Relationships between Organic Carbon and Fodichnia Morphology

TYLER E. HAUCK

Department of Earth and Atmospheric Sciences, University of Alberta, 1-26 Earth Sciences Building, Edmonton, Alberta, Canada, T6G 2E3, Email: thauck@ualberta.ca

SHAHIN E. DASHTGARD

Department of Earth and Atmospheric Sciences, University of Alberta, 1-26 Earth Sciences Building, Edmonton, Alberta, Canada, T6G 2E3

MURRAY K. GINGRAS

Department of Earth and Atmospheric Sciences, University of Alberta, 1-26 Earth Sciences Building, Edmonton, Alberta, Canada, T6G 2E3

RRH: RESOURCE DISTRIBUTION CONTROLS ON FODICHNIA MORPHOLOGY

LRH: HAUCK ET AL.

Keywords: Organic carbon, *Chiridotea caeca,* Pascichnia, Intertidal, Neoichnology, Bioturbation

ABSTRACT

Grazing trackways of the Valviferan isopod Chiridotea caeca *are examined to establish relationships between trackway complexity and morphology, and the distribution of food (organic carbon). These isopods burrow up to 1 cm beneath the surface within ripple troughs and plane-bedded sand of the upper intertidal zone. The burrows are grouped into three forms based on trackway complexity and the degree of looping and trackway crossover in planview. Sediment samples taken directly from the furrows of the trails are used to establish the total organic-carbon content associated with each type of burrow morphology. There is an increase in organic-carbon content from burrows of low complexity (linear), to burrows of high complexity (convolute with many crossovers), suggesting that benthic food content directly influences the behavior of* C. caeca*, which is manifest in the trackway morphology.*

Detailed study of trackway architecture further reveals a relationship between C. caeca *and food content leading to the recognition of three grazing styles, which are directly associated with the plan-view morphology of the trackway. The categories reflect the depth at which the isopod tunnels in the sediment. Graphical analysis of weight percent organic carbon against grazing style shows that there is a positive correlation between deep burrowing and high benthic food content.*

The morphology of C. caeca *trackways differs from deep-sea turbidite- and flysch-deposits. In the abyssal environment resources are replaced slowly, and food distribution is comparatively low and uniform, leading to regular meanders and complex traces that do not crossover existing tracks. Within the intertidal zone,* C. caeca *encounters sporadically distributed but abundant resources that are replenished semi-diurnally. The resultant* *burrows exhibit increasing crossover with increasing food content, representing a once-over feeding strategy that is deigned to rapidly harvest high-value, renewable resource. This suggests that complex fabrics in sub-sea settings (with abundant crossing over) may be characterized by similarly abundant and regularly replenished food.*

INTRODUCTION

Although never demonstrated, the distribution of benthic food is to be a major control on behavior of infaunal animals and the resultant burrow habits. At Waterside Beach, Bay of Fundy, Canada, burrows constructed by *Chiridotea caeca* are commonly observed on the foreshore surface during low tide. These trackways can be grouped based on the degree of complexity and crossover (i.e. plan-view morphology). The trace of the surface tracks constructed by this isopod is compared to benthic food content to assess the relationship between trackway architecture and organic carbon content.

Much work has been done on classifying burrows and trackways (trace fossils) in terms of ethological and behavioral implications. Seilacher's (1953) ethological classification represents the first successful attempt and is still largely in use today (Simpson, 1975; Pemberton et al., 2001). Seilacher's system included activities such as resting (Cubichnia), dwelling (Domichnia), crawling (Repichnia), grazing (Pasichnia), feeding (Fodinichnia), and farming (Agrichnia). Regarding animal response to food content (as opposed to type of feeding), only deep-sea trace fossil assemblages within the *Nereites* ichnofacies have received much attention. Those studies were conducted within both turbidite- and flysch- (Raup and Seilacher, 1969; Seilacher, 1974; Ekdale, 1985; Seilacher, 1986; Bromley, 1990; Wetzel, 1991; Wetzel and Uchman, 1998; Hayes, 2003; Uchman, 2003). The *Nereites* ichnofacies is typified by horizontal grazing-, feeding-, and dwelling-traces with well-developed meanders produced by deposit feeders and scavengers (Seilacher, 1967a, 1967b). Regular feeding patterns within ichnofacies *Nereites* are primarily associated with Repichnia, Pascichnia, Agrichnia, and Fodichnia. The complex traces produced by organisms that live in abyssal environments are thought to represent maximum exploitation of evenly distributed resources in broadly uniform substrates (Raup and Seilacher, 1969; Seilacher, 1986). Meander patterns and other systematic reworkings (such as spirals) represent an animal response to environmental stimuli, such as food input and availability. In other words, benthic-food content directly influences the nature of the bioturbation (Wetzel, 1991). In fact, these two statements—deep-sea resources are evenly distributed, and deep-sea meander patterns represent a response to food availability—are obviously at odds with each other and sporadically distributed meander-form burrows are best interpreted as animal exploitation of patchy resources.

In examples where meandering trails are more ubiquitous it is likely that improved food availability gives rise to dense populations of benthic infauna. High population densities have also been attributed to the development of meandering and spiraling trails whereby spatial competition restricts the feeding territory of an individual (Hayes, 2003). It has been further suggested that where benthic-food content is very high (i.e., littoral zone), behavioral specialization is not requisite (Wetzel, 1991). Evidence of organism behavior in response to benthic food content are found in Paleogene Flysch deposits in the Polish Carpathians, where high benthic food content in surface sediments results in high levels of grazing and near surface feeding burrows (Wetzel and Uchman, 1998). To summarize, it is generally thought that a decrease in food content leads to increasingly specialized feeding behaviors. This thinking is anecdotal as the aforementioned relationship has not been tested in modern sedimentary environments.

Traces in the lacustrine *Mermia* ichnofacies also exhibit complex meanders and spirals (Buatois and Mangano, 1998). However Buatois and Mangano (1998) also reported that traces in lacustrine deposits are less specialized than those found in the *Nereites* ichnofacies. They suggest that the highly specialized feeding strategies in the deep-marine realm reflect scarcity of food (following earlier interpretations), whereas the low specialization of grazing traces in the lacustrine *Mermia* ichnofacies reflect abundance and accessibility of food (Buatois and Mangano, 1998). Although Buatois and Mangano (1998) offer a sound rationale for the differences between those lacustrine trace fossils and their *Nereites* Ichnofacies counterparts, it should be noted that lacustrine basins are extremely short lived compared to marine basins, a factor that may have severely limited the development of specialized feeding behaviors in quiescent fresh waters.

Richter was the first to interpret meandering and spiraling *Helminthoida* traces observed in turbidites (Osgood, 1975). He attributed them to a sediment-eating organism that grazed either on or in the sediment so as to maximize exploitation of the local food resource (Osgood, 1975). Richter proposed three behavioral characteristics evident in *Helminthoida:* phobotaxis, thigmotaxis, and strophotaxis (these terms, derived from the biological literature have been recapitulated several times since: Raup and Seilacher, 1969; Osgood, 1975; Papentin and Röder; 1975; Hayes, 2003). Phobotaxis is avoidance of other animal's tracks and earlier self-made tracks, thigmotaxis aids the animal in moving parallel and in close proximity to existing tracks and strophotaxis reflects the ability of an organism to make 180° turns (Raup and Seilacher, 1969). The tracks produced by *C. caeca* in the intertidal zone of Waterside Beach show rudimentary phobotaxis and poorly developed strophotaxis. Thereby *C. caeca* trails display a lesser degree of complexity in the regularity of looping.

Chiridotea caeca

Our species identification of the isopod is based on comparative morphology of Richardson (1905) and McLaughlin (1980). *Chiridotea caeca* is a marine, Valviferan isopod of the Chaetiliidae Family (Fig. 2). It is found in sandy intertidal zones of the western North Atlantic from New Brunswick to Florida (Richardson, 1905; Griffith and Telford, 1985; Mcdermott, 2001). Griffith and Telford (1985) consider a similar species, *C. coeca,* to be carnivorous; however, *C. caeca* at Waterside Beach was observed scavenging for food as well. During the study, the isopod began foraging for food once the retreating tide had exposed the local foreshore. The isopods seemingly exploit organics that settled on the sand flat during high tide. During high tides, *C. caeca* remains buried under a thin, 1 cm veneer of sediment to escape predation from fish (Griffith and Telford, 1985). Organisms collected from Waterside Beach range in length from 4 to 13 mm, with a width approximately half the length of the isopod.

Adaptations for burrowing by a similar species, *Chiridotea coeca,* were studied by Griffith and Telford (1985). They observed that upon initiation of burrowing the first three pair of gnathopods (the foremost three pair of appendages) are driven into the sediment, while the posterior pleopods (small ‘flippers’ on the underside of the ‘tail’) beat rapidly (Fig. 2). This motion generates a current of water that effectively drives the animal into the sand. Once the first half of the organism is buried in the sand, the pleopods beat more slowly, inducing a respiratory current. The pereiopods, which are the four pair of appendages used for walking (Fig. 2), are responsible for the majority of forward motion. As *Chiridotea* moves into the water-saturated sand, particles are displaced horizontally and vertically around the body, leaving a collapsed burrow.

Study Area

Waterside Beach is located along the New Brunswick coastline of the Bay of Fundy, Canada, approximately midway up Chignecto Bay (Fig. 1). The study area is a 20 000 m^2 area in the southeast region of Waterside Beach (Fig. 1C). Mean spring tidal range exceeds 12 m. The extreme tidal range and shallow bathymetric gradient exposes a wide intertidal zone, presenting an opportunity to study animal-sediment relationships on the beach at low tide.

Methods

A 20 000 m^2 area of Waterside Beach was chosen for study due to high incidence of burrowing activity by *Chiridotea caeca*. The beach is separated into three distinct zones, based on beach slope and the observed sedimentary structures. The first occurs at the top of the beach and consists of plane-bedded sands crosscut by rills and runoff chutes. The second area consists of ebb-current modified wave ripples that are generally water saturated throughout the tidal cycle. The third and lowermost zone is entirely wave-ripple laminated. Multiple observation stations were set within each of the three zones. The wave-rippled zone encompasses an area of higher topographic relief. This area proved to be an exceptional region to conduct detailed studies of the tunnels of *C. caeca,* because the sands were not water saturated. Therein the preserved trackways were well defined and their complexities easily observed.

One meter by one meter and 0.5 m by 0.5 m stations were erected to detail and photograph tracks. At each station, sediment was collected to assess total organic carbon content (TOC). Control samples were taken from unburrowed sediment for comparative purposes. Population counts of *C. caeca* and detailed observations were taken at each station.

The beach-normal physiography was contrived through transects. Sedimentary structures and other notable features were photographed. Shallow trenches and surface observation were the primary means of collecting neoichnological data. Box cores, measuring 23 cm by 15 cm by 8 cm, were collected across the study area and x-rayed to image sedimentary structures in the vertical plane. The box cores were inserted into the sediment normal to the sedimentary structures observed on the surface. Sediment within the core was extracted and transferred to a 2 cm deep tray, which was subsequently imaged using a Soyee portable x-ray system (SY-31-100P). Two 1000 g samples of sediment were taken from the upper 3 to 4 cm of the study area for determination of the average grain size. These samples were sieved through screens of phi sizes –2 ϕ (4 mm) to 4 ϕ (0.0625 mm). Samples collected at individual stations for TOC were subjected to loss-on-ignition (LOI) analysis following the procedure prescribed by Heiri et al. (2001). Samples were dried for 24 hours at 105° C to remove interstitial water, and then disaggregated with mortar and pestle. Dried samples were placed in a high temperature oven and cooked at 550° C for 4 hours to remove organic carbon. Dry weights were measured before and after LOI and the weight percent difference plotted against burrow morphologies.

RESULTS

Sedimentology

Medium-grained sand (1 to 2 ϕ) is the dominant grain size within the study area, although the portion of fine-grained sand increases in the offshore direction. Figure 3 shows x-ray images of box cores taken from these sands. Figure 3A is taken from the plane-bedded sand in the upper intertidal zone (zone 1). Near the bottom of Figure 3A, landward-directed ripple cross-laminations are overlain by plane-beds. The plane beds dip seaward at the same angle as the beach surface. Above the plane beds, wave-rippled sand passes vertically into a massive to blurry appearing bed that may represent crypto- (*sensu* Howard and Frey, 1975) or cryptic-bioturbation (Bromley, 1990; Saunders and Pemberton, 1990; Gingras et al., 2002). The primary sedimentary structures in the cryptically bioturbated zone are destroyed by the tunneling activity of *Chiridotea caeca.*

In Figure 3B, the box core was taken from the current-modified wave ripple zone (zone 2). At the base of the core, seaward-dipping trough-cross beds occur with granule- and pebble-lined foresets. Above this are landward-dipping current-ripple laminae, which are in turn overlain by weakly defined (mottled) plane beds (Fig. 3B). Similar to Figure 3A, this bedding distortion likely results from the tunneling activity of *C. caeca.* Above the plane-bedded zone, bedding disruption increases reflecting an increase in biogenic reworking of the sediment.

Neoichnology

The majority of the endobenthic traces in the area comprise vertical and horizontal structures constructed by polychaetes. One such structure is the mucous-bound, vertical tube of the Bamboo worm, *Clymenella torquata.* The tubes are observed as chimneys in all areas except for the plane-bedded sands. Another burrow commonly observed is the slender, vertical, mucous-bound tube of the threadworm, *Heteromastus filiformis.* These two vertical structures are analogous to *Skolithos* burrows. Surface runoff commonly exposes high densities of these tubes, with many tubes washed out of the sediment and deposited in ripple troughs (Fig. 4A). Low occurrence of the carnivorous polychaete *Nephtys sp.* is noted. *Nephtys sp.* propel themselves through the sediment using their proboscis and paristoltic movements of their body (Navichnia, *sensu* MacEachern et al., 2006). As such, they disrupt the sediment, but do not leave behind an evident burrow in the sand. Another abundant trace is that formed by the worm *Paraonis fulgens*. *P. fulgens* produce multi-level horizontal spiral and meandering burrows within the sand (Fig. 4B). This feeding pattern optimizes food uptake in a given area (Papentin, 1973; Papentin and Röder, 1975; Bromley, 1990); however, the behavior is quite poorly understood.

Surface tracks other than those made by *C. caeca* were produced by gastropods (Fig. 4C). The snails produced *Aulichnities*-like (Ekdale, 1985) traces consisting of a shallow groove, with slight displacement of sand laterally to create small ridges on either side of the groove. The gastropod tracks look very similar to those tracks produced by *C. caeca* when the isopod is not tunneling under the sediment, but rather plowing its way across the surface (Figs. 4C, 6C). For *C. caeca* (in this study), this type of trackway is termed ‘surface locomotion’, which is described and discussed in detail below.

Trackway Morphology and Architecture of *Chiridotea caeca*

The burrowing activity of the Valviferan isopod *Chiridotea caeca* is restricted to ripple troughs or run-off chutes in plane-bedded sands. Moreover, bioturbation is most prevalent, but not restricted to water-saturated sands. As the tides retreat the sands dewater resulting in a shift of burrowing activity to the more water-saturated sands. Tracks made by *C. caeca* are classified into three plan-view morphologies – sinuous to linear (Fig. 5A, B), looping (Fig. 5C, D), and convolute (Fig. 5E, F). Trackway classification depends on the plan-view geometry of the trail and the degree of crossover. Crossover is negligible in linear tracks, but increases from looping to convolute (Fig. 5). Loops become obscured by increasingly numerous crossovers (Fig. 5E, F).

Convolute tracks are the most prevalent, followed by looping and then linear. The *C. caeca* population densities are highest in areas dominated by convolute tracks and lowest in areas characterized by linear tracks. Thirty-two to eighty-eight isopods per m^2 were counted in convolute-trackway dominated areas versus 12 to 24 isopods where looping is the main trackway morphology. Stations dominated by linear tracks range from 4 to 12 isopods / m^2.

In addition to the track morphologies described, tunnels exhibit different architectures corresponding to the depth of burrowing. The trackway may thus be subdivided into three groups based on the observed burrow architecture, including: collapsed tunnels (Fig. 6A), excavations (Fig. 6B), and surface locomotion (Fig. 6C). Collapsed-tunnel trackways are the deepest penetrating burrows and develop when the isopod tunnels through the sediment in the same fashion as that described by Griffith and Telford (1985). Collapsed tunnel tracks occur mostly within ripple troughs. Moreover, the majority of collapsed tunnel tracks are associated with complex trackway morphologies. Excavations are tracks that are left after the isopod plows near to the sediment surface leaving a trail similar to that of a gastropod (Fig. 4C). Surface locomotion trackways are the shallowest penetrating structures and preserve the most surface detail. These tracks comprise twinned shallow grooves separated by a slender bulge (Fig. 6C). In surface locomotion, and to a lesser extent excavation-type tracks, small pits are observed where the isopod stops moving and digs deeper into the sediment. Surface locomotion and excavation-type tracks are almost always employed where an isopod has crossed ripple crests.

Total Organic Carbon Content

Total organic carbon (TOC) content in the study area is relatively low, ranging from 0.97% to 1.80%. Figure 7 is a plot of burrow morphology (i.e. convolute, looping, linear, and no tracks) versus TOC content. There is a direct relationship between TOC levels and bioturbation intensity. Sediments exhibiting convolute trackway morphologies have the highest levels of TOC, whereas unburrowed sediments have the lowest (Fig. 7). Linear regression of the TOC highest value, average value, and lowest value (through each trace morphology) shows a negative slope in the direction of the unbioturbated sediments.

Figure 8 shows the architectural classification of trackways plotted versus TOC. Therein is demonstrated a direct relationship between the TOC of the sediment and the penetration depth of the track. Collapsed tunnels occur in sediments with the most TOC, plowed excavations show medial TOC values, and surface locomotion trackways in sediments contain the least TOC. Linear regression shows a negative slope in the direction of shallow track depth (surface locomotion).

INTERPRETATION AND DISCUSSION

The low diversity and high abundance of traces in the study area is a reflection of the moderate energies and dependable food supply of the upper intertidal zone. Shifting substrates, long periods of subaerial exposure, and exposure to both fair weather and storm weather contribute to the low diversity of organisms in this environment. Vertical, agglutinated Domichnia, and the rare occurrence of horizontal traces are typical of the *Skolithos* ichnofacies (Seilacher, 1967a, 1967b; Bromley, 1990; Pemberton et al., 2001). Vertical traces include those of the worms *Clymenella torquata* and *Heteromastus filiformis.* These deeply penetrating and reinforced structures are less likely to be destroyed by the shifting substrate (Bromley, 1990), whereas the delicate *Paraonis* spirals have a low preservation potential.

The study area has high numbers of the isopod *Chiridotea caeca,* which in part demonstrates the isopods preference for medium-grained sandy substrates (Griffith and Telford, 1985). They also showed that *C. coeca* preferentially ‘tunnels’ in substrates of this grain size. *C. caeca* will also show a preference for water-saturated sands, which are easier to move through and provide a means for respiration. This was observed in the general trend of higher population in areas of high water saturation, a trend that is progressively exaggerated throughout the tidal cycle.

Trackway Morphology, Architecture, and TOC Content

C. caeca, as a grazing scavenger, is most likely extracting detrital organic matter from the sand. Zaslavskiy (1981) has shown that detrital organic matter consists of lipids, proteins and carbohydrates, with lipids highest in concentration. Benthic food content in sediment also consists of molecular-sized organics, which can coat grains and mix with interstitial pore fluids (Zaslayskiy, 1981). Due to the low amount of sand found within the gut of *C. caeca,* it is probable that the isopod is selectively extracting detrital organic matter from the sediment. This includes fragments of tissues of organisms, aggregates of detrital organic matter, and pelobacteria (Zaslayskiy, 1981). Alternatively, Mcdermott (2005), in lab experiments, observed *C. caeca* predating on sympatric benthic fauna such as a species of haustoriid amphipod and two types of polycheates. This suggests that *C. caeca* is both a scavenger and a predator.

Looping and crossovers are coincident with high TOC, high numbers of individuals, and observable water saturation. However, the measurable correlation between trackway morphology and TOC (Fig. 7) demonstrates the propensity of *C.caeca* to crossover or loop in response to elevated TOC. Whereas linear trails represent the simplest behavior observed, and occur in the sand with the lowest TOC. This trend suggests that benthic food content in the sand directly influences the behavior of *C. caeca.* Two anomalously low TOC values measured in sediment characterized by trace looping may represent partial consumption of the organic carbon by the grazing isopods: average and highest TOC values are still measurably higher in sediment characterized by the looping behavior.

Looping and convolute trackways can be described as a form of meandering behavior, with crossover displaying a penchant for the higher food concentrations in the sediment (Fig. 9). Seilacher (1986) describes regular meanders as tracks in which successive lobes are guided by existing lobes without ever crossing over. Regular meanders are found in a wide variety of environments. Meandering is most prevalent and complex in deep-sea environments where systematic foraging is the most efficient means to extract food from the sediment (Seilacher, 1986). Phobotaxis, thigmotaxis, and strophotaxis are exercised by organisms in this environment partly as an evolutionary adaptation to the type and frequency of food deposition. Behavioral adaptation in *Chiridotea caeca*, namely the method by which food is extracted from the surroundings, does not display such a high degree of complexity in the intertidal area where food resources may be concentrated, patchy, and rapidly renewed.

The isopod strategy aims to utilize the highest concentrations of food available in a rapid manner. This is evidenced in the crossing over of previous tracks, which displays less efficiency in coverage of the entire substrate when extracting food. Where the food content is low, no specialized Pascichnial behavior is employed, and linear trackways are observed (Figs. 5A, B): these are essentially motility traces representing an isopod 'run' in a search for concentrated food. With increasing food content, a more specialized 'meandering' behavior is observed, culminating in looping trackways (Figs. 5C, D). Where the food content is high, the specialized behavior breaks down and successive loops are obscured (Figs. 5E, F): this represents a feeding frenzy of sorts and any attempts at once-over strategies are abandoned. Wetzel (1991) suggests that with high enough food content, behavioral specialization is not exercised (although that is a specialized behavior in of itself). This dataset certainly supports those interpretations.

A correlation also exists between track architecture and TOC content. Collapsed-tunnel tracks have the highest TOC content, followed by excavations, and finally surface locomotion. As above, the single anomalous low TOC value measured in sediment characterized by deeper collapsed burrows may represent partial reduction of the TOC by the higher numbers of isopods—average and maximum TOC values are still highest in association with this behavior. In terms of food content, the collapsed tunnels can be described as a Pascichnial feeding structure from which the isopod grazes upon organic detritus from the sediment. Lower levels of food cause the organism to change its behavior, as seen in the shift to excavations and surface-locomotion tracks. It can be inferred from observations that surface locomotion, in a similar fashion to linear tracks, is exercised when traveling between areas of high food content, and are thus a Repichnial trace. Behavior associated with collapsed tunnels is usually only exercised in ripple troughs. This is positively correlated with higher TOC. Moreover, collapsed-tunnel tracks are often associated with some degree of looping behavior within ripple troughs (Fig. 5E, F).

In summary, this study shows that feeding behavior of the isopod *C. caeca* can be correlated to the TOC in sediment. We contend that this represents an animal response to an exploitable food resource. Track morphologies are more complex, or convoluted, with increased TOC. Tunneling, the type observed in Figure 6A, as opposed to more epibenthic locomotion like that of the excavations and surface locomotion tracks, also correlates with higher values of TOC. Although intertidal feeding patterns have a low preservation potential the animal response to abundant but patchy food can likely be applied in sub-sea settings. The apparent analogy provided herein to Wetzel's (1991) deeper-water interpretations support the validity of broader application.

CONCLUSIONS

Although it has never been demonstrated, the organic content (i.e. available food) of a substrate is commonly used to explain variations in burrow morphology in sedimentary rocks. This is a hypothesis for good reason: the hypothesized relationship could not be established with fossil examples, and deep-sea examples, where the behavior is prevalent, are too inaccessible to assess. Thereby an intertidal proxy provides the first measured correlation between animal behavior and sediment TOC.

Our general findings include: (1) the neoichnology of the upper intertidal zone at Waterside consists of structures typical of a stressed *Skolithos* ichnofacies; (2) the burrow morphology of the isopod *Chiridotea caeca* is variable, however increases in animal looping and crossover correlate with increases in organic carbon content; and (3) the relationship between burrow architecture and TOC indicates that deeper tunneling correlates with higher levels of organic carbon, with levels decreasing as burrowing becomes shallower.

ACKNOWLEDGMENTS

Funding for this research under which this data was collected was generously provided by the Natural Sciences and Engineering Research Council (NSERC), BP Canada, Talisman Energy, Nexen Energy, Devon Energy, ConocoPhillips Houston, and Petro Canada.

FIGURES

FIGURE 1 – Map of the study area. (A) Location of the Bay of Fundy in Canada. (B) Location of Waterside Beach in the Bay of Fundy at high tide with the study area indicated.

FIGURE 2 – Sketch of *Chiridotea caeca.* A small, dorso-ventrally flattened isopod. The function of the labeled appendages is described in the text.

FIGURE 3 – Xrays from two box cores within the study area. (A) Box core taken from the sheet-bedded sands adjacent to the steeply dipping foreshore. (B) Box core taken from the current-modified wave ripples further down the foreshore. Notice the blurred laminations in both xrays. This is likely a product of the burrowing of *C. caeca*.

FIGURE 4 – Images of neoichnological structures occurring with *C. caeca*. (A). Mucous-lined burrows of *Heteromastis filiformis* (white arrows) that have accumulated in a wave-ripple trough. *C. caeca* trackways (black arrows) also occur in the trough. The round hole near the top of the image is the result of water drainage from the sample tray. (B) Delicate, mucous-lined spirals of *Paraonis fulgens.* (C) Similarities between the gastropod (*Littorina littorea*) track (white arrow) and the 'surface locomotion' track of *C. caeca* (black arrow).

FIGURE 5 – Trackway morphology of *C. caeca*. Large-scale example (A) and close up (B) of linear burrows displaying no crossover. (C) and (D) Looping burrow morphology displaying moderate crossover. (E) and (F) Convolute burrows displaying high crossover.

FIGURE 6 – Trackway architecture of *C. caeca*. (A) Collapsed tunnels are the deepest penetrating structure and contain the highest organic carbon contents. (B) Excavation tracks are of moderate depth and contain moderate amounts of organic carbon. (C) Surface locomotion tracks that contain the lowest amounts of organic carbon.

FIGURE 7 – Graph of organic carbon weight percent versus burrow morphology. Linear regression shows that high organic carbon content is associated with crossover (convolute tracks). Organic carbon contents drop progressively with looping tracks (intermediate crossover), linear tracks (no crossover), and unbioturbated sediments. Linear regression slopes are negative in the direction of unbioturbated sediments for high-, average-, and low points of each burrow morphology.

FIGURE 8 – Graph of organic carbon weight percent versus burrow morphology. Linear regression shows that high organic carbon content is associated with greater depth of the burrow (collapsed tunnels). Organic carbon contents drop progressively with excavations (intermediate depth) and surface locomotion tracks. Linear regression shows negative slopes in the direction of surface locomotion for high-, average-, and low points of each burrow morphology.

FIGURE 9 – Model depicting feeding patterns associated with C. caeca in intertidal deposits of Waterside Beach. Increasing food content correlates with increasing crossover and increasing complexity.

REFERENCES

Bromley, R.G., 1990, Trace Fossils; Biology and Taphonomy: Unwin Hyman, London, 280 p.

Buatois, L.A., and Mangano, G.M., 1998, Trace fossil analysis of lacustrine facies and basins: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 140, p. 367-382.

Ekdale, A.A., 1985, Paleoecology of the marine endobenthos: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 50, p. 63-81.

Gingras, M.K., MacMillan, B., Balcom, B.J., Saunders, T., and Pemberton, S.G., 2002, Using magnetic resonance imaging and petrographic techniques to understand the textural attributes and porosity distribution in *Macaronichnus*-burrowed sandstone: Journal of Sedimentary Research, v. 72, p. 552-558.

Griffith, H., and Telford, M., 1985, Morphological adaptations to burrowing in *Chiridotea coeca* (Crustacea Isopoda): Biological Bulletin, v. 168, p. 296-311.

Hayes, B., 2003, In search of the optimal scumsucking bottomfeeder: American Scientist, v. 91, p. 392-396.

Howard, J.D., and Frey, R.W., 1975, Regional animal-sediment characteristics of Georgia estuaries: Senckenbergiana Maritima, v. 7, p. 33-107.

MacEachern, J.A., Bann, K.L., Pemberton, S.G., and Gingras, M.K., 2006, The ichnofacies paradigm: High-resolution paleoenvironmental interpretation of the rock record: *in* MacEachern, J.A., and Gingras, M.K., eds., Applications of Ichnology to Subsurface Datasets: SEPM Society of Sedimentary Geology, Tulsa, OK, p. 1-33.

Mcdermott, J.J., 2001, Biology of *Chiridotea caeca* (Say, 1818)(Isopoda: Idoteidae) in the surf zone of exposed sandy beaches along the coast of southern New Jersey, USA: Ophelia, v. 55, p. 123-135.

Mcdermott, J.J., 2005, Food habits of the surf-zone isopod *Chiridotea caeca* (Say, 1818) (Chaetiliidae) along the coast of New Jersey, U.S.A.: Proceedings of the Biological Society of Washington, v. 118, p. 63-73.

Osgood, R.G.J., 1975, The paleontological significance of trace fossils: *in* Frey, R.W., ed., The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology: Springer-Verlag, New York, p. 87-108.

Papentin, F., 1973, A Darwinian evolutionary system III: Experiments on the evolution of feeding patterns: Journal of Theoretical Biology, v. 39, p. 431-445.

Papentin, F., and Röder, H., 1975, Feeding patterns: The evolution of a problem and a problem of evolution: Neues Jahrbuch fur Geologie und Palaontologie, v. 148, p. 184-192.

Pemberton, S.G., Spila, M., Pulham, A.J., Saunders, T., MacEachern, J.A., Robbins, D., and Sinclair, I.K., 2001, Ichnology and Sedimentology of Shallow to Marginal Marine Systems: Ben Nevis and Avalon Reservoirs, Jeanne d'Arc Basin: Geological Association of Canada, St. John's, 343 p.

Raup, D.M., and Seilacher, A., 1969, Fossil foraging behavior: computer simulation: Science, v. 166, p. 994-995.

Richardson, H., 1905, A monograph on the isopods of North America: Bulletin of the Washington Government Printing Office, v. 54, p. 346-355.

Saunders, T., and Pemberton, S.G., 1990, On the palaeoecological significance of the trace fossil *Macaronichnus*: *in*: Sedimentologists, A.o., ed., 13th International Sedimentological Congress, Nottingham, England.

Seilacher, A., 1953, Uber die methoden der palichnologie 1: Studien zur palichologie: Neues Jahrbuch fur Geologie und Palaontologie, v. 96, p. 421-452.

Seilacher, A., 1967a, Bathymetry of trace fossils: Marine Geology, v. 5, p. 413-428.

Seilacher, A., 1967b, Fossil behavior: Scientific American, v. 217, p. 72-80.

Seilacher, A., 1974, Flysch trace fossils: Evolution of behavioral diversity in the deep sea: Archaeologica Venatoria, v. 3, p. 233-244.

Seilacher, A., 1986, Evolution of behavior as expressed in marine trace fossils: *in* Kitchell, J.A., and Nitecki, M.H., eds., Evolution of Animanl Behavior: Paleontological and Field Approaches: Oxford University Press, New York, p. 62-87.

Simpson, S., 1975, Classification of trace fossils: *in* Frey, R.W., ed., The Study of Trace Fossils: A Synthesis of Principles, Problems, and Procedures in Ichnology: Springer-Verlag, New York, p. 39-54.

Uchman, A., 2003, Trends in diversity, frequency and complexity of graphoglyptid trace fossils: Evolutionary and palaeoenvironmental aspects: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 192, p. 123-142.

Wetzel, A., 1991, Ecologic interpretation of deep-sea trace fossil communities: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 85, p. 47-69.

Wetzel, A., and Uchman, A., 1998, Deep-sea benthic food content recorded by ichnofabrics: a conceptual model based on observations from Paleogene flysch, Carpathians, Poland: Palaios, v. 13, p. 533-546.

Zaslayskiy, Y.E.M., 1981, The content and biochemical composition of organic detritus in marine sediments: Oceanology, v. 21, p. 736-740.

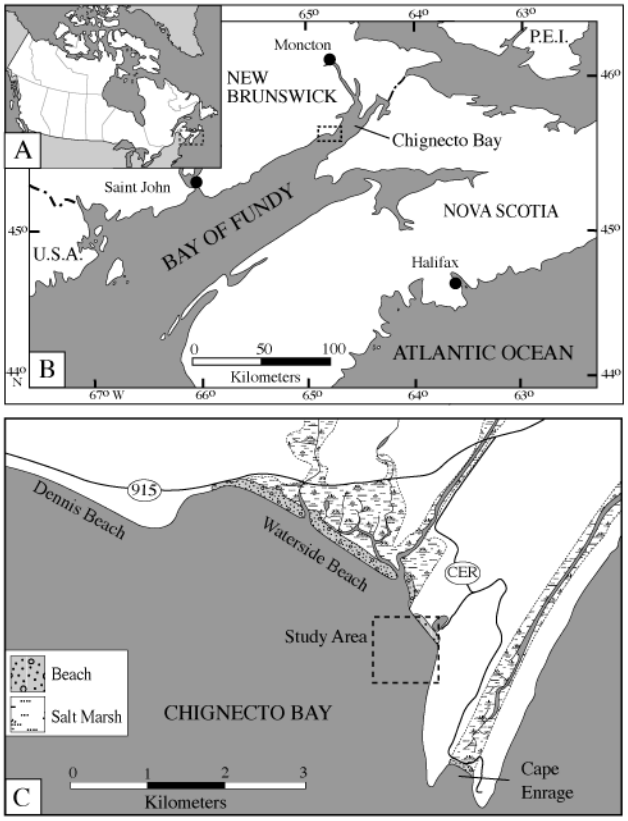

Figure 1, Hauck et al.
(1 column width)

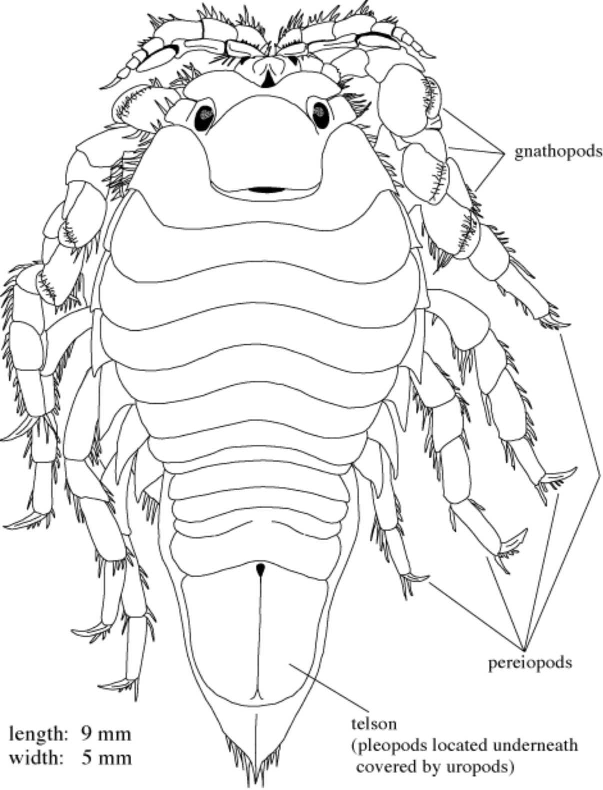

Figure 2, Hauck et al.
(1 column width)

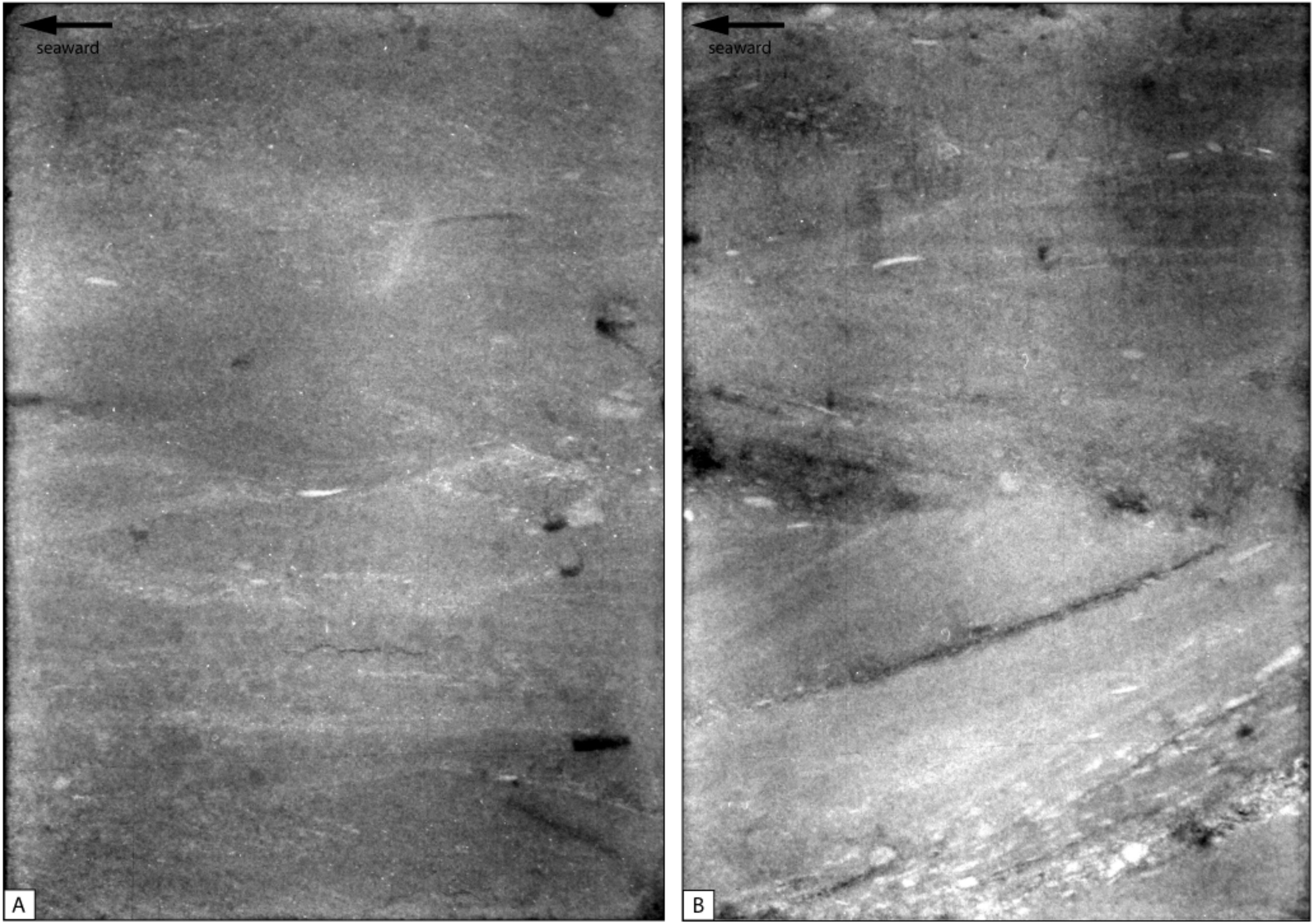

Figure 3, Hauck et al.
(2 column width)

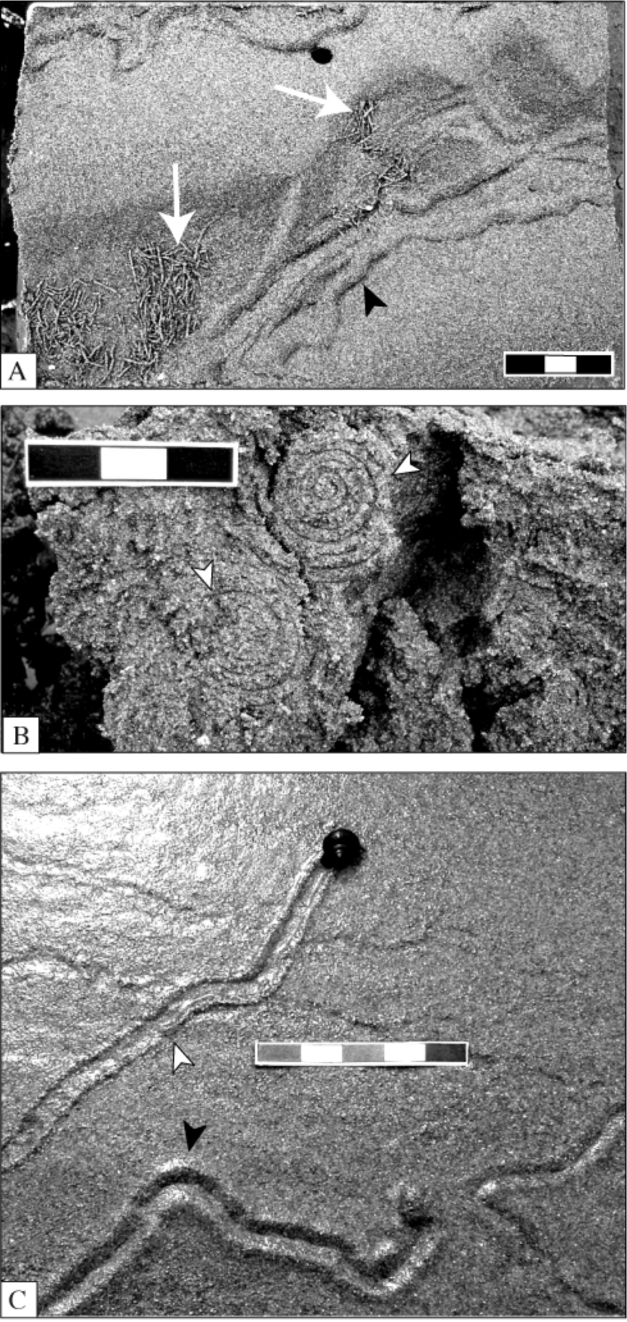

Figure 4, Hauck et al.
(1 column width)

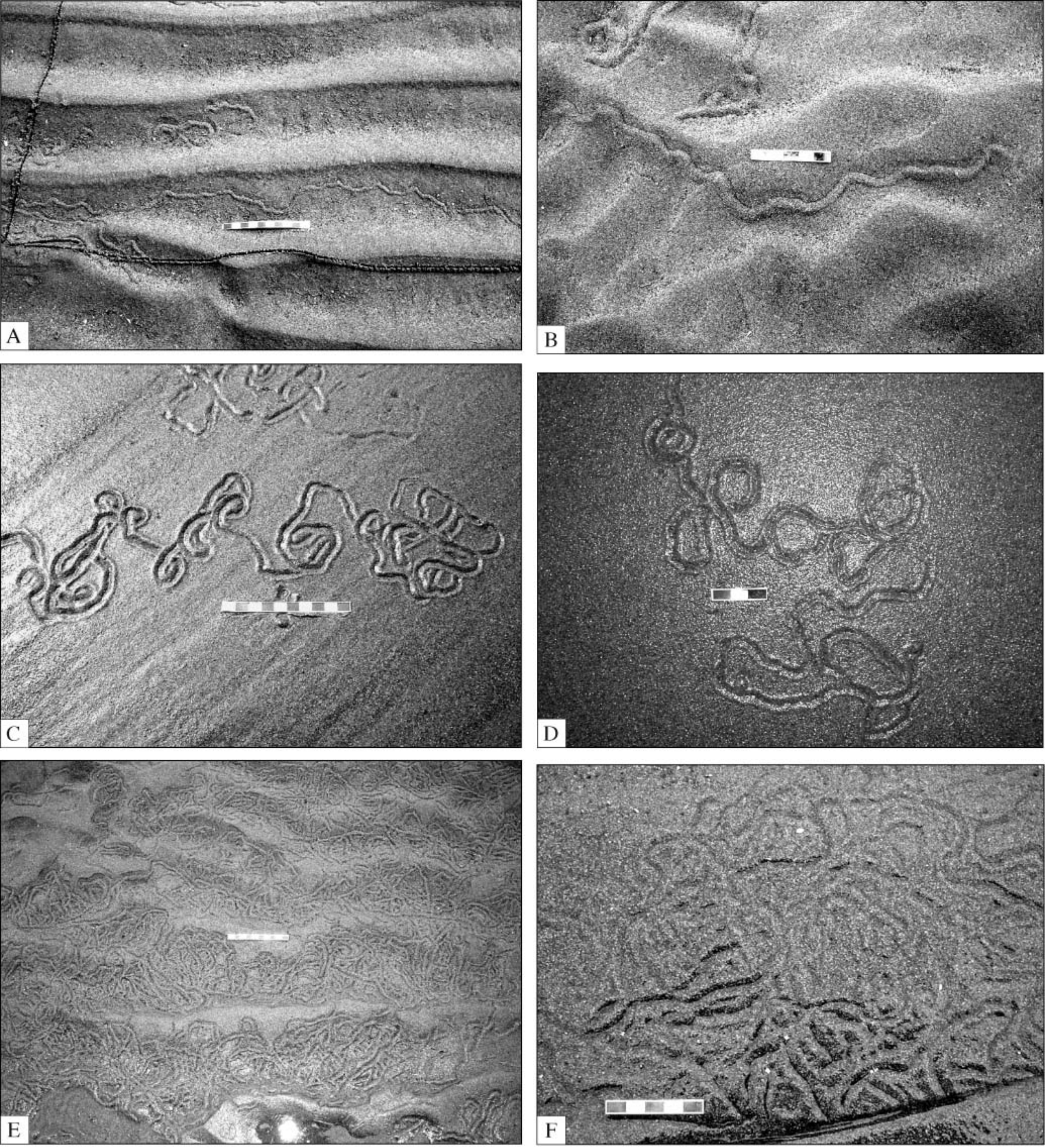

Figure 5, Hauck et al.
(2 column width)

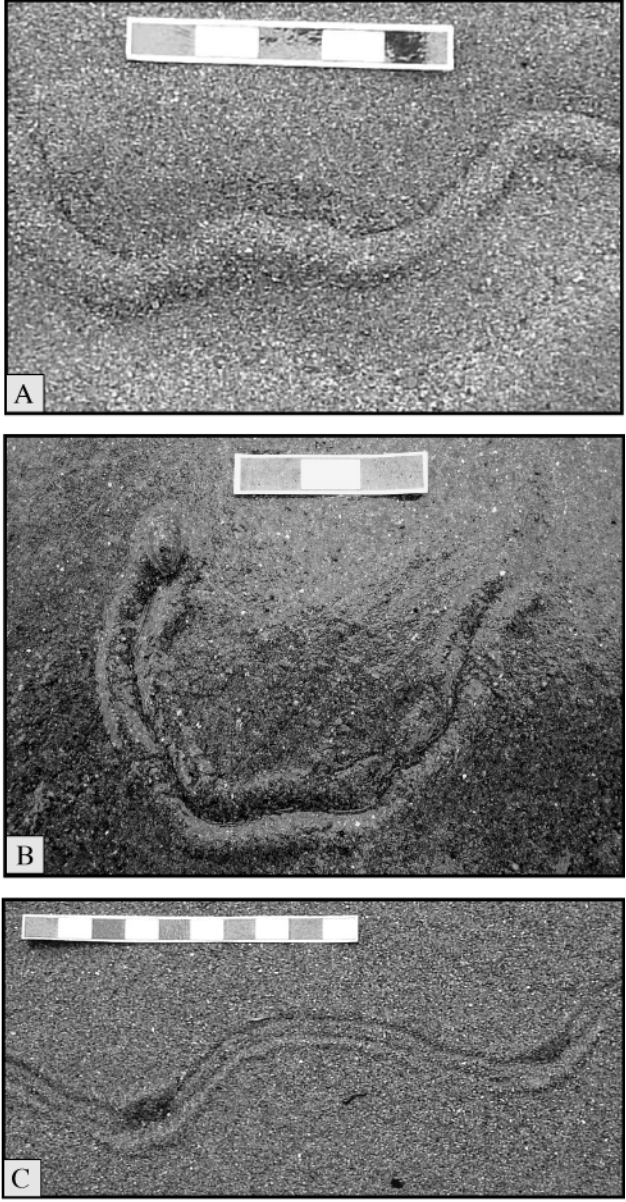

Figure 6, Hauck et al.
(1 column width)

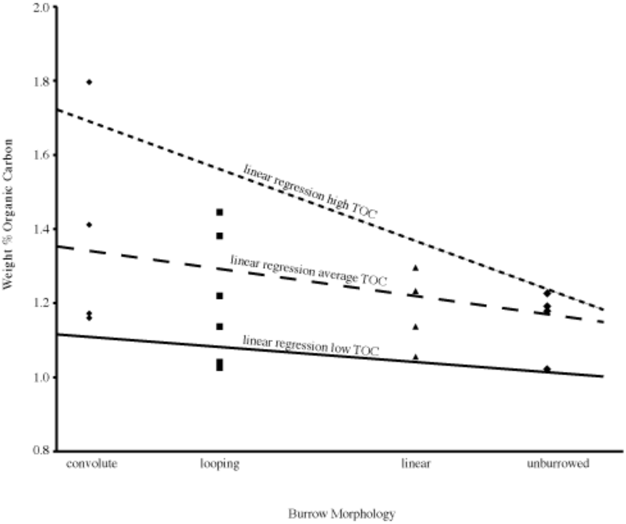

Figure 7, Hauck et al.
(1 column width)

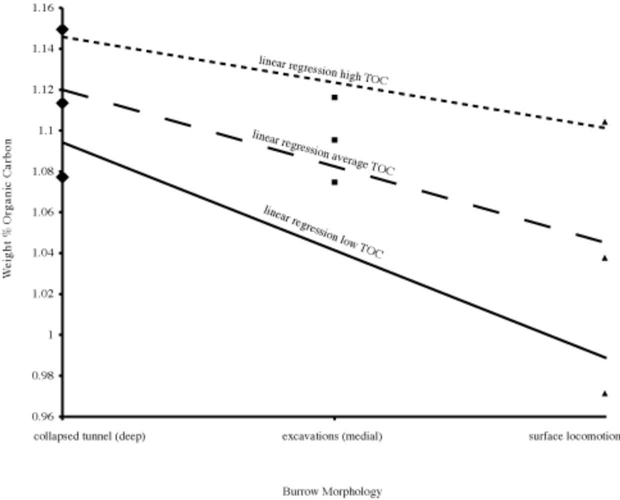

Figure 8, Hauck et al.
(1 column width)

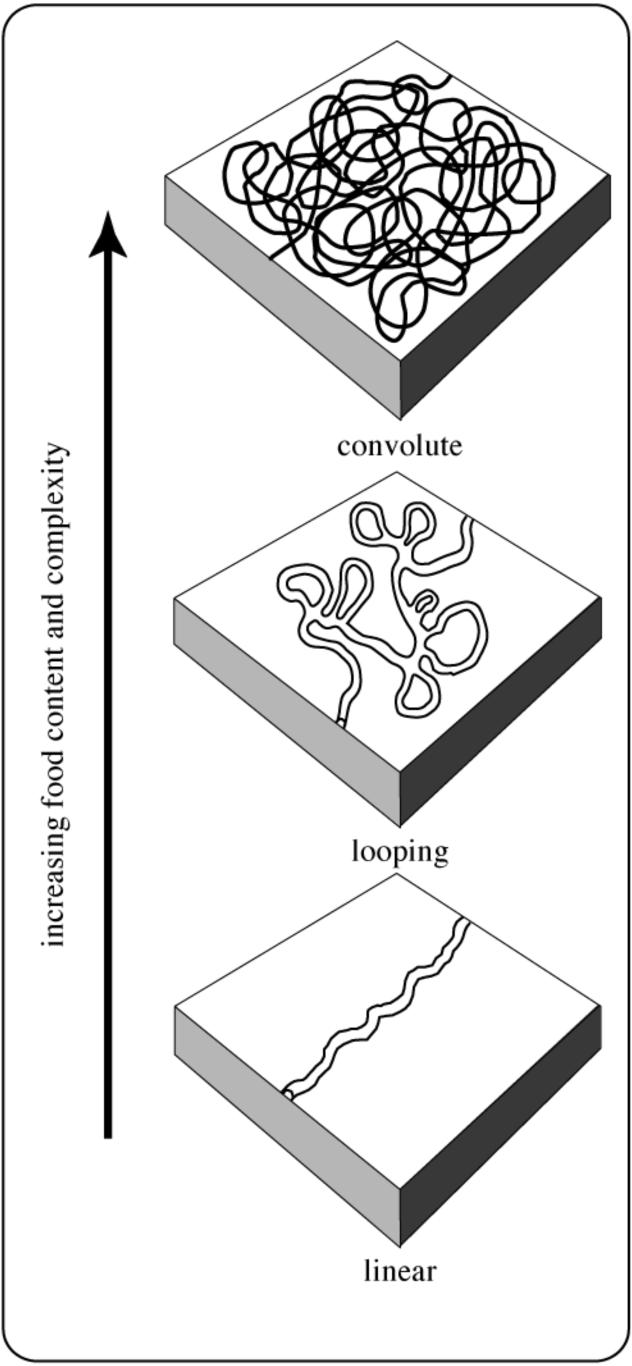

Figure 9, Hauck et al.
(1 column width)