opponent's thumb, while the dactyl acts similarly against the outer manus. (Ritualized component no. 11, p. 490.)

Heel-and-ridge. In high-intensity combat, the pollex tip rubs or taps the oblique ridge of the opponent, while the dactyl curves around the opponent's heel or taps with its tip against that region. (Ritualized component, no. 12, p. 490.)

Hepatopancreas. A digestive gland, consisting mostly of two large lobes that underlie the paired hepatic regions of the carapace. Formerly often termed the *liver.*

Herding. During a waving display, a male maneuvers a female toward his burrow. (Component no. 14, p. 496.)

Heterogony. (Replaced in current usage by *Allometry.*)

High-rise. A posture, occurring in the threat behavior of both sexes and in the courtship of males, in which the crab raises its body high on the extended ambulatories. (Agonistic component no. 13, p. 480.)

Holotype. In taxonomy, "the single specimen, designated or indicated as 'the type' by the original author at the time of the publication of the original description." (Mayr, 1969: 404.)

Hood. A concave, arching structure erected by a male in display phase beside his burrow. (P. 500; Pls. 48, 49.)

Hybridization. "The crossing of individuals belonging to two unlike natural populations, principally species." (Mayr, 1969: 405.) See also *Hybridization, allopatric*; *Subspecies.*

Hybridization, allopatric. "Hybridization between two allopatric populations (species or subspecies) along a well-defined contact zone." (Mayr, 1969: 397.)

Inactor. In combat, the opponent holding his major claw temporarily motionless. (P. 487.)

Ischium. On a maxilla, maxilliped, cheliped, or ambulatory, the third segment from the proximal end; in each of these appendages it is distal to the basis. (Figs. 1, 2.)

Instigator. In combats between two burrow-holders, the crab that approaches his future opponent; except for this approach, he does not necessarily ever become an actor. In combats between an aggressive wanderer and a burrow-holder, the wanderer is apparently always the instigator. Because of the usual high degree of ritualization, the words *aggressor* and *attacker* are not used.

Instrument. In combat a structure on the actor's claw used during the performance of a component.

Intensity, low. (1) In threat postures and motions, a general term for slight motions of the major cheliped toward an encroaching crab, in which the fingers are separated only partly if at all and the body little raised on the ambulatories; often accompanied by feeding. (Fig. 84.) (2) In combat, a component in which only the outer surfaces of the claws come into contact. (3) In waving display, the motion of the major cheliped is relatively slow when compared with that of high intensity, the tip of the claw usually does not reach as high in the air, in lateral waves the waving motion may be straight rather than circular, and, finally, any special motions occurring in advanced courtship are absent; often accompanied by feeding, low-intensity display usually indicates relatively simple territoriality rather than threat toward a particular male or definite courtship of a female. There is no sharp dividing line distinguished between low and high intensities in any of the three uses.

Intensity, high. (1) In threat postures and motions, the major dactyl is raised so that the fingers of the claw are widely separated and the body is raised on the extended ambulatories. (2) In combat, a component in which a part of each claw enters the gape of the opponent. (3) In waving display, the major cheliped moves at the maximum speed attained by the species, and describes the widest arc; in both threat and courtship, but particularly in courtship, special motions of both the major cheliped and of the other appendages sometimes involved in sound production are often included. Actual feeding only very rarely accompanies high-intensity behavior of any kind, the motions of the minor cheliped that often occur at these times being incomplete; they are here interpreted as displacement feeding under conditions of conflict.

Interdigitated-leg-wag. The more distal segments of one or more ambulatories overlap those of a parallel individual with accompanying rubbing or vibration. (Sound component no. 16, p. 484.)

Interlace. In high-intensity combat, each manus lies within the gape of the opponent, the bases of the two chelae coming almost into contact; the proximal prehensile edge of one pollex then rubs along one or both predactyl ridges of the opponent. (Ritualized component no. 9.)

Isolation, reproductive. "A condition in which interbreeding between two or more populations is prevented by intrinsic factors." (Mayr, 1969: 410.) Cf. *Mechanism, isolating.*

Jerk. In waving display, one of a series of short motions of the major cheliped that lifts or lowers the appendage with short pauses between. In this contribution the period of motion alone is counted as the jerk. No wave is described as including jerks unless either the upward or downward sweep, or both, are broken by at least one pause; a wave with a pause only at its peak, however, is not considered to be a jerking wave.

Jerking-oblique-wave. In waving display, the major cheliped unflexes obliquely upward with jerks at least during its rise. (Component no. 6, p. 496.)

Jerking-vertical-wave. In waving display, the flexed major cheliped is moved up and down with jerks at least during its rise. (Component no. 2, p. 496.)

Keel. A sharp ridge armed or smooth, at or close to the dorsal or ventral margin of part of a cheliped or ambulatory.

Kick. See *Leg-wave.*

Lagoon. A body of seawater, sometimes brackish, usually elongate, and always largely cut off from the surf of the open ocean. Sometimes the barrier is a reef, which may be largely submerged; sometimes it is the upper part of a beach or a stretch of dunes. Communication with the open sea is often by a permanent channel, as on coral atolls; sometimes, on continents and larger islands, a connection occurs only at spring tides or during heavy rains. Direct connection with a stream, if any, is frequently intermittent. Except on small atolls, lagoons are often bordered by mangrove swamps. The word *lagoon* and its translations are often used imprecisely, with variable implications, in different parts of the world. The above remarks cover its use in the present contribution. Cf. *Estuary.*

Lateral-circular-wave. In waving display the major cheliped is completely unflexed, then raised and returned to rest position from above the eyes. (Component no. 5, p. 496.)

Lateral-straight-wave. In waving display, the cheliped is completely unflexed, then returned to the flexed position in the same plane. (Component no. 4, p. 496.)

Lateral-stretch. A threat posture in which at least the major cheliped is unflexed to the side. (Agonistic posture no. 10, p. 479.)

Lateral-wave. In waving display, a general term for a motion of the major cheliped in which the claw is unflexed to the side. See also *Lateral-straight-wave* and *Lateral-circular-wave.*

Lectotype. "One of a series of syntypes which, subsequent to the publication of the original description, is selected and designated through publication to serve as 'the type.'" (Mayr, 1969: 406.)

Left-clawed. The cheliped on the crab's left side is enlarged.

Leg. See *Ambulatory.*

Leg-side-rub. Stridulation involving the more posterior ambulatory meri and the sides of the carapace. (Sound component no. 6, p. 483.)

Leg-stamp. The turned-under dactyls of two or more ambulatories strike the ground. (Sound component no. 11, p. 484.)

Leg-stretch. In waving display the crab raises its body with each wave. (Component no. 10, p. 496.)

Leg-wag. Stridulation involving rubbing of the ambulatory meri. (Sound component no. 5, p. 482.)

Leg-wave. In waving display, two or more ambulatories are raised on a side, often in a kicking motion; their meri however do not make contact and therefore there is no stridulation. (Component no. 12, p. 496.)

Legs-out. Posture assumed by a non-receptive female; when descending into her burrow she leaves the ambulatories of one side projecting in the air. (Agonistic posture no. 14, p. 480.)

Lek. A restricted locality in which males in many species of birds and other animals congregate in the breeding season. Here they defend individual territories from encroaching males and court females. In a restricted sense, the word is used of associations in which the strongest males hold territories near the center and do most of the mating. Leks in the restricted sense are not yet known to occur in *Uca.*

Leptochelous. The pollex and dactyl of the major cheliped are unusually long and slender in comparison with most individuals in the same species of similar carapace size. Cf. *Brachychelous.*

Line, raised. A ridge, long and very low, not paralleling similar structures. Cf. *Stria.*

Lunge. A threat pattern of high intensity. One male, with claw pointed forward, makes a feint toward another. (Agonistic component no. 5, p. 479.)

Major. Adjective preceding either the noun *side* or the name of an appendage or one of its segments; the word indicates that the location of the area is on the same side of a male as the large cheliped.

Major-manus-drum. Vibration of the manus of the major cheliped against the ground. (Sound component no. 9, p. 483.)

Major-merus-drum. Vibration of the merus of the major cheliped against an anterior part of the carapace. (Sound component no. 7, p. 483.)

Major-merus-rub. Stridulation in which part of the major merus rubs against an adjacent part of the carapace. (Sound component no. 1, p. 482.)

Mandible. One of the two small jaws, heavily calcified and meeting in the midline, in the buccal cavity. In a ventral view of the crab they lie underneath the three pairs of maxillipeds and two pairs of maxillae. Morphologically the mandibles are anterior to the first maxillae. (Fig. 37.)

Mangrove. Any of a number of shrubby and arboreal plants associated on sheltered coasts of the tropics and subtropics and in their brackish river deltas. Members of such a community are characterized most conspicuously by stilt roots. The community itself is called in English *mangrove* or *mangroves.* Macnae (1968) suggested substituting the word *mangal* to distinguish the forest community from its individual plants; the suggestion was published too late to be followed here, but its use in the future would certainly be sensible.

Manus, pl. *mani.* The sixth segment from the proximal end of a cheliped or ambulatory, it is simultaneously the predistal segment. On each of the two chelipeds its ventral distal portion is produced, forming the lower part of the chela, the pollex; the manus and pollex together are termed the *propodus* (*q.v.*). In discussions of the major cheliped, the word *manus* signifies its outer side, plus its dorsal and ventral margins. Cf. *Palm.* (Figs. 1, 2.)

Manus-rub. In low-intensity combat, the outer mani of the opponents rub longitudinally. (Ritualized component no. 1, p. 488.)

Margin, antero-lateral. On the dorsal part of the carapace, that portion of the side margins immediately behind the antero-lateral angle.

Margin, dorso-lateral. On the dorsal part of the carapace, a long raised line, smooth, beaded, or tuberculate, starting at the posterior end of the antero-lateral margin and continuing posteriorly and somewhat toward the center. (Figs. 1, 3.)

Margin, suborbital. On the antero-ventral part of the carapace the lower edge of the orbit; it is usually more or less crenellate at least near its outer angle. (Figs. 2, 3.)

Margin, vertical lateral. On the side of the carapace the long raised line extending upward from the ventral margin, directed toward or reaching the junction between the antero-lateral and dorso-lateral margins; often obsolescent at least in upper part. (Fig. 3.)

Maxilliped. Any one of six mouthparts, consisting of three pairs. The third pair, the outermost, includes broad, flat segments that fit closely over the buccal cavity. The second pair, in a ventral view of the crab, underlies the third pair and is external to, and overlying, the first pair. The first pair is external to and overlies the maxillae. Morphologically the maxillipeds are posterior to the maxillae. (Figs. 2, 33, 36.)

Mechanisms, isolating. "Properties of individuals that prevent successful interbreeding with individuals that belong to different populations." (Mayr, 1969: 405.)

Megalops. A post-embryological stage of crab development occurring after the zoea and before the crab molts into the first crab stage. In most crabs, including all *Uca*, both zoea and megalops are free-swimming. In *Uca* the few larvae so far identified are pelagic but most individuals of many species probably pass even their early stages in brackish water and a few far up tidal streams. Cf. *Zoea.*

Membrane-vibration. Air or air and water inside the epibranchial chambers vibrate against the membranes at the chelipeds' proximal ends. (Sound component no. 13, p. 484.)

Merus, pl. *meri.* On a third maxilliped, the more distal of the two large segments that cover the buccal cavity; on a cheliped or ambulatory, the fourth segment from the proximal end; on each of these appendages the merus is distal to the ischium. On chelipeds and ambulatories it is the most proximal large segment; it is always longer than broad and is followed distally by a short carpus. (Figs. 1, 2, 33.)

Microhabitat. A local subdivision of a habitat.

Mill, gastric. See *Stomach.*

Minor. Adjective preceding either the noun *side* or the name of an appendage or one of its segments; it indicates that the area is on the same side of a male as the minor cheliped. Cf. *Major.*

Minor-chela-tap. The tip of the claw on the minor cheliped strikes the ground several times. (Sound component no. 10, p. 484.)

Minor-merus-rub. Stridulation in which the merus of the minor cheliped rubs against an adjacent part of the carapace. (Sound component no. 2, p. 482.)

Minor-claw-rub. Stridulation in which the claw of the minor cheliped rubs the suborbital crenellations. (Sound component no. 3, p. 482.)

Minor-merus-drum. Vibration of the merus of the minor cheliped against the anterior part of the carapace. (Sound component no. 8, p. 483.)

Minor-wave. In waving display, the minor cheliped moves similarly to the major. (Component no. 9, p. 496.)

Mound. A low elevation with rounded top on the carapace or an appendage.

Mud. "The result of the reaction and interaction of alluvium and living organisms." (Macnae, 1956; 40.)

Mud flat. Expanses of muddy land left uncovered at low tide. Most occur near river mouths that often open into sheltered bays. In the tropics the flats are often partly bordered with mangroves.

Neotype. "A specimen selected as type subsequent to the original description in cases where the original types are known to be destroyed or were suppressed by the [International Commission on Zoological Nomenclature]." (Mayr, 1969: 407.)

Niche. "The precise constellation of environmental factors into which a species fits or which is required by a species." (Mayr, 1969: 407.) Cf. *Habitat*; *Biotope*.

Orbit. One of the pair of elongate trenches extending along most of the anterior part of the carapace, in which the eyestalk and eye lie when not in use. (Fig. 3.)

Osmoregulation. See *Regulation, osmotic*.

Ovary. In non-breeding *Uca* females, each of the two egg-bearing glands is confined in the coelomic cavity to a region between the heart and the posterior branchial region. In breeding individuals each ovary extends conspicuously far forward and laterally and they are in part joined in the midline. (Fig. 77.)

Overhead-circling. In waving display a component in which the cheliped does not return to the flexed rest position during a series of waves but describes aerial circles above the crab's body. (Component no. 8, p. 496.)

Palm. On a cheliped, the inner surface of the propodus, proximal to the pollex; in other words, the inner side of a claw proximal to the fingers. (Figs. 2, 44.)

Palm-leg-rub. Stridulation resulting from rubbing of the major palm against the anterior side of the first ambulatory. (Sound component no. 4, p. 482.)

Palp. The segments of a maxilliped distal to the merus.

Paratype. "A specimen other than the holotype which was before the author at the time of the preparation of the original description and was so designated or indicated by the original author." (Mayr, 1969: 408.)

Pattern, fixed action. See *Component*.

Pereiopod. See *Ambulatory*.

Phase. A temporary state that is characterized in males by one of a number of general behavior patterns. (P. 505.)

Phase, aggressive wandering. A male moves apparently at random through a population that includes displaying males, punctuates his passage with threats toward them, engages them in combat, makes superficial burrow explorations, and attempts unsuccessfully to mate.

Phase, display. In males the temporary condition characterized by waving display, burrow-holding, threat, combat, and courtship.

Phase, non-aggressive wandering. A male moves through a population or forms part of a drove, feeding near the tide's edge. He does not threaten or enter into combat, often passes close to displaying males in a crouching posture, does not hold a burrow during low tide, does not wave, and does not court.

Phase, territorial. A condition intermediate between the aggressive wandering phase and the display phase, often or usually very brief to absent. At this time a male holds a burrow and threatens other males but does not wave or court.

Phase, underground. A male remains underground in his burrow throughout one or more low-tide periods; the period of submersion is usually several days unless the crab is undergoing a period of hibernation or aestivation.

Phenetics, numerical. "The hypothesis that relationship of taxa can be determined by a calculation of an overall, unweighted, similarity value." (Mayr, 1969: 408.) See also *Taxonomy, numerical*.

Pheromone. An external secretion selectively affecting the behavior of conspecifics.

Phylogeny. "The study of the history of the lines of evolution in a group of organisms; the origin and evolution of the higher taxa." (Mayr, 1969: 409.)

Pile. A group of short, thickly set setae, often occurring in patches on the carapace and appendages; the appearance is reminiscent of velvet or fur.

Pillar. A tower-like structure built of substrate raised by a male in display phase beside his burrow. (P. 500.)

Pit. An indentation in the integument, small to minute and more or less rounded.

Pleopod. One of the paired appendages arising on the ventral sides of certain abdominal segments. In males there are only two pairs, one on each side of the first two segments; the first of these consists of the two genital organs or gonopods. Females have one pair on each of the first five segments; they are modified for holding the egg-mass.

Pollex; pl. *pollices*. On a cheliped's claw, the fixed finger, which is the ventral, distal extension of the propodus. (Figs. 1, 2, 42, 44.)

Pollex-base-rub. In high-intensity combat a component performed when the inactor has partly descended his burrow, leaving the claw projecting. The actor rubs the prehensile edge of his pollex against the outer pollex base of his opponent. (Ritualized component no. 5, p. 489.)

Pollex-rub. In low-intensity combat the outer sides of the pollices rub longitudinally. (Ritualized component no. 2, p. 488.)

Pollex-under-and-over-slide. In high-intensity combat, one pollex slides in turn along the ventral and dorsal edges of the opposing pollex. (Ritualized component no. 3, p. 488.)

Population, local. "The individuals of a given locality which potentially form a single interbreeding community." (Mayr, 1969: 409.)

Pore. The genital opening of the male, located on the distal end of the gonopod. (Fig. 58 *D, E.*) Cf. female's *Gonopore*.

Posing. A rigid posture adopted occasionally by individuals of both sexes in which the chelipeds are usually unflexed and the carapace tilted toward the sun. (P. 506.)

Post-megalops. The first littoral stage or instar; also known as the first crab stage. Cf. *Zoea* and *Megalops*.

Prance. A motion in which a male walks stiffly on the bent-under dactyls of the ambulatories. Possibly sounds are produced. (Agonistic component no. 12, p. 479.)

Pregape-rub. In high-intensity combat the tips of the dactyl and pollex rub longitudinally along the distal outer manus and palm, respectively, of the opponent. (Ritualized component no. 10, p. 490.)

Process, inner. A structure on the distal end of the gonopod arising on the inner side but often displaced anteriorly by torsion. Its shape varies from a large and tumid projection to a slender transparent spine. (Fig. 58; p. 464.)

Prolonged-leg-stretch. In waving display the crab holds his body high off the ground throughout a series of waves. (Component no. 11, p. 496.)

Propodus. In crustaceans generally, the predistal segment of a leg-like appendage; in this contribution, confined to either of the two chelipeds in *Uca*; it there consists of the manus and its distal extension, the pollex. The propodus on the ambulatories in this contribution is termed the *manus* (*q.v.*). (Fig. 2.)

Pubescence. See *Pile*.

Raised-carpus. A threat posture of low intensity. The major carpus is raised while the claw points obliquely down. (Agonistic component no. 1, p. 479.)

Rap; rapping. Terms used by Crane (1941.1ff.) in previous descriptions of waving display; they were equivalent to the present general term *drumming*. The behavior formerly called *rapping* was found to include manus-drums, merus-drums, and ritualizations of both. (P. 483.)

Region (of carapace). An area, usually convex, separated from its neighbors by narrow grooves.

Region, branchial. (Paired.) A large lateral region overlying the branchial cavity. (Fig. 1.) The region includes two other areas with names used in this contribution, the epibranchial and metabranchial regions (see below).

Region, cardiac. (Unpaired.) The central area on the carapace bounded anteriorly by the mesogastric, laterally by the branchial, and posteriorly by the intestinal regions. (Fig. 1.)

Region, epibranchial. (Paired.) The anterior part of the branchial region. It is bounded anteriorly and externally by the margins of the carapace and internally by the hepatic region. (P. 471.)

Region, hepatic. (Paired.) An antero-lateral area bounded anteriorly by the orbital region, internally by the mesogastric region and other gastric areas, and both externally and posteriorly by the branchial region. (Fig. 1.)

Region, intestinal. (Unpaired.) The most posterior of the central areas of the carapace, bounded anteriorly by the cardiac region, laterally on each side by the branchial region and posteriorly by the carapace margin. (Fig. 1.)

Region, mesogastric. (Unpaired.) The central area of the carapace that is bounded posteriorly by the cardiac region and laterally by the hepatic and branchial regions. (Fig. 1.) Anteriorly lie other gastric areas.

Region, metabranchial. (Paired.) The posterior, larger part of the branchial region, it is bounded anteriorly by the epibranchial part of the branchial region and the hepatic region, and internally by the mesogastric, cardiac, and intestinal regions; it overlies the cavity containing the large gills. (P. 469.)

Region, orbital. (Paired.) The area immediately behind the eyebrow and adjacent parts of the upper margin of the orbit. (Fig. 1.)

Region, pterygostomian. (Paired.) On the antero-ventral part of the carapace, the area external to the buccal cavity. (Fig. 2.)

Region, suborbital. (Paired.) On the antero-ventral part of carapace, the area immediately behind the suborbital margin. Paired. (Fig. 2.)

Regulation, osmotic. "Osmotic regulation may be defined as the regulation of the total particle concentration of such fluids at levels different from those of the external medium." (Robertson, 1962: 323.)

Reversed-circular-wave. In waving display as in the usual lateral-circular-wave, except that the cheliped is unflexed at a high point and flexed into rest position at a lower level. (Component no. 7, p. 496.)

Rhythm, circadian. An endogenous rhythm with a cycle roughly 24 hours in length.

Rhythm, endogenous. A cycle under physiological control that continues to operate for a time on its previously established schedule in the absence of the appropriate external stimuli.

Rhythm, lunar. An endogenous rhythm with a cycle roughly 28 days in length.

Rhythm, semi-lunar. An endogenous rhythm with a cycle roughly 14 days in length.

Rhythm, tidal. An endogenous rhythm with a cycle roughly 12.4 hours in length, its particular temporal characteristics changing continually in accordance with the tidal schedule prevailing locally.

Ridge. An elongate, narrow elevation of the integument with a more or less sharp edge that is sometimes tuberculate or otherwise armed. Cf. *Stria*; *Line, raised*; *Rugosity*; *Crest*.

Ridge, distal at dactyl base. The more distal ridge, usually tuberculate, on the upper distal part of the major palm. (Fig. 43.)

Ridge, oblique; *ridge, oblique tuberculate*. On the upper, distal part of the major palm, a raised area with its projecting edge usually sharply ridge-like but sometimes blunt; usually with tubercles extending from the carpal cavity to the vicinity of the proximal ventral part of the pollex. (Fig. 43.)

Ridge, proximal at dactyl base. The more proximal ridge, usually tuberculate, on the upper distal part of the major palm; vertical or nearly so in its upper part, its lower portion curves distally to merge with the tubercles of the inner row on the dactyl's prehensile edge. (Fig. 42.)

Right-clawed. The cheliped on the crab's right side is enlarged.

Ritualization. In the evolution of an animal's behavior, changes in a movement and certain associated structures so that they come to serve as a signal in communication, or as a different signal, or to function in some other social capacity. (P. 519.)

Rugosity. A roughness of the integument, usually in the form of short, blunt, irregular ridges, nontuberculate, irregularly shaped, and arranged in groups, the alignment of the individual rugosities being roughly parallel.

Sac, pericardial. (Paired.) A water-absorbing organ in the posterior part of the branchial cavity. (Fig. 78.) It aids in controlling the maintenance of moisture.

Salinity. The proportion of dissolved materials in seawater. Measured in parts per thousand (°/00). Normal seawater ranges, depending on latitude, between 34°/00 and 37°/00.

Sand. "A material consisting of comminuted fragments and water-worn particles of rocks (mainly siliceous) finer than those of gravel; often *spec.* as the material of a beach, desert, etc." (*The Shorter Oxford English Dictionary*, 3rd ed.)

Semi-unflexed-wave. In waving display the cheliped is partly unflexed as it is raised. (Component no. 3, p. 496.)

Series. (1) "In taxonomy, the sample which the collector takes in the field or the sample available for taxonomic study." (Mayr, 1969: 411.) (2) In waving display a group of waves and their associated motions performed by an individual in an uninterrupted sequence.

Serration. One of a series of somewhat compressed tubercles occurring on the margins of appendages; each is more or less triangular with the apex directed toward the distal end of the segment.

Seta, adj. *setose*. An unjointed appendage, either soft and hair-like or a stiff bristle. Setae vary greatly in microscopic characteristics and many are doubtless sensory in function; they occur plentifully on most parts of the body and jointed appendages.

Seta, spoon-tipped. On a mouthpart, especially on the merus of the second maxilliped, a seta ending in a more or less concave expansion, usually lobed or pectinate. (Figs. 36, 37.)

Sonagram. "A graphic representation of the vocalization of an animal." (Mayr, 1969: 411.)

Speciation. "The splitting of a phyletic line; the process of the multiplication of species; the origin of discontinuities between populations caused by the development of reproductive isolating mechanisms." (Mayr, 1969: 412.) Cf. *Speciation, Allopatric*; *Speciation, sympatric*.

Speciation, allopatric. "Species formation during geographic isolation." (Mayr, 1969: 397.)

Speciation, sympatric. "Speciation without geographic isolation; the acquisition of isolating mechanisms within a deme." (Mayr, 1969: 412.)

Species. "Groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups. . . ." (Mayr, 1969: 412.) Cf. *Subspecies*; *Population, local*; *Isolation, reproductive*; *Mechanisms, isolating*.

Species-specific. An attribute characteristic of a species; often used in connection with behavior patterns or their components.

Spermatophore. A capsule containing spermatozoa transferred through the male gonopod into the female gonopore.

Spine. A long, pointed tubercle.

Sternum. The segmented, ventral surface of the body lying between the proximal segments of the two chelipeds and of each pair of ambulatories. (Fig. 2.) In males the narrow abdomen folds forward into a groove that runs longitudinally down the sternum's midline. In adult females the broad abdomen, folded similarly forward, almost covers the sternum.

Stomach. A general term for the central part of the gut. Its most conspicuous component is the so-called gastric mill, a muscular sac with hard, internal ridges located between the lobes of the hepatopancreas. (Fig. 80.)

Stria. In this contribution used only of a ridge or raised line, very small to minute in all dimensions—length, height, and thickness; usually more or less parallel to other such structures; it may be unarmed, beaded, or tuberculate. This meaning of the word is included among the definitions given, for example, in *The Shorter Oxford English Dictionary*, 3rd ed.; there it appears as follows: "2.

Chiefly in scientific use. A small groove, channel, or ridge." Cf. *Ridge*; *Line, raised.*

Stria, postero-lateral. A stria on the postero-lateral part of the carapace, behind and usually external to the postero-lateral end of the dorso-lateral margin; when fully developed there are two, more or less parallel to each other, on each side. (Figs. 1, 3.)

Stridulation. Sound production by a single individual performed by rubbing, tapping, or vibrating one part of the body against another, either or both of which are suitably armed. The parts involved may be those of an appendage against the carapace or of two or more appendages against one another.

Style. A slender projection of the eyestalk beyond the distal end of the eye (cornea).

Subdactyl-and-subpollex-slide. In high-intensity combat, the upper edge of one dactyl moves to and fro longitudinally along the prehensile edge of the opponent's dactyl, while the prehensile edge of the pollex moves similarly along the lower edge of the opponent's pollex. (Ritualized component no. 4, p. 489.)

Subdactyl-and-suprapollex-saw. In high-intensity combat, one dactyl's prehensile edge moves transversely across part of the prehensile edge of the opponent's pollex. (Ritualized component no. 15, p. 491.)

Subgenus. An optional taxonomic category, consisting of a group of species the members of which appear to be more nearly related to one another than they are to other members of the genus.

Subspecies. "A geographically defined aggregate of local populations which differs taxonomically from other such subdivisions of the species." (Mayr, 1969: 412.)

Substrate. A general term for the terrestrial components of a biotope, composed partly or largely of inorganic matter, such as mud or sand.

Superspecies. "A monophyletic group of entirely or largely allopatric species." (Mayr, 1969: 412.) In the present contribution the term is used as follows: a group of allopatric species, each of which appears to be more closely related to its neighbors within the superspecies than to other members of the genus, with the occasional exception of sympatric members of its alliance. The term has no official taxonomic standing. In headings the name is enclosed in brackets, as suggested by Amadon 1966: 245). Cf. *Alliance*; *Allopatry.*

Supraheel-rub. In high-intensity combat, the dactyl rubs vertically against the heel of the opponent's manus, the pollex meanwhile lying against his palm. (Ritualized component no. 13, p. 491.)

Sympatry. "The occurrence of two or more populations in the same area; more precisely, the existence of a population in breeding condition within the cruising range of individuals of another population." (Mayr, 1969: 413.) In the present contribution, use of the word is restricted as follows: in the broad sense sympatry indicates the occurrence of more than one species of *Uca* in the same area, within sight of one another and without physical barriers between the populations; in the restricted sense it indicates such an occurrence of members of the same subgenus, particularly of those showing the closest interspecific relationship, as among members of an alliance (*q.v.*). Adj.: *Sympatric*; in this study used also as a n. (cf. allopatric).

Synonym. "In nomenclature, each of two or more different names for the same taxon." (Mayr, 1969: 413.)

Synonymy. "A chronological list of the scientific names which have been applied to a given taxon, including the dates of publication and the authors of the names." (Mayr, 1969: 413.)

Syntype. "Every specimen in a type-series in which no holotype was designated." (Mayr, 1969: 413.)

Systematics. "The science dealing with the diversity of organisms." (Mayr, 1969: 413.)

Tapping. In combat of both low and high intensities, part of the prehensile edge of the dactyl, the pollex, or both tap against part of the opponent's dactyl or propodus. Tapping sometimes forms a part of a number of ritualized components. (P. 491.) Cf. *Vibration*; *Claw-tap.*

Taxon, pl. *taxa.* "A taxonomic group that is sufficiently distinct to be worthy of being distinguished by name and to be ranked in a definite category." (Mayr, 1969: 413.)

Taxonomy. "The theory and practice of classifying organisms." (Mayr, 1969: 413.)

Threat. Aggressive postures and motions confined in males to individuals in the aggressive wandering, territorial, and display phases; in females they appear when approached by an aggressive wanderer, or when in a non-receptive phase. Although in males threats usually precede combat, the behavior appears far more often than combats. See agonistic postures and motions, and discussion; pp. 478, 516.

Thumb. (1) In older literature the fixed finger or pollex on a cheliped. (2) On the male gonopod, a subdistal structure (Fig. 56). Equivalent to the *palpus* of von Hagen, 1962.

Tomentum. See *Pile.*

Tooth. A tubercle, larger than the other tubercles in the same series and usually of a different shape.

Topotype. "A specimen collected at the type-locality." (Mayr, 1969: 413.) Such specimens are not necessarily given official taxonomic status.

Torsion. A characteristic of the male gonopod in some species in which part of the distal end is twisted so that one or more of its structures are displaced from their more usual positions. (P. 464.)

Tubercle. A small projection on the integument, either blunt or more or less conical, but of widely diverse shapes and sizes. Usually in series or groups. When very small in comparison with adjacent armature, the structure is here termed a granule, the name being imprecise. If larger and, particularly, different in shape from its neighbors, it is called a *tooth.* See also *Serration, Spine, Crenellation,* and *Edge, Beaded.*

Type. "A zoological object which serves as the base for the name of a taxon." (Mayr, 1969: 413.)

Type-locality. "The locality at which a holotype, lectotype or neotype was collected. (Cf. *topotype.*)" (Mayr, 1969: 414.)

Type-species. The species in a genus or subgenus which was designated as its type.

Upper-and-lower-manus-rub. In high-intensity combat the prehensile edges of one claw rub along the upper and lower margins of the opponent's manus. (Ritualized component no. 7, p. 489.)

Upset. In combat, an unritualized final component in which one crab is turned completely upside-down. The rarest of all combat components. (Forceful component no. 2, part, p. 488.)

Vertical-wave. In waving display, the flexed cheliped moves up and down. (Component no. 1, p. 496.)

Vibration. In sound production and in combat the rapid tapping by an appendage against the carapace, another appendage, or the substrate, or, in ritualized waving display, certain motions in the air. For present practical purposes, the word is confined to motions repeated at rates faster than 50 per second. At this rate, a blur on the film results when motion picture film is exposed at 24 frames per second, giving, when the frames are viewed through a dissecting microscope, a convenient means of distinguishing in combat between tapping and vibration. Vibration is here used synonymously with *drumming*, as employed in the names of certain behavioral components. Cf. *Tapping.*

Walking leg. See *Ambulatory.*

Wanderer. (1) A male in a non-aggressive phase, characterized by lack of attachment to a particular burrow. See *Phase, non-aggressive wandering.* (2) A receptive female at least in the subgenera *Minuca* and *Celuca*, as she moves through a displaying population.

Wanderer, aggressive. See *Phase, aggressive wandering.*

Wave. A general term for the rhythmic raising and lowering of the major cheliped during waving display. (P. 494.)

Wave, diminishing. In waving display, a wave lower than its predecessor in a single series.

Wave, primary. In waving display, the first and highest wave in a series.

Whitening, display. Temporary color lightening during the display phase of males and less often of females; it is characterized by the expansion of white chromatophores at least on the carapace. (P. 466.)

Withdrawal. Behavior associated with combat, in which a burrow-holder descends partway or entirely into his own burrow. (P. 491.)

Zoea, pl. *Zoeae.* One of the aquatic larval stages of crabs. Its outstanding morphological features are the occurrence of one or more large spines on the carapace. See also *Megalops.*

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Note: For abbreviations of serial publications "The World List of Scientific Periodicals" has been used. In the few cases where a particular periodical appeared to be unlisted, I have abbreviated it in this bibliography in a form consistent with that of the "World List," except that unusual words are spelled out.

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Indexes

Index to Scientific Names

Entries in **boldface** are the names of subgenera, species, and subspecies of the genus *Uca* which in this contribution are considered valid. Page numbers in boldface refer to the principal treatment of each of these entries, in accordance with the topics listed and described on pp. 10–13.

Several of the subheadings provided for the longer entries serve only as general guides. For example, the subheading "evolution" may include references to apparent phylogeny, morphological responses to ecological pressures, and possible derivations of behavioral components.

General Index

This index includes geographical localities, names of persons, and subjects.

Geographical Localities. Only major areas are listed, such as names of countries and certain islands. Page references to the species recorded from an indexed locality are given under the subheading "recorded spp.", followed by the first page of each pertinent species treatment in the Systematic Section (for example, "recorded spp., 77ff, 284ff"). These lists include species recorded from the locality in print, on specimen labels in material examined, or both. Some lists include records considered by the present author to be erroneous; the most questionable are also referred in the entry to additional page numbers; minor queries are discussed within the species treatments. The locality indexed, such as "India," as well as names of smaller places included within the area, occur chiefly in these treatment topics: Introduction, Range, Field Material, Type Material and Nomenclature, and References and Synonymy, as well as in Material Examined (Appendix A). Incidental references to indexed localities occurring in non-systematic sections are omitted when the geographical information is not directly important to the context, as in locality identification of behavioral observations.

Names of Persons. Both collectors and donors of material, as given on the labels of occasional preserved specimens, are listed as donors. Page numbers in boldface refer to citations of a writer only as the author of a scientific name. When further material involving the same person appears on the same page, the page number appears also in roman.

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