Journal of the Royal Society of Western Australia, 91: 175–198, 2008

Ichnological studies of the Western Australian soldier crab *Mictyris occidentalis* Unno 2008: correlations of field and aquarium observations

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Manuscript received January 2008; accepted May 2008

Abstract

The Western Australian soldier crab, *Mictyris occidentalis* Unno, spends most of its life cycle in-faunal in sandy tidal environments, and produces up to 16 different types of ichnological products: back-filled burrows, cavities, circular pustular structures, clots, craters, dactyl prints, discard pellets, eruption structures, excavation pellets, exit holes, hollow shafts, linear pustular structures, mat pustular structures, rosettes, scrape marks, and surface-parallel tunnels (with their floors and roofs). These are the result of the crabs working the sediment at different stages of their life cycle, whether or not they emerge, and their working of the sediment at different times of the tide. Soldier crabs have three phases to their ichnological behaviour corresponding to their life stages. Newly arrived recruits and juvenile crabs are cryptic, and develop sediment surfaces strewn with clots. Crabs in the early to middle stage of their life cycle also are cryptic, and develop subsurface cavities during high water, and subsurface cavities and sediment surfaces covered in pustular structures during low water. Adult crabs exhibit cryptic and emergent phases, and develop the most complex range of ichnological products – during high water, they form subsurface cavities, and during low water they develop cavities in the subsurface as well as sediment surfaces covered in pustular structures, exit holes, dactyl prints (sometimes), discard pellets, and rosettes. Mapping of crab activity and the boundaries of their workings at various scales shows there was a variability in crab behaviour as to whether adult crabs emerged or not, whether working of the sediment surface took place, where in the population emergences or subsurface workings took place, and in the subsurface whether the crabs were active or inactive. Similar variability in crab behaviour was observed in the aquarium. Our study showed a direct correlation between field and aquarium ichnological patterns, and the aquarium observations provided explanation of the field results.

Keywords: soldier crab, *Mictyris occidentalis* Unno, aquarium, ichnology

Introduction

The soldier crab *Mictyris occidentalis* Unno occurs extensively along the coast of Western Australia between Shark Bay and the Broome region (Fig. 1). The prevailing perception is that this crab, in common with other soldier crabs belonging to *Mictyris* elsewhere in the world, forms "armies" emergent above the sediment surface (Cowels 1915, Cameron 1966, Yamguchi 1976) and, indeed, while there is a part of the life cycle of *M. occidentalis* where it does present itself for part of the low tide as vast numbers of individuals at the surface, in fact the species spends most of its life in-faunal (cryptic) in the substrate. However, whether in-faunal, or emergent for short periods, this crab leaves a plethora of biogenic sedimentary structures as evidence of its complex behaviour that is useful information in the construction of its life stages and various activities it undertakes, and in interpreting fossil evidence of the species.

Ichnology is the study of animal traces, particularly those of fossil organisms (Frey 1975; Ekdale *et al.* 1984; Bates & Jackson 1987). Students of modern sedimentary environments began to apply the term "ichnology", originally defined for fossil traces, to modern traces, and as a result, the distinction between modern and fossil traces became blurred. More recently, the discipline of ichnology has been formally subdivided into neoichnology (the study of modern traces [Garrison *et al.* 2007]), and palaeoichnology (the study of fossil traces). We use the term "ichnology" in the sense that it is the study of traces, and that it is an umbrella term to encompass both "neoichnology" and "palaeoichnology". However, throughout the paper, while the terms "ichnology" and "ichnological" are used, the reader should be aware that products of the modern soldier crab fall into the realm of neoichnology.

Ichnology has long been an important discipline in the tool kit of zoology. The identification and description of species-specific mammal and reptile burrows, scats and other traces, for instance, have assisted in the surrogate identification of the presence of species, and to interpret their behaviour (Triggs 2004; Southgate 2005; Thompson & Thompson 2007a, 2007b). Similarly, burrows and other traces of invertebrate fauna have been studied as part of their ecology, autoecology, sedimentology and biogeochemistry, especially in tidal marine environments

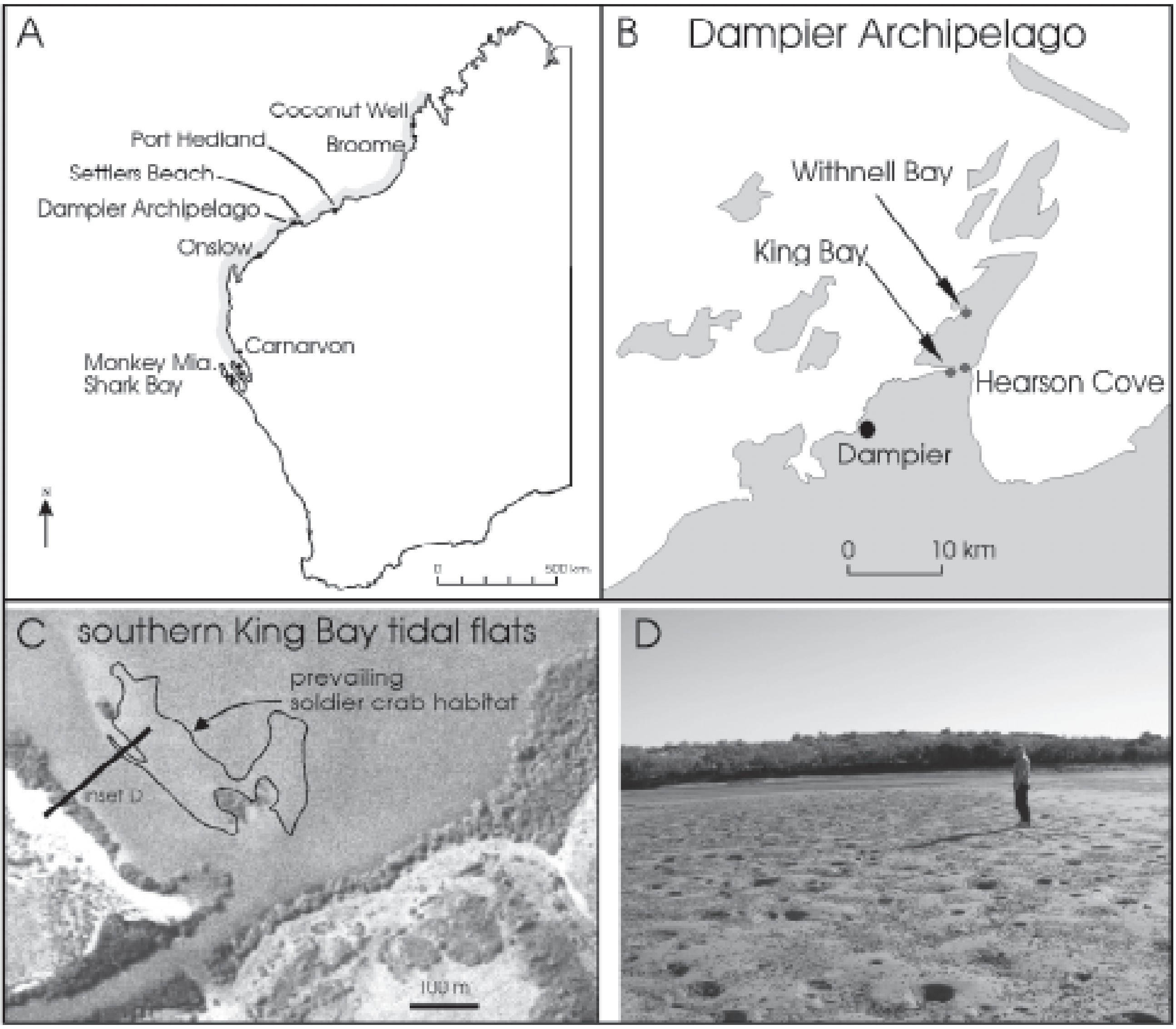

Figure 1. Location of study sites. A. General location of soldier crab *M. occidentalis* along the Western Australian coast (grey line), and location of study sites. Note that the occurrence of *M. occidentalis* will not be continuous along the coast but related to available habitat. B. Location of study sites in the Dampier Archipelago region. C. Location of soldier crab habitat in southern King Bay, the Dampier Archipelago. D. Surface of habitat in southern King Bay showing stingray-pocked surface.

(Frey 1975; Reineck & Singh 1980; Carney 1981; Ekdale *et al*. 1984). All such ichnological studies, whether of vertebrate or invertebrate fauna, have provided invaluable insights into the ecology, autoecology, and animal-habitat relationships for those species investigated (McCall & Tevesz 1982), and the more detail that has been garnered, the more insights have flowed from such work.

To our knowledge, to date, no studies have comprehensively described the ichnology of *Mictyris*, *i.e.*, all of its burrowing, foraging, and trace-producing activities. If they have any ichnological component in their scope, most studies have focused on only one aspect of soldier crab ichnology (such as its burrow structure; Cowles 1915; Takeda & Murai 2004), or have briefly described ichnological products as background information to autoecological studies (Quinn 1983; Rossi & Chapman 2003) and ecological impact studies (Dittmann 1996; Sadao 2001; Sadao 2002; Webb & Eyre 2004). We suggest that ichnological features in their own right are important aspects of the soldier crab life history and autoecology. A study of soldier crab ichnological features can assist researchers in a number of ways, *e.g.*, to determine the presence of soldier crabs even though they may not be emerging during a particular (settlement or early to middle) stage of their life cycle, to determine what is the predominant life stage of the population at the time of observation (qualitatively determining the relative abundance of juveniles to adults), and to determine the extent of patchy crab foraging activity on the tidal flat, and hence information about crab behaviour. Ichnology and ichnological products also form the basic temporal and sedimentologic framework to designing further studies on soldier crabs in regards to crab-and-sediment relationships, soldier crab predator associations, relationships and responses, soldier crab accessing and processing of food, nutrient recycling, and geobiochemistry, amongst others.

In this project, the need for laboratory/aquarium studies grew from field observations and experiments where it became difficult to determine and explain the apparent lateral movement of soldier crab populations suggested by the patchy patterns of activity of the populations, and the various patterns of the biogenic traces. The aquarium studies added to and corroborated field observations, allowing proper interpretation of the latter since the crabs in the aquarium directly and unequivocally replicated ichnological patterns observed in the field. Also, the aquarium studies provided insights into soldier crab behaviour not readily apparent on the tidal flat, such as behaviour during times of inundation at high tide. The results of the field and ichnological aquarium studies additionally provided data to interpret the former presence of the soldier crabs from their traces. Such information is useful in interpreting Pleistocene tidal flat rocks, and (earlier) Holocene beach rocks, thus pointing to the presence of *Mictyris* populations in the past.

Previous work on crab behaviour in aquaria has been undertaken for other species, *e.g.*, those of *Dotilla*, *Uca*, and *Portunus* (Palmer 1973; Avent 1975; Crane 1975; Phillips & Cannon 1978; Furota 1996; Takeda *et al*. 1996; Nakasone & Murai 1998; Pope 2000; Rodriguez *et al*. 2000; Yamaguchi 2001; Arshad *et al*. 2006; Koukkari & Sothern 2006), and they have been useful in documenting biorhythms of particular species with respect to tidal cycles and useful to studies of other behavioural aspects. Some studies have been undertaken on species of *Mictyris* in the aquarium, but these have tended to focus on physiological aspects of a given species (Kelemec 1979; Quinn 1986; Maitland & Maitland 1992; Ahsanullah & Ying 1993; Henry 1994), or in the laboratory/aquarium to document some particular burrowing behaviour (Cowles 1915; Takeda & Murai 2004). To date, no studies have involved the ichnology of *Mictyris* in the detail of the aquarium study presented here.

We also draw attention to the work of Knox & Miller (1985) who similarly used aquarium studies to correlate with and interpret field observations, and showed that the one organism can produce a range of ichnological products (though the variability of the ichnological products in their study was not due to variable behaviour, as is the case in our study, but to the organism interacting with a variable sediment). Using gastropods, Knox & Miller (1985) investigated the environmental controls on the gastropods' trails and showed that different morphology could be generated under different environmental conditions. In the aquaria, with sediment of various grainsizes, composition, and consolidation, they found that the one species of gastropod produced trails that varied in depth (of ploughing), cross-sectional shape, and traverse ridging. The authors could relate these laboratory results to tidal flat sub-environments that also varied in sediment properties.

The purpose of this paper is to comparatively describe behaviour and the variety of the ichnological products of *Mictyris occidentalis* in the aquarium and on the tidal flat, and to describe those traces useful to interpreting *M. occidentalis* behaviour and life patterns in the field. The paper begins with description of the behaviour of the crabs on the tidal flat to provide a background setting for the species, and the types of ichnological products that the crab generates, as a baseline for what to expect and what to explain in the aquarium studies.

In this paper, we describe the ichnological patterns of the Western Australian soldier crab in the field and in the aquarium to a level of detail not previously provided for a Western Australian tidal-flat marine organism. This was undertaken because *M. occidentalis* yields a complexity of ichnological products that, in addition to being genus-specific, reflects its ontological stage, and complex behaviour related to the stage of the tide. The results have been invaluable, supplementing studies in the biogeography, ecology, and autoecology of *M. occidentalis* in Western Australia.

Terms and definitions

Since soldier crabs, as a result of their unique behaviour in their subsurface feeding and surface foraging, leave characteristic imprints on the tidal flat as various structures which can later become palaeoichnological traces, it is necessary to define appropriate terms. Some soldier crab-created structures can be related to terms already existing in the general literature, *e.g.*, back-filled burrow, while terms employed for *Mictyris* biogenic structures by other authors are briefly mentioned and if they are not employed here, reasons are given. The terms used in this paper are presented with definitions in Table 1.

Materials and methods

Methods involved a field work component and a laboratory component. Field work was focused on a sandy tidal flat in southern King Bay, Dampier Archipelago, Western Australia (Fig. 1). In order to replicate the natural environment of the soldier crab as near as possible in the aquarium, field work involved description of the natural setting of the soldier crab habitat in terms of sediment type, documentation of the micro-topography, depth to the water table at the habitat, frequency of tidal flooding (inundation), temperature of the water, and density of population. Field work was supplemented by observations and photography of soldier crab ichnological products in the following additional sites in Western Australia: Shark Bay, Onslow, Maitland River Delta, Withnell Bay and Hearson Cove (in the Dampier Archipelago area), Settlers Beach (Cape Lambert area), Port Hedland, Broome, and Coconut Well (north of Broome).

In the field, the subsurface and near-surface crab traces were documented by excavations and planing of the surface. Crab activity in pelletising the surface, or creating a pustular surface was documented by video camera and still photography. Observations were undertaken mostly during the day-time low tide, and 10 night-time low tides. To determine the depth at which the crabs resided in the subsurface, we undertook excavations, as well as coring with 10 cm diameter PVC pipes to 1 m depth (to extract *in situ* sediment with crabs therein), box coring to 30 cm depth, and systematic planing of the surface.

Table 1

Terms and definitions employed in this paper for soldier crab biogenic structures on or in the substrate

Term	Definition in this paper	Previously used terms
back-filled burrow	vertical to horizontal, cylindrical tube generally 10–15 mm diameter, of disturbed sediment; a burrow that has been back-filled with sediment by an in-faunal vagile crab	term already established in the ichnological literature
cavity	small, unattached, equant (up to 2 cm across), to linear (up to 4 cm long), air-filled hole in sediment occupied by soldier crab in the subsurface; air bubble may have a thin layer of geopetal muddy water on the bottom during high tide inundation; size of cavity depends upon size of crab; a specialised type of burrow formed in the subsurface by soldier crabs in all stages of their life cycle	burrow; however, the term "burrow" on its own is too broad to be applied to the range of specialised structures described herein; also the term "burrow" often carries implication that the structures are linearly extended; the term "igloo" has been used for a pellet-roofed air-filled chamber just beneath the sand surface for a species of *Dotilla* (Takeda *et al*. 1996); this term does not convey the notion of the deeper subsurface cavities encountered in this study, and so is not used here
circular pustular structure	elevated (2–10 mm relief), circular area, 1–5 cm in diameter, composed of packed excavation pellets or packed discard pellets (see below for general "pustular structure"); generated by a subsurface crab not laterally mobile, *i.e.*, formed from below in a single place; isolated, individual pustular structure also referred to as "pustule" in this paper	coined in this paper
clot	small (< 3 mm) lump(s) of sand on tidal-flat surface pushed up mainly by a very small juvenile crab (< 3 mm) that is residing in a cavity, or feeding just below the sediment surface; clot size related to crab size	coined in this paper
crater	roughly circular raised ring of sand surrounding a central depression, produced by the circular burrowing motion of a crab	coined in this paper
dactyl print	short, narrow impression in fine sand or mud film on sediment surface made by dactyl of walking leg; several dactyl prints in line comprise a track	coined in this paper
discard pellet	single round ball of sand formed from sand filtered in the buccal cavity; it is placed on the tidal flat surface during the surface feeding activity of the crab, or placed from below from within a surface-parallel tunnel onto/into the surface by the feeding activity and/or excavation from the tunnel; size of the pellet depends on crab size – they range in size from 2–5 mm, but tend to be similar in size for a given age group; a crab with a carapace length of 6 mm will construct a pellet of 2 mm, and a crab of carapace length of 15 mm will construct a pellet of 5 mm	pseudofaecal pellet (Cameron 1966, Quinn 1983): this term is not used in this paper as it describes not what the ichnological product is, but what it resembles
eruption structure	flange or lip of sand surrounding an exit hole	coined in this paper
excavation pellet	single round ball of sand formed by the crab as it excavates sediment usually to form a surface-parallel tunnel; the ball of sand is placed from below onto/into the surface, with other such pellets, to form the roof of the subsurface tunnel; size of the pellet depends on crab size – they range in size from 2–8 mm; generally, the excavation pellet is not as cohesive as a discard pellet	coined in this paper
exit hole	circular opening 5–15 mm in diameter created by a crab exiting the substrate and commencing surface activities; may be on the undisturbed sediment surface or within a pustular structure	coined in this paper
hollow shaft	vertical or inclined tunnel to the surface 20–50 mm long and up to 10 mm diameter generally constructed by adult crabs; may be manifest at the surface by an exit hole or a rosette, or a pustular structure; a specialised type of burrow formed by a crab exiting the sediment	burrow; however, the term "burrow" on its own is too broad to be applied to this specialised soldier crab structure
linear pustular structure	elevated (2–10 mm relief), linear, oblate, to sinuate, to multifurcate area composed of packed discard pellets and excavation pellets (see below for general "pustular structure"); they are 1–3 cm wide and up to 20 cm long; generated by a subsurface crab that is laterally mobile; isolated, individual linear pustular structure also referred to as "linear pustule" in this paper	coined in this paper

Table 1 (cont.)

Term	Definition in this paper	Previously used terms
pustular structure	general term for any elevated (2–10 mm relief), circular, linear, oblate, to sinuate, to multifurcate, or matted area composed of packed discard pellets and excavation pellets; three types are recognised: (1) circular types; (2) linear, oblate, to sinuate, to multifurcate types; and (3) mat types; isolated, individual pustular structure also referred to as "pustule" in this paper	hummock (Quinn 1983; Webb & Eyre 2004); we use the term hummock to describe the macroscale mounds on the tidal-flat surface produced by stingray feeding
mat pustular structure	elevated (2–10 mm relief) area of disturbed sediment composed of coalesced circular, linear, oblate, to sinuate, to multifurcate pustular structures; the mats can range in size from *circa* 20 cm to tens of metres	coined in this paper
rosette	isolated, somewhat circular, raised mound, usually 3–4 cm in diameter, comprising a central plug and an outer ring that has a vague radial structure; formed by crab burrowing into the sediment for re-entry, excavating and disposing of the sand radially as it corkscrews into the sediment	mound (various authors)
scrape mark	short linear scratch in sediment surface where a crab has scraped up sand with its cheliped to pack into the buccal cavity	generally used term for other tidal flat crabs
tunnel	shallow linear, sinuate, to multifurcate surface-parallel structure, 1–4 cm wide; composed of a floor excavated from the underlying sediment, and upper part enclosed by a pustular roof; formed by crab working in the near-surface forming a surface-parallel trough enclosed by a pustular roof	gallery (Webb & Eyre 2004): has connotations of a passage with at least one open side; it is not considered to be appropriate to describe this totally enclosed soldier crab structure
tunnel floor	the basal concavity of a tunnel, excavated from the underlying sediment	coined in this paper
workings	any soldier crab biogenic structures on the sediment surface; so termed because the sediment has been "worked over" by the soldier crab	coined in this paper

For the aquarium observations, a glass aquarium (50 cm x 30 cm by 30 cm deep) with a basal outlet valve was set up, and sediment from the soldier crab habitat at King Bay tidal flat was placed therein to create a sloping surface, with 30 cm depth of sediment at one end of the aquarium and 5 cm at the other end, mimicking the sloping edge of a stingray feeding excavation hollow (Fig. 2). Thirty soldier crabs from the King Bay site were placed in the aquarium, replicating the density of the crabs in the natural environment. The crabs and sand were covered in seawater. The seawater was changed every two days. Sediment in the aquarium was left to oxygenate and deoxygenate with the processes of water exchange, crab burrowing, and crab inactivity, so that effectively the subsurface sand replicated the natural environment of the tidal flat, in contrast to Kelemec (1979) who oxygenated the sand in an aquarium experiment by diffusing oxygen from below.

Four aquarium experiments were conducted. The first was in the field for one week for the purpose of determining whether soldier crabs could survive aquarium conditions and to determine on a preliminary basis their response to aquarium conditions. In the field, the aquarium and its sediment content rested on a sand mound on the tidal flat surface so that it was naturally inundated twice daily by spring tides (at low tide, the water in the aquarium was siphoned off to simulate low tide). The second aquarium experiment was carried out in a laboratory in Perth for 9 months with the aim of observing soldier crab behaviour and documenting biogenic structures by observation, mapping of aquarium walls, and intensive video camera filming and still photography. The third aquarium experiment was carried out in a laboratory for 3 months with the aim of further intensive photography. The last experiment was carried out in a laboratory for 1 month with the purpose of observing bioturbation in layered sediment.

In the first experiment, in the field, the temperature of the water, sediment and air was the same as ambient environmental conditions. In the second experiment, the temperature of the seawater was regulated by a heater, bringing the water temperature to *circa* 25°C. In the third, the entire aquarium system was placed in a temperature-regulated room in which air temperature and water temperature were kept to 28°C. In the fourth, the experiment was conducted during the Perth summer, and the temperature was not regulated. In this way the laboratory aquarium experiments, which ran for a total of 13 months, were conducted over the Perth summer and winter, without winter temperatures affecting the crabs.

Over the time of the experiments, twice daily, and daily for several days every fortnight, seawater was placed in the aquarium for half a day, and then emptied to replicate semi-diurnal spring tides and neap tides. One low tide was simulated during the day-time, and one during the night-time. Every month, to replicate maximum neap tidal conditions (that were documented at the soldier crab habitat in King Bay), the aquarium was left inundated for two days. The water in the aquarium was emptied and replenished either by siphoning, or by basal efflux from the tank through the outlet valve (Fig. 1). With the siphoning or the efflux of water from the aquarium to simulate a low tide, two levels of water were achieved (Fig. 2): 1. the water level was brought down to 5 cm from the base of the

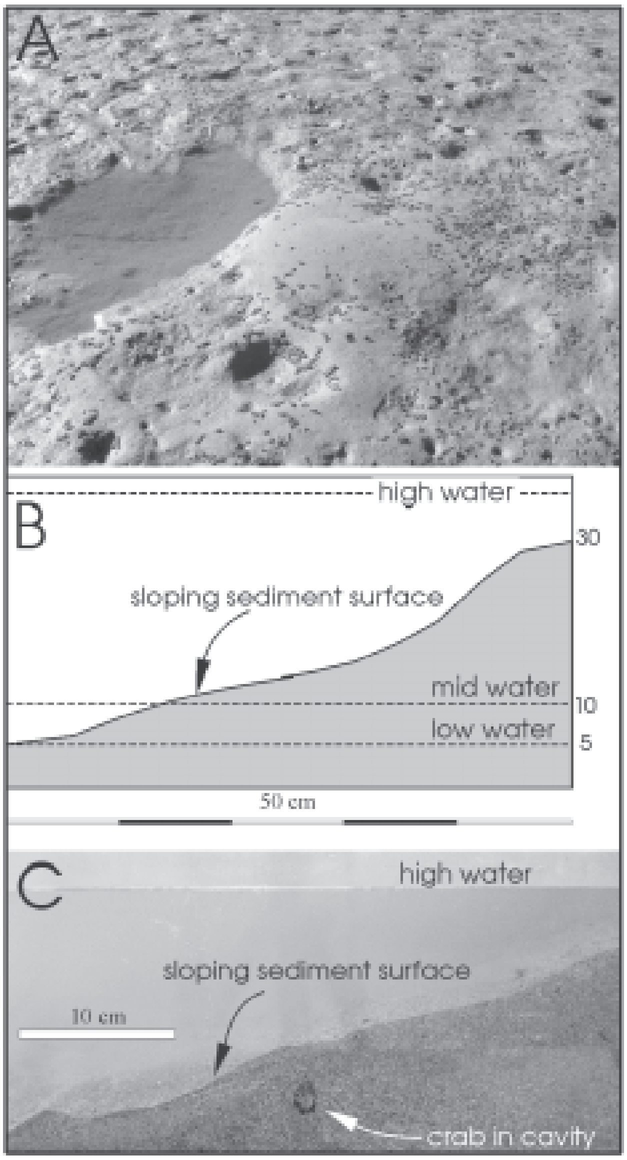

Figure 2. Experimental design. A. Basis for the geometry of the sand in the aquarium – field photograph of a stingray-generated water-filled hollow, with its adjoining mound of sand. B. The three levels of water attained in the aquarium; at high water, all surfaces are flooded; at mid water, simulating a neap tide, the water table is 20 cm below the high point of the sand; at low water, simulating a spring tide, the water table is 20–30 cm below the high point of the sand. C. Portion of the side view of the aquarium at high water, with the sloping sand surface simulating the hollow-to-mound relationship shown in A.

aquarium, with the water table 25 cm from the surface of the sand at the upper slope to simulate maximum spring tide conditions; and 2. the water level was brought down to 10 cm from the base of the aquarium, with the water table 20 cm from the surface of the sand at the upper slope to simulate moderate spring tide conditions. For the latter situation, a pool of water was left at the lower slope of the sand.

Once it became apparent from aquarium observations that the crabs, as a result of their subsurface activities, were producing structures *within* the sediment as well as on the sediment, in the fourth set of aquarium experiments the sand was artificially laminated in order to be able to trace the development of biogenic (bioturbation) structures.

The behaviour of the crabs and the ichnological products of the crabs in the aquarium were documented by video camera, by photography of the walls and surface of the aquarium, and by observation and drawings (directly tracing from aquarium walls onto transparent sheets). Most of the observations were undertaken during day-time low water, but several of the night-time low water periods were also documented. For video camera filming, the camera was set up on a stand and allowed to run continuously for 3 hours. For example, for low water activity, as soon as the water was at its low level, the camera was activated and allowed to run for 3 hours continuously. In this manner, there was a record of the onset of the crab activity and its progression. Filming was undertaken of the surface and of one of the aquarium walls. For high water activity, the camera also was run for 3 hours so that there was a continuous record of crab activity as exposed along the aquarium walls. In total approximately 25 hours of film footage was obtained for later analyses.

Additionally, 50 hours also were logged in directly observing the crabs constructing cavities, maintaining cavities, moving vertically upwards to exit (and creating vertical hollow shafts), spiralling downwards to re-enter the sediment, and creating vertical hollow shafts to progress from the surface to lower depths. This was an important component of the study as there was direct observation of the action and the product undertaken and generated by the crabs, respectively.

This study, in terms of observing and experimenting with the soldier crabs in the field, is based on decades of field work. Commencing in 1980, one of us (VS) visited the King Bay site on a quarterly basis between 1980–1982 and 1985–1988 for 2 consecutive days, and on a monthly basis between 1982 and 1985 for 1 day each month, amounting to *circa* 200 hours of observations and experimentation. Commencing in 1997, both of us visited the King Bay site on a yearly to quarterly basis between 1997 and 2007 for 3–4 days at a time, amounting to 40 man-days (or *circa* 200 hours) of observations and experimentation.

Mapping of crab activity and the boundaries of their workings was undertaken using enlarged high-resolution aerial photographs at a scale of 1:500. At this scale, trees, megaripples, creek lines, other tidal drainage lines, and other tidal landforms and features were evident, and were used as medium-scale landscape markers to provide location and orientation for mapping the outlines of crab workings. Between these medium-scale landmarks, boundaries of the workings were established by direct mapping onto the aerial photographs, supplemented by (metre-length) pacing to the nearest metre.

Mapping at the smallest scale of the increase in workings in quadrats was undertaken by photography. A series of fifteen replicate 25 cm x 25 cm quadrats were randomly spread over the tidal flat surface immediately after the tidal flat surface was exposed, and photographed from time zero on a 15-minute basis for a total of 3 hours. These photographs provided the basis

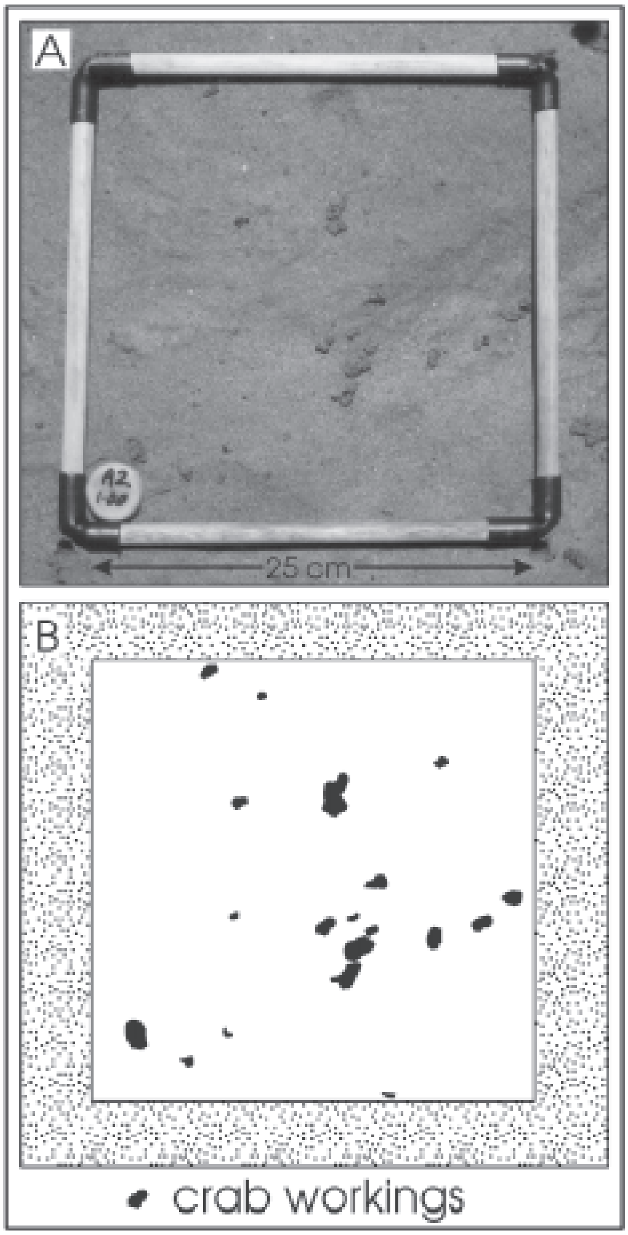

Figure 3. Quadrat (25 cm x 25 cm in size) in the field, with crab workings appearing within the quadrat, and tracing of the workings for use in Figure 5.

for tracing the initiation and progression of the various crab workings such as clots, pustular structures, and rosettes, that appeared on the surface (Fig. 3).

The soldier crab habitat in King Bay, Dampier Archipelago

The soldier crab habitat in southern King Bay is a sandy, mid-tidal to high-tidal flat, specifically a sandy ebb-tidal delta located at the mouth of a tidal creek (Semeniuk *et al.* 1982; Semeniuk & Wurm 1987; and Fig. 1). Occurring between levels of *circa* mean low water neap tide (MLWN) and mean sea level (MSL), it is exposed during all spring tides for several hours, and exposed during most neap tides for a few hours, however, on some neap tides the habitat is not exposed at all. While the habitat receives some low-amplitude waves from the open head of King Bay (Semeniuk & Wurm 1987), the environment is a relatively low-energy site located within the King Bay embayment. In this environment, some mud does accumulate and as such the substrate habitat of the soldier crab is a slightly muddy, fine to medium sand (mean sand grainsize is 125 µm and mud content is *circa* 3%). The sediment has *circa* 0.5% organic matter as detritus.

The surface of the habitat is pocked with 20–50 cm diameter feeding excavations of stingrays, hence in detail the habitat is undulating, composed of a series of pools and low sand mounds (Fig. 1). In general, the water table under the tidal flat on a low spring tide is 10–20 (-30) cm below the surface. Soldier crabs inhabit the undulating sand surface, and more specifically the sand mounds adjoining the pools. Excavations and box cores indicate that the soldier crabs are located in the upper 10–20 cm of sediment surface during low tide periods.

The sediment that underlies the tidal flat where the soldier crab resides is invariably pigmented at shallow depths by iron sulphide. At depths of 10–30 cm and greater, the sediment is medium grey to dark grey. At 0–10 cm, the sediment is medium grey to light grey. The surface layer, < 1 mm thick, is commonly oxidised to light grey or a buff/tan tone. Pellets created by the crabs from the shallow subsurface and surface tend to mirror the pigmented sediment from which they are derived.

Crab workings are commonly reworked by tidal currents and small amplitude waves during spring tides. During neap tides, tidal currents are of smaller magnitude, and crab workings have a higher chance of preservation. We have observed soldier crab workings surviving the previous high-tidal current reworking: the workings are not always distinct, but reduced to a series of rounded lumps. Also, following a high tide, especially during neap tide periods, and depending on the sedimentary budget of suspended mud in the region, there may be a thin film of mud or very fine sand on the sediment surface, the thin film of mud being deposited as a result of lag / settling lag processes (*cf.* Postma 1967; Reineck & Singh 1980); during these times, soldier crab ichnological products stand out in contrast, and dactyl prints and tracks are best preserved.

Field observations

Soldier crabs in the field exhibit a range of trace activities, as determined by direct observation and excavations. Figures 4–6 illustrate a range of structures produced by the soldier crabs from tidal flat settings.

At King Bay, but supplemented by observations elsewhere, soldier crabs spend most of their life cycle as in-fauna in the sandy environment. There are three phases to their ichnological behaviour corresponding to their life stages:

1. newly arrived recruits and juvenile crabs in the early stage of their life cycle – a cryptic phase;
2. crabs in the early to middle stage of their life cycle – a cryptic phase; and
3. crabs in the adult stage – exhibiting cryptic and emergent phases.

Immediately after the ebb tide exposes the surface, the sediment is still very wet and there is an absence of scrape marks and soldier crab dactyl prints, even though there is the opportunity for preservation of such traces because of the thin film of mud on the sediment surface formed by scour lag / settling lag processes. Such mud can preserve surface traces and activities of fauna, *e.g.*, the activities of fish feeding. This indicates that there was no soldier crab surface activity during the high tide.

Crab ichnological activities are described below, focusing on those that occur at low tide. During a low tide, in all cases the crabs begin their activities that are manifest as ichnological products on the surface when the sand is exposed long enough (within one to two hours) for it to drain free of phreatic interstitial water, but is still cohesive with pellicular moisture. This occurs during day-time low tides and night-time low tides.

When a population is composed of newly-arrived recruits (sizes 1–2 mm) and/or individuals in the early (juvenile) stage of their life cycle (sizes 2–3 mm) [composed of very small, almost translucent crabs, and grey-blue juvenile crabs], during a low tide the surface becomes speckled with small clots of sand as a result of settlement and juvenile recruit workings (Fig. 4A). Generally, these crabs remain in the subsurface, and in excavating a small hole (cavity) therein, dispose of the sand onto the surface as a small aggregate *circa* 1–2 mm in size. These are scattered on the surface above the individual crabs. At this stage, the crabs may also create craters (Fig. 4B). They do this by opening the roof of their near-surface cavity exposing themselves to the surface, and excavating and depositing excavation pellets as a ring of sand around the opening; later, when the crabs descend to lower depths, they will fill the central concavity from below with more excavation pellets, leaving a single circular pustule where the crater once was.

When a population is in the early to middle stage of their life cycle (sizes 3–5 mm), composed of grey-blue juvenile and sub-adult crabs, during a low tide the surface becomes "pustular" as a result of crab workings. Again, the crabs remain in the subsurface, but their workings are the result of their creating shallow, meandering surface-parallel tunnels, the roofs of which are a mass of small cohesive pellets of sand, formed as a consequence of their feeding and excavation activity. In the first instance, cryptically, within 1–2 centimetres of the surface, the crab scrapes and excavates a proportion of sand from the near-surface, places it in its buccal cavity to extract its food, then rolls the food-depleted sand into a small ball, 2–3 mm in size, which it jettisons as a discard pellet to one side or attaches it to the roof of the developing tunnel. Some of the pellets are also formed by excavation and aggregated into the roof as balls of sand (excavation pellets). For the discrete surface pellets, the term "discard pellet" is used to make a distinction from the feeding pellets of crabs such as *Scopimera*, which aggregate sand on the surface into small balls or pellets from which they extract food particles. As a result of this soldier crab activity, the upper 1–2 centimetres of the sand is transformed into a labyrinth of tunnels the roofs of which are constructed of the material excavated from the tunnels. As such, the sediment surface becomes generally composed of linear to meandering areas of pustular sand, *and elevated* by 2–10 mm above the former sediment surface as the material of the tunnels is transferred to the roofs (Figures 4C and 4D). Thus the roofs of the tunnels are composed of aggregated discard pellets and excavation pellets of sand. Carefully removing the cover of sand pellets exposes the surface-

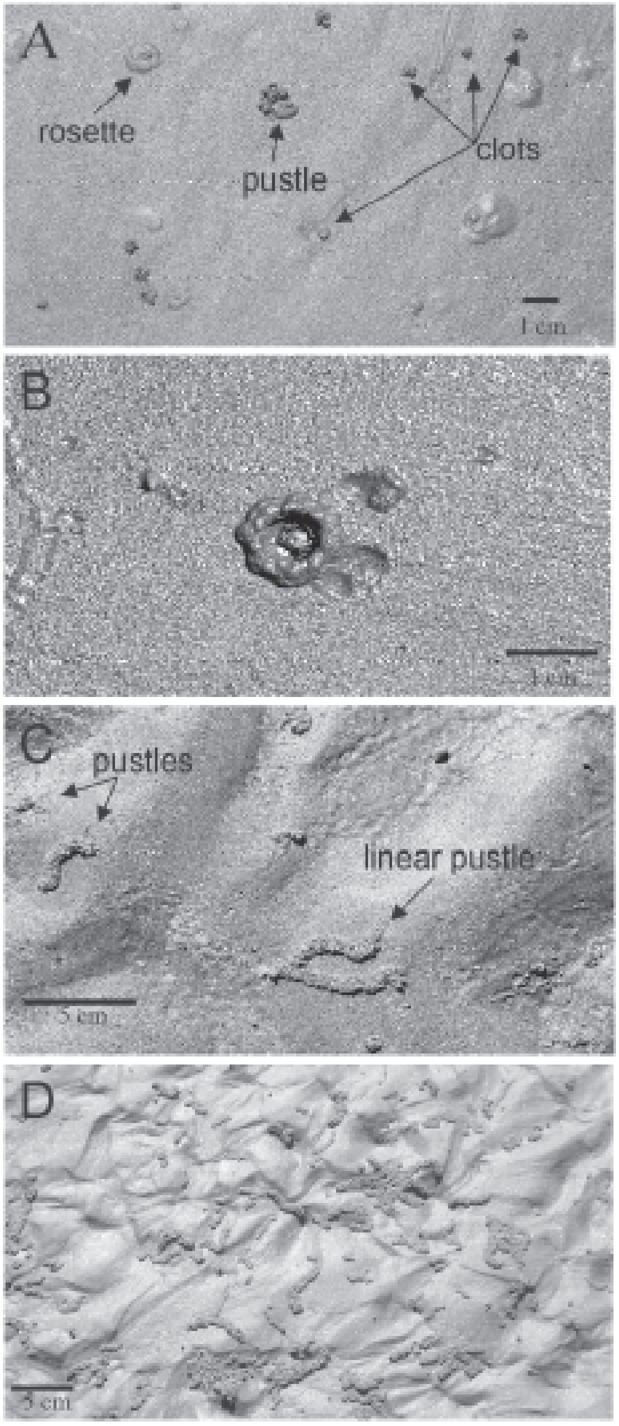

Figure 4. Photographs of types of surface workings by crabs of the settlement phase and juveniles. These workings are generated by crabs mostly working in the subsurface. A. Overview of a field of clots. B. Crater, with crab present in the central concavity. C. Circular pustular structure and linear to meandering pustular structures. D. Overview of a more complex field of linear to meandering pustular structures.

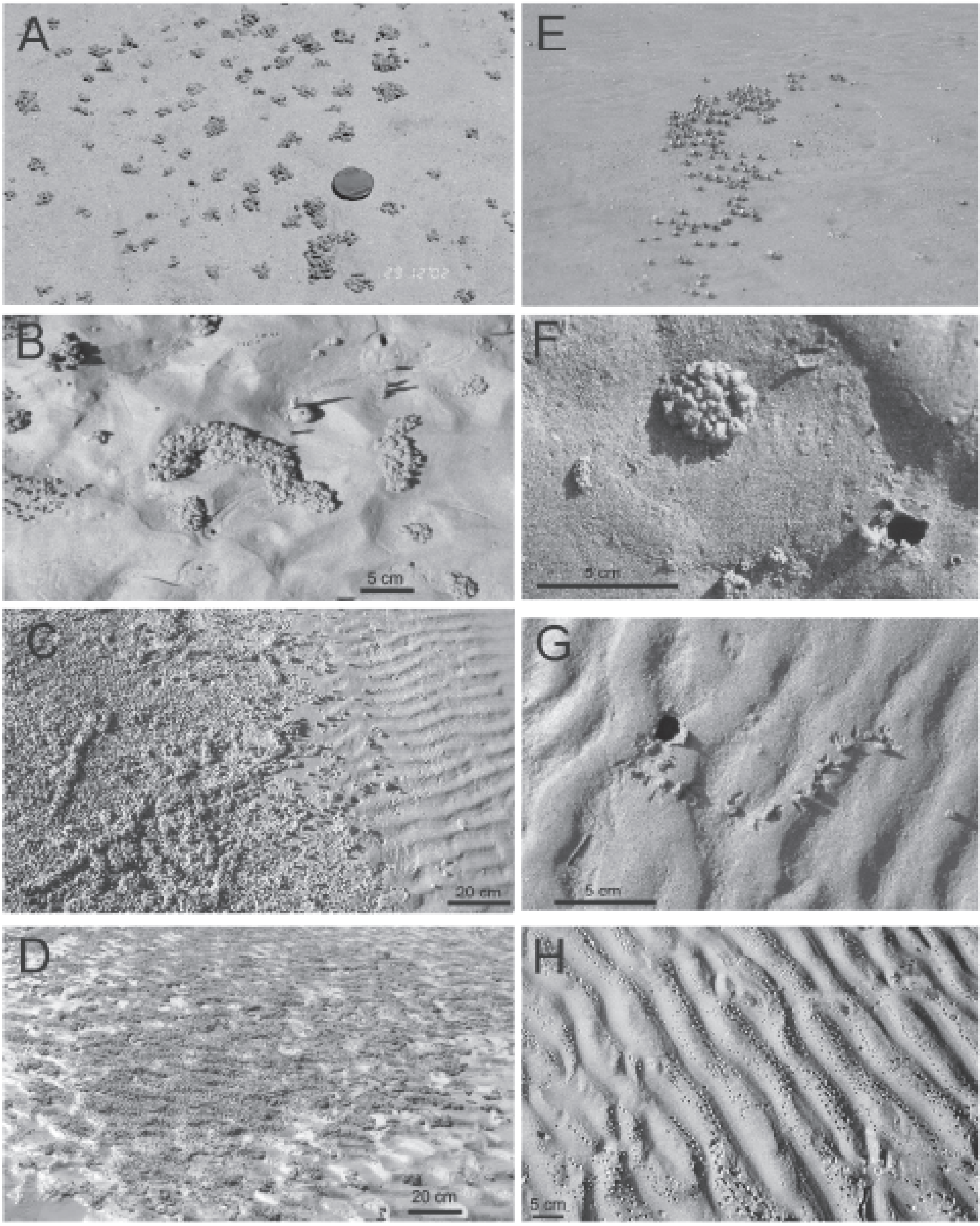

Figure 5. Photographs of types of surface workings by adult crabs. These workings are generated by crabs working the sediment in the subsurface and on the surface. A. Field of circular pustules (lens cap is 50 mm diameter). B. Circular pustular structure and meandering pustular structures. C. Zone of soldier crab workings adjoining a rippled sand flat; the workings consist of a mat of pustular structures generated by coalescing circular pustular structures and meandering pustular structures, and discard pellets. The majority of the workings are discard pellets. A prominent meandering pustular structure is evident to the middle left of the photograph. D. A mat of pustular structures generated by coalescing (mainly) meandering pustular structures and circular pustular structures; discard pellets are also common. E. Swarm of soldier crabs walking over a tidal flat sparsely covered in discard pellets. F. Exit hole with eruption structure, and (re-entry) rosette. G. Exit hole with eruption structure, and a trail of scrape marks with discard pellets. H. A row of discard pellets along the crests of ripples, where the soldier crab was preferentially walking.

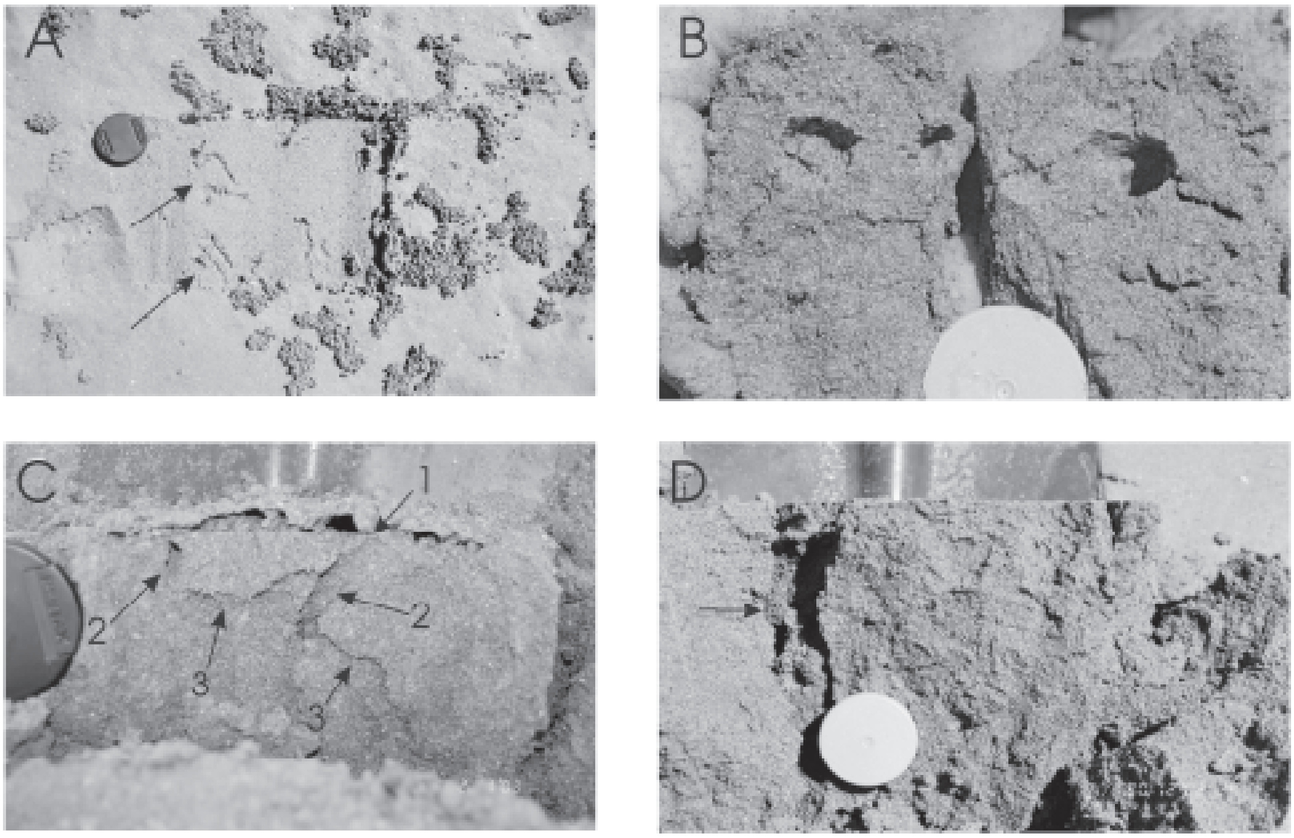

Figure 6. Excavations in the field to illustrate soldier crab ichnological structures. Lens cap in A and C is 50 mm diameter; film cannister cap in B and D is 35 mm diameter. A. Planed surface to remove the pustular structures to 1 cm depth to reveal the underlying horizontal tunnels. Arrows show tunnels below the surface. B. Equant cavity located *circa* 2 cm below the sediment surface. C. The tunnel under a pustular roof (arrow 1), hollow shafts (arrow 2); arrow 3 points to artificially generated cracks. D. A hollow shaft leading up to an exit hole.

parallel labyrinth of tunnels (Fig. 6A). The activity of the crabs in constructing the shallow surface-parallel tunnels mainly begins some 30 minutes to *circa* 60 minutes after the tide has fallen low enough that the water table is 10–20 cm below the sediment surface, and as a result, the water in the sediment changes from phreatic to pellicular water. Once it begins, the activity of producing the tunnels and creating a pustular surface continues for up to 150 minutes depending on the phase of the tidal cycle (Fig. 7). Figure 7 shows the increase in surface workings in time for 5 quadrats. In this instance, while there were workings evident as pustular structures, and even though the crab population was adult, there were no emergences of crabs during this particular low tidal period.

As the crabs work the immediate subsurface for food, the surface aggregations of pustular structures become longer and begin to coalesce. The end result may be a tidal flat surface completely covered in pustular structures that appear like a mat on the surface.

Because the discard pellets and excavation pellets that comprise the tunnel roofs are derived from sediment > 1 mm in depth and are deposited into the surface sediment, there is a contrast in colouration of the meandering to linear pustular structures. These pellets tend to be light grey to mid-grey amidst a surface tone of buff/tan and light grey, hence they stand out in tonal relief. Having a higher moisture content than surface sand, these pellets from the subsurface have a less well-defined spherical shape.

During this stage of the crab population's life cycle, the crabs also construct cavities which are separate from the surface-parallel tunnels. Excavations expose centimetre-sized, rounded to equant cavities located 1–5 cm below the surface. As mentioned earlier, these cavities are holes in the sand but with a geopetal lining of mud on their floor.

When soldier crabs are in the adult stage of their life cycle (sub-adult and adult, sizes 7–10 mm, and up to 16 mm, with the population composed of deeper blue to sky blue soldier crabs), during a low tide three types of activity ensue: 1. the surface becomes pustular as a result of crab workings composed of circular pustules (Fig. 5A), or linear/meandering pustular structures (Figures 5B and 5C), and the surface, with intensive working over by the crabs develops into a pustular mat (Figures 1D and 5D), as described earlier; 2. some crabs also may construct cavities; and 3. a proportion of the resident adult population emerges.

When the crabs emerge (Fig. 5E), there is an abundance of exit holes which are circular, often with eruption margins (Figures 5F and 5G). Emergent crabs wander on the surface feeding. Thousands may emerge in this manner, feeding and creating the impression of the soldier crab "armies" (Fig. 5E). Crabs have been documented emerging mainly during day-time low tides, but there are

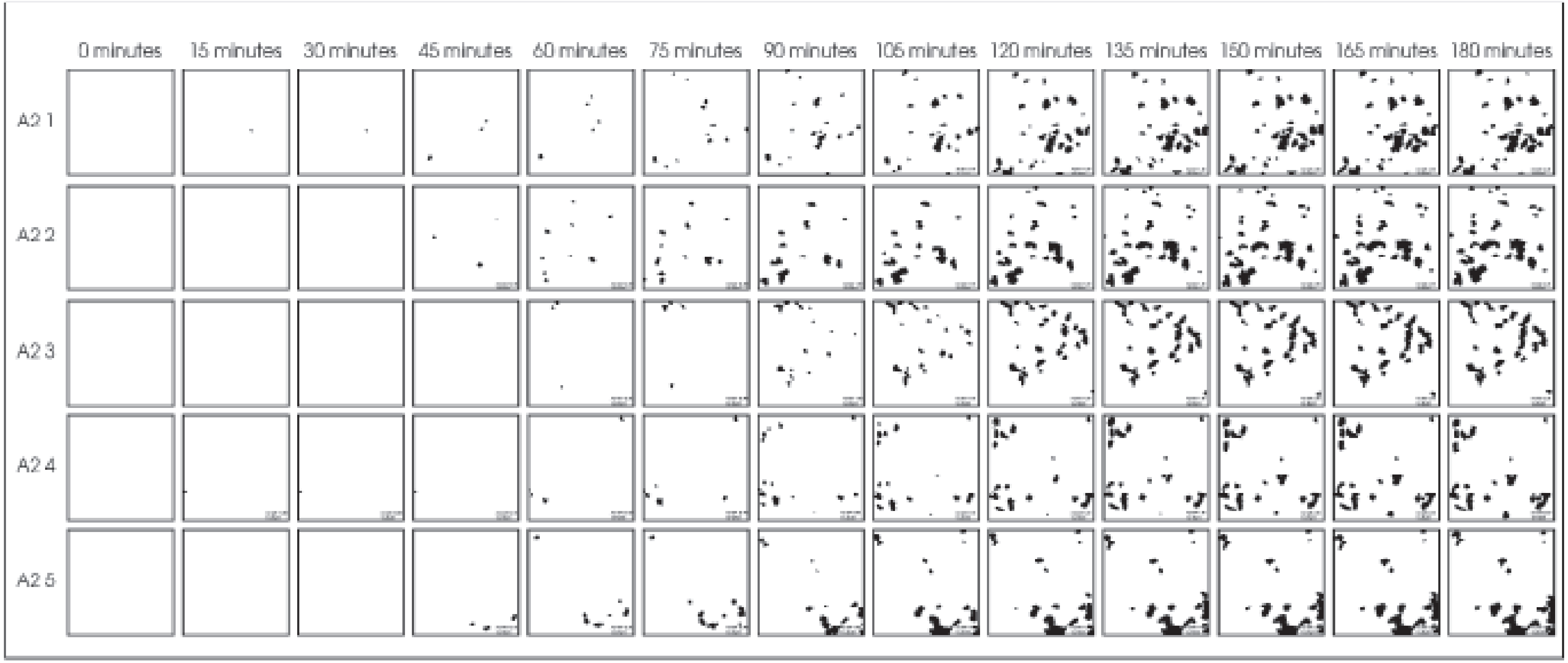

Figure 7. Increase in density of workings in five quadrats over 3 hours. In quadrats A2-1 and A2-4, one circular pustular structure appears at 15 minutes; at 45 minutes, circular pustular structures have appeared in four of the quadrats; by 90 minutes the workings have become conspicuous; most workings have ceased by 120 minutes. Quadrats are 25 cm x 25 cm.

exit holes evident during some of our night-time observations, though no observations of mass swarming. When the crabs emerge and forage on the surface, they generate scrape marks (Fig. 5G) in their harvesting of sediment for extraction of food, and the surface becomes covered in small discard pellets (Figures 5G and 5H). Several scrapings may be undertaken before the crab accumulates enough sediment in its buccal cavity to discards a pellet of sand. The discard pellets are placed a short distance away from where the sand was scraped. Depending on whether the crabs are relatively slowly wandering in their foraging, or rapidly moving over the surface, this distance can range from 5 mm to *circa* 25 mm, and locally up to 100 mm. Depending on how mobile the crab has been during feeding, the discard pellets can be arranged in meandering lines, or randomly, or in localised patches. Sometimes, ripple crests exert a control on the direction of crab wandering, and the line of discard pellets follows the ripple crest. (Fig. 5H).

The discard pellets, derived from the oxidised surface sand that has lower moisture content than the underlying sand, tend to be tan/buff in colour, similar to the surface sediment, and are more cohesive as spherical balls. They contrast with the colour of the pellets that comprise the meandering to linear pustular structures, hence they are conspicuous. Depending on the abundance of emergent crabs, and for how long they stay emergent, the surface may be littered with scattered discard pellets, or densely packed with an abundance of such pellets.

Dactyl prints are locally present when there is a thin film of mud or very fine sand on the sediment surface, but this ichnological feature is not common.

Eventually, the crabs re-enter the subsurface and do so by corkscrewing into the sediment, producing a distinct rosette pattern (Fig. 5F) As the crabs corkscrew in, they excavate the sand and pile it to one side as they rotate inwards, thus producing a rosette of excavated material (hence the vague radiating structure to the rosette), and finally as they descend to a level below that of the surface sediment, they upwards pack the central hole so that the final morphology of the trace commonly is a rosette of excavation discards and a central plug (Fig. 5F). Crabs were observed corkscrewing in both clockwise and anticlockwise directions, showing no sign of "handedness".

When the crabs rapidly exit or re-enter the sediment, they may leave vertical to near-vertical holes.

Figures 6B–6D illustrate a range of subsurface structures developed by the crabs. Figure 6B illustrates an equant cavity located *circa* 2 cm below the sediment surface. Figure 6C illustrates hollow shafts, and the tunnel under a pustular roof. Figure 6D illustrates a hollow shaft leading up to an exit hole.

At the stage where adult crabs are producing a pustular surface, exit holes, scrape marks, discard pellets, and rosette structures, there also may be local occurrences of clots. Investigation of these show that crabs smaller than the mean size of the population are present as juvenile recruits that arrived later than the main population.

In the field there was a variability in behaviour. One group of crabs would emerge apparently *en masse* in one location on one day, and another group elsewhere which remained in the subsurface on the first day, would emerge on another day. For any emergences, there would be a (usually small) proportion of crabs remaining in the subsurface. Emergent groups generally produced pustular structures before appearing on the surface. Further, on the third day, both groups may have produced pustular structures but had no emergences, then on the fourth day, both groups produced only pustular structures, but of a different plan shape. A third group may have remained subsurface for all four days, but emerged *en masse* in their resident location on the fifth day. In Figure 7, where the workings were mapped in detail in quadrats, there were no emergences on that particular low tide, but a local nearby emergence of crabs on the next day. Mapping of areas of pustular workings

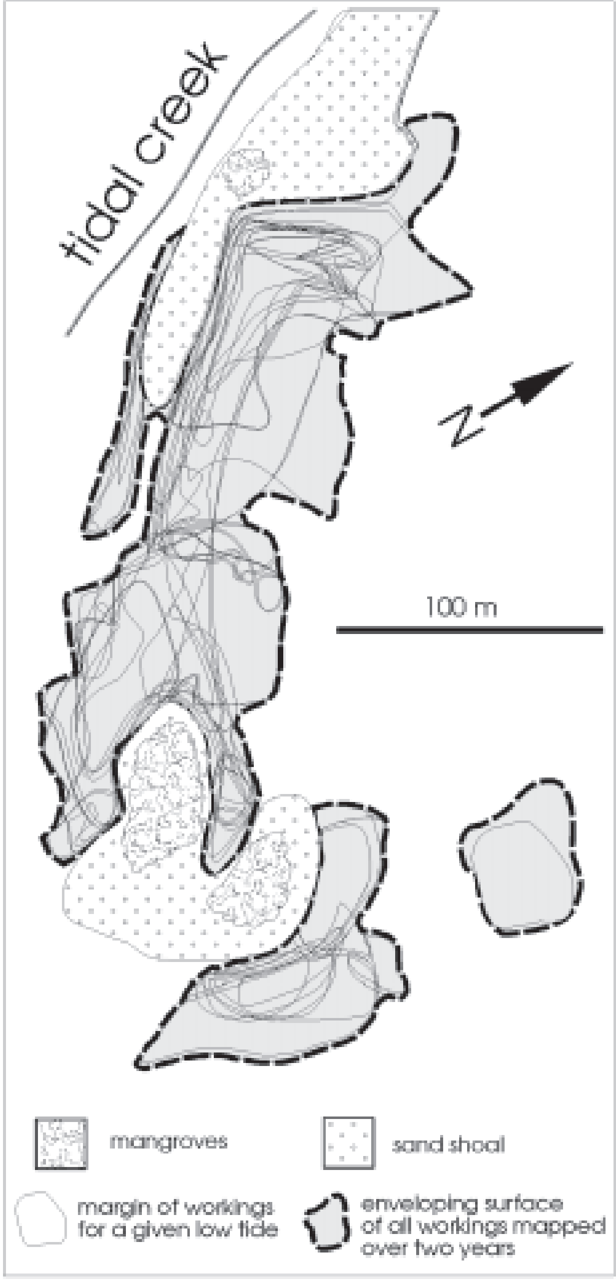

Figure 8. Map showing the overall distribution of the workings of crabs in southern King Bay over two years.

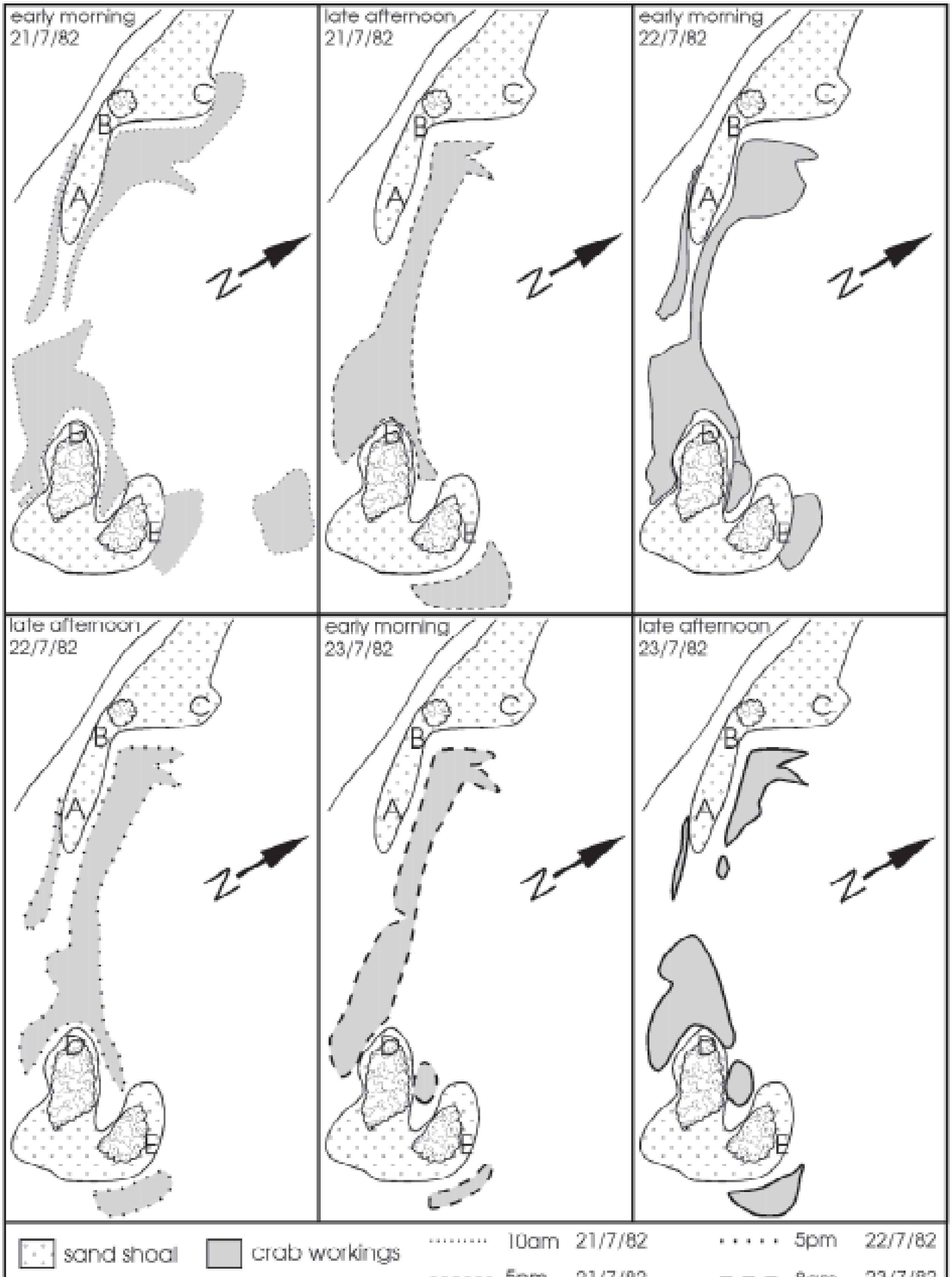

Figure 9. Maps of the workings of crabs in southern King Bay during six day-time low tides over three days.

shows that the boundaries of clusters of crabs within the large population resident within the habitat could change on a daily basis. Details of mapping are provided in Figures 8 and 9.

Figure 8 provides some background on the soldier crab habitat and the longevity of locations of crab activity as a prelude to describing the variability of soldier crab activity in this environment: there are some small mangrove copses inhabiting the crest of two tidal shoals that are part of the ebb-tidal fan in southern King Bay (Semeniuk & Wurm 1987). A distribution pattern of the soldier crabs, encompassing occurrences over two years (1981–1982) as determined by daily and monthly mapping, is shown in Figure 8; all mapped occurrences of the workings of the crabs are presented in this Figure, with an enveloping surface showing the maximum area that the crabs inhabited in southern King Bay. Soldier crabs had not inhabited the sites of the mangrove copses nor the upper parts of the sandy shoals above *circa* MSL. Their habitat preference here was the tidal flat between MSL and MLWN, along the margins of the shoal where the mud content is < 5%, which approximately is parallel to topographic contours and to the crests of the shoals [the soldier crabs also generally had not inhabited the higher energy margins of the tidal creek, between MLWN and MSL, where tidal current flow and strong sediment mobility precludes their establishment]. As such, their overall distribution is circumferential to the shoals.

The distribution and variability of the crab workings over a three-day period with two tides a day are shown in Figure 9. For these three days, the crabs did not emerge, indicating that any variation in location of ichnological activity can not be the result of their emergence, migration, and then re-entry into the subsurface in new locations, hence generating a new location of ichnolgical activity. Without emergence, the variation of crab ichnological activity is the result of clusters or patches of crabs behaving variably in the subsurface from site to site. In detail, there is variability from tide to tide and from day to day, as will be described below. To facilitate description of the patterns, the two shoals are internally labelled as to their elongate spits and lobes as A, B, C, D and E.

On the morning low tide of 21st July 1982, the patches of crab workings occurred as thin strips projecting eastwards from either side of elongate spit A; the southern thin strip was absent during the afternoon low tide of the same day, reappeared on the morning and afternoon low tides of 22nd July 1982, was absent for the morning low tide of 23rd July, and was diminished in area for the afternoon low tide of 23rd July (Fig. 9). At the same time, crab workings appeared circumferential to the sand shoal lobe C on the morning low tide of 21st July 1982, but not again for the next five low tides. The re-entrant in the shoal (area B) showed crab workings that, while generally in the same location, expanded and contracted in area from day to day. Similarly, the sand shoal lobe of area D showed a fairly consistent circumferential occurrence of crab workings, but the detailed shape and the extent of the areas varied from low tide to ensuing low tides. The location north east of lobe E showed patches of crab workings that varied in occurrence and in shape, and in areal extent.

Results from the aquarium

Mictyris occidentalis placed in the aquarium in the field and in the laboratory showed that these soldier crabs survived aquarium conditions. They grew from juvenile and sub-adult to fully adult while in the laboratory environment. The first experimental batch that was placed in the aquarium in the laboratory were sub-adult crabs initially and grew to be adults (with growth of mean carapace length from 5 mm to 14 mm) over nine months before they were released into the field at their place of capture. Figures 10–13 show the general results of the aquarium observations.

In the aquarium, the crabs carried out the same activities as they do in the natural environment. Their surface working and subsurface working activities occurred during the day-time and night-time. While they have been observed to emerge mainly during day-time low water, there have been some that emerged during night-time low water, as evidenced by their exit holes.

Whether in the sub-surface or emergent on the surface, the crabs inhabited the full length and width of the aquarium, producing ichnological structures across the whole sediment surface (Figures 10 and 11): meandering to linear, shallow surface-parallel tunnels; re-entry rosettes; and discard pellets (as will be described later). Fortuitously, many of the 30 crabs also carried out their activities alongside the aquarium wall (with up to 10 at a time located along the aquarium wall), maintaining cavities, forming vertical to oblique back-filled burrows and creating the shallow surface-parallel tunnels, thus providing the opportunity to observe their activity in the subsurface. As such, there were direct observations of how crabs produce their ichnological structures which were useful for interpreting those in the field.

The first important observation of the aquarium conditions was that if tides were consistently mimicked, there was no emergence of crabs when the sediment was inundated at high water (simulating the high tide). The second important observation was that the crabs may continue their activity in the subsurface when the sediment was inundated on the high water.

The ichnological behaviour of the crabs is described in a framework of two water-level conditions:

1. that of high water, simulating high tide when sediments are inundated;
2. that of low water, simulating low tide with the water table at 20 cm to 5 cm below the sediment surface.

Activities during high water

At high water, all crabs remained buried and produced cavities at depths of 5 cm to 15 cm, rarely to 20 cm (Figures 10A and 10B). These cavities essentially housed the crabs in an air-filled cavity that was *circa* 25% larger in diameter than the crab's size, and no crabs resided in the sand without being in such cavities. Within this cavity the crabs continually modified the wall of the open structure, so that over minutes to several hours the cavity slowly migrated vertically (upwards or downwards), or laterally (Fig. 13). In other words, the cavity was continually being modified and was migrating. Within the cavity, the crab maintained the air

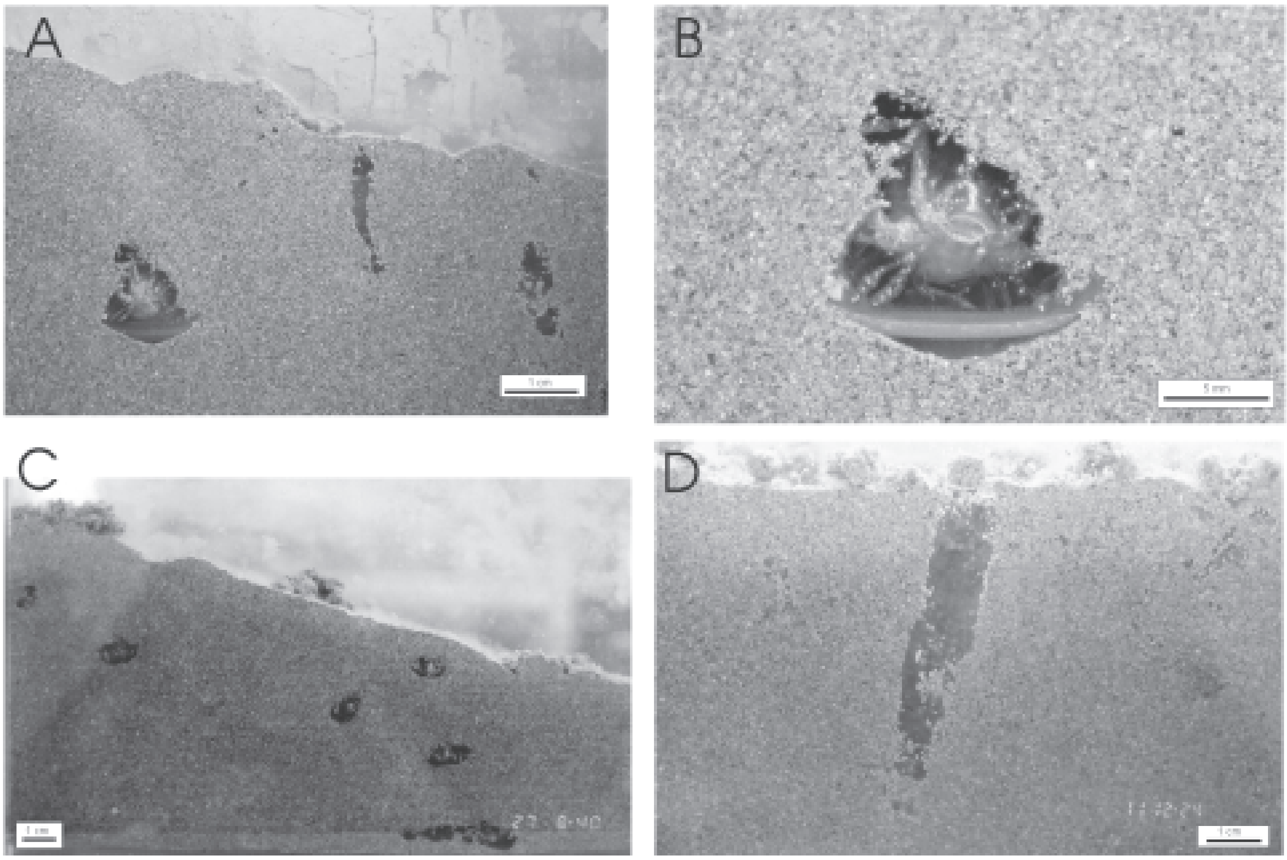

Figure 10. Photographs of crab activities in the aquarium. A and B are of crabs when inundated. C and D are of crabs at low water. A. To left, crab in air-filled cavity with geopetal sludge on floor; to right, crab in another cavity; in the centre is a linear cavity; the sediment surface is comprised of former circular pustular structures that have collapsed with inundation. B. Close-up of (A) showing crab and geopetal sludge in cavity. C. Five crabs in cavities in the subsurface, and two circular pustular structures on the surface. D. Hollow shaft leading to an exit hole.

pocket and the ovoid cavity shape by employing the chelipeds and the first two pairs of walking legs to scoop or push the sand and the last two pairs of walking legs to act as stabilisers. Water seeped into the cavity creating on the floor of the cavity a pool of geopetal mud sludge < 1 mm deep, up to 2 mm deep (Figures 10A and 10B). The crab, orientated in a dorsal surface upwards position, was feeding from this sludge, using its chelipeds and front walking legs in synchronous or alternating motions to scoop the muddy material into its buccal cavity. In this context, the feeding activity of the crab did not produce any discard pellets, and the crab directly utilised the muddy soup as feeding material. Occasionally the crab would scoop sand from the one side of the cavity and pack that material into its buccal cavity, then remain motionless for a short period except for lateral movements of the third maxillipeds. This material would be discarded as a semi-liquid unconsolidated mass and pushed to the opposite side of the cavity with outward sweeping motions of the chelipeds.

During intra-cavity activities such as feeding, cavity maintenance or migration, the crab appeared to attain inverted or lateral body orientations as well as the conventional dorsal surface upwards position with an equal facility.

Not all crabs were active at the one time. From a population of 30 crabs in the aquarium, a maximum of 10 were visible at any one time along the walls, and of these, activity was observed usually in 5 crabs at a time. During such times, the other crabs were under the sand in the interior of the aquarium and were not visible.

Activities during low water

During low water, a proportion of crabs emerged and some stayed subsurface. Those crabs along the aquarium walls provided the opportunity to document that even though the water table had fallen to below the level of a given cavity, and that while other crabs were constructing shallow surface-parallel tunnels or had emerged creating a hollow shaft and exit hole (Fig. 10D), some crabs remained in the subsurface in their cavities (Fig. 10C). Feeding motions of these crabs were the same as under conditions of high water except that there was no geopetal sludge in the bottom of the cavity and the material discarded from the buccal cavity was more cohesive but still not pellet-shaped as in surface discard pellets. Often these subsurface crabs remained relatively inactive. This inactivity may have lasted from minutes to hours, with the crab remaining motionless. When the aquarium was again inundated, these crabs returned to

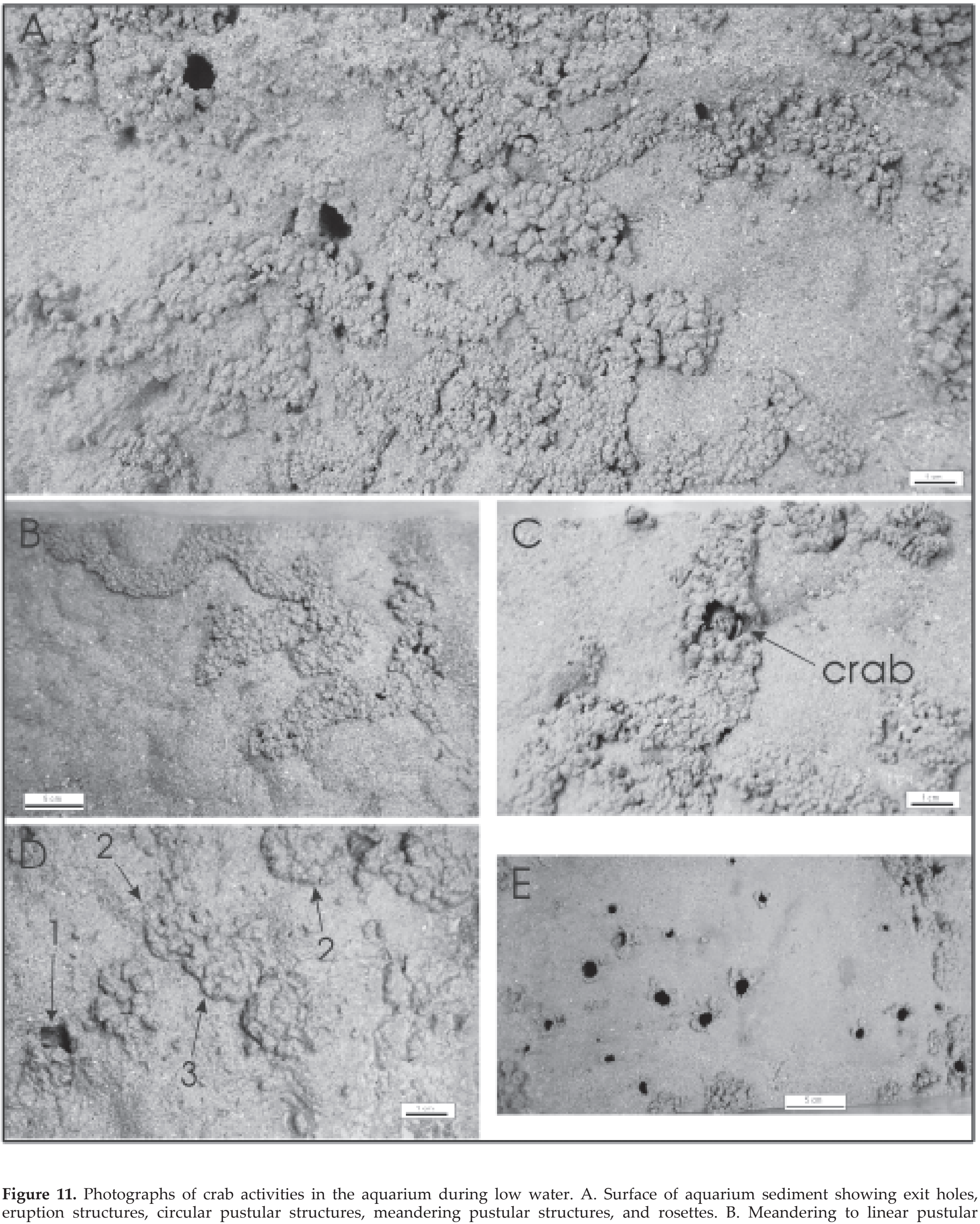

Figure 11. Photographs of crab activities in the aquarium during low water. A. Surface of aquarium sediment showing exit holes, eruption structures, circular pustular structures, meandering pustular structures, and rosettes. B. Meandering to linear pustular structures. C. Meandering pustular structures with crab in the tunnel exposed by an open roof. D. Eruption structure around an exit hole (arrow 1), rosettes (arrow 2), and circular pustular structures (arrow 3). E. Twenty exit holes, some with eruption structures, and several circular pustular structures.

their feeding and cavity-migrating activity, or still remained inactive.

Generally, whether during day-time or night-time, the activity of the crabs on the surface either in constructing shallow surface-parallel tunnels or emerging, was within 15–60 minutes of low water (the artificial low tide), and sometimes up to 150 minutes after the low water, though some crabs created circular pustules within minutes of low water (to re-excavate their cavity). The majority of crabs constructed shallow surface-parallel tunnels (Figures 11A, 11B and 11C). Those crabs active along the aquarium walls showed that the tunnel construction was achieved by creating discard pellets and attaching them to the roof of a developing tunnel, and by forming excavation pellets and also attaching them to the roof of a developing tunnel.

For a given period of low water, during the day-time low water periods, a minority of crabs usually emerged, and these formed exit holes with eruption margins. Where located along the aquarium wall, the exit holes commonly were the upper termination of a vertical to near-vertical hollow shaft showing that the crabs rapidly ascended the sand, then exited, leaving the hollow shaft in their wake rather than a back-filled structure (Figures 10D and 12). Sometimes, all the crabs in the aquarium emerged at the one time so that all 30 crabs were on the surface.

While on the surface, the crabs would feed, creating scrape marks and then discard pellets. Walking on the surface also created some dactyl prints. Eventually, the crabs re-entered the sediment in staggered intervals creating re-entry rosettes with a central plug.

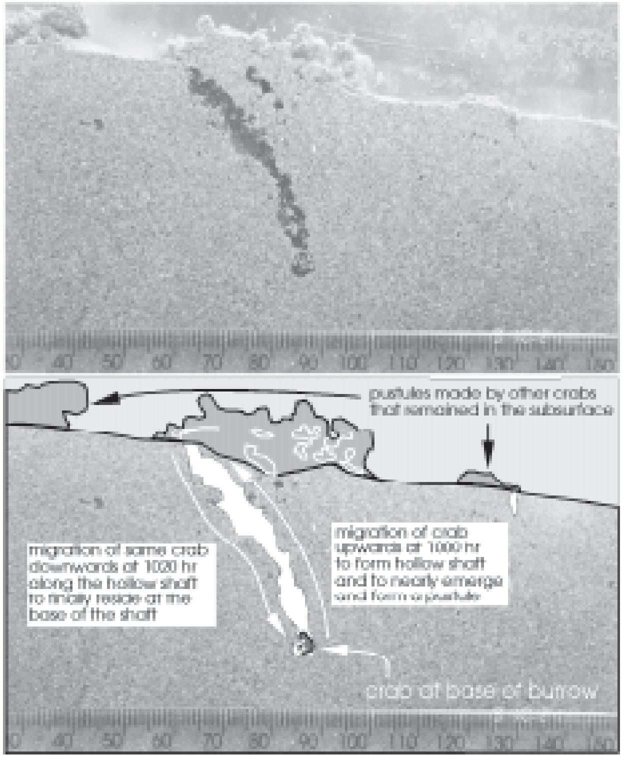

Figure 12. Photograph and annotated tracing of aquarium wall showing the observed movement of one crab upwards and downwards within a hollow shaft. Scale in millimetres.

Again, for the low water activities, not all crabs were active at the one time. From the population of 30 crabs, a maximum of 10 were visible at any one time along the walls, and of these, activity was observed usually in 5–9 crabs at a time (Fig. 10C).

Figure 13 illustrates the variability of crab behaviour for six low water periods. The crabs variably emerged, or created pustular structures, or remained active or inactive in cavities, and their activities were not synchronised. Further, the mobility of individual crabs at the same time of observation varied temporally, and in terms of speed of their movement, direction(s) of their movements, and how far they moved.

The activity of the crabs on the surface mimicked that in the field. Generally, immediately after the sediment surface was exposed at low water, the surface was devoid of ichnological structures. If the crabs remained in the subsurface, progressively in time, the surface of the sand was covered in circular pustules, or linear pustular structures (Fig. 11). If the crabs emerged, the surface initially was covered in circular pustules, or linear pustular structures by those crabs that remained in the subsurface or that were about to emerge, and was additionally, for those crabs that had emerged for a given low water episode, pocked with exit holes and covered with discard pellets and rosettes. The numbers of crabs that created pustular structures, or meandering pustular structures, or those that emerged to create exit holes, discard pellets, or rosettes, varied from low water period to low water period, from no emergences, to a maximum number of 30 (all of them).

An important aspect of the activity of the crabs in the aquarium was its variability:

1. during a given period of low water, not all crabs were active at the same time (where visible along the aquarium walls, some remained inactive in their cavities, some were active in their cavities, some excavated surface-parallel tunnels, and some emerged);
2. during another period of low water, most crabs might have been inactive at the same time, remaining in their cavities; *i.e.*, there were no emergences and no development of pustular structures;
3. during another period of low water, all crabs appeared to be active at the same time, but some remained active in their cavities, some excavated surface-parallel tunnels, and some emerged; and
4. during yet another period of low water, all crabs emerged at the same time.

Subsurface sedimentary structures

The aquarium provided the opportunity to observe the movement of the crabs in the subsurface of the sediment and the sedimentary structures that were created as a consequence. Some of this description has already been provided above, but is re-iterated here in the context that there is a focus now on subsurface sedimentary structures of what are traditionally viewed as biogenic sedimentary structures rather than the surface ichnological features.

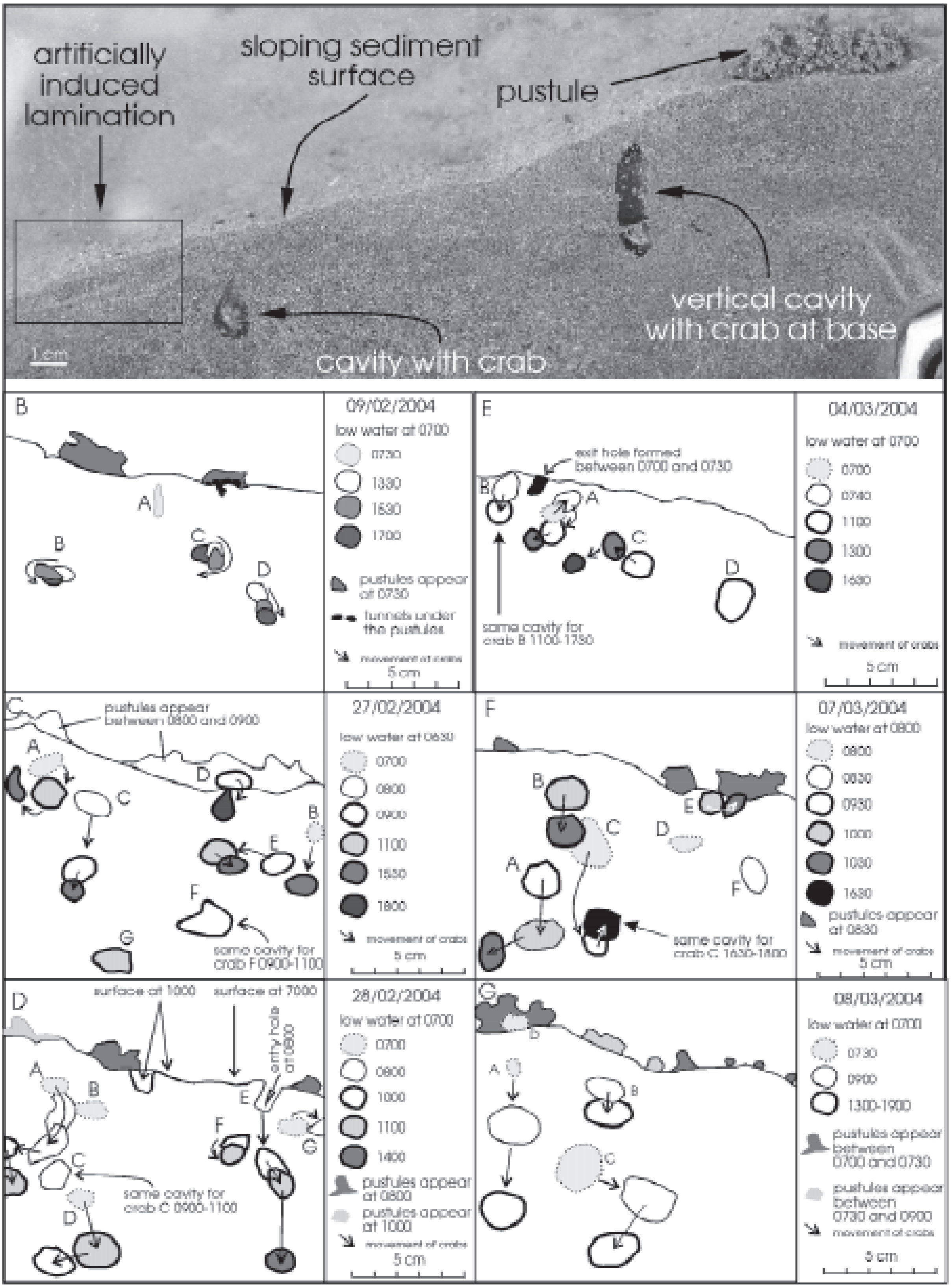

Figure 13. Results of the aquarium observations. A. Side view of the aquarium, one hour after low water, showing sloping sediment surface, pustule on surface, and two crabs in the subsurface, one in an equant cavity *circa* 2 cm below the surface, and the other in a vertical cavity located 1–4 cm below the surface. B–G. Tracings of the aquarium walls showing, for a given day, the number of crabs visible along the glass wall, the location of a cavity at a given time, the migration of the cavity in time, pustules on the surface and when they appeared, and the number and time that any crabs emerged. For a given frame, the crabs are notated A, B, C, D, *etc*. Since all crabs are approximately the same size, deriving from the same cohort, the size of cavity in these views is dependent on cut of cross-section: tangential sections appear as small cavities, and median sections show maximum size of a cavity.

The movement of the crabs in the subsurface is of two types:

1. vertical movement to rapidly emerge onto the sediment surface; this produces a vertical to near-vertical hollow shaft; and
2. lateral, vertical and downwards movement of the cavity; this produces a blurred bioturbation structure wherein the sediment appears swirled.

Where the sand was artificially laminated in the aquarium to trace the development of biogenic (bioturbation) structures, the process of burrowing and cavity migration left a bioturbated zone of vertical corridors, swirls and mottled material in the upper 15 cm of the sediment (Fig. 14). Burrow back-filling and cavity wall modification by the crabs created a wall-parallel lamination that was highlighted by sand grainsize variation, fine mud lamination, and by iron-sulphide diagenesis (grain pigmentation). For example, movement of the crabs to the surface and to the subsurface via vertical hollow shafts ultimately resulted in the development of vertical to near-vertical bioturbation structures that were emphasised (highlighted) by diagenetic colouration (varying degrees of iron sulphide pigmentation).

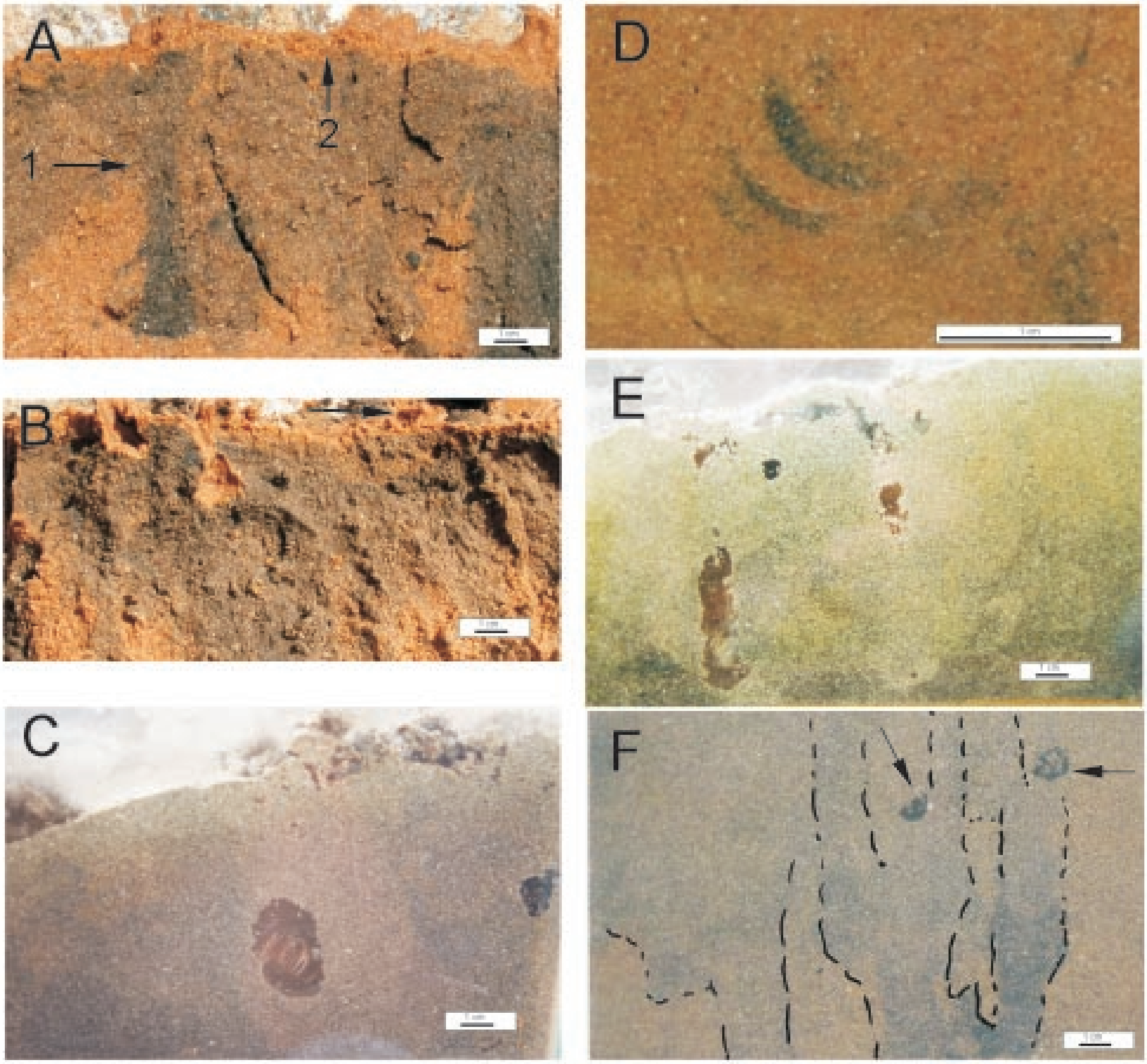

Figure 14. Bioturbation structures generated by soldier crabs. A. Field photograph illustrating general mottled brown (oxidised) and grey (iron sulphide pigmented) sand, with vertical back-filled burrow structures (arrow 1), and surface oxidised zone (arrow 2). B. Field photograph illustrating general vertical back-filled burrow structures highlighted by brown and grey sand. The near-surface layers have cavities that have an oxidation halo. Pustular structure is on the surface (arrow). C. Photograph of aquarium wall showing crab in cavity, and vertical zone of bioturbation generated by this mobile crab, highlighted by brown and grey sand. D. Back-filled burrow, with back-filling highlighted by brown and grey sand. E. Crabs in equant and linear cavities, and general bioturbated (swirled) nature of the sediment (particularly evident in lower middle and lower right of the aquarium). F. Vertical back-filled structures highlighted by brown and grey sand; two crabs in their cavities are arrowed (margins of corridors of grey and brown sand outlined on aquarium wall).

Summary of soldier crab ichnological products

The soldier crab *M. occidentalis* can produce up to 16 different types of ichnological products. These are the result of the crabs working the sediment at different stages of their life cycle, whether or not they emerge, and the working of the sediment at different times of the tide. The various ichnological products and a summary of their formative biogenic processes have been listed in Table 1 [note that components of integrated ichnological products are not treated as separate products, *i.e.*, a tunnel floor is part of a tunnel, not a separate structure, and the term "workings" refers to the total aggregation of ichnological products that occur on tidal flats]. Most of the ichnological products are distinct and diagnostic of particular activities. Clots, craters, circular pustular structures, dactyl prints, the discrete discard pellets on the surface, eruption structures, exit holes, hollow shafts, linear pustular structures, rosettes, scrape marks, and surface-parallel tunnels exemplify this. However, the roofs of surface-parallel tunnels are composed of excavation pellets and discard pellets, and it has not been possible to macroscopically separate these after they have formed. Mat pustular structures are not the result of a separate activity but one of coalescence of other structures.

Discussion and conclusions

Observations of soldier crabs in the aquarium were very useful because the crabs replicated activities observed in the field. In addition, the aquarium could be used for observations of crab behaviour not readily apparent in the field. Results from the first aquarium experiment in the field and subsequent laboratory experiments showed that soldier crabs rapidly became acclimatised to aquarium conditions, did not display aberrant behaviour after an initial settling-in period, and could survive for an extended time and grow to a larger than average size in aquarium conditions that replicated the temperature and tidal regime of their natural habitat. The aquarium also provided the opportunity to vary the environmental conditions to ascertain crab responses (as will be described in later papers).

For both field and aquarium situations, the initiation of surface activities by the crabs producing clots, pustules and linear to meandering to mat pustular structures was within 15–60 minutes of sediment exposure, when the sand was sufficiently dewatered, though we did notice that the aquarium crabs generally tended to initiate workings earlier.

Initially, while the results from field work emphasised the ichnological products on the sediment surface, and indeed the aquarium results reinforced and explained these phenomena, the aquarium observations provided insights into the behaviour of the crabs in the subsurface under simulated both high-tide and low-tide conditions. Knowledge that the crabs remain active under high-tide conditions is particularly important because the crabs *spend more than 50% of their time under high tides*, and previous to our laboratory observation it was not known what activities *M. occidentalis* carried out during times of inundation. The aquarium observations showed that their burrowing, migration and feeding continues in the subsurface during inundation. Other tidal crabs from genera such as *Scopimera*, *Uca*, and *Ocypode*, which are generally surface feeders, clearly wait out the high tides in their burrows to re-emerge on the low tide (Hill & Hunter 1973; Crane 1975; Gherardi *et al.* 1999; Gherardi & Russo 2001). They then re-excavate their burrows, and undertake feeding on the surface during low tide (by creating feeding pellets, or by scraping diatom-rich material off the surface, or by scavenging detritus, respectively), to then re-bury themselves and wait out the next high tide in their burrows, safe from predators that invade their habitat on the flooding tide. Their specialised surface feeding activities do not continue into the subsurface. This study shows that the activities of the soldier crab take place during both high tide and low tide and hence can be a 24-hours-a-day exercise. Moreover, both the surface activities (during low tide) and subsurface activities (during low tide and high tide) involve feeding – the former, feeding from the surface sediment, resulting in the generation of discard pellets that form the roofs of the surface-parallel tunnels and in a surface litter of discard pellets, and the latter, feeding from the geopetal sludge flooring the cavities and from the sand of the cavity walls. The soldier crab, *M. occidentalis*, is a cryptic (in-faunal) animal, spending most of its life cycle as in-fauna, and, as such, in hindsight it was to be expected that it undertook its feeding activities in the subsurface during high and low tides.

There is a difference in strategy of feeding and products of feeding between low and high tide. Because at low tide the sand is cohesive with pellicular water, and this pellicular water largely is the only water available for the crab to slurry the fine-grained organic material in its buccal cavity for feeding. Thus *M. occidentalis,* during a low tide, in extracting pellicular water from the ball of sediment it has scraped up, produces cohesive discard pellets (on the surface or in the construction of the roofs of surface-parallel tunnels), leaving a (pellicular water depleted) discard pellet behind. Some species of *Mictyris* (*M. longicarpus*), while on the sediment surface, have been observed taking up water from surface pools which they then store internally and use for particle size separation in the feeding process (Dittmann 1996).

Sand generally cannot remain cohesive when it is water-saturated (Webster 1919; Carrigy 1970; Reineck & Singh 1980; Groger *et al.* 2003; Kleinhans & van Asch 2005; Nowak *et al.* 2005; Breien *et al.* 2007), unless it is held by an organic gelatinous matrix (*cf.* Bathurst 1967). Consequently, in order for the sand to remain cohesive as pellets, and to ensure that the roofs of the tunnels do not collapse, soldier crab activity that is manifest on the surface does not begin until the water content of the sand changes from being saturated to being pellicular. Thus, a determining factor for the development of a majority of the traces is cohesive sand with a film of pellicular water coating the sand grains, a feature that is conditional on the sand being exposed to the drying action of sun and wind some time after its exposure by a falling tide. Hence, soldier crabs do not work the sediment to create surface-parallel tunnels while the sand is under water. They also generally do not work the sediment to create surface-parallel tunnels in sediment recently exposed by a falling tide. Similarly, the creation of discard pellets does not take place in water-saturated sand, but in sand that has pellicular water. The early onset of workings in the aquarium, as noted above, may be due to more rapid draining of interstitual water under aquarium conditions, resulting in the development of sand with pellicular water sooner than would occur under field conditions.

Because the sand is not cohesive under high tides, *M. occidentalis* does not produce discard pellets during times of inundation. Rather, it directly utilises the water seeping into its air-pocket cavity, feeding directly on the sludge that accumulates on the cavity floor. We conclude that this sludge, in fact, is the material being extracted from the film of pellicular water that coats the sand grains when *M. occidentalis* is feeding at low tide. In the former situation (high tide), the crabs directly utilise fine-grained material that seeps into their feeding cavity. In the latter situation, the crabs harvest this film of sludge off the sand into their buccal cavity and leave behind a pellet of sand, depleted of fine-grained material and packed into a neat ball by their walking legs.

Discard pellets of *M. occidentalis* superficially appear similar to the feeding pellets of the sand bubbler crab *Scopimera* (in this case, in our observations in Western Australia, the sand bubbler crab is *Scopimera inflata*). However, there is a difference in arrangement of pellets and associated structures derived from feeding by *M. occidentalis* as compared to those derived by feeding by the sand bubbler crab. As described earlier, *M. occidentalis* emerges from an exit hole, and in its wanderings on the surface scrapes up sand, leaves scrape marks in isolation, moves away from the scrape site, and continues to gather sand until the ball of sediment is large enough to discard as a pellet. It deposits the discard pellet a short distance from the scrapings. The exit hole, the scrape marks and the discard pellets are in three unrelated locations. *S. inflata*, on the other hand, emerges from its burrow, and initially begins its foraging close to the burrow entrance. It scrapes up sand into a ball that rests on the sediment surface, and it gathers its food from the surface of the ball (the pellet). The pellet is bordered by scrape marks. Once the sediment is depleted of food, the crab moves a short distance in a radial line away from its burrow entrance and scrapes up more sand into a separate ball that rests on the sediment surface. This practice continues as the sand bubbler crab progressively moves further and further from the burrow entrance, leaving a line of pellets and scrape marks. In this case, the burrow entrance hole, the scrape marks and the feeding pellets are all locationally related.

In terms of burrow permanence, many crab species have fixed burrows (to which they return on the rising tide, as mentioned above), re-excavating or cleaning out their burrows on exposure at the next low tide, or have a permanent burrow entrance. Species of the fiddler crab *Uca* are an example of the former, and species of the ghost crab *Ocypode*, or the mangrove grapsid crabs are examples of the latter (Hill & Hunter 1973; Crane 1975; Gherardi *et al.* 1999; Gherardi & Russo 2001; Breitfuss *et al.* 2004). Other crabs, while adapted to shifting sand under wave and tidal action, or whose burrows collapse under water-saturated conditions, may re-establish their burrows in a single fixed position during the ensuing interval of the low tide. For example, species of the sand bubbler crab *Scopimera* reside in a burrow that collapses at high tide (Gherardi *et al.* 1999). They re-excavate their burrows during low tide such that there is a permanent vertical burrow (whose entrance is surrounded by radiating rows of feeding pellets). The activities of *M. occidentalis* stand in contrast to the above. Their surface-parallel tunnels are ephemeral or transient structures, effectively similar to gastropods that forage and move through the sediment in the near-surface, creating a trail of ploughed sediment. The cavities of the soldier crabs also are generally ephemeral, transient structures, but can remain as a short term temporary (static) feature. In summary, the soldier crab, *M. occidentalis*, whether on the surface or in the subsurface, is generally mobile and, as such, creates a complex range of ichnological products that are ephemeral and transient. Our conclusion, therefore, is that the behaviour of *M. occidentalis*, in contrast to many other crabs, is ichnologically complex.

However, *M. occidentalis* is not alone in exhibiting such complex ichnological behaviour. Some degree of complexity, though not to the same level as *M. occidentalis*, was documented by Gherardi *et al.* (1999) for the Scopimerinae crab, *Dotilla fenestrata*. These authors related the variety of burrow-oriented activities of *D. fenestrata* to be the result of rigid and plastic patterns, essentially an adaptation to the vagaries of intertidal habitat. Gherardi *et al.* (1999) concluded that the activity of *D. fenestrata* could be classified in a number of stereotyped behavioural patterns, the occurrence of which may change throughout the low water or on the basis of the crabs' relative size, according to an expected schedule. Digging, for instance, was more pronounced in larger individuals and mostly occurred when the crab emerges or just before it seals itself inside the burrow at the flooding tide. However, in contrast, maintenance of their burrows was a constant behaviour. Gherardi *et al.* (1999) documented the range of adaptive flexible behaviour in *D. fenestrata*; this included: the presence within the same population of both burrow-centred crabs and wanderers; the construction by the burrow-centred crab sub-population of two types of burrows (feeding-trench burrows and igloos); and significant differences in the behavioural budgets of the inhabitants of the two burrows. The ability of this species to 'switch' modes of activity allows responses to both the predictable and unpredictable elements of intertidal environments. However, while there is relative complexity in behaviour of *D. fenestrata*, manifest to some degree in the abundance and types of its ichnological products, *M. occidentalis* appears to be a far more complicated crab in terms of its in-faunal or epi-faunal behaviour in relation to tides, its life stage, and its feeding strategies (whether emergent, in subsurface tunnels, or in subsurface cavities).

Our aquarium observations allowed us to identify that the creation of cavities is an important part of soldier crab activity, and this suggested a re-investigation of the crab in the field to find similar products of such activity. The details of the cavities in terms of their size, shape, and geopetal mud floors obtained from aquarium observations facilitated recognition of such features in the field, confirming that what was observed in the aquarium also was a feature of the natural tidal-flat environment (Fig. 6B).

Subsurface cavities formed by crabs have been documented by other authors (*e.g.*, Cowles 1915), though they have ascribed different functions to them. Maitland (1986), for instance, in describing large membranous disks on the meral segments of *Scopimera* and *Dotilla*, considered that these crabs retreated on the high tide to an subsurface air chamber within which they continued to breathe air until the low tide. In effect, these subsurface cavities were considered by Maitland (1986) to be breathing chambers. We consider the cavities of *Mictyris occidentalis* to be a feeding chamber, a resting chamber, as well as a breathing chamber. In a study of the soldier crab, *Mictyris longicarpus*, from Eastern Australia, Maitland & Maitland (1992) concluded that the species is an obligate air-breather. Their gill chambers were modified for both water circulation and air-breathing in that water circulates through lower gill compartments, and upper regions of the gills are air-filled, functioning as lungs. This duality of function of the breathing chambers enables the crabs to operate on the surface, explains their need for an air-pocket in the subsurface at high tide, and how they survive if the air-pocket collapses. From aquarium observations, Maitland & Maitland (1992) also describe *Mictyris longicarpus* as constructing an "igloo" (or domed sand roof) above a pocket of air at the sediment surface prior to flooding by the tide, and then descending, with the pocket of air, to 10–30 cm depth, to wait out the high tide [this "igloo" is analogous to the rosette structures described for *Mictyris occidentalis* in this paper]. In this respect, the behaviour of *Mictyris longicarpus* overlaps with *Mictyris occidentalis* of this study. In another paper, Takeda *et al.* (1996) described "igloo" construction in the ocypodid crab *Dotilla myctiroides*. In addition to constructing its vertical burrow, *Dotilla myctiroides* rotates in the sand to form a circular wall of sand pellets around it and subsequently roofs the wall with pellets (the domed sand roof mentioned above). The resulting burrow structure, also termed an "igloo" by Takeda *et al.* (1996), encloses a small quantity of air together with the crab itself. Takeda *et al.* (1996) considered that such air chambers greatly facilitated vertical movement of the crab, and that the making of an "igloo" was an adaptation to enable construction of an air chamber in semi-fluid sand, where vertical burrows cannot be constructed, because the sand was not sufficiently firm to prevent collapse. Again, in contrast, we consider the cavities of *Mictyris occidentalis* to be a feeding chamber, a resting chamber, and a breathing chamber, regardless of the consistency of the sand. Takeda & Murai (2004) also documented *Mictyris brevidactylus*, a soldier crab from Southeast Asia, constructing two types of air chambers, one near-surface for feeding, and the another, a deeper ovoid form for residency. In this context, *Mictyris brevidactylus* appears to be constructing surface-parallel tunnels and subsurface cavities, similar to *Mictyris occidentalis*.

Discovery of distinctive subsurface bioturbation structures evident in aquarium studies also directed us to revisit the field environment to investigate and focus on similar structures in the sediment. The characteristics of bioturbation structures meant that *M. occidentalis*, in addition to its other obvious ichnological structures, left diagnostic subsurface structures in the sand, that (if all other ichnological products were to be erased by processes such as wave action or cavity collapse) could remain as a signature of the former presence of these crab (Fig. 14).

An important conclusion to emerge from this study was that the ichnological products of the soldier crab relate to the life stage of the species, to whether or nor the adult crab emerged, and to the tides. There are three periods of ichnological products related to life stages of the crabs. Populations dominated by crabs in their settlement phase and early stage of their life cycle develop sediment surfaces strewn with clots. Populations dominated by crabs in the early to middle stages of their life cycle develop sediment surfaces covered in pustular structures, and concomitantly create subsurface cavities. Populations dominated by crabs in the middle to late stage of their life cycle develop sediment surfaces covered in pustular structures, cavities in the subsurface, exit holes, (sometimes) dactyl prints, discard pellets, and rosettes. Mixed-sized populations resulting from continuous or pulsed juvenile recruitment into the population therefore create a mix of ichnological products.

The observation of variability in behaviour in the crab population in the aquarium had direct implications to interpreting the activity of crabs in the field where there was also variability in behaviour. The aquarium observations confirmed that the crabs did not always behave consistently as similar units. There was consistency in crab behaviour in that they built the same types of structures at the same time of tide: *e.g.*, pustular structures were produced on the low tide; exit holes, the formation of discard pellets, and rosettes also were produced only on the low tide. The development of cavities occurred on low and high tides. But outside of these patterns specific to the whole species, the crabs appeared to have independent behaviour. Thus, while there may have been emergences *en masse*, or large areas worked into pustular surfaces, it was not predictable that all crabs would all emerge throughout the entire habitat at the same time, and that all crabs in the subsurface worked the sediment to create a pustular surface, or that all crabs in the subsurface worked in their cavities at the same time. Rather, the emergences and development of pustular surfaces, and the periods of quiescence of surface activity was variable from site to site in the habitat (measured in terms of several metres), even though the entire habitat (measured in terms of several tens of metres to hundred of metres) was populated by these crabs in the subsurface. The variability of behaviour of the crabs in the aquarium could have been interpreted as an aberration or artifact of the behaviour of crabs imprisoned in a tank, but in fact, once the factor of behavioural variability was determined, it correlated with observation of crab behaviour in the field, and explained observations of the behaviour of natural crab populations in our studies over decades. That is, the behaviour of the crabs in the natural environment has similarly been sporadic or variable. In contrast, *Scopimera* and species of *Uca* in a given burrowing population generally all behave similarly at the same time (there are generally no absentees or deviations from the individual pattern, so if one crab emerges and feeds, then all crabs appear to emerge and feed). But soldier crabs are variable in behaviour: under the same conditions of exposure, light, wind, pellicular water content, and salinity, not all individuals act the same way; some emerge, some tunnel, some stay in the subsurface; then the next day all may emerge; and for the ensuing days the variable behaviour continues. This was particularly emphasised by the aquarium studies because clearly all external factors of exposure, light, wind, pellicular water content, and salinity were similar throughout the aquarium, yet individuals in the population of 30 crabs did not respond uniformly.

The variability of preservation of soldier crab ichnological products also relates to the tidal cycle, *i.e.*, whether it is a period of spring tide or neap tide. Spring tides are associated with more swift tidal current velocities, and crab ichnological products have a higher chance of reworking during an ensuing high tide. During neap tides, with the thin film of mud deposited by scour lag / settling lag processes, soldier crab ichnological products stand out in contrast, and have the best chance of preservation; also, dactyl prints and tracks, if present, are best preserved on the mud films.

In summary, the key points deriving from aquarium observations of crab activity below the sediment surface was that there were cavities, that crabs were feeding from sludge at the base of the cavity, that there was subsurface movement of the crabs, (laterally and vertically, and similar movement, axiomatically, of the cavity around them), that vertical hollow shafts were produced by a crab in the process of emerging and re-entering the sediment, and that the subsurface activity could produce distinctive bioturbation patterns. There was a range of ichnological products generated by the same organism depending on stage of life, time of tide, and whether the crab emerged or not.

The key soldier crab traces, in chronological order of development from time of high tide to time of low tide, are: cavities, clots, excavation pellets and discard pellets, meandering pustular-sand-roofed surface-parallel tunnels, exit holes, dactyl prints, scrape marks, surface-deposited discard pellets, and rosettes. The discard pellets forming the tunnel roof and the surface discard pellets are formed the same way, but one is attached by the crab to the roof from below, the other is formed on the surface by emergent crabs, albeit the latter contain more pellicular water and are initially less cohesive, and are also more pigmented.

Our study showed a direct correlation between field work and aquarium observations, and provided explanation of the field results. All ichnological products observed in the aquarium had their counterpart in the natural environment. Interestingly, while the aquarium study was set up to observe and explain what was documented in the field, and to add to our understanding of the ichnological behaviour of the crabs, it resulted in the observation of additional features such as mud-floored cavities and bioturbation structures that initially were not readily apparent or interpretable in the field, and that now could be targeted specifically for discovery and investigation in the field.

The ichnological results of the paper also can be useful paleoichnologically in Quaternary rocks for the identification of soldier crab workings and interpretation of tidal environments that soldier crabs inhabit.

Acknowledgements: Assistance in field work was provided by T A Semeniuk and P A S Wurm in the 1980s and by M Brocx, L Mustapah, and A Benz between 1997–2007. Assistance with laboratory work was provided by P Clifford. Their help is gratefully acknowledged. For VS, this work is part of VCSRG R&D Project Nos. 1 and 3. Thanks also go to Associate Professor A Kinnear for assistance and advice.

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