TRANSACTIONS
OF THE
ROYAL SOCIETY OF NEW ZEALAND

BIOLOGICAL SCIENCES

VOL. 11 No. 4 JUNE 5, 1969

The Morphology of Stridulatory Structures in the Genus *Ovalipes* Rathbun

By W. STEPHENSON,
Department of Zoology, University of Queensland, Brisbane.

[*Received by the Editor, February 2, 1968.*]

INTRODUCTION

IN their review of stridulation in crabs, Guinot-Dumortier and Dumortier (1960) refer to two species of *Ovalipes, O. punctatus* (de Haan) and *O. ocellatus* (Herbst). Stephenson and Rees (1968) have shown that recent authors have confused at least five species under the name of *O. punctatus,* and that there are differences in the details of the presumed stridulatory structures in these species. Stridulating structures similar to those in *O. ocellatus* occur in *O. guadulpensis* (Saussure) and there are comparable structures in *O. iridescens* (Miers) and *O. molleri* (Ward). In *O. georgei* Stephenson and Rees, the presumed stridulatory devices differ from those in all the other species of the genus. For these reasons the present study encompasses all the known species.

Ovalipes species have been divided by Stephenson and Rees (1968) into four subgroups:—(1) *O. punctatus* subgroup comprising *O. punctatus, O. trimaculatus* (de Haan), *O. catharus* (White), *O. australiensis* Stephenson and Rees and *O. elongatus* Stephenson and Rees. (2) *O. georgei* subgroup comprising *O. georgei.* (3) *O. iridescens* subgroup comprising *O. iridescens* and *O. molleri.* (4) *O. ocellatus* subgroup comprising *O. ocellatus* and two forms of *O. guadulpensis.*

The general approach of Guinot-Dumortier and Dumortier (1960) was to infer stridulation from examination of structures showing special modifications almost certainly associated with sound production. Two types of structures were considered: the *pars stridens* or " râpe " (rasp), which is usually stationary, and the plectrum which usually engages it.

In " *O. punctatus* " conspicuous striae on the under surface of the hand of the cheliped evidently form a rasp, and in males two modified structures could engage them. These are the raised collar on the merus and the modified dactyl of the first pair of walking legs. Balss (1921), in an earlier review of stridulatory structures in decapods, considered the dactyl as the plectrum, but Guinot-Dumortier and Dumortier (1960) followed Rathbun (1930) and Barnard (1950) in considering the merus as the effective structure on the grounds that it " paraît beaucoup plus fonctionnel ".

To resolve these differences of opinion attempts were made to engage the rasp with each type of plectrum, using large preserved male specimens of *O. australiensis*

Published by the Royal Society of New Zealand, c/o Victoria University of Wellington, P.O. Box 196, Wellington.

Trans. R. Soc. N.Z., Biol. Sci., Vol. 11, No. 4, *pp. 43–71, 7 figs., 2 pls.*

from eastern Australia which had retained flexibility of their joints. Both engagements could be effected with ease and produced very audible sounds in air, each sound having distinctly different qualities. Similar results were obtained with large males of *O. catharus* from New Zealand. It seemed most probable that both plectra would be functional in the living animal.

Engagement of the rasp by other less obviously modified plectra could also be effected with ease, as could engagement of the two obvious plectra with a number of less obvious rasps. Once the dynamic approach of attempting engagements of structures and listening for sound production had been embarked upon, it became evident that a great variety of structures could readily be engaged to produce sounds. A few additional engagements appeared to involve " unnatural " forced movements.

In *O. australiensis* and *O. catharus* females and small males showed a smaller range of stridulatory possibilities than large males, and in general feebler sounds were produced. This indicated that, if the various sounds were produced in living specimens, they would offer possibilities of size and sex recognition. Comparison of structures in males of *O. australiensis* and *O. catharus,* and of the engagements which were easily effected, indicated further possibilities of interspecific recognition, and this seemed to apply throughout the *O. punctatus* subgroup.

In the other subgroups many unmodified structures produced sounds, with each subgroup having differently modified sound-producing structures. These results offer a meaningful approach to the evolution of stridulatory structures in the genus as outlined in the discussion of the present paper.

It remains uncertain how many of the sounds are produced by the different species in nature. Study of preserved specimens showed that while morphologically distinct structures can be engaged individually, many presumably normal movements give several simultaneous or sequential engagements. This would result in a smaller effective vocabulary (of more complex patterns) than the initial listings might indicate.

For a complete study it would have been necessary to investigate all species under natural conditions, but this would present impossible difficulties because:

(1) Some species are evidently rare, and one (*O. georgei*) is only known from the few preserved type specimens.

(2) Knowledge of specific distributions (Stephenson and Rees, 1968) indicates that investigations in many parts of the world would be necessary.

It was then hoped to study live specimens of the local species (*O. australiensis*). Unfortunately, while this species was frequently recorded in Southern Queensland in 1965, no specimens have been obtained since, in spite of intensive efforts. There has been similar failure to obtain live material through the kind offices of Drs. Griffin and Yaldwyn of the Australian Museum. Even if live specimens had been obtained, difficulties would have remained. Many of the sounds produced by movements of preserved specimens are indistinguishable either by ear or by Sonagraph records (see below), and it would be necessary to observe specimens while they were producing sounds. In aquaria sounds associated with social behaviour, and particularly with sexual behaviour, might well be suppressed and confirmation of extent and possible functions of all truly natural sounds would require observations under field conditions. Much more information on the species under field conditions is required before this study could commence.

Recent information (Wears, personal communication) indicates an abundance of *O. catharus* in the Wellington area in accessible habitats. There is also a probability of social organisation in this species, and clearly the next logical step in the investigation would be work on the New Zealand species.

METHODS

Using flexible preserved specimens, one part of the body was moved against another. Initially observations were made in air, and the sounds noted, but were repeated upon specimens placed in water and sounds were recorded by hydrophone on a tape recorder (speed 7½ in./sec.). The hydrophone employed ("Fish Fone" by Engineering Research Corp., Shreveport, Louisiana) did not permit high fidelity recordings, particularly in the high frequencies, but proved adequate for present purposes.

Recording conditions were kept as constant as possible throughout, including distance of source from hydrophone (*c.* 2cm), and both tone and volume controls of the tape recorder. Recordings were converted into Sonagraph records by a standard procedure (half speed tape, Sonagraph frequency setting 85r to 6K, shaping switch HS, narrow band selector) at standard levels of record reproduction (10) and mark level (7½). Recordings were calibrated with an oscillator.

In spite of the attempts at constancy, it was impossible to eliminate variations in (a) the speed of the plectra moving over the rasps, and (b) the pressure between the engaging surfaces. Retrials on the same specimen showed these particularly affected the clarity of the pulses as analysed by the Sonagraph. Hence too detailed comparisons of the Sonagraph records were not made and only a selection is given below (see Pl. 1). False echoes from the walls of the container could have caused additional obscuring of the pulses, but were probably of minor importance because of the close proximity of the hydrophone to the sound source.

In one case (*O. georgei*) only type material with mostly inflexible joints is available, and some of the conclusions are drawn directly from structural features, following the method of Guinot-Dumortier and Dumortier (1960).

Throughout the investigations "natural" or "unnatural" movements were noted.

The general approach below is to list the individual engagements producing sound in a given species; in most cases an imposing list results. Simultaneous or sequential engagements which give a more realistic concept of the true range of stridulating possibilities, are then listed.

THE *O. punctatus* SUBGROUP

A. Large males of *O. australiensis*

Several cheliped structures which bear either striae or granules can act as moveable rasps, and produce sounds when engaged by several plectra on the walking legs. In addition several carapace structures produce sounds when different parts of the chelipeds move across them, with the cheliped areas sometimes acting as moving rasps and sometimes as moving plectra. In some cases because both cheliped and carapace structures are granular, they appear to act simultaneously as rasps. In describing cheliped/walking leg engagements it is convenient to list rasps and plectra, but for cheliped/carapace engagements it is simpler to list stationary and moving structures.

I. Cheliped/walking leg engagements

(a) *Rasps on cheliped* (Fig. 1A)

(i) The conspicuous striae on the under surface of the palm (Fig. 1A–a) merge distally into a granular area (Fig. 1A–b), and the two areas are best considered as a unit.

(ii) The above merge into rows of granules on the immovable finger (Fig. 1A–c) but these are conveniently considered as separate.

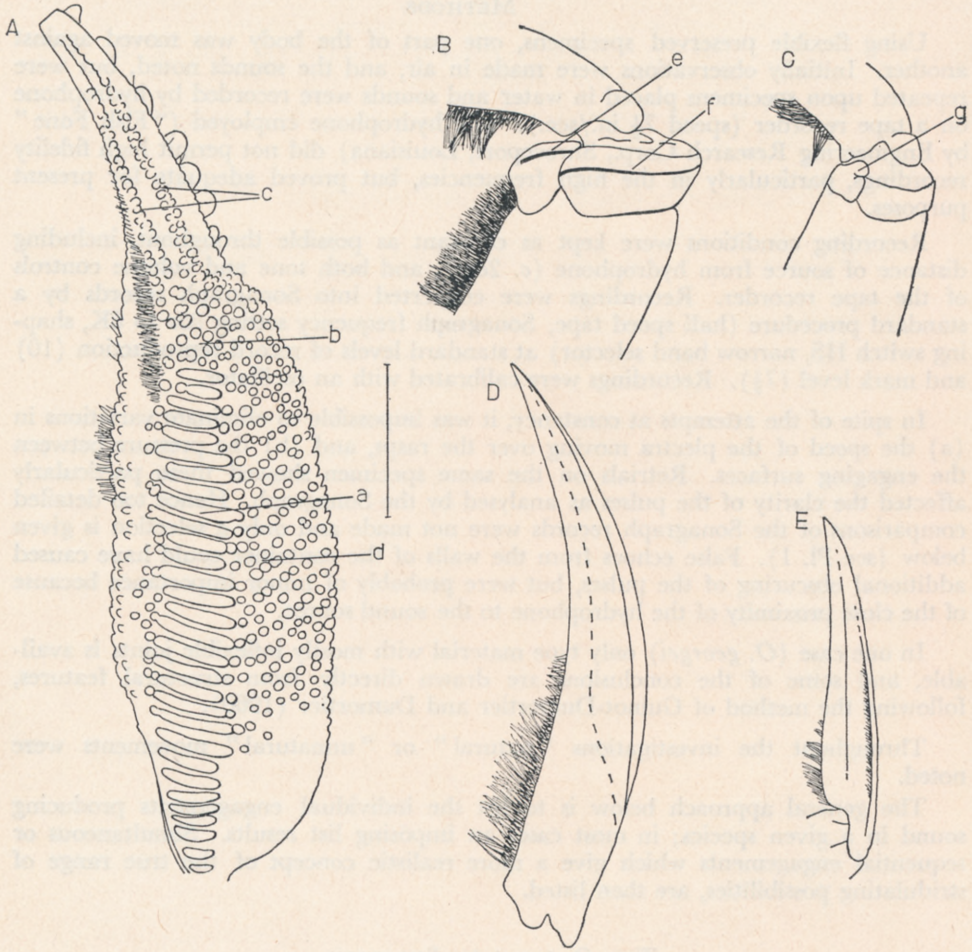


FIG. 1.—*O. australiensis* Stephenson and Rees. A. Ventral surface of palm and immovable finger of left cheliped; a—striae, b—distal granules under palm, c—rows of granules under immovable finger, d—granules on outer surface of palm. B. Dorsal view of collar on merus of first right walking leg; e—inner boss, f—outer boss. C. Dorsal view of collar on merus of second right walking leg; g—rounded bosses. D. Dorsal view of dactyl of first walking leg. E. Dorsal view of dactyl of second walking leg, outer edge on right. Scale = 10mm.

(iii) The palm striae merge into granules on both inner and outer surfaces of the palm. Those of the outer surface (Fig. 1A–d) engage by both longitudinal movements (iiia) and dorsoventral movements (iiib) to produce sounds.

(b) *Plectra on walking legs* (Fig. 1B–E)

The legs are numbered I-III below.

(i) Dactylus I (Fig. 1D), is considerably modified, triradiate in section, and with a strongly cornified tip. The following portions act as plectra: (a) tip, (b) upper inner carina, and (c), lower carina.

(ii) Dactylus II (Fig. 1E), is of more normal form, although with more distinct carination and more cornified tip than in most portunids. The following act as plectra: (a) tip, (b) upper carina, and (c) lower carina.

(iii) Dactylus III, as with second leg, except the tip does not act as plectrum. Plectra are: (b) upper carina and (c) lower carina.

(iv) Propodus I, outer edge is carinate (Fig. 2a) and acts as a plectrum.

(v) Propodus II, similarly.

(vi) Carpus I, upper surface is granular (Fig. 2b) and acts as plectrum.

(vii) Carpus II, similar.

(viii) Carpus III, similar.

(ix) Merus I bears a conspicuous collar consisting of two swollen areas, each bearing a cornified boss, each of which can act as a separate plectrum, although normally both would engage simultaneously. The outer boss (a) is the larger (Fig. 1B–f) and extends beneath to form an incomplete annulus; the inner boss (b) on the upper surface (Fig. 1B–e) is smaller than the outer boss and is strongly cornified.

(x) Merus II bears a collar in which only the inner area is swollen to form a pair of rounded bosses (Fig. 1C–g), which act as a plectrum.

Merus III has only a feebly developed collar which does not appear to act as a plectrum.

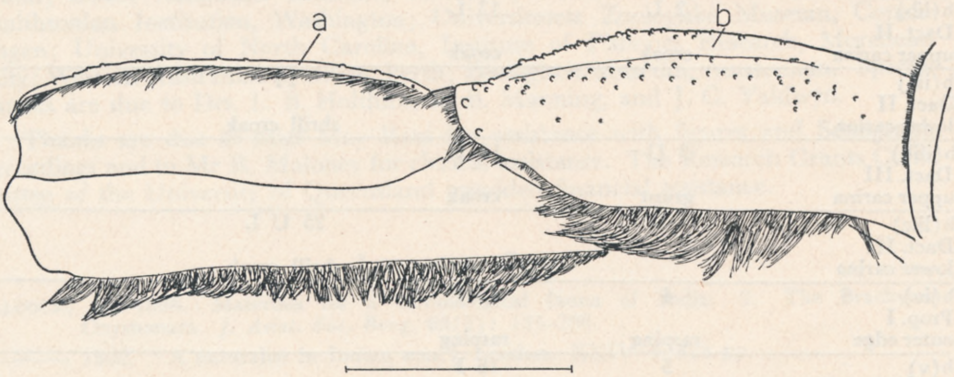


FIG. 2.—*O. australiensis.* Dorsomedian view of (a) propodus, and (b) carpus of first right walking leg. Scale = 10mm.

(c) *Engagements of rasps with plectra*

(i) *Individual engagements*

Table I shows that there are 29 anatomically possible methods of sound production. Six involve " unnatural " movements leaving 23 apparently functional ones, and it was difficult to determine which of these 23 were the most " natural ". It was also difficult to decide which produced the loudest sounds, although attempts were made.

Sonagraph records were made from tape-recordings, but did not facilitate distinctions between many of the sounds described as a " croak " or a " rasp ".

(ii) *Combined engagements*

These include the following, with numbering from Table I:— (9) + (10) + (19) + (20); (1) + (12); (2) + (13); (22) + (28) (by oblique movement).

(iii) *Individual variations*

Only variations of palm striae were examined. Numbers vary from 17 to 24, and there is considerable variation in the widths of individual striae, and the extent of fusion with the lateral granules. The overall pattern, reminiscent of a human fingerprint, has about the same potentiality for variation in structure, and presumably in details of sound production.

TABLE I.—Male *O. australiensis,* engagements of cheliped rasps by plectra on walking legs, and descriptions of sounds produced. The numbering of cheliped rasps (e.g., a(i), a(ii)) and of walking leg plectra (e.g., b(i), b(ii)) refer to listings in the text, and engagements of one with the other are given in arabic numbers. " Unnatural " or forced engagements are indicated by " U ", loud sounds by " L ", and faint ones by " F ".

Cheliped rasps Plectra	a(i) Striae and granules under palm	a(ii) Granules under imm. finger	a(iiia) Granules outer surface palm (longl. movt.)	a(iiib) Granules outer surface palm (D.V. movt.)
b(ia) Dact. I tip			22 shrill croak	28 L croak
b(ib) Dact. I upper inner carina	1 L croak	12 L croak		
b(ic) Dact. I lower carina			23 L shrill croak	
b(iia) Dact. II tip				29 L croak
b(iib) Dact. II upper carina	2 L croak	13 L croak		
b(iic) Dact. II lower carina			24 shrill croak	
b(iiib) Dact. III upper carina	3 U grunt	14 U croak		
b(iiic) Dact. III lower carina			25 U L shrill croak	
b(iv) Prop. I outer edge	4 rasping	15 F rasping		
b(v) Prop. II outer edge	5 rasping	16 F rasping		
b(vi) Carp. I upper surface	6 dull croak	17 dull croak		
b(vii) Carp. II upper surface	7 dull croak	18 U dull croak		
b(viii) Carp. III upper surface	8 U dull croak			
b(ixa) Merus I collar outer boss	9 L deep croak	19 L dull croak	26 L croak	
b(ixb) Merus I collar inner boss	10 L deep croak	20 dull croak	27 croak	
b(x) Merus II collar	11 deep croak	21 U dull croak		

II. Cheliped/carapace engagements

(a) *Cheliped—the moving structure*

The cheliped engages various carapace structures by both horizontal and by dorsoventral movements to produce sounds. The inner surfaces of the following joints, none of which show special modifications, are involved: (i) moveable finger, carina; (ii) immovable finger, carina; (iii) palm, upper carina often involving distal spine; (iv) palm, central carina; (v) palm, lower carina; (vi) palm, granular distal border; (vii) palm, boss on upper border; and (viii) wrist, spine. These structures are all obvious except for two which are (vi) which is near the lower portion of the articulation of the moveable finger, and (vii) which is near the upper portion of the articulation of the moveable finger.

The only cheliped area showing possible modification for engaging the carapace is (ix) the anterointernal upper surface of the arm (Fig. 3A–E), which bears a smooth hardened area (see Fig. 3A–a) which engages certain anterolateral teeth by horizontal movements.

(b) *Carapace—the stationary structures* (Fig. 3G)

Most engagements are with tips or granular edges of (i) suborbital tooth, (ii) first anterolateral tooth (Fig. 3G–a), (iii)-(vi) second to fifth teeth respectively.

Only a single carapace area shows possible modification associated with stridulation, and this is a clear arc of cuticle on the ventral surface just behind the anterolateral teeth (Fig 3G–b). The arc bears scattered granules, and is approximately equivalent to, but less modified than, the "*pars stridens* sous-orbitaire" of other

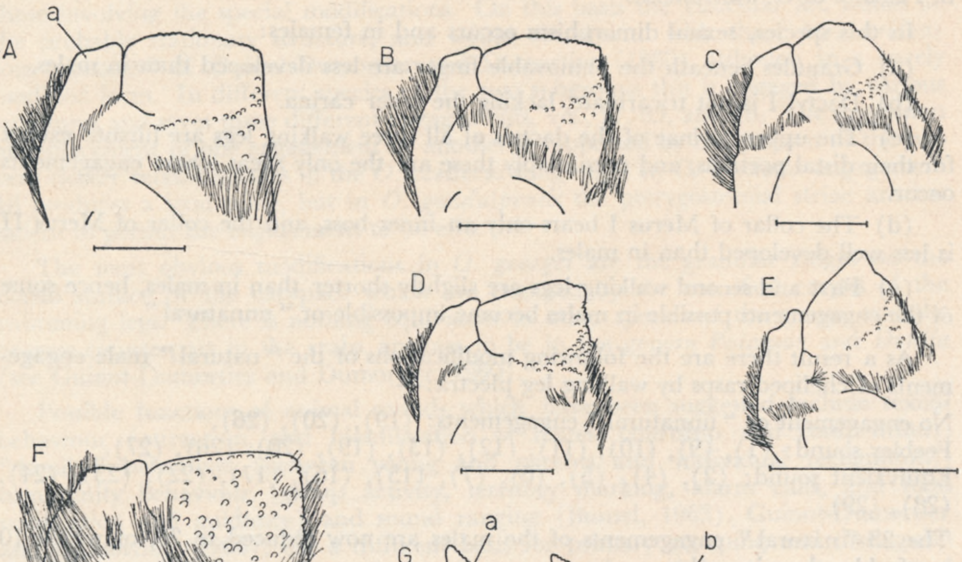


Fig. 3.—A–F. Dorsal views of distal upper border of arm of right cheliped, G. ventral view of ventral surface of left of front of carapace. Anterior sides on left and posterior sides on right; males except female in E. A. *O. punctatus* (de Haan), a—smooth hardened area. B. *O. australiensis* Stephenson and Rees. C. *O. trimaculatus* (de Haan). D. *O. catharus* (White). E. *O. elongatus* Stephenson and Rees. F. *O. georgei* Stephenson and Rees. G. *O. trimaculatus* (de Haan), a—first anterolateral tooth, b—cuticular arc. Scale = 10mm.

crabs as considered by Guinot-Dumortier and Dumortier (1960). It should be noted that pterygostomial striae occur in other subgroups of *Ovalipes,* but not in the present subgroup.

(c) *Engagements*

(i) *Individual engagements*

Dorsoventral movements of the chelipeds produce the engagements listed in Table II, and horizontal movements those in Table III. The number of methods of sound production which are anatomically possible increases to 69, and the number of apparently functional ones to 59. Again Sonagraph records did not facilitate distinctions between many of the sounds.

(ii) *Combined engagements*

For dorsoventral movements these include the following, with numbering from Table II: (31) + (37) + (38); (31) + (32) + (39) + (41) + (42); (33) + (37); (34) + (35) + (51); (36) + (52); (32) + (39) + (41) + (42) + (46) + (49); and (32) + (40) + (43) + (47) + (50). For horizontal movements, they include the following, with numbering from Table III: (54) + (55) + (56) + (63) + (64); (57) + (65); (58) + (59); (60) + (61); and (66) + (67) + (68) + (69).

B. Females of *O. australiensis*

In this species, sexual dimorphism occurs and in females:

(a) Granules beneath the immovable finger are less developed than in males.

(b) Dactyl I is not tricarinate, lacking the inner carina.

(c) The upper carinae of the dactyls of all three walking legs are hirsute except for their distal portions, and presumably these are the only areas where engagements occur.

(d) The collar of Merus I bears only an inner boss, and the collar of Merus II is less well developed than in males.

(e) First and second walking legs are slightly shorter than in males, hence some of the engagements possible in males become impossible or " unnatural ".

As a result there are the following modifications of the " natural " male engagements of cheliped rasps by walking leg plectra:—

No engagement or " unnatural " engagements: (19), (20), (26).
Feebler sound: (1), (9), (10), (11), (12), (13), (19), (20), (26), (27).
Equivalent sound: (2), (4), (5), (6), (7), (15), (16), (17), (22), (23), (24), (28), (29).

The 23 " natural " engagements of the males are now reduced to 20, of which 10 are feebler than in males.

No detailed investigation was made of the engagements of chelipeds against the carapace. These were generally similar to those in males.

C. Juveniles of *O. australiensis*

These resemble females in the details showing sexual dimorphism and in addition (a) lack any development of meral collars; (b) the upper carinae of the dactyls of all three walking legs are hirsute to their tips, and probably not involved as plectra; and (c) the lower carinae of the dactyls of the first and second walking legs are hirsute proximally, and presumably only the distal portions could act as plectra.

As a result there are the following modifications of the 20 " natural " female engagements of cheliped rasps against walking leg plectra:

TABLE II.—Male *O. australiensis,* engagements of carapace structures by dorsoventral movements of cheliped, and descriptions of sounds produced. The numbering of carapace structures (e.g., a(i), a(ii)) and of cheliped structures (e.g., b(i), b(ii)) refer to listings in the text, and engagements of one with the other are given arabic numbers. " Unnatural " engagements are indicated by " U ".

Cheliped Structure Carapace Structure	a(i) Mov. finger, inner carina	a(ii) Imm. finger, inner carina	a (iii) Palm, inside, upper carina and distal spine	a(iv) Palm, inside, central carina	a(v) Palm, inside, lower carina	a(vi) Palm, inside, granular distal border	a(vii) Palm, inside, boss on upper border	a(viii) Wrist, inner spine
b(i) Suborb. tooth	30 deep grunt	31 deep grunt				44 U croak		
b(ii) 1st AL tooth		32 deep grunt	33 grunt	37 croak or grunt		45 U croak	48 click or croak	
b(iii) 2nd AL tooth			34 grunt	38 croak or grunt	41 croak	46 croak	49 click or croak	
b(iv) 3rd AL tooth			35 grunt	39 croak or grunt	42 croak	47 croak	50 click or croak	
b(v) 4th AL tooth			36 grunt	40 croak or grunt	43 croak			51 croak
b(vi) 5th AL tooth								52 croak

TABLE III.—Male *O. australiensis*, engagements of carapace structures, by horizontal movements of chelipeds. All sounds produced are croaks; "unnatural" engagements are indicated by "U", deep croaks are indicated by "D". Remaining legend as for Table II.

Cheliped Structure / Carapace Structure	a(ii) Imm. finger, inner carina	a(iii) Palm, inside, upper carina and distal spine	a(iv) Palm, inside, central carina	a(v) Palm, inside, lower carina	a(viii) Wrist, inner spine	a(ix) Arm, anteroint. upper surface
b(ii) 1st AL tooth	53 U					
b(iii) 2nd AL tooth		54				66
b(iv) 3rd AL tooth		55	58	60	62	67
b(v) 4th AL tooth		56	59	61	63	68
b(vi) 5th AL tooth					64	69
b(vii) Cutic. arc		57 D			65	

No engagement or "unnatural" engagement: (1), (2), (9), (10), (11), (12), (13), (27).

Feebler sound: (4), (5), (6), (7), (15), (16), (17), (22), (23), (24).

Equivalent sound: (28), (29).

The 23 engagements of males and the 20 of females are reduced to 12, of which ten are relatively feeble.

Again no detailed investigation was made of the engagments of chelipeds against carapace.

D. Comparisons of males in other species of the *O. punctatus* subgroup with *O. australiensis*

No males are available in *O. elongatus,* and only a single male of *O. punctatus* with flexible joints was available (82mm, Oshoro, Japan, don. Hokkaido Imp. Univ.; coll. Madoka Sasaki, USNM). Several flexible males were available of *O. trimaculatus* and *O. catharus.*

I. Engagements of cheliped rasps with walking leg plectra

Throughout engagements were very similar to those in *O. australiensis* and the only minor differences noted were as follows:

(26)—loud noises in *O. australiensis* and *O. punctatus,* faint in *O. trimaculatus,* none in *O. catharus.*

(27)—loud in *O. australiensis,* faint in *O. trimaculatus,* none in *O. punctatus* and *O. catharus.*

(24) and (29)—" natural " engagements in *O. australiensis* and *O. punctatus,* " unnatural " in *O. trimaculatus* and *O. catharus.*

The sounds produced by equivalent engagements differed from species to species. Thus in *O. punctatus* compared with *O. australiensis*:

(i) The striae on the palm are larger, deeper, coarser and less numerous (13–20 cf. 17–24), producing more distinctly pulsed sounds. The same applies to the granules on the under surface of the palm.

(ii) The innermost carina beneath the immovable finger is conspicuously developed and bears large ovoid granules lying transversely, resembling a shorter version of the palm striae. Engagements produce louder and more pulsed sounds than in *O. australiensis.*

(iii) In engagement (11) (palm striae against 2nd meral collar), the inner boss is slightly less developed and the outer boss more developed, so that both act as plectra and not merely the inner boss as in *O. australiensis.*

(iv) In engagements (23) and (24), the first and second dactyls engage primarily with the salient central carina on the outside of the palm rather than with the lower one as in *O. australiensis.*

When *O. trimaculatus* is compared with *O. australiensis* the differences are as follows:

(i) The striae and the granules distal to them are smaller, more numerous (viz., 26–31 striae), shallower and finer, and give an increased frequency of pulses.

(ii) The under surface of the immovable finger is broadly rounded rather than carinate or bicarinate and is beset with small granules, again giving increased frequency of pulses.

(iii) The outer surface of the hand is more finely granular and with a relatively feebly-developed carina. Engagements produce feebler noises.

(iv) In engagement (26) the more salient inner boss of the first merus is more important than the outer boss in engaging with the outer surface of the palm.

When *O. catharus* is compared with *O. australiensis* the differences are as follows:

(i) The striae are shallower, smaller and slightly more numerous (viz., 20–26). The under surface of the immovable finger is not distinctly bicarinate, but is broadly rounded and with fine granulation (resembling *O. trimaculatus*). The result is a slightly increased frequency of pulses.

(ii) The outer surface of the palm is more finely granular and with a relatively feebly-developed carina (resembling *O. trimaculatus*).

(iii) While the dactyl of the first walking leg is tricarinate, the carina on the upper inner surface is relatively feebly developed, and that of the upper outer surface is less salient. Feebler sounds result.

(iv) No meral collars appear to engage with the outside of the palm.

II. Engagements of chelipeds with carapace structures

In general these appear to be similar in the different species of the subgroup and produce similar sounds. The only exceptions concern the cuticular arc and the upper surface of the arm. The former ranges from a small area bordered anteriorly by dense hairs and bearing very few granules in *O. australiensis,* to a relatively large area bordered posteriorly by fairly sparse hairs and bearing fine dense granules in *O. catharus*. Engagements with these areas produce sounds of different qualities in the different species.

The upper surface of the arm differs considerably in details from species to species (see Fig. 3A to E), but this seemed only to produce minor differences in the kind of sounds produced.

THE *O. georgei* SUBGROUP

This subgroup comprises the single species *O. georgei* in which the structures presumably modified for stridulation are a rasp consisting of a uniformly granular (almost striated) ridge on the posterior branchial region of the carapace (Fig. 4A) which is evidently engaged by a cornified carina on the carpus of the fifth leg (Fig. 4B). In addition the dactyl of the first walking leg is strongly triradiate.

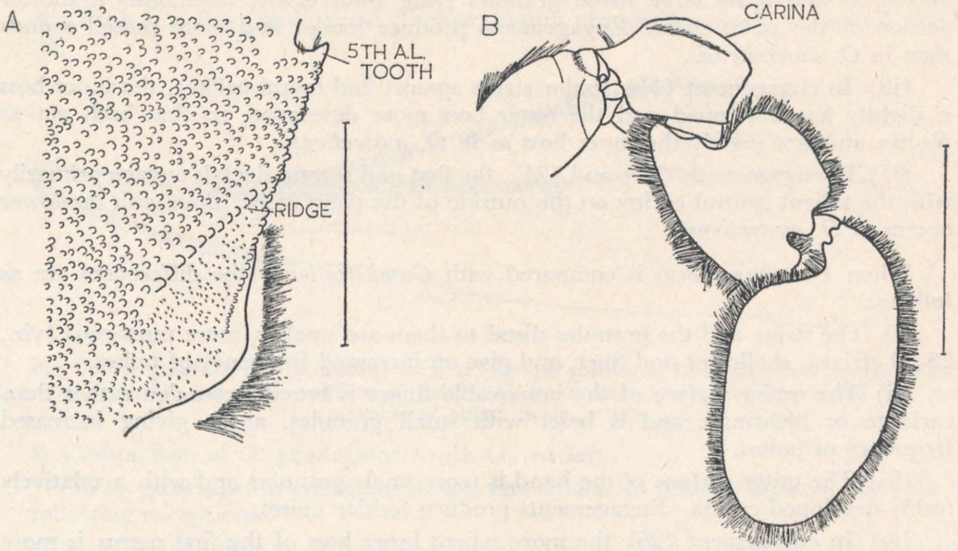


FIG. 4.—*O. georgei* Stephenson and Rees. Dorsal views of (A) right mesobranchial area of carapace; (B) right fifth leg. Scale = 10mm.

Unfortunately only male type material with almost inflexible and damaged legs was available, and only a few stridulating possibilities could be investigated by movements (see Table IV).

TABLE IV.—Male *O. georgei,* engagements of cheliped rasps by plectra on walking legs. All sounds produced are either rasping or croaking noises, " F " indicating a faint, and " L " a loud sound. Engagements indicated by " D " are based upon movements of disarticulated limbs. The numbering of cheliped rasps (e.g., a(i), a(ii)), and of walking leg plectra (e.g., b(i), b(ii)) refer to structures equivalent to those listed in the text for *O. australiensis.* Engagements in normal arabic numerals are the same as with *O. australiensis,* and those in italicised numerals are " related " to the equivalently numbered engagement in *O. australiensis.*

Plectra	Cheliped rasps		
	a(i) + a(ii) Granules under palm and imm. finger	a(iiia) Granules outer surface palm (longl. movt.)	a(iiib) Granules outer surface palm (D.V. movt.)
b(ia) Dact. I tip		22 D	*28* D
b(ib) Dact. I upper inner carina	1 D		
b(ic) Dact. I lower carinae		23 D	28 D
b(iia) Dact. II tip			29 F
b(iib) Dact. II upper carina	2 F		
b(iic) Dact. II lower carina		24	
b(iv) Prop. I outer edge	4 D		
b(v) Prop. II outer edge	5		
b(vi) Carp. I upper surface	6 D		
b(vii) Carp. II upper surface	7		
b(ix) Merus I collar	9 D L		

I. Cheliped/walking leg engagements

The under surface of the palm does not bear striae but distally is distinctly granular. These granules continue to the proximal portion of the immovable finger and in Table IV, " granules under palm " and " granules under immovable finger " are not separated.

The thirteen engagements, all producing rasping sounds or shrill croaks, compare with 23 " natural " engagements in males of *O. australiensis.* It should be noted that one engagement is additional to those in *O. australiensis* but is " related " to one in that species, as indicated by italicised type in Table IV.

II. Cheliped/carapace engagements

O. georgei possesses the same structures as in the *O. punctatus* subgroup with a particularly well-developed boss on the anterointernal upper surface of the arm (Fig. 3F) and a similar clear arc of cuticle under the anterolateral teeth. Because of inflexibility of the chelipeds engagements could not be effected but presumably the possibilities of sound production are comparable to those in *O. australiensis* as shown in Tables II and III.

III. Fifth leg/carapace engagements

The carpus of the fifth leg engages:

(a) A conspicuous granular ridge on the posterior branchial portion of the carapace. As this engagement involves the structures with the greatest modifications it seems possible that it is the main sound-producing mechanism. It certainly produced a loud rasping sound on the few occasions when the risk of moving type material was accepted.

(b) The granular posterolateral border of the carapace by a vertical movement producing a scratching sound.

The total number of engagements which produce sounds in males of *O. georgei* is probably of the order of 50–60. No females of this species are known.

The *O. iridescens* Subgroup

This subgroup comprises *O. iridescens* and *O. molleri,* and the most obviously modified structures, presumably for stridulation, are the rasps on the striated pterygostomial regions of the carapace. These are engaged by plectra consisting of projections on the distal portions of the ischia of the chelipeds (Fig. 5).

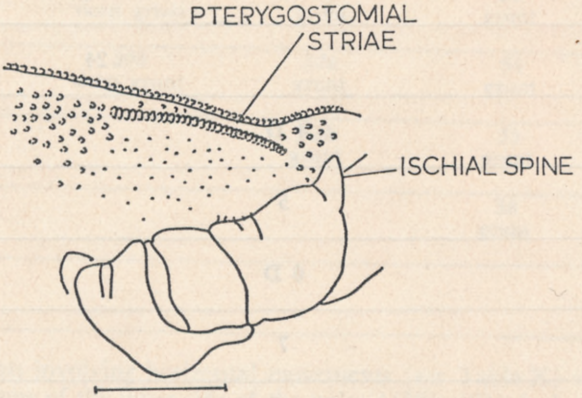


Fig. 5.—*O. iridescens* (Miers). Ventral view of pterygostomial striae and ischium of cheliped. Scale = 5mm.

The dactyls of the second and third walking legs are multiradiate and strongly cornified, particularly in the males. Some additional and some conspicuously loud sounds are produced by engagements involving these structures.

A. Moderate sized males of *O. iridescens*

The main investigations were made upon males with carapace breadths 45.7–49.4mm. Additional comments on larger males, females and juveniles are given later.

I. Cheliped/walking leg engagements

As in *O. georgei,* the under surface of the palm does not bear striae but is granular, the granules continuing to the immovable finger. In Table V, " granules under palm " and " granules under immovable finger " are not separated.

TABLE V.—Male *O. iridescens,* engagements of cheliped by plectra on walking legs, and descriptions of sounds produced. General legend as for male *O. australiensis* in Table I. Engagements in italicised numerals are additional to those in *O. australiensis,* but "related" to those in that species, additional engagements with no counterpart in *O. australiensis* are shown in bold type.

Cheliped rasps Plectra	a(i) + a(ii) Granules under palm and imm. finger	(additional rasp) Granules under arm	a(iiia) Granules outer surface palm (longl. movt.)	a(iiib) Granules outer surface palm (D.V. movt.)
b(ia) Dact. I tip			22 shrill rasping	28 rasping
b(ib) Dact. I upper carina	1 (?U) rasping	**1** faint rasping		
b(ic) Dact. I lower carina	*1* rasping		23 shrill croak	
b(iia) Dact. II tip			*23* F grunt	29 F rasping
b(iib) Dact. II upper carina	2 shrill croak			
b(iic) Dact. II lower carina		**2** grunt	24 dull grunt	
b(iiib) Dact. III upper inner carina	3 L shrill rasping	**3** L shrill croak		
b(iv) Prop. I outer edge	4 L rasping			
b(v) Prop. II outer edge	5 rasping			
b(vi) Carp. I upper surface	6 croak			
b(vii) Carp. II upper surface	7 F croak			
b(ix) Merus I boss	9 F grunt			

The under surface of the arm is also strongly granular, and movements showed that it could act as a rasp. (Re-investigation of males of *O. australiensis* showed similar granulation but none of the engagements which were attempted appeared "natural".) Hence in Table V, there is an additional rasp and bold numerals are used to indicate these additional engagements. There are 17 "natural" engagements compared with 23 in males of *O. australiensis.*

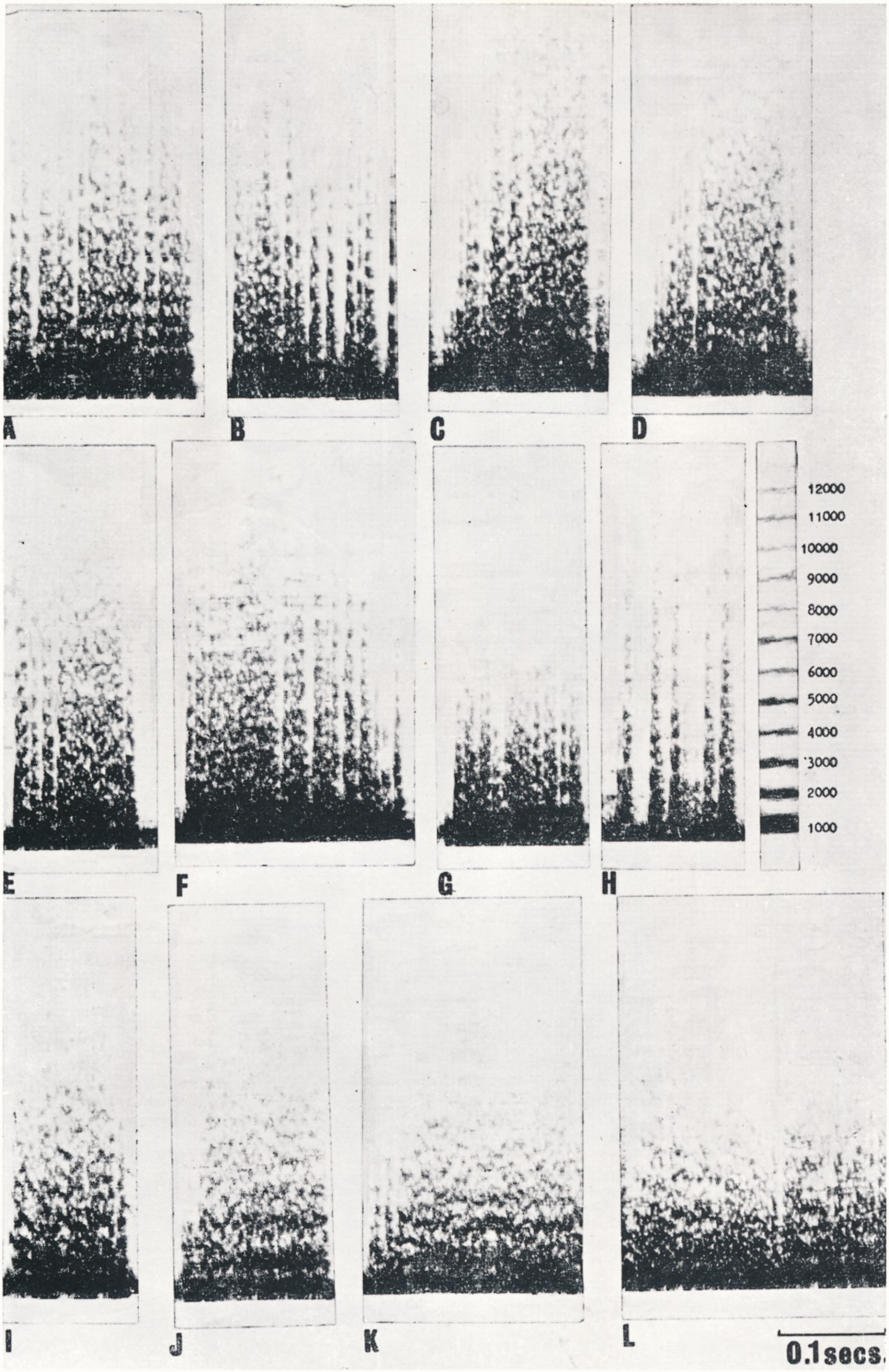
II. Cheliped/carapace engagements

Dorsoventral movements of the chelipeds give engagements additional to those in *O. australiensis,* e.g., inner carina of immovable finger against second and third anterolateral teeth. In Table VI the numbered engagements which are "related" to others in *O. australiensis* are again shown in italicised type.

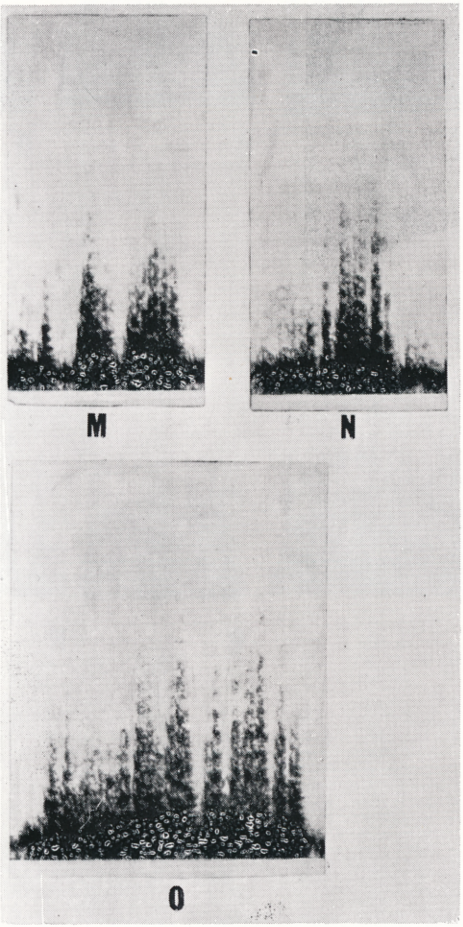
The upper carina on the inside of the palm does not engage as such, but the distal two spines on this carina do engage. The bold numerals used to indicate these

TABLE VI.—Male *O. iridescens,* engagements of carapace structures by dorsoventral movements of cheliped. General legend as for Table II. All sounds produced are grunts, with deep grunts indicated by "D". Engagements in italicised numerals are additional to those in male *O. australiensis,* but are "related" to engagements in that species. Engagments in bold numerals have no obvious counterpart to those in previous tables.

Cheliped Structure / Carapace Structure	a(i) Mov. finger, inner carina	a(ii) Imm. finger, inner carina	(additional) Palm, inner upper surface distal spine	(additional) Palm, inner upper surface subdistal spine	a(vi) Palm, inside, granular distal border	a(vii) Palm, inside, boss on upper border
b(i) Suborb. tooth	30 D	31 D				
b(ii) 1st AL tooth	*30a* D	32 D	**4**			48
b(iii) 2nd AL tooth	*30b* D	*32a* D	**5**			49
b(iv) 3rd AL tooth	*30c* D	*32b* D	**6**	**8**	47	50
b(v) 4th AL tooth			**7**	**9**	*47*	*50*



Sonagraph recordings of engagements in males from three subgroups, involving modified and unmodified structures. Vertical scale frequencies, horizontal scale time. *O. australiensis*. A. Engagement 1, "loud croak", involving two modified structures. B. Engagement 9, "loud deep croak", involving two modified structures. C. Engagement 29, "loud croak", involving unmodified structures. D. Engagement 15, "faint rasping", involving unmodified structures. *O. iridescens*. E. Engagement 17, "loud croaking rasp", involving two modified structures. F. Engagement 4, "loud rasp", involving unmodified structures. G. Engagement 3, "loud shrill croak", involving modified plectrum. H. Engagement 29, "faint rasping", involving unmodified structures. *O. ocellatus*. I. Engagement 16, "loud rasping", involving unmodified structures. J. Engagement 18, "loud croaking rasp", involving two modified structures. K. Engagement 57, "loud rasping", involving two unmodified structures. L. Engagement 6, "faint rasping", involving two unmodified structures.



Sonagraph recordings of separate and sequential engagements in male *O. australiensis*. Scales as in Plate 1. M. Engagement 57, " dull croak ". N. Engagement 65, " croak ". O. Engagement 57 + 65.

replacement and additional engagements continue seriatim from those in Table V. The central carina inside the palm is rounded, and engagements produce no significant sound, while neither the lower carina inside the palm nor the inner wrist spine engage.

There are a total of 20 dorsoventral engagements in males of *O. iridescens* compared with 21 in *O. australiensis.*

TABLE VII.—Male *O. iridescens,* engagements of carapace structures by horizontal movements of chelipeds and descriptions of sounds produced. General legend as for Table II. Loud sounds indicated by " L ", faint by " F ". Engagements in italicised numerals are additional to those in male *O. australiensis,* but are " related " to engagements in that species. Engagements in bold numerals have no obvious counterpart to those in previous tables.

Cheliped Structure Carapace Structure	a(i) Mov. finger inner carina	a(ii) Imm. finger inner carina	a(vii) Palm, inside, boss on upper border	a(ix) Arm, anteroint. upper surface	(additional) Ischial peg
b(i) Suborb. tooth		*53a* F rasping			
b(ii) 1st AL tooth	10 F rasping	53 F rasping			
b(iii) 2nd AL tooth	11 F rasping	*53b* F rasping	**13** croak		
b(iv) 3rd AL tooth	12 F rasping	*53c* F rasping	**14** croak		
b(v) 4th AL tooth			**15** croak		
b(vi) 5th **AL** tooth				69 rasping	
b(vii) cutic. arc				16 L rasping	
(Additional) Pterygostomial striae					**17** L croaking rasp

Horizontal movements of the chelipeds (see Table VII) do not involve engagements of dorsal, central or lower carinae of the inside of the palm or of the inner wrist spine. Instead the boss on the upper side of the palm near the articulation of the movable finger engages certain anterolateral teeth. Bold numerals are given for these additional engagements.

An additional plectrum, one of the special modifications in this subgroup, is the ischial peg. Its engagements have no parallel in the species previously considered, and are again indicated in Table VII in bold type.

There are a total of 13 horizontal engagements in males of *O. iridescens* compared with 16 in *O. australiensis.*

III. Fifth leg engaging carapace structures

The carpus of the fifth leg engages the granular postlateral border of the carapace by a vertical movement to produce a scratching sound; this engagement is similar to one occurring in *O. georgei.*

The total number of engagements producing sounds in moderate-sized males of *O. iridescens* is approximately 50.

B. Large males of *O. iridescens*

Only two larger males were available. In a 62.8mm damaged specimen, the left cheliped had apparently regenerated after damage and is much smaller than the right and many of the listed engagements involving this appendage were not observed. The right (disarticulated) cheliped gave normal sounds compared with medium-sized males except for engagement **16** (anterointernal upper surface arm/cuticular arc) which was feeble. The same applied to both chelipeds of a 112.4mm male with chelipeds disarticulated.

In neither of these specimens was the sound produced by engagement **17** (ischial peg/pterygostomial striae) noticeably louder than in medium-sized males.

C. Females of *O. iridescens*

Engagements appeared identical with those in medium-sized males.

D. Juveniles of *O. iridescens*

These were as with medium-sized males except that the smaller the specimen the fainter and shriller the sounds produced. In addition in small specimens, engagements involving the second anterolateral tooth (viz. *30a, 30b,* **5, 11,** *53,* **13**) become more difficult to effect, because the tooth is less projecting.

E. Comparison of *O. molleri* with *O. iridescens*

In male and female *O. molleri* engagements closely resemble those in *O. iridescens* with the following minor differences:

(1)–(9) fainter, because of smaller granules under palm and immoveable finger (rasp a(i) + a(ii)).

1, 2, 3 louder because granules under arm better developed.

(*32b*), (*47*) *and* (*50*) do not occur because arm longer.

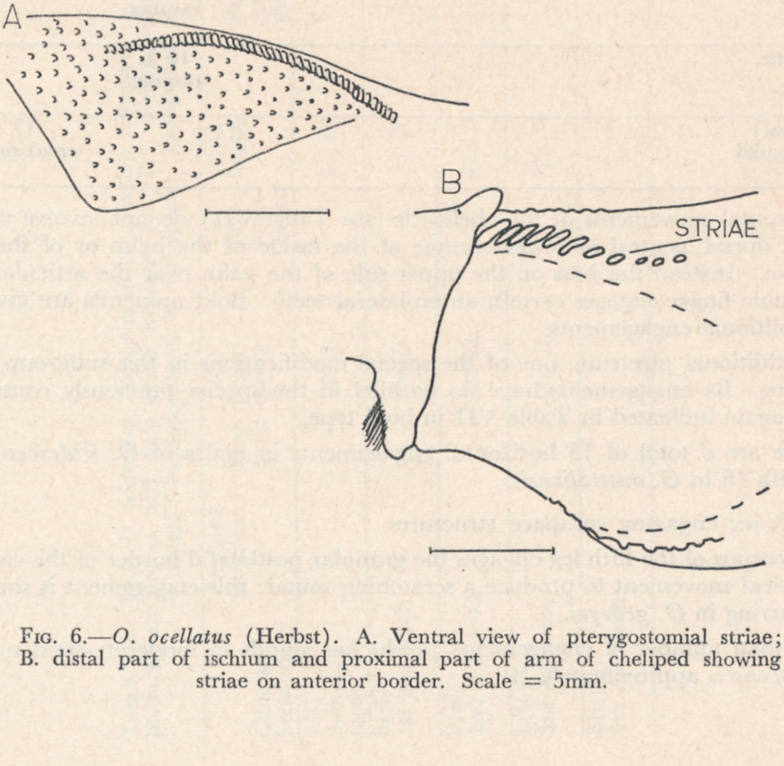


Fig. 6.—*O. ocellatus* (Herbst). A. Ventral view of pterygostomial striae; B. distal part of ischium and proximal part of arm of cheliped showing striae on anterior border. Scale = 5mm.

(69) and 16 impossible to distinguish because the granular cuticular arc (rasp b(vii)) lies close to the fifth anterolateral tooth (rasp b(vi)).

In juveniles of this species, engagement 16 (anterointernal upper surface arm/cuticular arc), is much more strongly engaged than in medium-sized specimens. This is comparable with the difference between medium-sized and large specimens of *O. iridescens*.

THE *O. ocellatus* SUBGROUP

This subgroup comprises *O. ocellatus* and two forms of *O. guadulpensis*. The only obviously modified structures presumably for stridulation are the rasps on the striated pterygostomial regions of the carapace, which are engaged by plectra consisting of striae on the proximal anterior borders of the arms of the chelipeds (Fig. 6A, B).

A. Moderate-sized males of *O. ocellatus*

The main investigations were made upon males of *O. ocellatus* with carapace breadths 53.5 to 66.9mm. Additional comments on larger males, females and juveniles are given later.

I. Cheliped/walking leg engagements

The under surface of the palm bears a narrow band of granules with an almost squamiform arrangement, which extends along the immoveable finger. Another band of granules on the under surface of the arm is comparable with one of the additional

TABLE VIII.—Male *O. ocellatus,* engagements of cheliped rasps by plectra on walking legs. All sounds are raspings, with faint indicated by " F ". " Unnatural " engagements are indicated by " U ". Numbering of rasps, plectra, and engagements as in previous tables.

	Cheliped rasps	
Plectra	a(i) + a(ii) granules under palm and imm. finger	Granules under arm
b(ib) Dact. I upper carina	1	
b(ic) Dact. I lower carina		1
b(iib) Dact. II upper carina	2	
b(iic) Dact. II lower carina		2
b(iiib) Dact. III upper carina	3 U	3
b(iv) Prop. I outer edge	4	
b(v) Prop. II outer edge	5	
b(vi) Carp. I upper surface	6 F	
b(vii) Carp. II upper surface	7 F	
b(ix) Merus I boss	9 F	

rasps in *O. iridescens*. These rasps are engaged by most of the usual plectra as listed in Table VIII. The outer surface of the palm is not granular and so no engagements of this surface are listed. There are only 10 " natural " engagements of which three are so feeble as to have doubtful stridulatory significance.

II. Cheliped/carapace engagements

Engagements involving dorsoventral movements of the chelipeds are given in Table IX, in which, as compared with Table II (*O. australiensis*) and Table VI (*O. iridescens*), the smaller number of listed cheliped structures, and hence of engagements will be noted. The absence of carinae on the inside of the palm eliminates engagements (37)–(47). The relatively lengthy arm eliminates (41)–(43) and (52), (53).

The total number is 15.

TABLE IX.—Male *O. ocellatus,* engagements of carapace structures by dorsoventral movements of chelipeds. Numbering of rasps, plectra, and engagements as in previous tables.

Cheliped Structures Carapace Structures	a(i) Mov. finger, inner carina	a(ii) Imm. finger, inner carina	a(iii) Palm, inside upper carina	a(vii) Palm, inside, boss on upper border
b(i) Suborb. tooth	30 deep grunt	31 grunt	*33* click	
b(ii) 1st AL tooth	*30a* deep grunt	32 grunt	33 grunt	48 click or croak
b(iii) 2nd AL tooth	*30b* deep grunt	*32a* grunt	34 grunt	49 click or croak
b(iv) 3rd AL tooth		*32b* grunt	35 grunt	50 click or croak
b(v) 4th AL tooth			36 grunt	
b(vi) 5th AL tooth				

Engagements involving horizontal movements (see Table X) exclude the central and lower carinae of the inner side of the palm ((58)–(61) inclusive) and the inner wrist spine ((62)–(65) inclusive).

An additional engagement involves the specially modified structures in this species viz. the striae on the anterior border of the arm with the pterygostomial striae. This engagement **18**, produces the loudest noise of all engagements in this species, and has been mentioned previously by Hansen (1921), Balss (1921), Rathbun (1930) and Guinot-Dumortier and Dumortier (1960).

Engagements **19** and **20** involve cheliped and carapace structures previously listed, but are additional engagements, not possible in the other species. Although the engagements of the upper surface of the arm with the third, fourth and fifth anterolateral teeth and with the cuticular arc, are separately listed ((*69a*), (*69b*), (69), **16**), they are extremely difficult to engage separately and individually.

The total number of engagements is 20, but of these three are so faint as to have doubtful stridulatory significance.

B. Large males of *O. ocellatus*

Two specimens, with carapace breadths 85.4 and 87.0mm were available.

TABLE X.—Male *O. ocellatus,* engagements of carapace structures, by horizontal movements of chelipeds. Loud sounds are indicated by " L ", faint sounds by " F ". Numbering of engagements is as in previous tables, with additional engagements 18, 19 and 20.

Cheliped Structure Carapace Structure	a(i) Mov. finger inner carina	a(ii) Imm. finger, inner carina	a(iii) Palm, inside, upper carina and distal spine	a(vii) Palm, inside, boss on upper border	a(ix) Arm, anteroint. upper surface	(additional) Arm, striae on anterior border
b(i) Suborb. tooth	19 rasping	*53a* rasping				
b(ii) 1st AL tooth	10 rasping	53 rasping	*54* rasping	20 click		
b(iii) 2nd AL tooth	11 rasping	*53b* F rasping	54 rasping	13 click		
b(iv) 3rd AL tooth	12 F rasping		55 rasping	14 click	*69a* rasping	
b(v) 4th AL tooth			56 F rasping		*69b* rasping	
b(vi) 5th AL tooth					69 rasping	
b(vii) Cutic. arc			57 L rasping		16 L rasping	
(Additional) Pterygostomial striae						18 L croaking rasp

Differences compared with the medium-sized males were:

(1) In the 85.4mm male, the granules under the palm and arm are rounded, presumably due to wear. The engagements listed in Table VIII produced at most very feeble sounds in this specimen. In the other unworn specimen " normal " sounds were produced.

(2) In both specimens, the inner carina of the movable finger engages dorsoventrally with the third anterolateral tooth to give an additional engagement (*30c*). There is a similar horizontal engagement (*53c*), which does not occur in medium-sized males of *O. ocellatus,* but which is the same as one occurring in males of *O. iridescens.*

(3) As in *O. iridescens,* the anterior border of the arm engages fewer anterolateral teeth in large males than in medium-sized ones. Thus engagements (69), (*69a*) and (*69b*) do not occur.

Overall in *O. ocellatus* as in *O. iridescens* there are fewer sound-producing engagements in large males than in medium-sized ones.

C. Females of *O. ocellatus*

Engagements resemble those of medium-sized males, excepting that in Table VIII, engagements **1** and **2** are performed with the upper carinae of their respective dactyls, not the lower ones.

D. Juveniles of *O. ocellatus*

Engagements generally resemble those in females (allowing for more feeble and high-pitched sounds) although the following do not occur: (*32b*), (*33a*), (56), and **12**. Because there is no obvious boss on the inside of the arm, the following also do not occur: **13, 14, 20.**

Summarising: in *O. ocellatus* the total number of engagements is of the order of 35 in large males, 40 in smaller males and females, and 32 in juveniles. In a worn specimen of a large male, some 10 engagements produced virtually no sound, leaving 25.

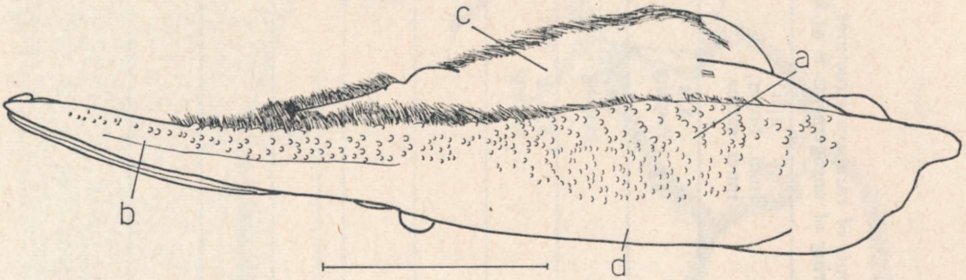


FIG. 7.—*O. guadulpensis* (Saussure) form a. Ventral surface of hand and immoveable finger of right cheliped; (a) under surface of palm, (b) immovable finger, (c) inner and (d) outer surfaces of palm. Scale = 10mm.

E. Comparison of *O. guadulpensis* with *O. ocellatus*

In *O. guadulpensis* engagements are very similar to those in *O. ocellatus* with the following exceptions:

(1)–(9) louder than in *O. ocellatus* because the granules under the palm are better developed (Fig. 7).

3 is unnatural, and (*32a*), (*32b*) and **12** do not occur.

16, an apparently important engagement in *O. ocellatus* does not occur in *O. guadulpensis.* This is because the pterygostomial striae are so salient that the more distal portion of the upper border of the arm cannot engage the cuticular arc.

Three additional engagements of the suborbital tooth (b(i)) by chelipeds occur. These are: dorsoventral movement involving boss on palm (a(vii)); horizontal movement involving dorsal carina and distal spine inside palm (a(iii)); and boss on upper distal border of palm (a(vii)). For reference purposes these are listed as (*48a*), **21** and **22**, respectively.

Three engagements which occur in medium-sized males of *O. ocellatus* do not occur in male *O. guadulpensis*. These are the same three not occurring in large *O. ocellatus*, viz. (69), (*69a*) and (*69b*).

In female *O. guadulpensis* the above three engagements did occur.

No juveniles were available for study.

Summarising: in *O. guadulpensis* the total number of engagements is again of the order of 35 in large males (carapace breadths 73.0–82.5mm) and medium-sized males (carapace breadths 55.5–64.5mm). In females there are approximately 38 engagements.

DISCUSSION

The results have shown that the number of engagements of pairs of structures which seem anatomically capable of sound production in different species of *Ovalipes* ranges from 59 in males of *O. australiensis* to 35 in large males of *O. ocellatus*.

These numbers appear excessive from many points of view. Busnel (1963), noting that the number of sound signals which make up the repertory in a species increases as one goes higher up the animal kingdom, quotes Tembrock (1957) with 36 signals in the fox as the maximum known number apart from man. In invertebrates older work on the honey bee (Martin, 1880) gave 26 signals, but in more recent work (Hansson, 1945) smaller numbers are given (10–12).

If each of the engagements in a given species produced a different kind of sound, the multiplicity of engagements would be more understandable. Taking *O. australiensis* as the best studied example, only a few obviously different sounds are produced, which have been described as " croak ", " dull croak ", " deep croak ", and " rasping ". Examination of Sonagraph records revealed little more differentiation than was apparent by listening alone. It permitted the expected distinction between sounds involving a short pulse-train when only a short series of projections was engaged (Pl. 2M, 2N), and those involving a long pulse-train where a long row of striae or granules was involved (Pl. 1A, 1B). (The term " pulse-train " is here used as defined by Broughton, 1963.) It also confirmed the distinctions between " deep " sounds in which lower frequencies preponderate (Pl. 2), and shriller sounds in which there is an appreciable high frequency component (Pl. 1E, 1F). In some cases distinct harmonics were evident in the Sonagraph records (Pl. 1A), but in most cases virtually all frequencies in the audible range were represented at approximately equal intensities, allowing for attenuation which was probably instrumental (Pl. 1C, 1F). These sounds, aptly described as " white noise ", are known from other crustaceans (see Hazlett and Winn, 1962a, b; Fish, 1964; Tavolga, 1965), and all gave very similar Sonagraph records. The use of these records was valuable in showing the considerable variations which could be induced by altering the pressure exerted on the engaging surfaces, and the speed of movement. This made distinctions between many of the " white noises " virtually impossible. Examination of Sonagraph recordings revealed one common factor, again expected. All the sounds met Fring's (1964, p. 157) requirement for effective acoustic signalling. In his words they are " . . . sharply structured, full of rapid attack and decay periods (transients) ".

The difficulty in distinguishing many of the sounds by ear or from recordings was in some cases paralleled by difficulties in effecting individual engagements. Particularly in cases where the suborbital and anterolateral teeth were engaged by either dorsoventral or horizontal movements of the cheliped the " normal " tendency was to engage all teeth in a single movement, and precise positioning was required to effect the separate engagements. It is almost certain that movements by the animal would produce many practically simultaneous engagements by dorsoventral movements and sequential ones by horizontal movements. This would greatly reduce the number of effective engagements, and would mean that many of the noises which are indistinguishable on an auditory basis, do in fact, merge during their production. In a living animal one could expect fewer, louder, more prolonged and acoustically more complex sounds than those produced by the single engagements. (See Pl. 2.) There still remain an embarrassingly large number of sound producing methods.

A minority of these involve structures which show obvious modifications and these modifications are different in each of the subgroups. Thus in the *O. punctatus* subgroup in both sexes there are rasps composed of striae on the under surface of the palm of the cheliped, while in males the only obvious plectra are modifications of the dactyl and merus of the first walking leg. In *O. georgei* there is a granulated ridge on the dorsal surface of the carapace and a cornified carina on the carpus of the swimming leg. The dactyl of the first leg is modified as in the *O. punctatus* subgroup, but there is not a correspondingly modified rasp. In the *O. iridescens* subgroup the striated pterygostomial region is engaged by an ischial peg, while in the *O. ocellatus* subgroup pterygostomial striae are engaged by short striae on the upper borders of the arms. It is evident that the occurrence of structures modified for sound production is a generic feature, but this is difficult to reconcile with the fact that the structures showing modifications are so different. Previously (Stephenson and Rees, 1968) it was suggested that the genus had evolved from a form with an inherent tendency to stridulate.

The present results offer an alternative explanation. Several of the engagements are common to all species of the genus, and also to both sexes (where these were available for study). The precise number depends upon whether two adjacent areas —under the palm and under the immoveable finger—are considered separate (as they are in the *O. punctatus* subgroup) or a unit. If the latter, there are 14 common engagements as follows:

(a) Rasps of granules or striae under the palm and immoveable finger engaged by plectra on the four most distal joints of the walking legs, and particularly those of the first leg. These engagements have been tabulated as 1 (including *1*), 2, 4, 5, 6, 7, and 9.

(b) Suborbital and first anterolateral teeth engaged by the inner surfaces of the fingers during dorsoventral movement of the chelipeds. These engagements tabulated as 30 (including *30a*), 31 and 32, would normally be combined almost simultaneously.

(c) First to third anterolateral teeth engaged by a boss on the inner side of the palm during dorsoventral movement of the chelipeds. Engagements 48, 49, and 50 are involved; again these would be combined simultaneously.

(d) Fifth anterolateral tooth engaged by horizontal movement of the upper surface of the arm—engagement 69.

It is now postulated that the ancestral *Ovalipes* possessed the above methods of potential sound production, and that many of them were actually employed.

In the *O. punctatus* subgroup some of these ancestral methods have become augmented by special morphological developments. Thus in males engagements 1 and 9 involve both modified rasps and modified plectra, while further engagements which produce noises involve modified rasps but relatively unmodified plectra (engagements 2, 4, 5, 6, 7, 10 and 11) or, modified plectra but relatively unmodified rasps (engagements 12, 19, 20, 26, and 27). Several of the sounds which are produced when only a single modified structure is involved are apparently as loud as those involving two modified structures (e.g., 2, 10, 12, 19 and 26) and it is difficult to believe that they do not produce sounds in living animals.

This is supported by study of *O. georgei,* which has the dactyl and merus of the first walking leg of the male modified in a manner comparable to the species of the *O. punctatus* subgroup, but has no correspondingly modified rasps. Either the dactyls in the two subgroups are not modified for stridulation, or *O. georgei* can in this instance produce functional sounds from unmodified rasps. The latter is the much more likely alternative, particularly since at least one conspicuously loud sound can be produced (engagement 9).

In the *O. iridescens* subgroup the second and third walking legs are modified, being multiradiate and, in males, strongly cornified. Again there are no obviously modified rasps, and again the production of loud noises in certain cases (engagements 3 and 3) strongly suggests that the modifications are functional for sound production. While in this species there are some engagements additional to the common generic pattern, their relationships to it are obvious.

In both the *O. iridescens* and *O. ocellatus* subgroups there is a conspicuously modified rasp comprising the striae of the pterygostomial region, but in each subgroup a different plectrum is moved horizontally across it. The simplest way to account for the evolutionary development of these structures would be to assume that a horizontal movement of the chelipeds across the anterior ventral surface of the carapace produced minor noises, which have been augmented and replaced by those involving the special modifications. On this basis the cuticular arc would be the probable stationary structure, and would correspond with the "*pars stridens* sous-orbitaire" of Guinot-Dumortier and Dumortier (1960) although in a barely modified form. In different species of the two subgroups this is engaged by various structures and gives three different engagements, viz., 57, 65, and **16**. The suggestion of replacement of one engagement by another is supported by comparison of the two very closely related species in the *O. ocellatus* subgroup. In *O. ocellatus* engagement **16** produces a loud noise, but in *O. guadulpensis* the pterygostomial striae are too salient to permit the engagement to be effected.

The most obvious modifications in *O. georgei* are the granular ridges on the dorsal surface of the carapace which are engaged by the cornified carpus of the swimming legs. There is nothing equivalent in other species of the genus, and the nearest counterpart in the crabs appears to be in the genera *Potamon* and *Dotilla* (see Guinot-Dumortier and Dumortier, 1960).

Possible functions of animal sounds which have been suggested include sexual behaviour (attraction, and identification of mates, courtship and competition), "family" behaviour (between young and parents and individual recognition), community behaviour (group activity, territory marking, alarm calls, and food notification and guidance) and sound ranging (Busnel, 1963). Guinot-Dumortier and Dumortier (1960), use a different basis for primary grouping and distinguish between sounds mostly concerned with the same species and those mostly concerned with other species. The former would include sexual attraction, advertisement to the opposite sex, menace towards the same sex, territory advertisement, collective grouping signals, and information signals such as warnings of predators. The latter, which are all evidently intended to intimidate other species, may also act as warning signals to individuals of the same species.

In most cases where stridulatory structures have been described in crustaceans, sounds have not been heard, but are presumed to be produced (Guinot-Dumortier and Dumortier, 1960; Dumortier, 1963a). In still fewer cases have the significance of the sounds been suggested or established. Of these, intimidation or warning sounds are known from several groups involving such crab genera as *Acanthocarpus* (Rathbun, 1937); *Calappa* (Fish, 1964); *Matuta* (Alcock, 1896, 1902; also unpublished personal observations); *Menippe* (Crane, 1947); *Ocypode* (Alcock, 1902; Crane, 1941; Guinot-Dumortier and Dumortier, 1960; also unpublished personal observations). Other crustaceans producing intimidation sounds include palinurids (Moulton, 1957; Fish, 1964), alpheids (Verrill, 1908; Votz, 1938; Johnson, 1943; Johnson, Everest and Young, 1947; Pope, 1949; Moulton, 1957; Nicol, 1960; Cohen and Dijkgraff, 1961; Haslett and Winn, 1962a; Fish, 1964); and in special circumstances *Gonodactylus* (see Haslett and Winn, 1962a, but also Dumortier, 1963). Territorial advertisement or sexual menace apparently occurs in a few cases such as *Uca* (Dembowski, 1925; Green, 1961; Altevogt, 1959; von Hagen, 1962) probably in *Ocypode* (Alcock, 1902; Lankester, 1909) and possibly in palinurids (Dijkgraff, 1955; Linberg, 1955). It has been effectively demonstrated in alpheids by Haslett and Winn (1962a). Maintaining collective grouping is involved in some cases such as palinurids (Moulton, 1957; Green, 1961; Fish, 1964), *Dotilla* (Guinot-Dumortier and Dumortier, 1960) and *Uca* (Burkenroad, 1947). Sexual attraction is involved in *Uca* (Burkenroad, 1947; Altevogt, 1959; von Hagen, 1961, 1962; Salmon and Stout, 1962; Salmon, 1965, 1967), and possibly in *Metaplax, Ilyoplax* and one *Sesarma* species (Tweedie, 1954).

The structures modified for stridulation are better developed in males than in females in the *O. punctatus* and the *O. iridescens* subgroups (no females are available in *O. georgei*). It seems that production of the attendant sounds by males is a secondary sexual characteristic, but whether this works at the level of male/male or male/female is unknown. The fact that females have considerable potential vocality suggests that sound communication may also be involved in collective grouping. Small differences occur between the details of the modified structures in individuals of a species, and this suggests a possible method of recognition of individuals within the group.

Unfortunately little data exists upon whether or not species of *Ovalipes* do live gregariously. There is a suggestion of this in the " irregularity " of data upon catches in most of these species as recorded in Stephenson and Rees (1968). Local data upon *O. australiensis* are illustrative. For many years before 1965 only isolated records were obtained, and the vast bulk of Queensland data comes from two trawled catches. Intensive enquiries have failed to reveal later specimens from the same areas and these are still urgently required for aquarium studies. Wear (personal communication) has made the most valuable observations to date upon sociality in *Ovalipes* by noting the regular occurrence of groups of females of *O. catharus* in the Wellington district. They occur at night, in numbers of three to nine, spaced around the perimeter of shallow circular or cresent-shaped depressions up to 18in diameter, just below low tide level.

In each of the subgroups differences between the obviously modified stridulatory structures are of diagnostic importance. It seems most probable that the different qualities of the sounds produced would be important to the species themselves. Whether they act primarily in maintaining the cohesion of groups or to reinforce specific boundaries is conjectural. Two facts are possibly significant. The first is in the Australasian region three species occur apparently in similar habitats, and with one case of overlapping distribution, viz., *O. australiensis* and *O. catharus* in Victoria and South Australia (Stephenson and Rees, 1968). The second fact is that the species are extremely similar, with the main distinctions in " non-adaptive " features which might serve as species indicators. These are pigmentation and the stridulatory structures.

If sound production is to be significant to individuals of a species, they must be able to receive vibrational stimuli. There is now a great wealth of evidence that the otocysts (statocysts) and many of the cutaneous hairs of crustaceans act as vibration receptors (see reviews by Green, 1961; Cohen and Dijkgraff, 1961; and Frings, 1964).

In the *O. iridescens* subgroup there are unique structures which may act as special vibration receptors, and if so these species would really " hear " in the sense of Cohen and Dijkgraff (1961). The structures are two extremely thin cuticular areas on the branchiocardiac portions of the carapace (Stephenson and Rees, 1968). It seems probable that, for conspicuously thin cuticle to occur where thick cuticle would be expected, some special functional service must be performed. The citing of the areas does not suggest resonating structures concerned with sound transmission and it is unfortunate that the chances of obtaining live specimens of either species (*O. iridescens* and *O. molleri*) are remote.

ACKNOWLEDGMENTS

I am deeply grateful to the Directors and Curators of Crustacea in the following Museums for most kindly placing most or all of their *Ovalipes* collections at my disposal. The Australian Museum, Sydney; Canterbury Museum, Christchurch; Dominion Museum, Wellington; Macleay Museum, University of Sydney; Museum of Comparative Zoology, Harvard; National Museum, Melbourne; Queensland Museum, Brisbane; Queen Victoria Museum, Launceston; South African Museum, Natal; South Australian Museum, Adelaide; United States National Museum, Smithsonian Institution, Washington; Universitetets Zoologiske Museum, Copenhagen; University of North Carolina, Institute of Fisheries Research, Morehead City; Western Australian Museum, Perth; Zoologisch Museum, Amsterdam. Special thanks are due to Drs. L. B. Holthuis, R. B. Manning, and J. C. Yaldwyn.

Thanks are due to Miss May Rees for assistance with figures and Sonagraph recordings and to Mr R. Maloney for clerical assistance. The Research Grants Committee of the University of Queensland provided financial assistance.

LITERATURE CITED

ALCOCK, A., 1896. Materials for a carcinological fauna of India. 2. The Brachyura Oxystomata. *J. Asiat. Soc. Beng.* 65(2): 134–296.

——— 1902. " A naturalist in Indian seas." London. XXIV + 328 pp.

ALTEVOGT, R. Ökologische und ethologische Studien an Europas einziger Winkerkrabbe *Uca tangeri* Eydoux. *Z. Morph. Ökol. Tiere* 48: 123–46.

BALSS, H., 1921. Über Stridulationsorgane bei Dekapoden Crustaceen. *Naturw. Wschr.* 20: 697–701.

BARNARD, K. H., 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Ann. S. Afr. Mus.* 38: 1–824.

BROUGHTON, W. B., 1963. Method in bio-acoustic terminology. *In* Busnel, R. G. (Ed.) " Acoustic behaviour of animals." Elsevier Publishing Co., Amsterdam: 3–4.

BURKENROAD, M. D., 1947. Production of sound by the fiddler crab, *Uca pugilator* Bosc, with remarks on its nocturnal and mating behaviour. *Ecology* 28(4): 458–62.

BUSNEL, R. G., 1963. On certain aspects of animal acoustic signals. *In* Busnel, R. G. (Ed.) " Acoustic behaviour of animals." Elsevier Publishing Co., Amsterdam: 69–111.

COHEN, M. J.; DIJKGRAFF, S., 1961. Mechanoreception. *In* Waterman, T. H. (Ed.) " The physiology of Crustacea." Academic Press, New York, Vol. 2: 65–108.

CRANE, JOCELYNE, 1941. Eastern Pacific Expeditions of the New York Zoological Society XXVI. Crabs of the genus *Uca* from the West Coast of Central America. *Zoologica* 26(3): 145–208.

——— 1947. Ibid. XXXVIII. Intertidal brachygnathous crabs from the West Coast of Tropical America. *Zoologica* 32(2): 69–95.

DEMBROWSKI, J., 1925. On the " speech " of fiddler crab *Uca pugilator*. *Pr. Inst. M. Nenk.* 3(48): 1–7.

DIJKGRAFF, S., 1955. Lauterzeugund und Schallwahrnehmung bei der Languste (*Palinurus vulgaris*). *Experientia* 11: 330–1.

DUMORTIER, B., 1963. Morphology of sound emission apparatus in Arthropoda. *In* Busnel, R. G. (Ed.) "Acoustic behaviour of animals." Elsevier Publishing Co., Amsterdam: 277–345.

FISH, M. P., 1964. Biological sources of sustained ambient noise. *In* Tavologa, W. N. (Ed.) "Marine bio-acoustics." Pergamon Press, Oxford: 175–94.

FRINGS, H., 1964. Problems and prospects in research on marine invertebrate sound production and reception. *In* Tavolga, W. N. (Ed.) "Marine bio-acoustics." Pergamon Press, Oxford: 155–73.

GREEN, J., 1961. "A biology of Crustacea." London: XV + 180 pp.

GUINOT-DUMORTIER, DANIELE; DUMORTIER, B., 1960. La stridulation chez les crabes. *Crustaceana* 1(2): 117–55.

HAGEN, H. O. VON, 1961. Nächtliche Aktevat von *Uca tangeri* in Südspanien. *Naturwissenschaften* 48: 140.

——— 1962. Freilandstudien zur Sexual und Fortpflanzungsbiologie von *Uca tangeri* in Andalusien. *Z. Morph. Ökol. Tiere* 51: 611–725.

HANSEN, H. I., 1921. "Studies on Arthropoda." Gyldenalske Boghandel, Copenhagen: 80 pp.

HANSSON, A., 1945. Lauterzeugung und Lautauffassungsvermögen der Bienen. *Opusc. ent. Suppl.* VI: 1–124.

HASLETT, B. A.; WINN, H. E., 1962a. Sound production and associated behaviour of Bermuda crustaceans (*Panulirus, Gonodactylus, Alpheus,* and *Synalpheus*). *Crustaceana* 4: 25–38.

——— 1962b. Characteristics of sound produced by the lobster, *Justinia longimanus. Ecology* 43: 741–2.

JOHNSON, M. W., 1943. Underwater sounds of biological origin. O S R D, Sec. 6.1—Sr. 30–412, No. 1270. (Quoted from Fish, M. P., 1964.)

JOHNSON, M. W.; EVEREST, F. A.; YOUNG, R. W., 1947. The role of snapping shrimp (*Crangon* and *Synalpheus*) in the production of underwater noise in the sea. *Biol. Bull.* 93: 122–38.

KRAUSS, F., 1843. Die Südafrikanischen Crustaceen. Eine Zusammenstellung aller bekannten Malacostraca, Bemerkungen über deren Lebenweise und geographische Verbreitung, nebst Beschreibung und Abbildung mehrerer neuen Arten: 1–68. Publisher: E. Schweizerbart.

LANKESTER, E. W., 1909. "A treatise on Zoology. Pt. VII Appendiculata (Third Fascicle: Crustacea)." London: viii + 346 pp.

LINDBURG, R. G., 1955. Growth, population dynamics, and field behaviour in the spiny lobster *Palinurus interruptus* (Randall). *Univ. Calif. Pub. Zool.* 59: 157–247.

MARTIN, D. R., 1880. "Les abeilles, Enchiridion apicole ou Manuel d' Apiculture rationnelle." *Ed* Gounouilhon. Bordeaux (quoted from Busnel, R. G., 1963).

MOULTON, J. M., 1957. Sound production in the spiny lobster *Panulirus argus* (Latreille). *Biol. Bull.* 113: 286–95.

NICOL, J. A. C., 1960. "The biology of marine animals." Pitman, New York. xi + 717 pp.

POPE, ELIZABETH C., 1949. *Crangon*—the noisy pistol prawn. *Aust. Mus. Mag.* 9: 326–8.

RATHBUN, MARY J., 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atecyclidae, Cancridae, and Xanthidae. *Bull. U.S. natn. Mus.* 152: XVI + 609 pp.

——— 1937. The oxystomatous and allied crabs of America. *Bull. U.S. natn. Mus.* 166: VI + 272 pp.

SALMON, M., 1965. Waving display and sound production in the courtship behaviour of *Uca pugilator*, with comparisons to *U. minax* and *U. pugnax*. *Zoologica* 50: 123–49.

——— 1967. Coastal distribution, display and sound production by Florida fiddler crabs (Genus *Uca*). *Anim. Behav.* 15: 449–59.

SALMON, M.; STOUT, J. F., 1962. Sexual discrimination and sound production in *Uca pugilator* Bosc. *Zoologica* 47: 15–20.

STEPHENSON, W.; REES, MAY, 1968. A revision of the genus *Ovalipes* Rathbun, 1898 (Crustacea, Decapoda, Portunidae). *Rec. Aust. Mus.* 27(11): 213–61.

TAVOLGA, W. N., 1965. Review of marine bio-acoustics. State of the art: 1964. Tech. Rept. Navtradevcen 1212–1. U.S. Naval Training Center, Port Washington, N.Y. 100 pp.

TEMBROCK, G., 1957. Zur Ethologie des Rotfuchses (*Vulpes vulpes* L.), unter besonderer Berücksichtigung der Fortpflanzung. *Zool. Gart. Lpz.* 23: 289–532.

TWEEDIE, M. W. F., 1954. Notes on graphsoid crabs from the Raffles Museum. Nos. 3, 4 and 5. *Bull. Raffles Mus.* 25: 118–28.

VERRILL, A. E., 1908. Decapod Crustacea of Bermuda. *Trans. Conn. Acad. Sci.* 13: 60–123.

VOLZ, P., 1938. Studien über das "Knallen" der Alpheiden, nach Untersuchungen an *Alpheus dentipes* Guérin und *Synalpheus laevimanus* (Heller). *Z. Morph. Ökol Tiere* 34: 272–316.

PROFESSOR W. STEPHENSON,
Department of Zoology,
University of Queensland,
Brisbane, Queensland.