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## BURROWING AND BURYING BY THE CRAB *MACROPHTHALMUS HIRTIPES*

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### ABSTRACT

*Macrophthalmus hirtipes* (Jacquinot, 1853) excavates burrows under water in soft, muddy sand that remains waterlogged at low tide. The crabs are immersed for at least 4 h in every tide. The burrows are usually single, blind-ending, slightly curved passages; their openings do not appear to be deliberately closed by the crabs. Excavation is effected by using one set of walking legs as a scoop while the other set provides sideways traction.

Burrow openings are readily obscured by water movement, so that apparent burrow density does not give a true indication of the number of crabs in an area, but only indicates how many have been active recently; the true density may be found by sieving.

The burrowing activity of *M. hirtipes* is compared with that of other ocyppodid crabs, and the functions of burrows are discussed. A distinction is made between excavating a burrow and rapid burying, because the two behaviours are very different, and must involve different adaptations and selection pressures.

## INTRODUCTION

*Macrophthalmus* (= *Hemiplax*) *hirtipes* (Jacquinot, 1853) is an ocypodid crab of the subfamily Macrophthalminae, and was transferred from *Hemiplax* to *Macrophthalmus* by Barnes (1967).

Beer (1959) described the fighting and defensive behaviour of *Macrophthalmus hirtipes* and the grapsid crab *Helice crassa* (Dana). He found that both species occupied burrows, but said: "On no occasion did I see *Hemiplax hirtipes* constructing a burrow, and I suspect that the crabs of this species occupy burrows built by the other". This seemed unusual because the ability to dig burrows is widespread among ocypodids, and has been reported in the genera *Macrophthalmus* and *Heloecius* (Griffin 1965, 1968), *Uca* (Pearse 1912, Crane 1941a, Altevogt 1955), *Ocyopode* (Cott 1929, Crane 1941b, Tweedie 1950, Barrass 1963, George & Knott 1965, Hughes 1966), *Dotilla* (Tweedie 1950), and *Scopimera* (Tweedie 1950, Fielder 1970). The present work is hence an investigation of burrowing and associated activity in *M. hirtipes*.

## METHODS

Field observations were made at Papanui Inlet, Otago Peninsula (45° 50' 45" S, 170° 40' 42" E). The study area was a gently sloping expanse of muddy sand to seaward of the junction between Papanui Inlet Road and Sheppard Road. On 27 June 1973, the tide rose 1.9 m above datum (annual range 1.6–2.2 m), and the zone occupied by *M. hirtipes* was immersed for 4.0–5.5 h.

Excavation of burrows was observed in the field during November and December 1970; February, May, and October 1971; and February and April 1973. I took notes while standing close to the burrowing crabs, some of which were caught and placed on the substrate surface, in shallow water, so that their 'rapid burying' method could also be noted. Additional observations were made on captive animals housed in a 40×25×18-cm laboratory aquarium containing a 5-cm layer of substrate from the field study area covered by 1–2 cm of sea water.

On 7 April 1973 (water temperature 19°C) a 70-m transect was laid down the shore, from a point 3 m to seaward of the sea wall bounding the road to a point beyond the zone of burrows; there were no burrow openings between the sea wall and the start of the transect. The number of burrow openings in a 0.25-m<sup>2</sup> quadrat was counted at 2-m intervals down the transect. The tide took approximately 0.75 h to rise and 1.2 h to fall along the transect; the height difference along the transect (23 cm) indicated a mean slope of 0.2°. On 27 June 1973 (water temperature 4°C) another transect was laid, parallel to the first but 2 m to the west. Burrows were counted as before; there were approximately eight burrows per m<sup>2</sup> in the 3 m of muddy sand between the sea wall and the beginning of the transect this time.

The substrate was too soft and wet to investigate burrows with a trowel, so the middle finger of the right hand was used to feel the shape of the passages; this method was suitable for burrows with an opening larger than 1 cm across. A ruler was used to measure the width of the burrow opening, the path of excavated material, and the length and depth of the burrow. The angle of descent near the entrance was found by placing a 5-cm probe into the burrow opening, and reading the angle from a pointer attached to the probe; the pointer passed across the face of a protractor held with the base parallel to the substrate surface. On 25 February 1973 a sample of 25 burrows and their occupants was measured. This sample was chosen by walking across the crab zone and stopping every five paces to investigate the nearest burrow with an opening larger than 1 cm. Additional observations were made at other times on the shape and angle of the burrows.

On 7 April 1973, 50 crabs were sexed and measured to determine the sex ratio, size variation, and distribution in the study area. Measurements, to the nearest mm, were made across the carapace at the level of the second pair of lateral spines, and along the median axis. The sample was chosen in the same way as before.

The permanence of the burrows was studied by plotting their positions in the aquarium every morning for 9 days with three crabs 'in residence'; and by mapping burrows in three permanent 25×25-cm quadrats pegged out at Papanui Inlet, at 5 m, 31 m, and 41 m from the sea wall. The position of each burrow entrance and its associated excavated material was mapped on graph paper on 7 April 1973, and again 1 day and 8 days later. On the last visit some shallow depressions in the quadrats were investigated manually, and some proved to be associated with partly occluded burrows. Therefore, on 26 May 1973 (water temperature 7°C), burrow openings were counted in four separate 25×25-cm quadrats, placed in an irregular line across the transect, 13 m from the sea wall. Then the substrate below these four areas was removed to a depth of 10 cm by pushing a 25×25-cm metal quadrat box into the substrate and carefully removing the box with a spade. The total 0.025 m<sup>3</sup> of substrate was then washed through a colander with 3-mm circular holes. The crabs so obtained were measured and sexed, except for those < 0.8 cm in carapace width, which showed no obvious sex differences and were classed as juveniles.

## RESULTS

The sexes were equally represented in the sample of 50 *M. hirtipes* examined on 7 April 1973, and there were equal proportions of males and females in the upper and lower halves of the 'crab zone' of the transect. No females were in berry. Most individuals were small; the mean carapace widths were 1.17 cm (S.D. 0.3 cm) for males, and 1.11 cm (S.D. 0.25 cm) for females. There were a few large crabs in the population with a carapace width up to 3.5 cm, and smaller ones (< 0.8 cm carapace width) which were excluded because of the sampling method used. These small crabs made up 36% of the sample obtained by sieving, however.

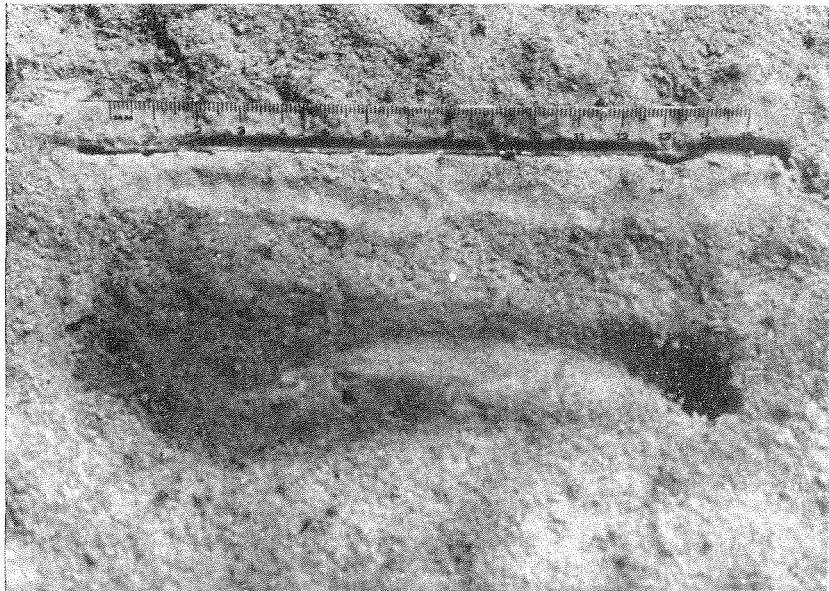


FIG. 1—*Macrophthalmus hirtipes* burrow, at Papanui Inlet, Otago Peninsula, 4 July 1971; recently excavated, dark, subsurface material is conspicuous against the lighter surface material.

Active crabs were usually seen feeding and burrowing under shallow water as the tide fell, but they may also be active at other times when the water is too deep to see them. During low tide the crabs were generally out of sight beneath the substrate, but on two warm days (20 November 1970, air temperature 22°C; 6 April 1973, air temperature 17°C) they were feeding in the open after the tide fell. These crabs frequently visited burrows to crouch at the entrance in the water and pump it around their bodies.

The crabs began to burrow by digging the tips of their right or left walking legs into the substrate. The set of legs used for digging was folded into a scoop, and the other set was used to drag the crab along the surface. The body was held low over the excavated material, and sometimes movement was assisted by the leading cheliped and the fourth trailing pereopod. The shallow depression first formed was enlarged into a tunnel; the darker excavated material was deposited at the end of a tongue- or fan-shaped path extending on a line from the burrow (Fig. 1). The crabs deposited the material by simply standing erect, or by pushing it through the opening between the chelipeds. The excavated material was too loose to form a distinct heap, but some crabs patted it down with alternate movements of the chelipeds. A series of photographs taken in the laboratory on 13 November 1970 shows a crab removing material from its burrow, which is in substrate material brought from the field study area (Fig. 2).

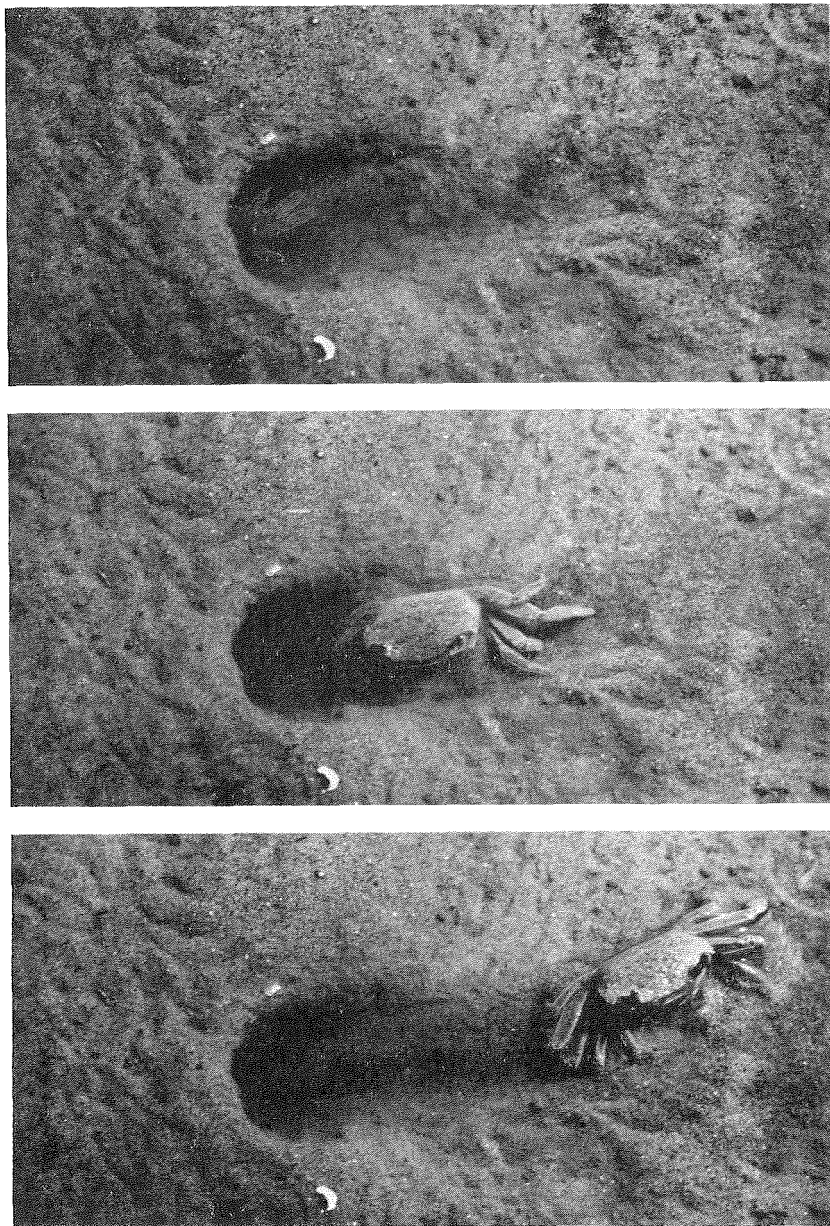


FIG. 2.—Burrowing activity of *Macrophthalmus hirtipes* held in a laboratory tank, 13 November 1970 (crab and sediment from Papanui Inlet, Otago Peninsula): *Upper*—the leading (left) legs of a crab are visible at the entrance to its burrow; *Middle*—the crab emerges, using its left legs for locomotion and its right legs for carrying the excavated material; *Lower*—the crab is about to release the excavated sandy material, visible under the “scoop” formed by its right legs.

TABLE 1—Dimensions of 25 *Macrophthalmus hirtipes* and their burrows, Papanui Inlet, Otago Peninsula, 25 February 1973

DIMENSION	MEAN	S.D.
CRABS	(cm)	(cm)
Carapace width (across 2nd spines)	1.4	0.4
Carapace length (median axis)	0.9	0.3
BURROWS		
Length of path of excavated substrate	14.5	4.2
Width of burrow entrance	2.6	1.2
Length of burrow	17.3	4.8
Maximum depth below substrate surface	6.0	1.5
Angle of descent at entrance	(degrees from horizontal) 35.5	6.4

If a crab was alarmed while away from a burrow, on soft ground under water, then it usually buried itself. The sequence of burying movements was quite different from that of burrowing. First the crab probed the surface with the tips of its legs and chelae, then pushed its body forwards and downwards into the substrate. Next, the body was rocked backwards and upwards, and sand was shovelled away from the underside with the chelipeds. This sequence was repeated until the crab was hidden, with only the eyestalks protruding above the substrate.

#### BURROWS

Each burrow consisted of a single passage descending from the surface at an angle of  $36 \pm 8.5^\circ$  S.D. ( $n = 100$ ). The passage felt well formed beneath the surface, and did not collapse when walked over by a human observer. The slope usually decreased along the passage, which levelled out to become parallel to the surface in the larger burrows. Most burrows (94%,  $n=50$ ) had blind endings, the remaining 6% sloped up to the surface again, and had two openings. Twenty-five percent were straight, 45% were slightly curved to the left or right ( $<90^\circ$ ) and a further 24% were more strongly curved ( $>90^\circ$ ). Each burrow seemed to be the same width throughout, and there was no evidence that *Macrophthalmus hirtipes* deliberately closed the entrance to its burrow. The dimensions of 25 occupied burrows are shown in Table 1.

Burrows were often conspicuous in the muddy sand, which remained waterlogged at low tide, and were more plentiful in the upper 35 m of the transect than the lower 35 m, where the substrate was firmer and contained more sand.

When three small crabs were kept in the laboratory aquarium, 21 burrow openings were recorded over a 9-day period. Sixty-two percent of these openings lasted for less than a day, 28.5% were in the same position for 2 consecutive days, and 9.5% were in the same position for

TABLE 2—Permanence of *Macrophthalmus hirtipes* burrows in three 25×25-cm fixed quadrats, Papanui Inlet, Otago Peninsula

	DATE (April 1973)		
	7	8	15
Total number of burrow openings recorded	36	35	15
Number of burrow openings in same position as previous visit	..	4 (11%)	0
Number of burrow openings within 5 cm of a previously recorded burrow	..	14 (39%)	4 (11%)
Number of burrow openings previously recorded but no longer present	..	18 (50%)	31 (89%)
		36	35
Number of burrow openings not previously recorded	..	16/35(59%)	11/15(73%)

3 days. Burrow openings were also transient in the field; only 11% of a sample of 36 burrows were in the same position 1 day later, and there were none in the same position 1 week later. (Table 2).

On 26 May 1973, sieving confirmed the suspicion that there could be more crabs in an area than was suggested by the number of burrows apparent at the surface. For example, there was only one burrow opening at the surface of 0.25 m<sup>2</sup> of substrate, but 22 crabs in the underlying 10 cm (0.025 m<sup>3</sup>) of sediment. The open burrow was made by a large male of 3.3-cm carapace width. In this sample, 45% of the crabs were male, 18% female, and 36% juvenile.

#### DISCUSSION

The distribution of *Macrophthalmus hirtipes* at Papanui Inlet was similar to that found by Stephenson (1970) at Porirua Harbour, near Wellington, where the crabs were most common in areas immersed for more than 6 h during each flow and ebb of the tide. In the present study, crabs of this species were most plentiful in areas immersed for 4.0–5.5 h. This variation may be due to local conditions, and particularly to the availability of suitable substrate. Stephenson also found ovigerous females concentrated near low-water mark in early June. There were no ovigerous females at Papanui in the sample examined on 7 April 1973, and the sexes were evenly distributed over the habitat at that time. Beer (1959) found *M. hirtipes* more concentrated near the lower tidal limit than *Helice crassa*. He considered it possible for *M. hirtipes* to occupy *H. crassa* burrows, because the two species sometimes occupied the same areas. However, the burrows of the two species differ in several ways: *H. crassa* usually burrows in firm sand, which remains in distinct piles outside the entrance, and the sand is sometimes used to plug the burrow.



Most ocypodid crabs which have been studied live higher up the intertidal zone than *M. hirtipes*, and are most active when their part of the beach is exposed (Pearse 1912, Cott 1929, Crane 1941a & b, Tweedie 1950, Altevogt 1955, Barrass 1963, George & Knott 1965, Hughes 1966, Fielder 1970). *M. hirtipes* seems unusual because it is most active under water; even its close relative *Macrophthalmus latifrons* is most active when exposed (Griffin 1968). Beer (1959) found *M. hirtipes* active when it was immersed during the rise and fall of the tide, but on two warm days during the present study I noted active crabs after the tide had receded. Warmth probably stimulates more crabs to activity, and indeed there seemed to be more surface signs of burrows on warm days than on cold days. There were more burrows visible on 7 April 1973, when the water temperature was 19°C, than on 27 June 1973 when it was 4°C (Fig. 3). Pearse (1912), Crane (1943), George & Knott (1965) and Griffin (1968) have commented on daily and seasonal differences in appearance of the burrows of other ocypodids.

*Macrophthalmus hirtipes* excavates a burrow by using one set of legs to carry the excavated material and by moving sideways, in the same way as most other ocypodids. The exceptions are *Scopimera inflata*, which pushes a pellet of sand ahead of the legs from the burrow, then carries it with the chelipeds (Fielder 1970); *Ocypode ceratophthalmus*, which carries two loads of sand at a time (Cott 1929); and *Dotilla mictyroides*, which can lie sideways in wet sand and spin around by running backwards, so that it becomes enclosed in a dome-shaped chamber (Tweedie 1950).

Descriptions of the burrows of ocypodids and accounts of burrowing are rather sporadic in the literature, and are more common in the earlier work reviewed by Schöne (1961). Recent work has concentrated on visual and acoustic communication between crabs.

The burrow of *M. hirtipes* seems to resemble that of its close relative *M. latifrons*, which descends obliquely at a shallow angle and has a single opening (rarely two or three) which is not deliberately closed with substrate material (Griffin 1965, 1968). Many ocypodids close their burrow openings, particularly in advance of the rising tide; possible exceptions are some upper-shore *Ocypode* (Cott 1929, George & Knott 1965). Most ocypodids live higher up the shore than *M. hirtipes* and *M. latifrons*, and are consequently exposed for longer periods. Typically their burrows go down steeply to the water table, and some end in a chamber or horizontal passage; depth ranges are 10–20 cm for *Dotilla* (Tweedie 1950), 16–75 cm for *Uca* (Pearse 1912, Altevogt 1955), and 15–130 cm for *Ocypode* (Cott 1929, Crane 1941b, Barrass 1963, George & Knott 1965, Hughes 1966). Crane (1941a) notes that *Uca* spp. “. . . on yielding mud had the shallowest holes, and large species high up on relatively dry muddy sand beaches, or along the banks of drying streams, dug deepest.” Depth seems dependent on substrate and on exposure time.

*Macrophthalmus hirtipes* has a shallow burrow, with an oblique entrance and without a distinct pile of excavated material. However, its

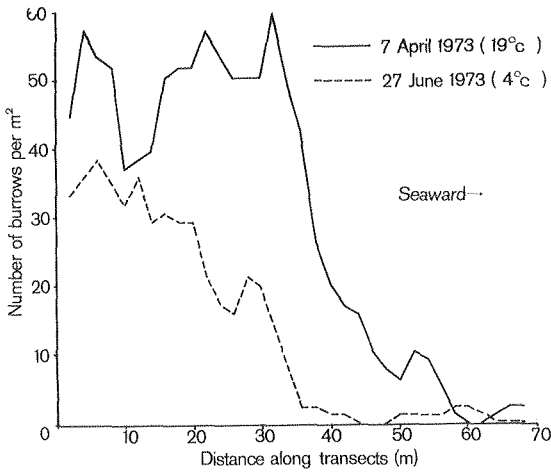


FIG. 3.—Distribution density of *Macrophthalmus hirtipes* burrows along adjacent transects, Papanui Inlet, Otago Peninsula, April and June 1973. Water temperatures are given with the dates. Curves smoothed by taking "sliding averages" for successive groups of three units.

habitat is waterlogged (thus obviating the need for deep burrows), and the surface of the substrate is too loose for vertical burrowing. The substrate is distinctly stratified; the light-coloured surface material is loose and easily disturbed, but the dark subsurface material is quite cohesive and difficult to sieve. When the water is disturbed by ripples the openings of the burrows begin to erode, and the dark excavated material is soon mixed with the surface material; even human footprints are completely obscured after 1 day. This suggests that the appearance of burrows at the surface depends on water movements and on how many of the crabs have been active recently, which would explain why apparent burrow density varies with time, and why there may be more crabs in an area than might be inferred by counting burrow openings.

The most important function of the burrow for *Macrophthalmus hirtipes* and other crabs is protection from predators. In those species which burrow further up the beach, the burrow also protects from extremes of temperature and desiccation. Burrows occasionally serve this function for *M. hirtipes* when crabs are active in the open on warm days. Miller (1961) stressed that the burrow is an important source of water for respiration and feeding in species, such as *Uca pugnax*, which filter small organic material from the sand or mud. He suggests that those species which use the burrow as a source of water are the most territorial, and defend one burrow and its surroundings for some time. Fielder (1970) found this relationship between marked territorial behaviour and use of the burrow for water in *Scopimera inflata*, and cites the work of Ono, who found that three species of upper-intertidal ocypodids

which used their burrows for water also defended fixed territories, whereas three lower-intertidal species used their burrows for shelter only, and were less attached to one place. This theory is consistent with the behaviour of *M. hirtipes*, as the burrow is not usually an important source of water and this crab does not defend fixed territories. Beer (1959) marked individual *M. hirtipes*, and found that they wandered over large areas when feeding, and that the males defended any burrow near at hand; Beer did not observe fighting by females. This evidence suggests that fighting between males may serve a sexual function rather than for territorial defence. In some species of *Uca* the burrow is used for mating, and Crane (1957) has suggested that this has evolved where there is a strong association between the burrow, territory, and courtship. Even the excavated material may serve a sexual function: Linsenmair (1967) showed that the sand pyramids of male *Ocypode saratan* attract the females to the mating sites, and Crane (1941a) found that only the courting males of certain *Uca* spp. build shelters over their burrows.

This and further studies on the ecology and behaviour of *Macrophthalmus hirtipes* may help to shed light on its taxonomic affinities. Barnes (1970) has remarked on the great similarity between *M. hirtipes* and certain sesarmine grapsids such as *Metaplex* and *Helice*. He considers that these modifications are convergent and associated with breathing and burrowing. Garstang (1897) suggested that the antero-lateral denticulations of sand-burrowing crabs function as a coarse sieve and are a modification associated with respiration beneath the surface. Lateral teeth are well developed in *M. hirtipes* and, with certain rows and patches of hair, may well prevent sand and mud from clogging the gill passages. However, this interpretation is complicated by the fact that the males and females have different distributions of hairs.

Barnes (1967) considers that the streamlined carapace and strong pereopods of *Macrophthalmus hirtipes* are adaptations for more efficient burrowing. He argues that a crab that can burrow beneath the surface of the substratum fastest at the approach of a predator is likely to be at a selective advantage. (This behaviour associated with rapid disappearance has been called burying in the present paper; it seems useful to distinguish it from excavating a burrow, which involves different movements and timing.) Garstang (1897) and Fielder (1970) have also used burrowing to cover both behaviours, although Garstang differentiates between burrows which are "permanent subterranean tunnels" and "temporary excavations, the sand, mud or gravel being in actual contact with their bodies when they are embedded". Burrowing and burying are both antipredator devices but it seems useful to distinguish them, especially when considering the relationships between morphology, ecology, behaviour and evolution. It may be that the resemblance between *M. hirtipes* and some grapsid crabs is based on a true relationship and is not due to convergent evolution. Wear (1968) says "the zoea larva of *Hemiplex hirtipes* is very similar to those of the genera *Cyclograpsus*, *Helice* and *Hemigrapsus*" and he believes that it is possible that the

family Ocypodidae is not a natural grouping. In this group it is difficult to distinguish homology from analogy and the larvae may show the true affinities, which are masked in the adults by common ecological adaptations.

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