



Biology of shallow marine ichnology: a modern perspective

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ABSTRACT: This study considers the construction and functionality of biogenic structures made by marine, vermiform nemerteans, polychaetes and hemichordates; marine crustaceans; motile bivalves; motile echinoderms; and sponges and sea anemones. We report on a range of modern biogenic structures similar to several known ichnogenera. Vermiform animals dominantly occupy vertical burrows that range from simple through helical shafts to Y- and U-shapes. Horizontal traces made by worms range in form, but are dominated by branching and variably sinuous to meandering burrows. Crustaceans primarily excavate open burrow systems that possess a range of architectures that are similar to either *Thalassinoides* or *Psilonichnus*. Smaller crustaceans, such as amphipods, mix the sediment. Bivalve traces vary in form, but generally preserve evidence of vertically oriented filter or interface-deposit feeding from a stationary location, rapid vertical escape, or horizontal grazing. Echinoderms dominantly preserve body impressions and motility traces, such as *Asteriacites*. An important class of biogenic structure, *Scolicia* and *Bichordites*, are made by urchins. Finally, sea anemones can generate large, penetrative, conical biogenic structures. Large, open horizontal networks serve as domiciles and deposit-feeding structures for crustaceans, but with worms similar burrow types are used more for passive carnivory and establishing an interface-feeding network. We report that the trace fossil *Gyrolithes* potentially represents mechanical ramps for shrimp, but is used as a sediment holdfast when made by worms. Finally, Y-shaped burrows are used for filter feeding in shrimp, and interface-deposit feeding in worms. These examples emphasize that inferences of behavior in the rock record are interpretive.

KEY WORDS: Ichnology · Neoichnology · Traces · Crustacea · Vermiforms · Bivalves · Echinoderms · Anemones

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INTRODUCTION

Ichnology is the study of trace fossils (or ichnofossils), which primarily constitute the fossilized trails and burrows of animals. Commonly, and inaccurately referred to as 'tracks and trails', these vestiges of animal activity reflect the behavior that animals employed in order to live, feed, move, or hide within their environments. Interpretation of the animal's behavior can lead to better interpretations of the depositional conditions, towards which ichnology is largely applied. Trace fossils are classified morphologically, and are assigned to

ichnogenera and ichnospecies on that basis (see Bertling et al. 2006 for a complete review of ichnotaxonomy). As such, trace-fossil names are taxonomically independent of the animal that made them. Below we present several trace-fossil names. These are used so that this summary paper can be linked to the ichnological literature.

Although trace fossils may owe much of their resultant morphology to their tracemaker, this relationship is rarely stressed in the ichnological literature. This is mainly because a large range of tracemakers can generate the same traces if employing broadly similar

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behaviors to survive comparable environmental conditions (Ekdale et al. 1984). Nevertheless, a better understanding of trace fossils can be obtained if modern animals are studied in the context of their trace-making behaviors. Herein, we explore the more common traces observed in modern environments and associate those traces to groups of animals. This paper particularly focuses on the infaunal behavior of invertebrates in marginal-marine and marine settings. The main groups of animals considered herein are: vermiform nemerteans, polychaetes and hemichordates; a range of marine crustaceans; bivalves; motile echinoderms; and, to a lesser degree, sponges and sea anemones. These groups of animals were chosen on the basis of their abundance in marine environments, the common occurrence of ichnofossils similar to their traces, and the many studies of their trace-making behavior. Animals that bore into hard substrates are not reported, as such studies have been previously performed and are not discussed here (e.g. Kelly & Bromley 1984, Bromley 1994). The aim of the present work is not to suggest limitations to the interpretations of trace fossils, but to increase the range of possible interpretations.

MATERIALS AND METHODS

Most data on modern traces are collected using 1 of 3 methods: (1) manual excavation of sediment in intertidal zones, with careful splitting of the sediment along and perpendicular to bedding planes; (2) resin or plaster casts of burrows, whereby a burrow is flooded with polyester, polyurethane resin, or plaster, and the cast is removed upon hardening of the substance (e.g. Bouma 1969); and (3) collection and slabbing of sediment box-cores followed by X-ray imaging (e.g. Gingras et al. 1999, 2001, Dashtgard & Gingras 2005a). Manual excavation is used in intertidal zones, casting has been conducted in intertidal and shallow subtidal settings, and box-coring is used from intertidal to deep waters. Another means of determining trace morphology is to place burrowing animals in aquaria and study the resultant burrow morphologies (e.g. Dafoe et al. 2008). Aquaria have also been used *in situ* in sedimentary studies and removed after a time for laboratory analysis (Dashtgard & Gingras 2005b).

RESULTS

Vermiform nemerteans, polychaetes and hemichordates

Worm-like animals represent a very important group of macroscopic bioturbators in marine settings. They

are diverse and can be exceedingly abundant: >10 000 species of marine polychaetes are known (Rouse & Fauchald 1998). Within the Polychaeta, most reported (ichnological) observations are associated with members of the subclasses Palpata (Glyceridae, Nephtyidae, Nereididae, Serpulidae, Sabellidae, Spionidae, Pectinariidae and Terebellidae) and Scolecida (Arenicolidae, Capitellidae, Maldanidae, Opheliidae and Paraonidae).

Nemerteans are often free swimming, but some are common burrowers (e.g. *Cerebratulus* of the family Lineidae), living infaunally in marginal-marine settings. Although less common, the burrows of vermiform hemichordates (class Enteropneusta or 'acorn worms') are well studied because hemichordates represent the 'evolutionary link' between invertebrates and vertebrates. Two important genera of enteropneusts are *Saccoglossus* and *Balanoglossus*. *Saccoglossus* favors shallow marine waters and *Balanoglossus* appears to be more abundant in deeper waters (Chris Cameron pers. comm.).

The commonest morphology of worm burrows is a simple vertical tube or shaft (Figs. 1A & 2A). From such tubes, worms filter feed in the water column (e.g. sabellariids), gather food from the sediment–water interface (e.g. terebellids, maldanids and glycerids), deposit feed (maldanids and capitellids), or engage in passive carnivory (e.g. *Cerebratulus*). More exotic uses of vertical tubes include gathering stock chemicals for chemobiosis (Romero-Wetzel 1987, Hertweck et al. 2005) or attracting vagile pore-living animals (Minter et al. 2007). The most common modification of the vertical shaft is transformation into a Y-form. This behavior is exemplified by nereid polychaetes, which are observed to extend their burrows laterally with serial Y-branches (Figs. 1C & 2B,C). A second common modification is the establishment of a basal tunnel, which can run horizontally and may be connected to the sediment–water interface laterally (Fig. 1C). The basal tunnel may be observed to branch. Where preserved in the rock record, these structures will generally be assigned to the ichnotaxa *Skolithos* (vertical shaft), *Polykladichnus* (Y-shape), *Planolites* (actively filled, horizontal tube), or *Palaeophycus* (lined tube). To varying degrees, such traces are made by nereids, glycerids, nephtyids, nemerteans and the hemichordate *Balanoglossus* (Gingras et al. 1999, Hertweck et al. 2005, 2007). Burrows that branch basally and possess a single vertical connection to the sediment–water interface, such as those commonly made by nereid and capitellid polychaetes, may produce traces similar to *Chondrites* (Hertweck et al. 2007).

Another common feature of worm-generated tubes is the addition of a lining. Lined vertical burrows are typically unbranched. Linings can be thin and litho-

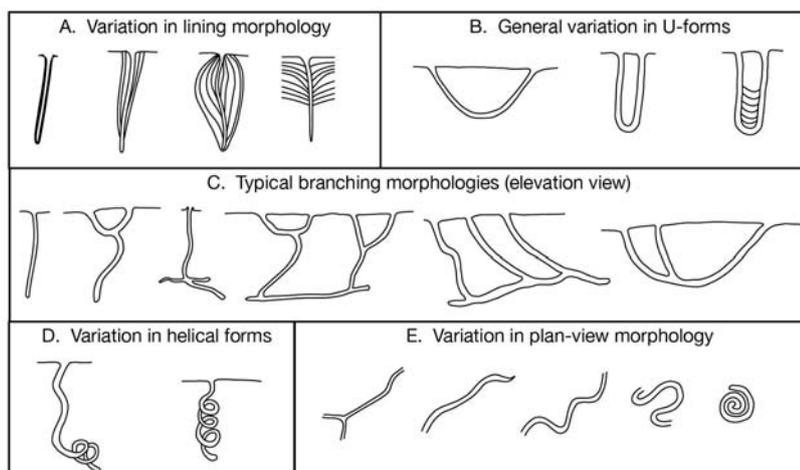


Fig. 1. Variations in worm burrows. (A) Burrow lining types: concentric and thin, through tapered or spindle-shaped. Also, *Tasselia*-like lining is shown on right. (B) Broad, narrow, and *Diplocraterion*-like U-shaped burrows. (C) Morphological variation in Y-shaped burrows. (D) *Helicolithus*- and *Gyrolithes*-type helical burrows. (E) Branching, sinuous, meandering, and coiled forms of intrastratal horizontal burrows

logically distinct, such as the brick-layer style sand tubes of pectinariids, or may comprise mucus-bound sediments, such as those installed by maldanid worms (Fig. 1; Bromley 1996). Although visibly discernible from their unlined counterparts, lined shafts are still assigned to *Skolithos* in the sedimentary record. Tubes with armored linings (i.e. lined with mucus and other material, such as sediment or shell fragments) may be ascribed to *Schaubcylindrichnus*. In some burrows, the lining is observed to be extravagantly over-thickened, typically with fine-grained clastics. This is commonly accompanied by a flaring of the lining, producing the spindle-shaped lining commonly observed in terebellid polychaete burrows (Aller & Yingst 1978, Nara 1995, Gingras et al. 1999), or a drum-shaped morphology (Wetzel & Bromley 1996). Flared or tapered structures in the rock record would be described as *Cylindrichnus* or *Rosselia* (Figs. 1A & 2H). In gravel-dominated sediments, terebellid polychaetes commonly deposit feed within the sediment and do not require a tube opening at the sediment–water interface. In these cases, the resultant burrow is similar in form to *Asterosoma* (Dashtgard et al. 2008).

A morphological advancement of the simple shaft is the U-shaped burrow, resulting in an *Arenicolites*-like trace (left and middle traces, Fig. 1B). Although similar in form to Y-shaped burrows (Fig. 1C), U-shaped burrows serve a fundamentally different feeding strategy. Nereid worms seem to generally employ a Y-morphology and are seldom observed in simple U-burrows, whereas animals that commonly use U-shaped burrows (such as arenicolids) show no predisposition to add a descending Y-branch. This seems to reflect basic

functionality: Y-burrows are more commonly used for interface feeding and protection, where access to the detritus-laden surface is enhanced by an extra opening, and extra openings reduce the risk of predation. U-burrows are more commonly dedicated to conveyor-belt feeding strategies (i.e. arenicolids; Swinbanks 1981) or filter feeding (spionids; Gingras et al. 1999). Basic U-form burrows can be modified by extending or shifting the U-structure and, thereby, generating a spreite. U-burrows with spreiten are assigned to the ichnogenus *Diplocraterion*, diminutive examples of which have been observed to be made by spionid polychaetes (Schäfer 1972, Pemberton & Frey 1985, Gingras et al. 2001) and arthropods (Richter 1926, Seilacher 1964, Schäfer 1972). Larger rock-record examples (such as *Diplocraterion habichi*) may well have been produced by nemerteans

or nereid polychaetes, but modern examples of large *Diplocraterion* have not been reported.

An important twist on vertical shaft architectures is the imposition of a corkscrew morphology, resulting in the trace fossils *Helicolithus* and *Gyrolithes* (Figs. 1D & 2F,G). Such traces have only been observed in modern settings in association with capitellid polychaetes (Howard & Frey 1975) and decapod shrimp (Dworschak & Rodrigues 1997; discussed in 'Materials and methods—Marine crustaceans'). The morphology is also observed as a component of some enteropneust burrows (*Saccoglossus*; Gingras et al. 1999), but, in those cases, the corkscrew generally resides at the terminal end of the lower burrow (Fig. 2F,G). Although the trace fossil *Gyrolithes* has been linked to salinity-induced stresses in the rock record (MacEachern et al. 1999), modern occurrences seem to be more strongly associated with either anchoring of the worm (e.g. *Saccoglossus*), a response to high-density colonization (e.g. capitellids; M. K. Gingras pers. obs.), or may represent a focused, 3D deposit-feeding structure (M. K. Gingras pers. obs.).

The range of morphologies on the horizontal components of worm burrows are expressed in their planiform configuration. As suggested above, worm burrows may branch near the surface. Such structures facilitate interface feeding, reduce the risk of predation, and possibly allow passive carnivory (all of these general behaviors are discussed in Seilacher 1964). Tubes or burrows may also be sinuous to meandering horizontal tunnels, with or without branches. Nereid polychaetes commonly construct 3D horizontal networks (Fig. 1E), from which branches extend to the

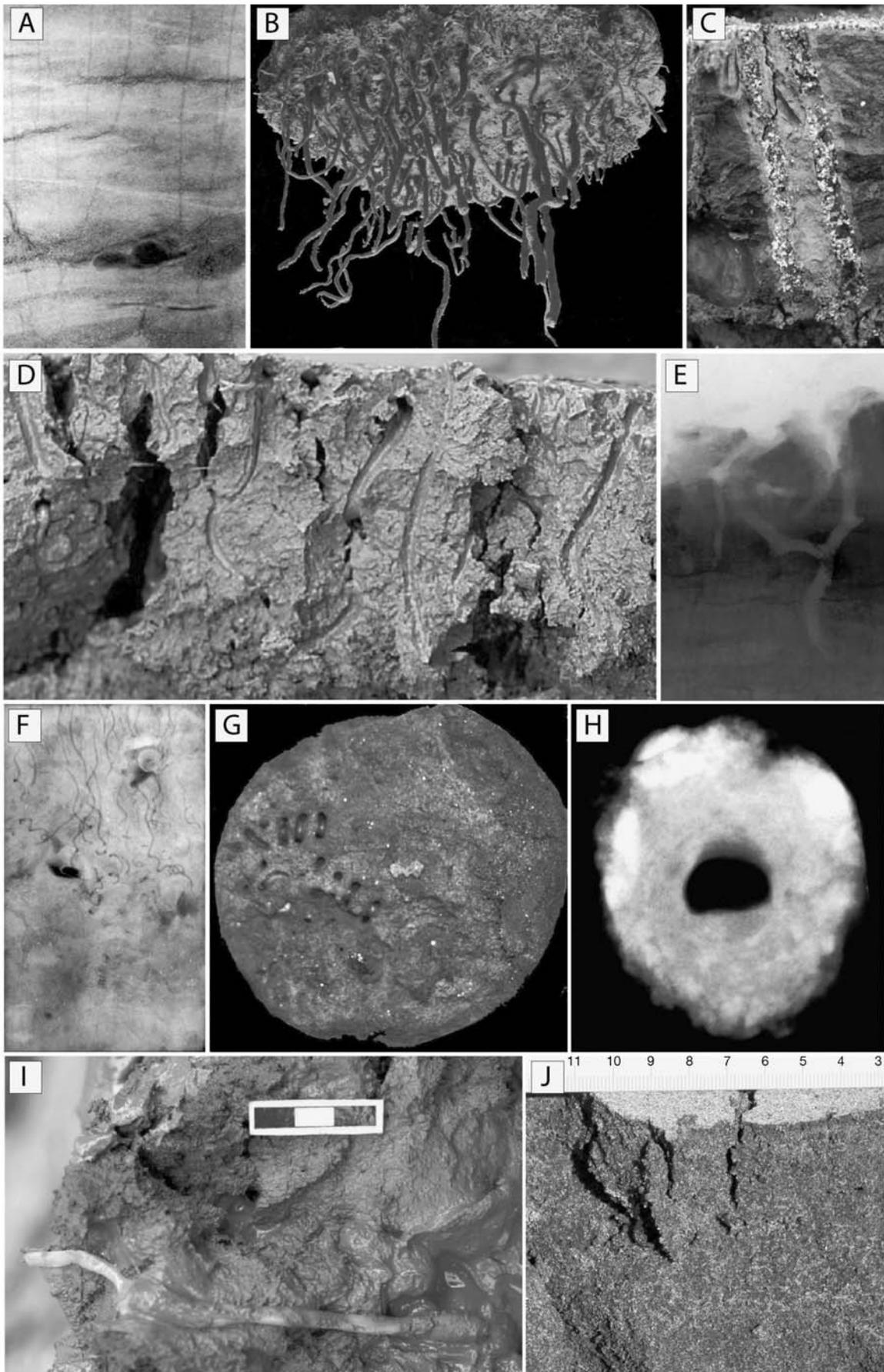


Fig. 2. Worm burrows. (A) Incipient *Skolithos* from tidal sands, Ogeechee Estuary (X-ray image); tracemaker not ascertained. Field of view: 12 cm. (B) Resin cast of Y-shaped burrows of *Nereis* from Kouchibouguac Estuary, Canada. Field of view: 34 cm. (C) Reamed vertical tube with concentric lining from Bay of Fundy, Canada. Field of view: 2.5 cm. (D) Nereid polychaetes and incipient *Polykladichnus* from muddy sediments of Shepody Estuary, Canada. Field of view: 15 cm. (E) X-ray image *Polykladichnus*, Bay of Fundy, Canada. Field of view: 14 cm. (F) *Saccoglossus* (enteropneust) burrows, X-ray image from Bay of Fundy, Canada. (G) Exposed parts of *Saccoglossus* burrows from shallow core (Willapa Bay, USA). Field of view: 10.5 cm. (H) Cross section of thickened burrow wall (*Rosselia*) from modern terebellid polychaete (Bay of Fundy, Canada). Field of view: 4 cm. (I) *Palaeophycus*-dwelling nemertean, *Cerebratulus*, Shepody estuary, Canada. Scale bar: 3 cm. (J) *Macaronichnus* made by opheliid polychaete, *Euzonus*. Pachena Beach, Vancouver Island

sediment–water interface. These burrow networks are semi-permanent structures that allow the worm to move quickly through the sediment and deposit feed over a larger area (Hertweck et al. 2007, Gingras et al. 1999, Dashtgard & Gingras 2005a). Opheliid polychaetes also move horizontally through the sediment and backfill their burrows as they relocate. Opheliids are, in part, deposit feeders that are constantly shifting in search of food (Clifton & Thompson 1978, Saunders & Pemberton 1990). As such, a permanent burrow structure would be impractical. Permanent horizontal burrow networks are similar to the trace fossil *Palaeophycus*, whereas temporary burrows of mobile feeders are similar to *Planolites*. Opheliids are also known tracemakers of *Macaronichnus* (Fig. 2G). Unbranched horizontal burrows are difficult to observe in modern settings, but have been inferred from X-rays of box-cores collected from deeper-water deposits (Wetzel 1991, 2002). Such burrow forms probably record deposit-feeding behaviors—such as that interpreted for the trace fossil *Chondrites*—and may be produced by polychaetes (Hertweck et al. 2005). Non-branched horizontal burrows are similar in morphology to the trace fossils *Planolites*, *Helminthopsis*, *Phycosiphon*, and *Cochlichnus*.

In summary, worm burrows from modern settings show a wide range of burrow morphologies that can be directly applied to the rock record. Some of the burrow forms, such as vertical shafts and branched horizontal burrow networks have a wide range of ethological uses. Other forms, such as Y- and U-shaped burrows, and corkscrew-shaped burrows seem to indicate more localized niches. Modifications on planiform morphology are dominantly dedicated to deposit-feeding initiatives.

Marine crustaceans

The range of burrowing marine arthropods is broad. Dominant in this group are isopods, amphipods and decapods, to which we restrict the discussion below. Isopods are a diverse order of crustaceans common to shallow marine waters. Amphipods include >7000 species of small, shrimp-like crustaceans, most of which

occupy marine settings. The order Decapoda includes crayfish, crabs, lobsters, prawns, and shrimp. In marine settings, the trace-fossil record is dominated by thalassinid shrimp and amphipods and, to a far lesser degree, the burrows of crabs, stomatopods, and lobsters (Fig. 3).

Isopods are relatively flat, robust animals that scavenge and deposit feed within the intertidal zones of modern sand-dominated shorelines. They excavate shallow burrows in the sediment during high tide, in order to avoid being eaten. As the falling tide exposes the sediment, the isopods move rapidly through water-saturated sediment, processing and extracting organic matter (Griffith & Telford 1985, Hauck et al. 2008). In some cases, the pathways of these small crustaceans are preserved as displaced sedimentary laminae produced by their infaunal, ‘sediment-swimming’ movement: these traces have no clear taxonomic affinity. The surface trackways constructed by isopods—straight to meandering to chaotically spiraling bedding-plane traces—can be ascribed to *Gordia*. Alternatively, where preservation is exceptional, a bilobate furrow may be evident, and the resulting trace can be classified as *Isopodichnus*.

Amphipods are another major group of burrowing organisms in marginal-marine settings. In sandy back-shore settings, talitrid amphipods construct vertical, unlined burrows similar in form to *Skolithos* (Dashtgard & Gingras 2005b). Within the intertidal zone, 2 main burrowing amphipods are commonly found, *Corophium* sp. and *Haustorius* sp. *Corophium volutator* is a mud-loving shrimp, which occurs in population densities up to 63 000 m⁻² in semi-firm mud substrates (Thurston 1990, Pearson & Gingras 2006). It constructs a U-shaped tube that, during high tide, allows the amphipod to breathe, feed, and evacuate waste material from the safety of its burrow. *C. volutator* burrows are similar to *Arenicolites*. With time, this tube is deepened resulting in the development of *Diplocraterion* (Fig. 4G) (Richter 1926, Seilacher 1964, Schäfer 1972). A second *Corophium* species, *C. arenarium*, is common in sandy substrates within the intertidal zone. *C. arenarium* constructs a single vertical shaft in sand as water flows freely through the burrow walls and does not require an exit shaft. These burrows are similar in

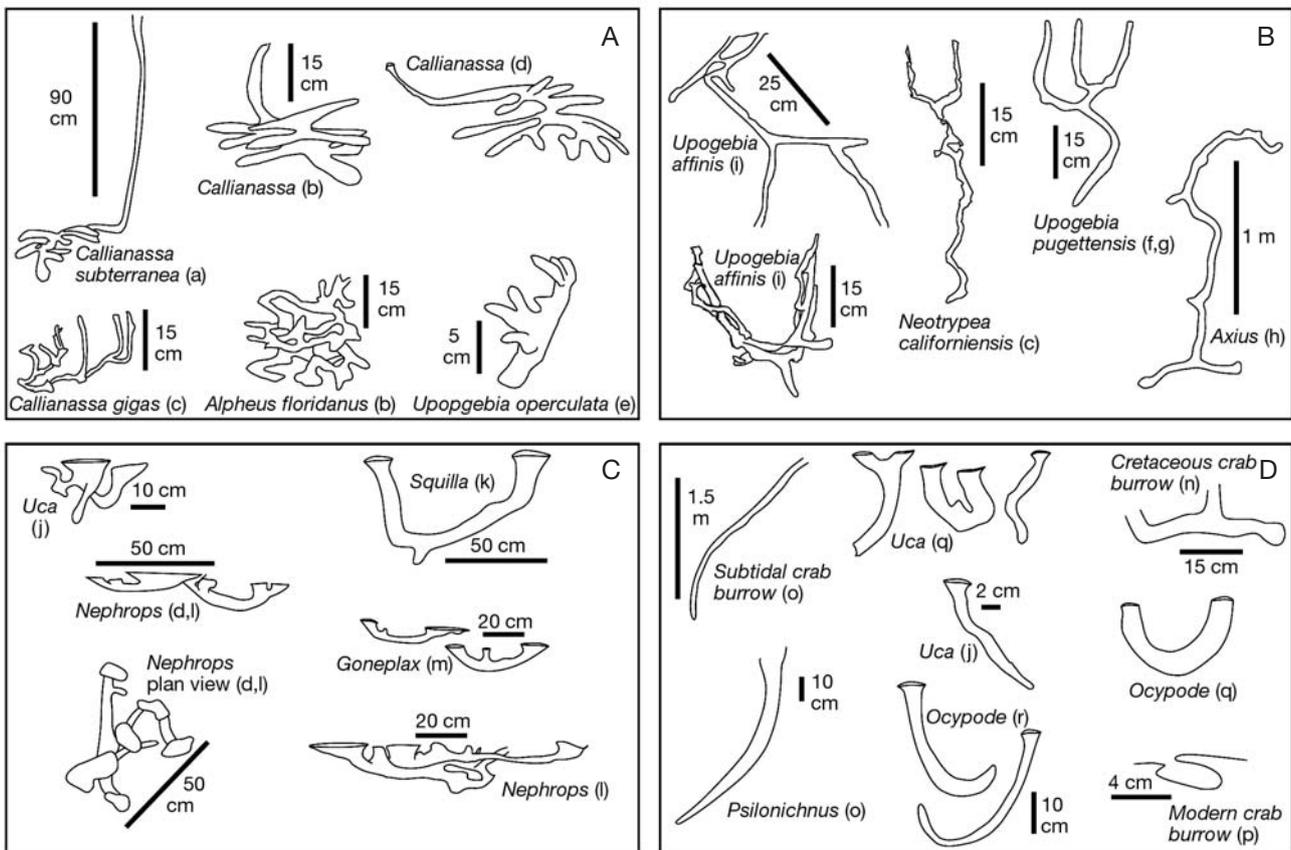


Fig. 3. Variations in crustacean burrows represented by schematic diagrams of resin casts and trace fossils. Thalassinid burrows with (A) a simple subapertural shaft and a complex deposit feeding architecture and (B) with modified U-shaped subaperture and simple or absent basal architecture. (C) Crab, lobster and mantis burrows with complex subaperture and no basal architecture; (D) Crab burrows with a simple J-, U-, or Y-shaped subaperture and no basal architecture. For (A,B) shafts and tubes have a circular cross-section and burrows are (A) commonly lined, or (B) rarely lined. For (C,D) irregular or ovate cross-sections are common and burrows are generally unlined. Note overall higher complexity of basal portion of thalassinid burrows compared to lobster and crab burrows. Lobster burrows demonstrate more complex branching in sub-aperture portion of burrow; crab burrows commonly display simplest architectures. Sources indicated by letters beside burrow schematics are as follows: (a) Atkinson & Nash (1990), (b) Shinn (1968), (c) Griffis & Chavez (1988), (d) Rice & Chapman (1971), (e) Kleeman (1984), (f) Dworschak (1982), (g) Stevens (1929), (h) Pemberton et al. (1976), (i) Frey & Howard (1975), (j) Basan & Frey (1977), (k) Myers (1979), (l) Farmer (1974), (m) Atkinson (1974), (n) Richards (1975), (o) Humphreys & Balson (1988), (p) Savazzi (1982), (q) Farrow (1971), (r) Frey et al. (1984), (s) Fürsich (1981)

form to *Skolithos*. The surface locomotion trackways of *Corophium* and of free-swimming marine amphipods have not been classified.

Haustoriid amphipods—a group of burrowing amphipods—also occur in intertidal settings. Haustoriids are commonly referred to as digger amphipods, as they move through the sediment by excavating and backfilling their burrow as they move. The smaller species of this group of amphipods are only a few millimeters long and tend to contribute to the formation of cryptobioturbation (see 'Biodeformational structures' below). Large specimens, however, disrupt the sediment (Fig. 4F) (Howard & Elders 1970).

Thalassinid shrimp are the best known of crustacean burrowers, producing traces conspicuous in their size and geometry. The basic form of most thalassinid

shrimp burrows is a vertical shaft connected to the sediment–water interface, which branches at depth (Shinn 1968, Griffis & Chavez 1988, James et al. 1990). The range of thalassinid traces is summarized in Fig. 3A and Fig. 4A,B. Fossilized, these traces are known collectively as *Thalassinoides*. The upper part of the burrow, referred to as the aperture, may split and narrow, forming a small Y-shape. This is rarely preserved in the rock record. Thalassinid shrimp burrows may display complex basal structures (Fig. 3A) including tiered and box-worked networks (Shinn 1968, Griffis & Chavez 1988, James et al. 1990). In general, thalassinid shrimp use the vertical shaft to maintain a connection to the sediment–water interface, and the basal network for deposit feeding. The large volume of thalassinid burrows also permits shrimp to moderate the burrow

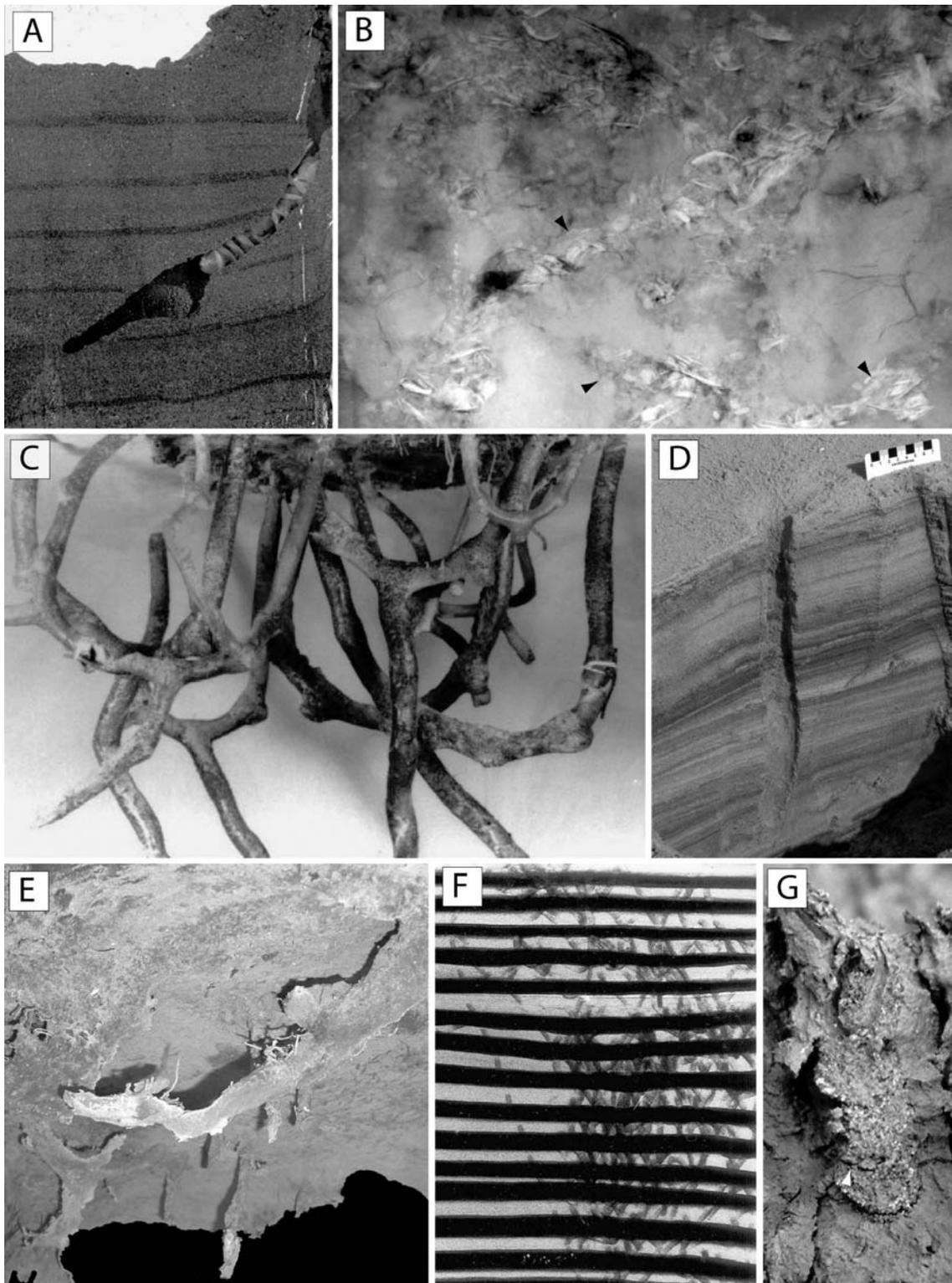


Fig. 4. Crustacean burrows. (A) *Neotrypaea californiensis* (thalassinid) in a laminated aquarium. Image shows swollen turning chamber and typical *Thalassinoides* morphology. Field of view: 14 cm. (B) X-ray of thalassinid burrows filled with shell material (black arrowheads), Ogeechee Estuary, USA. Field of view: 25 cm. (C) Resin cast of burrows of *Upogebia pugettensis* from Willapa Bay, USA. (D) Vertical part of incipient *Psilonichnus* made by crabs, Ogeechee Estuary, USA. (E) Resin cast of *Hemigrapsus oregonensis* from Willapa Bay, USA. Field of view ~20 cm. (F) Sediment mixing by haustoriid amphipods in thin-walled aquarium. (G) Incipient *Diplocraterion* made by amphipod *Corophium volutator*. Field of view: 2 cm

chemistry in intertidal settings and in locales characterized by salinity fluctuation (Thompson & Pritchard 1969). The genus *Upogebia* tends to maintain a Y-shaped burrow (Fig. 4C) (cf. *Polykladichnus*) that the animal employs for filter feeding, using the descending branch as a protective domicile (Stevens 1929, Dworschak 1982). This is a different use of the Y-structures constructed by worms, in that polychaetes activate this strategy for focused interface-feeding activities. Thalassinid shrimp are also known to make large, *Gyrolithes*-style helical burrows (Dworschak & Rodrigues 1997). These burrows are identical to those produced by vermiform animals, except that the trace is much larger and bioglyphs may be imprinted on the burrow wall (Wetzel 2007). It is more likely that the shrimp use such architectures to produce a spiral ramp for the easy maintenance of their domiciles, or that this is a response to high population densities within shrimp species otherwise not known for gregarious behavior.

Shrimp burrows may be pellet-, mud-, and mucus-lined (Pemberton et al. 1976, Frey et al. 1978) but can vary appreciably. These are normally used in shifting substrates and, in the rock record, would be considered stabilized variants of the trace fossil *Thalassinoides*. In general, pellet-walled shrimp burrows would be ascribed to the ichnogenus *Ophiomorpha*.

Modern crab burrows have many characteristics that are not generally seen in burrows made by other crustaceans (Figs. 3C,D & 4D,E). These include comparatively simple architectures (U-, Y-, and J-shaped), open apertures and irregular ovoid cross sections (Fig. 3C,D). Crab burrows are normally unlined (Atkinson 1974, Curran & White 1991, Gringras & Pickerill 2002) and can be interpreted as *Psilonichnus* (Frey & Pemberton 1987, Pemberton et al. 2001). Because crab burrows represent domiciles as opposed to combined feeding structures, complex basal geometries are absent. The architectures of crab and lobster traces are similar, although lobster burrows normally display shallower, sub-apertural branching (Rice & Chapman 1971, Farmer 1974) and possess more irregular burrow diameters (Fig. 3C,D). No widely used ichnogenus resembles the irregular burrows constructed by lobsters; although the term *Decapodichnus* is informally ascribed (Pemberton et al. 1984).

Marine bivalves

There are 3 main types of bivalve traces (Fig. 5): (1) vertically oriented filter- or surface-deposit-feeding from a stationary location, (2) horizontal motility reflecting grazing near the sediment–water interface, and (3) rapid vertical movement through the sediment as an escape mechanism. Additionally, bivalves pro-

cess reduced sediment-porewater compounds within their burrows.

Stationary, filter- and surface-deposit-feeding bivalves have been observed to produce columnar traces composed of 3 parts: (1) an ovate cavity situated around the bivalve; (2) possible equilibrichnial structures directly below or above the cavity, recording slight upward and downward movement; and (3) a vertical chimney or chimneys demarcating the location of the bivalve's extended siphon or siphons (Figs. 5 & 6A–C) (Gingras et al. 2007). Similar structures in the rock record include *Siphonichnus* (Stanistreet et al. 1980), *Scalichnus*—an equilibrium trace fossil produced by *Panopea* (see Hanken et al. 2001)—and, to a lesser degree, *Conichnus* which normally only possesses Features 1 and 2 of the 3 main bivalve traces above (e.g. Savrda & Uddin 2003). *Conichnus* represents the efforts of the animal to maintain a connection to the sediment–water interface (Fig. 5). In the case of *Siphonichnus*-type traces, the connection is maintained using a prehensile siphon. Notably, many bivalves also have a 'foot' that is capable of moving the organism up and down in the sediment, and producing equilibrichnia (menisci). Together, the siphon and the foot represent the primary means of sediment reworking.

A very common ichnofossil ascribed to bivalves is *Lockeia*. This is a small, almond-shaped depression indented by the foot of the bivalve during resting.

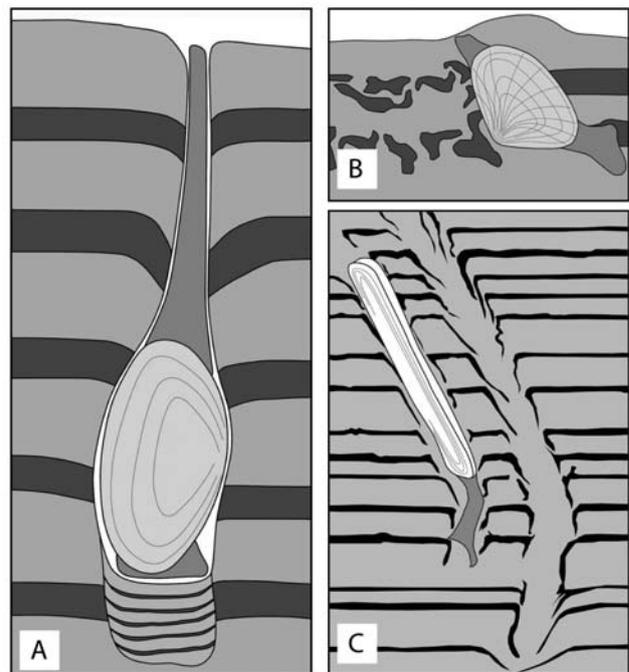


Fig. 5. Bivalve traces. (A) Vertically oriented bivalve produces *Siphonichnus*-type trace. (B) Disruption of sediment produced by horizontal movement of bivalve. (C) Escape structures (fugichnia) produced by upward escape behavior of mobile bivalves

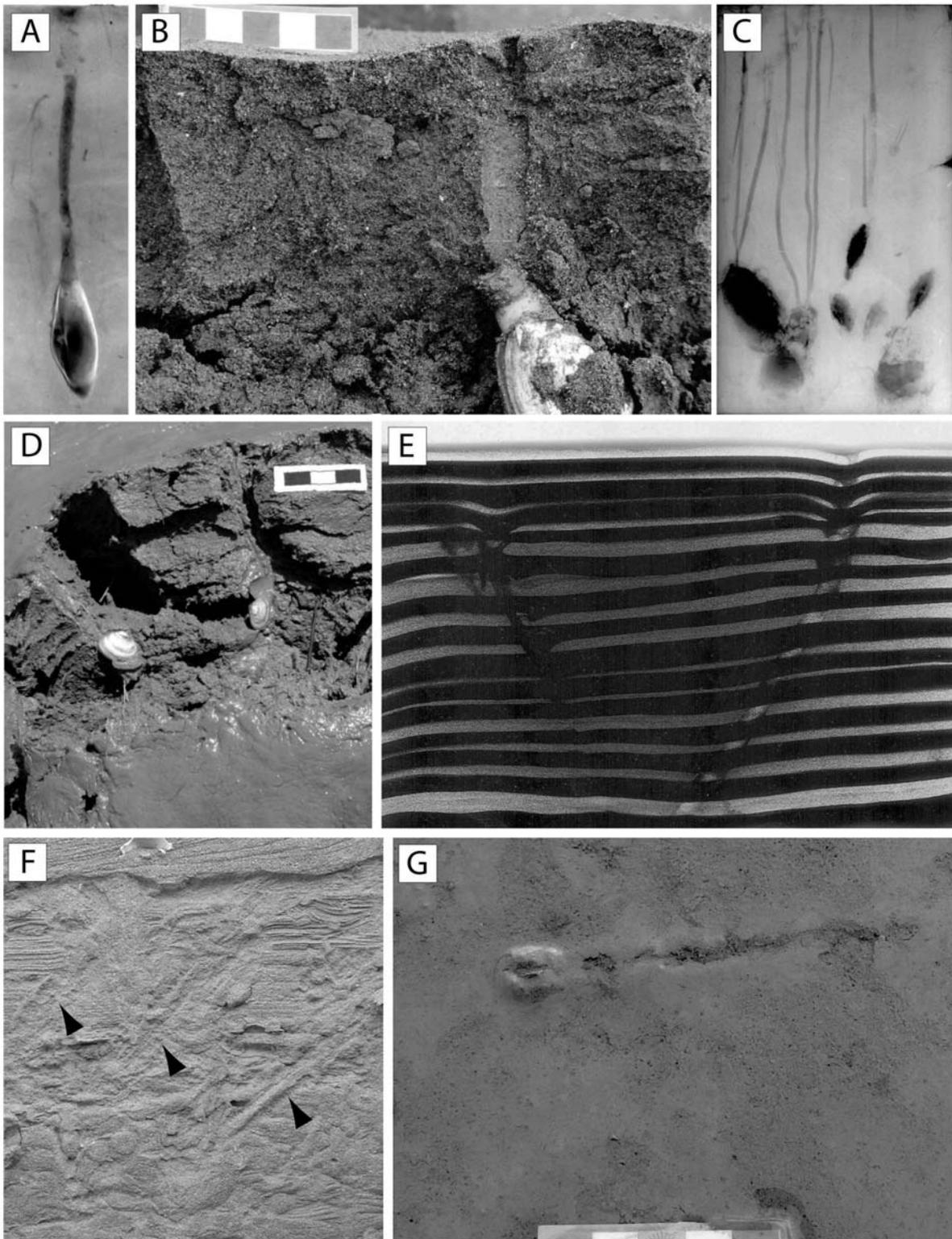


Fig. 6. Bivalve burrows. (A) *Mya arenaria* *in situ*; X-ray of shallow sediment core from Bay of Fundy, Canada. Field of view: 3.5 cm. (B) *M. arenaria* in sandy sediment, Bay of Fundy, Canada. Scale bar: 5 cm. (C) Split siphon of *Macoma balthica* results in paired connection to sediment–water interface. X-ray image from Kouchibouguac, Canada. Field of view: 14 cm. (D) *M. balthica* *in situ*, Shepody estuary, Canada. Scale bar: 3 cm (E) Razor clam adjustment structures in thin-walled aquaria. Field of view: 25 cm. (F) Resin peel of shallow box-core showing escape structure (black arrowheads point to escape traces) of modern razor clams. Field of view: 15 cm. Courtesy of B. C. Yang. (G) Horizontal trail of *M. balthica*

These structures are difficult to see in modern deposits, because they are preserved only at interstratal boundaries. They are best seen in bedding-plane views. Inferable structures have been identified in X-ray images, and very well-developed examples (found with preserved *in situ* shells of *Mya arenaria*) have been reported from Recent sediments in the Bay of Fundy (Dashtgard & Gingras 2005b).

Rapid vertical movements by bivalves are preserved almost solely as fugichnia (i.e. upwards-escape tracks). In modern deposits, this is caused by an abrupt sedimentation event and is observed as a wispy, downward deflection of sedimentary laminae. This behavior has been induced in aquaria, and captured in box-core peels (Figs. 5 & 6E,F), but in the rock record it is exceedingly difficult to distinguish such structures from those produced by the escape response of other animals.

Horizontal movements of bivalves leave furrows and produce lateral deformations ascribed to the pushing of the foot (Figs. 5 & 6G). This has been likened to the production of *Protovirgularia* in the rock record (Seilacher & Seilacher 1994). Much more complex (lateral) bivalve movements have been suggested in the case of *Hillichnus loboensis*, which was compared to the traces of modern tellinacean bivalves (Bromley et al. 2003), and in some complex bivalve motility tracks (Werner 2002).

Motile echinoderms

Motile echinoderms are represented by Eleutherozoa, which include the Asterozoa (starfish), Ophiurozoa (brittle stars), Echinozoa (sea urchins and sand dollars), and Holothurozoa (sea cucumbers). All of these animals leave distinctive traces in modern sediments.

Asteroids most commonly leave star-shaped resting traces preserved as the trace fossil *Asteriacites* (Gailard 1991). It is also recognized that asteroids create motility traces that record their movement across the seafloor. Less well known are the predation traces produced by asteroids digging into shallow sediment to feed on bivalves.

Ophiuroids may move along the seafloor in a manner similar to asteroids, and can leave similar resting traces. Unlike starfish, however, the brittle stars have been observed buried in sediment with their arms stretched above the sediment–water interface (Howard & Frey 1975). This filter-feeding behavior has been reported from various shallow marine settings. The resulting trace is a conical to chevron-shaped disruption of the sediment that has not been reported from the rock record (Fig. 7C), but which could be confused

with *Lingulichnus* or *Cylindrichnus* in poorly displayed cross-sections.

Echinoids—such as heart urchins (spatangoids)—can be extremely mobile, especially in sandy substrates. These animals move through the shallow sediment by passing sediment grains under their bodies using their tube feet. The resulting trace, shown from X-ray images of laboratory aquaria and sediment box-cores, can be a very finely and regularly backfilled passage (Fig. 7D,E) (Bromley & Asgaard 1975, Wetzel 1981, Fu & Werner 2000). Not all spatangoids produce a finely back-filled trace, however, with such traces ranging from laminated to crudely backfilled (Bromley & Asgaard 1975, Kanazawa 1995). The backfilled burrows produced by sand dollars (very thin and very shallow: M. K. Gingras pers. obs., Parksville, British Columbia, 2006), sea biscuits, and heart urchins are similar. However, identification of the resultant trace is dependent upon the size and shape of the tracemaker. Backfilled structures constructed by heart urchins are the most conspicuous of these trace fossils, due to their larger cross-sectional width. The very flattened form of sand dollar traces would likely inhibit their identification as trace fossils. Backfilled echinoid tunnels can be broadly classified as *Scolicia* or *Bichordites*, although true *Scolicia* and *Bichordites* should show evidence of a preserved axial canal or canals near the center of the trace fossil. Such details are hard to identify in modern sediments and are, in part, dependant on the grain-size of the sediment (Wetzel 1981). Sand dollars are known to orient themselves vertically within the sediment in a manner similar to brittle stars, such that part of their body is buried and part extends above the sediment–water interface (O'Neill 1978). This behavior is likely to produce small chevron-shaped disruptions virtually identical to the aforementioned brittle star's traces.

Sea cucumbers are probably responsible for a broader range of trace fossils than have been ascribed to them in the ichnological literature. They make crude, sinuous trails at the sediment–water interface and large, also crude, bow-shaped *Arenicolites*-type burrows in intertidal settings (Fig. 7A,B) (Howard 1968). Their ability to burrow infaunally suggests that at least some irregular disruptions of sediment in the rock record could be attributed to the burrowing activity of sea cucumbers.

Sponges and sea anemones

Although sponge traces are widely recognized as borings (e.g. Kelly & Bromley 1984, Bromley 1994, 1996), their traces in soft sediment are limited to cup-shaped resting marks. These traces range in size from

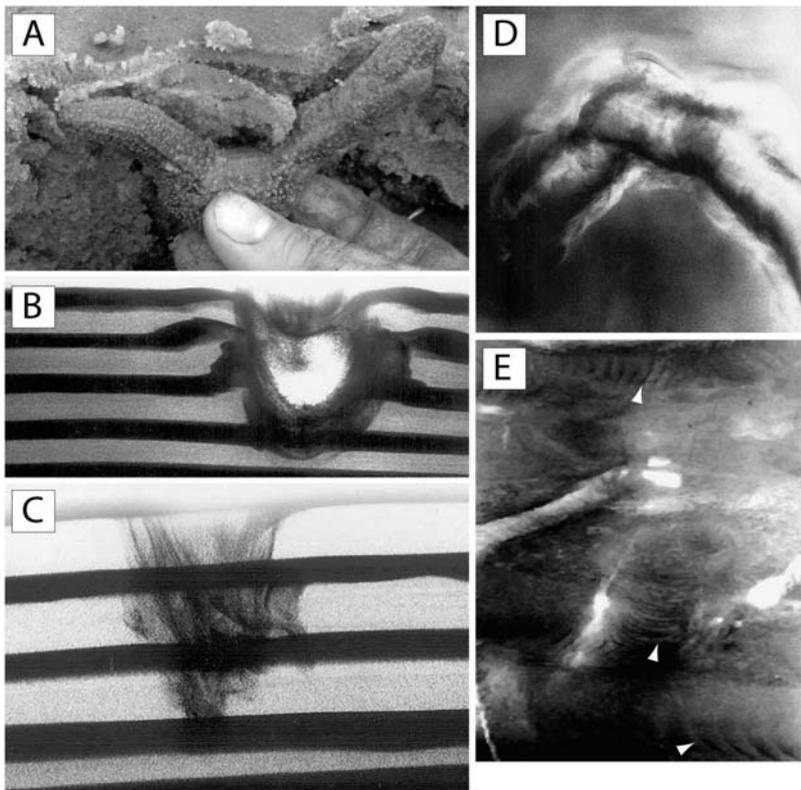


Fig. 7. Echinoderm burrows. (A) Sea cucumber, *Thyone*, living in *Arenicolites*-like burrow, Ogeechee Estuary, USA. (B) X-ray image of *Thyone* in thin-walled aquarium. Field of view: ~20 cm. (C) Typical intrusive structure produced by brittle star. Field of view: 13 cm. (D) X-ray image of sea urchin, *Moira*, from aquarium study. Field of view: 25 cm. (E) Digitized tracing of X-ray image of shallow sediment core bioturbated by heart urchins. Field of view: 14 cm. Arrowheads: mensiccate backfill of echinoid passage

centimeter-scale to decimeter-scale, and they generally do not exceed a few centimeters in depth. Sea anemones, in contrast, can produce large, penetrative biogenic structures. The burrowing anemone, *Cerianthus*, for example, may reach 70 cm in length, and can burrow to almost that depth within the sediment (Hargitt 1907). The animal protrudes out of its burrow to hunt, and retracts to nearly full depth to take shelter. Its iterative probing up through the sediment produces a collapsed, chevron-shaped trace fossil that is conical in cross-section (Fig. 8). *Cerianthus* is also very capable of re-establishing its position with respect to the sediment–water interface, such that its dwelling trace can show notable aggradation in response to sedimentation events. Only small anemones have been imaged from X-rays of box-cores, but their traces are nearly identical to the trace fossil *Conichnus*. Buck & Goldring (2003) noted the similarity of conical structures attributed to anemones and various structures produced by dewatering or degassing. This suggests caution should be used when interpreting potential anemone-made structures in the rock record.

Biodeformational structures

Biodeformation structures (sensu Schäfer 1956) include macro-scale deformation, and cryptobioturbation or cryptic bioturbation. Cryptic bioturbation is a common texture in marginal-marine depositional environments. The activities of meiofauna (animals between 0.1 and 1 mm) and very small macrofauna blur or mottle the original sedimentary fabric, resulting in the development of a cryptobioturbate texture (Howard & Frey 1975, Bromley 1996). Whereas the macrofauna discussed above either excavate a penetrative burrow or disrupt the sediment to the point that primary sedimentary structures are destroyed, meiofauna shift grains only slightly as they move and feed between them. In sandy substrates, the mass of meiofauna occupying the sediment may far exceed the macrofaunal population mass. Despite this, meiofaunal disruption of the sediment is commonly ignored, because some primary sedimentary fabrics are still visible even in 100% cryptobioturbated substrates. In tropical environments, complete homogenization of sediments by meiofauna has been reported to occur in as little as a few days (Thayer 1983, Bromley 1996).

Biodeformational structures are features such as ‘mantle and swirl’ (Schäfer 1956, Lobza & Schieber 1999, Schieber 2003) and sediment-swimming structures. Mantle and swirl structures occur where burrows cross sedimentary layers and obscure the bedding contacts, with the burrow infills displaying an array of complex, convoluted features due to mixing of soupy sediment. Sediment-swimming structures result from an animal passing through fluid-rich substrate. Such structures blur sedimentary laminae, but do not produce a distinct burrow, and develop mainly through the burrowing activity of macrofauna, such as nephtyid polychaetes and isopods. The biosedimentary textures generated are similar to cryptobioturbation.

DISCUSSION

The majority of marine trace fossils can be attributed to invertebrates. Studies from modern settings have revealed tracks and burrows analogous to many trace fossils, including *Arenicolites*, *Asterosoma*, *Cochlichnus*, *Conichnus*, *Cylindrichnus*, *Diplocraterion*, *Gordia*, *Gyrolithes*, *Helminthopsis*, *Isopodichnus*, *Ophiomorpha*, *Lockeia*, *Palaeophycus*, *Planolites*, *Polykladich-*

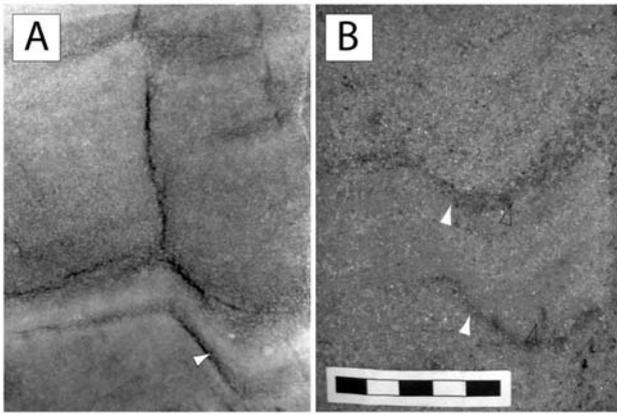


Fig. 8. Anemone burrows. (A) *Conichnus*-like structure from X-ray image, Ogeechee Estuary, USA. Field of view: 10 cm. (B) Slabbed box-core showing sediment disruption around anemone, Ogeechee Estuary, USA. Arrowheads: anemone trace. Scale bar: 5 cm

nus, *Protovirgularia*, *Psilonichnus*, *Rosselia*, *Scolicia*, *Siphonichnus*, *Skolithos*, *Taenidium*, and *Thalassinoides*, as well as biodeformational textures. This is a conservative list. More complex ichnofossils have been interpreted in the context of neoichnological data (e.g. *Neonereites* [Martin & Rindsburgh 2007] and *Hillichnus*). Some traces have been identified (in modern sediments) from deep-water studies, but the tracemakers are not known: *Zoophycos*, *Phycosiphon*, and *Chondrites* are commonly reported from sedimentary core, but without the tracemaker retained (Wetzel 1991). Other deep-water trace fossils (e.g. graphoglyptids or patterned trace fossils) are unknown from modern deposits or are only rarely reported. *Spirorhaphe*, *Cosmorhaphe*, and *Paleodictyon* have been observed as grooves in the tops of washed cores (without their tracemakers; Ekdale 1980), whilst *Paleodictyon* has been reported once from submarine surveys (Rona et al. 2003). Most trace fossils can be associated with a tracemaker only by inference. Analogues of other trace fossils probably will be discovered as studies of deep-marine settings increase.

A fundamental tenet of ichnology is that trace fossils should not be identified or characterized with respect to the inferred tracemaker, because fossil behavior is evolutionarily convergent. In other words, the behavior of a shrimp making a *Skolithos*-type trace is thought to be the same as a worm constructing a similar trace. However, many morphologically similar traces are produced for different reasons by different groups of animals. Large, open horizontal networks serve as domiciles and deposit-feeding structures for crustaceans, but are built by worms mainly for passive carnivory or for expanding an interface-feeding network. The trace fossil *Gyrolithes* potentially represents a mechanical ramp made by a shrimp or a holdfast produced by worms. Similarly,

Y-shaped burrows are used for filter feeding by shrimp, and interface deposit feeding by worms. These examples emphasize that inferences of behavior in the rock record are interpretive. Moreover, recurring associations of trace fossils (i.e. ichnofacies) are based upon the most likely (interpreted) behavior linked to a trace fossil. This does not reduce the utility of ichnofacies, but it does suggest that in settings characterized by lower diversities of trace fossils (e.g. brackish-water settings), the application of accepted ichnofacies can be extremely misleading.

Although linking a trace fossil to a tracemaker is not necessarily critical to an ichnological study, we contend that ichnological research can clearly benefit from such efforts. By understanding the life strategies employed by infauna in modern environments and how the traces they produce aid in survival, we can better assess the likely habits represented by individual and groups of trace fossils preserved in the rock record. Infaunal organisms respond to environmental stresses; by assessing organism and community response to various environmental stresses, it is possible to establish relations between ichnofossils, ichnological communities, and sedimentary processes. These links can be used to refine paleoenvironmental interpretations of the rock record and identify or predict spatial changes in the sedimentary environment.

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