

Resin Cast of Modern Burrows Provides Analogs for Composite Trace Fossils

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A neoichnological resin cast of modern burrows from a mudflat at Willapa Bay, Washington, reveals much of the architecture of the infaunal community present locally within sediments of this mudflat. The cast structures comprise Ppsilonichnus-, Skolithos-, Trichichnus-, Chondrites(?)-, Planolites-, Palaeophycus-, and Arenicolites-like burrows. The range of behaviors represented by these structures cannot be classified into an archetypal (Seilacherian) ichnofacies.

*The resin cast contains many coeval, composite burrows that may reflect certain commensal relationships. Notable composite associations include: (1) siphon shafts of *Mya arenaria* that are connected to and descend from crab domiciles; (2) an example of a pair of infaunal *Mya arenaria* that share a single siphonate shaft; (3) abundant *Heteromastus* burrows that connect to crab and bivalve burrows; and, (4) *Nereis* burrows that are connected to crab domiciles. It is suggested that such contemporaneous relationships, if passed into the fossil record, might be misinterpreted as representing tiering or faunal succession. The reported observations provide a new perspective on the potential significance of interpenetrating trace fossils and complex ichnofabrics.*

INTRODUCTION

Compound trace fossils are commonly recognized in the fossil record. Excellent examples include the transition of *Ophiomorpha* into *Thalassinoides* and then *Spongeliomorpha*, aptly described by Frey et al. (1978) and recently revisited by Schlirf (2000); *Planolites* grading into *Alcyonidiopsis* (Pickerill and Narbonne, 1995); *Cruziana* that are continuous with *Thalassinoides* (Zonneveld, 1999); and *Thalassinoides* that are continuous with *Phycodes* (Miller, 2001). In general, it is preferred that the sample be named after its predominant component (Pemberton and Frey, 1982; Pickerill, 1994).

Compound trace fossils are recognized as two taxonomically distinct ichnofossils that integrate with each other (Pickerill, 1994). The transition between forms can be abrupt or gradational, and both components are normally attributed to different burrowing behaviors used by a single tracemaker. Also, heterogeneous physical characteristics in the substrate may favor different modes of trace preservation, in which case the composite nature may result from taphonomic factors.

Composite ichnofossils, on the other hand, result from the amalgamation of the same and/or different ichnotaxa (Pickerill, 1994). These may occur in a variety of settings and they are common in the rock record. An example includes *Chondrites*-reburrowed *Thalassinoides* (Bromley and Frey, 1974) in which *Chondrites* were most dense near the wall and in the fill of *Thalassinoides*. A predatory *Rusophycus* trace observed in conjunction with *Helminthopsis* was reported by Pickerill and Blisset (1999). Bromley et al. (1999) noted the consistent occurrence of *Taenidium crassum* cross-cutting *Zoophycos* in Upper Cretaceous chalks from northwest Europe. They interpreted the rogue *Taenidium* as representing either predatory behavior on the *Zoophycos* trace maker, deposit feeding on the *Zoophycos*-maker's fecal material, or as an autocyclic iteration of the *Zoophycos*-maker following the completion of some component of the ichnofossil.

In the case of chance interpenetrations, examples are common in the rock record. These are usually interpreted as providing evidence of substrate tiering. Substrate colonization patterns also may be inferred from such data. This is exemplified by post-storm colonization in shoreface settings in which suspension-feeding structures, that are associated with thin storm beds, are cross-cut by grazing traces following storm abatement (Pemberton and Frey, 1984; Pemberton and MacEachern, 1996).

Although their occurrence is quite variable, the rationale for classifying composite ichnofossils has been proposed and is thoroughly discussed by Pickerill (1994). The recognition and analysis of composite ichnofossils can reveal a history of infaunal activity. Because interpenetrating ichnofossils are mostly interpreted to represent successive stages in generating a bioturbate texture, the potential for contemporaneous emplacement of the composite-ichnofossil elements is not usually discussed.

Observations of modern burrows show that the composite nature of some traces can be explained by coeval juxtaposition. The occurrence of contemporaneous composite traces in modern environments is mostly limited to smaller infauna advantaging themselves of the extended sediment-water interface created by the burrows of larger infauna which provides shelter from high hydraulic energy and predation.

This study focuses on composite traces that are preserved in a detailed resin cast from an intertidal flat. It provides four different examples of commensal, composite burrows and discusses how they might be observed in the rock record.

Location

Willapa Bay is located in the southwest corner of Washington and is separated from the Pacific Ocean by a 27-km-long spit (Fig. 1). The bay is mesotidal and has a tidal range of 2 to 3 m.

The intertidal flat is located on the eastern side of Willapa Bay, near the Bone River (Fig. 1). The flat is composed of muddy sand: locally, 60 to 85% of the sediment is finer than lower fine sand (3 ϕ).

Methods

The primary database for this study is a detailed resin cast of open burrows in a sandy mudflat. The cast dimen-

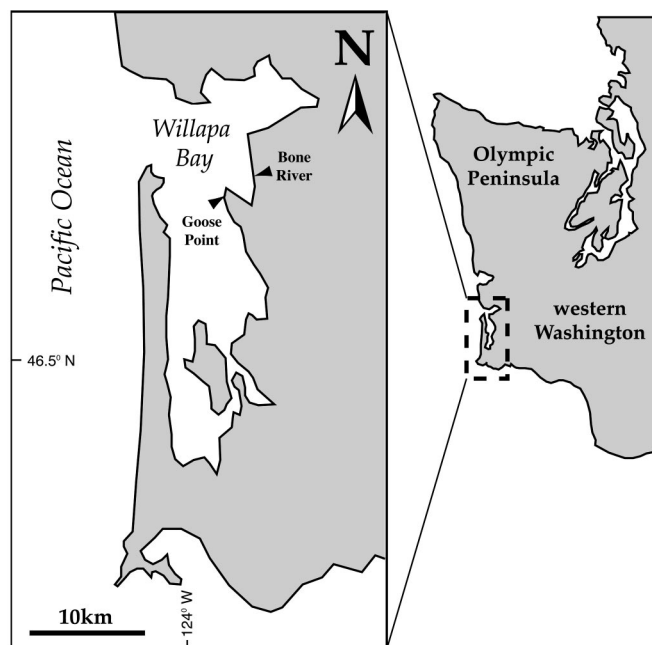


FIGURE 1—General location of the study area in Washington. Willapa Bay is located on the southwest corner of Washington, north of the mouth of the Columbia River.

sions are 90 x 35 cm (area) and the resin reached a maximum depth of about 24 cm. Data procured from the cast are supplemented by detailed observations of the sedimentology and neichnology of the modern tidal flat in that area.

To prepare the sample, a dam of sediment was piled around the perimeter of the casting area to a height of 5 to 8 cm. Polyester boat-repair resin catalyzed by methylethyl ketone peroxide (MEKP) provided the casting medium. Catalyst concentration was 100 ml of MEKP per liter of resin. Prior to adding the catalyst the resin was diluted with acetone (9 parts resin to 1 part acetone) to lower its viscosity. Because the viscosity increases markedly about 5 minutes after the addition of the MEKP, the resin was poured immediately following the introduction of the catalyst. To minimize sediment disruption, pouring was limited to one corner of the dammed area and was poured down a makeshift sluice. Penetration of the resin into open burrows was improved by oscillating the local water table with a hand pump about 1m away from the cast area.

Because the cast was poured in an intertidal setting, the timing was important. The sediment was prepared and the resin poured one hour after the tide had receded from the area of interest. The cast was submersed by the incoming tide about 90 minutes after the resin was poured. The cast was left to cure until the next low tide and was extracted almost a full day after it was poured. Excavation of the cast was done manually. It is helpful to resign oneself to becoming exceptionally muddy, and it is worth knowing that resin-cast excavation is at least a two-person job.

RESULTS

The burrows of at least 6 groups of organisms were preserved in this one resin cast (Fig. 2A-F). Among the most

conspicuous of these are the pendulous casts of *Mya arenaria* (Linnaeus), the Pacific coast's soft-shelled clam (Fig. 2A, C, and E). A bivalve is captured at the terminus of several of the clavate casts. The siphon casts indicate that the siphon length is between 9 and 12 cm long. In the resin cast, burrows of *Mya* occur in three configurations: (1) as solitary *Skolithos*-like traces descending from the mudflat surface; (2) paired (dual tracemakers; see below) at the base and sharing a *Skolithos*-like shaft; and (3) as solitary traces descending from the base of *Psilonichnus*-like traces.

The largest and most robust of the trace casts are the rather spiky *Psilonichnus*-like traces produced by the intertidal crab *Hemigrapsus oregonensis* (Dana) (Fig. 2A, B, D, E, and F). The resin casts have an oval to almond-shaped cross-section that is generally less than 1 cm high and 2.5 cm wide. The lowermost component of the tunnels are gently ramped to horizontal. They taper distally and terminate bluntly. Near the aperture, the burrows ramp steeply upwards. Some of the crab traces are networked near their tops, connecting to adjacent crab traces with inclined tunnels that characteristically exhibit approximately 60° branches. Surrounding the crab-burrow casts, and especially on the tunnel floors, small sail-shaped projections protrude from the cast surface (Fig. 2B). These are trample markings and chelae marks as observed in fossil burrows from the local Pleistocene outcrop (Gingras et al., 2000). The burrow's ovate cross-section, simple J-shape, and reclined morphology are similar to *Psilonichnus upsilon* as described by Frey et al. (1984) and are identical to Pleistocene *Psilonichnus* reported from Willapa Bay by Gingras et al. (2000).

Smaller burrows are distributed almost ubiquitously throughout the cast (Fig. 2A, B, D, and F). These represent the small, commonly branched shafts and tunnels of the threadworm *Heteromastus*. The shafts are generally about 1 mm in diameter. Although the burrows most resemble *Trichichnus*, their tracemaker, *Heteromastus*, has been associated with other trace forms including *Gyrolithes* and *Chondrites*(?) (Gingras et al., 1999). The small burrow casts connect to the larger traces, including the *Skolithos*-like bivalve traces and the *Psilonichnus*-like crab burrows, and descend from the mudflat surface. They are not observed connected to the *Palaeophycus*-like *Nereis* tunnels that are discussed later. Wherever the threadworm burrows connect to a larger burrow, they are approximately normal to the larger burrow's surface.

Small *Arenicolites*-like trace casts are rarely observed connected to the apertural portion of the crab burrows (Fig. 2B). These have a small diameter (< 1mm), are about 3 mm wide, and are about 7 to 10 mm long. Bromley and Frey (1974) reported similar burrows in association with burrows of *Upogebia affinis* (Dana) and interpreted them to be the burrows of the tracemaker's larvae. Curran (1976) reported similar structures. In the current case, careful sectioning of the sediment reveals that these are the burrows of *Corophium*, an abundant amphipod in the bay.

Three well-cast burrows of the polychaete *Nereis virens* (Sars) are present on the resin cast. These are the largest worm burrows represented on the cast (diameter = 4 mm). The *Nereis* burrows have a Y-shaped aperture that connects to the sediment/water interface. Away from the ap-

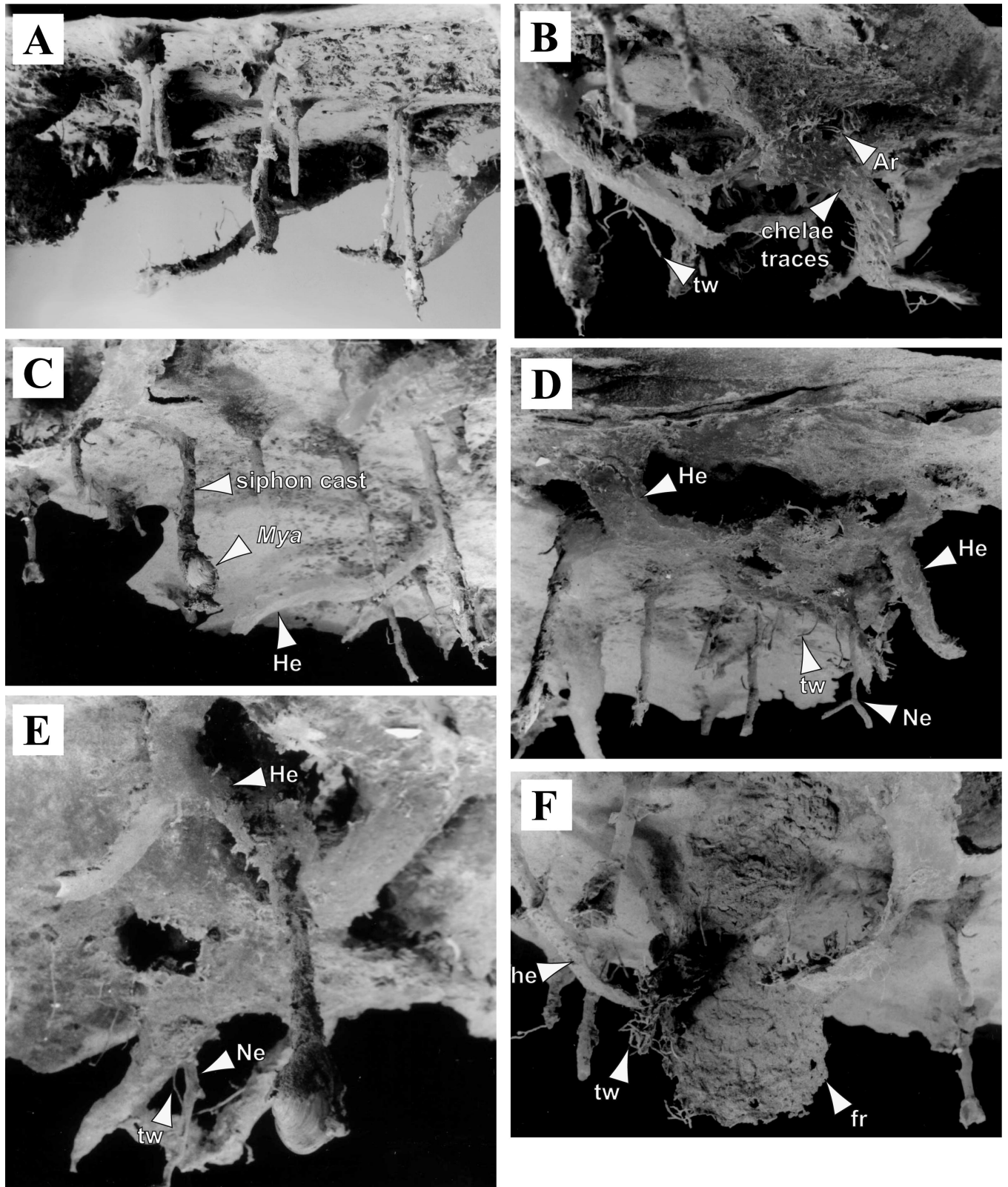


FIGURE 2—Details of the studied resin cast. (A) General configuration of the cast showing preserved bivalve burrows in the foreground and crab burrows in the background. (B) Chelae traces emplaced by the intertidal crab *Hemigrapsus* are easily seen at the base of the simple J-burrow. *Arenicolites*-like burrows (Ar) and small *Trichichnus*-like (tw) burrows are the work of isopods and threadworms, respectively. (C) Close up of the bivalve *Mya* and its preserved siphonate passage. Crab burrow is emphasized in the background (He). (D) The burrow of *Nereis* (Ne) are shown attached to a *Psilonichnus*-like crab burrow (He). The work of threadworms is also preserved (tw). (E) Bivalve burrow descending from the base of a crab burrow (He). Also note the *Nereis* (Ne) and the threadworm burrow (tw). (F) Part of the conical fracture that surrounded the siphon of the large *Macoma balthica* (fr). Several small worm burrows radiate from the fracture (tw).

erture the burrows are inclined to horizontal and have several branches (Fig. 2D). These burrows most resemble the trace fossils *Palaeophycus* (excavation reveals a mucus-rich organic lining) and *Skolithos*. Some sections resemble small *Thalassinoides*. The *Nereis* burrow-casts are observed connected to the casts of the crab- and bivalve-burrows.

Finally, a cone-shaped, wafer-like void was captured in the casting process (Fig. 2F). This void represents thin concentric fractures. Such features are locally present around large, reamed siphon passages made by the bivalve *Macoma balthica* (Linnaeus). The main siphon passage was not cast because the bivalve blocked the shaft with sediment when the resin was poured.

In summary, four notable composite biogenic structures are present in the resin cast: (1) burrows of the bivalve *Mya arenaria* that descend from crab-excavated *Psilonichnus*-like burrows; (2) a pair of *Mya arenaria* that share a siphon shaft that bifurcates near its bottom; (3) abundant *Heteromastus* burrows that are openly connected to crab and bivalve tunnels and shafts; and (4) nereid burrows that are connected to the crab traces.

The resin cast demonstrates the pervasiveness of broadly coeval composite traces. Notably, such relationships are generally not reported from the rock record. Taphonomic considerations and recognition criteria are discussed in the next section.

INTERPRETATION AND SIGNIFICANCE

The resin cast details the architecture of a portion of the macrofaunal colonizers of the Willapa Bay mudflat. It is stressed that only open burrows are cast; therefore, infauna that do not maintain open burrows are not represented. For example, burrows of the polychaete *Nephtys* are not observed even though the worm was exhumed several times while studying the mudflat. This is because *Nephtys* is known to 'bolt' or 'swim' through sediment and commonly does not maintain an open burrow (Clifton, 1984).

Evidently, the most common burrower in the immediate area of the cast is the threadworm *Heteromastus*; its burrows are pervasively distributed in the substrate. Threadworm burrows commonly descend to a depth of 25 cm, making them among the deepest structures in the mudflat. X-rays of the sediment confirm that *Heteromastus* burrows locally dominate the bioturbate texture of these mudflats.

Less abundant, but perhaps more conspicuous, are the *Hemigrapsus*, *Mya*, and *Nereis* burrows represented in the resin cast. These animals respectively introduce *Psilonichnus*-, *Skolithos*-, and *Palaeophycus*-like burrows to the substrate. Mixed ethologies are commonly inferred from trace fossil data in estuarine deposits (Pemberton et al., 1982; Buatois et al., 1997) and are decidedly common in both the modern and ancient record at Willapa Bay (Gin-gras et al., 1999).

The resin cast reveals the extent to which burrowing animals construct and live in coeval, composite biogenic structures. All of the 6 major trace types observed in the cast are present in some type of a composite arrangement. Incipient *Psilonichnus* occur with *Skolithos*, *Palaeophycus*, *Arenicolites* and *Trichichnus/Chondrites*(?), all of which appear to use the crab's domicile as an extension of the

sediment-water interface. *Skolithos*-like siphon structures are connected to *Palaeophycus* and *Trichichnus*-like burrows. Even the large, concentric fractures surrounding the large siphon trace are well used by threadworms.

Although it is useful to consider the larger biogenic structures as simply contributing to the area afforded by the sediment-water interface, there are several practical points that suggest composite traces represent a commensal relationship. For instance, threadworms that connect to the larger crab and bivalve burrows can access oxygenated water while being located further away from surface predators. Also, the crab burrows tend to maintain a volume of water in them when the tide is out (Ricketts et al., 1985), a luxury the threadworm would not enjoy otherwise. Organic detritus, including crab feces, is more abundant in the burrow as well because the domiciles provide excellent detritus traps during flood- and ebb-tide. Thus, even though the occurrence of these composite traces might be attributed to other random devices, such as larval dispersion and undirected bioturbation, benefits for at least one of the organisms are likely.

Another of the relationships observed in the resin cast consists of two specimens of *Mya* using the same siphon passage. Such a relationship may have had advantages while the organisms are relative juveniles, because the energy expenditure related to burrow maintenance could have been shared. Perhaps as the animals matured, and their resource demands increased, condominium living was no longer convenient (Fig. 3).

Composite, contemporaneous traces provide an interesting taphonomic scenario. In the case of threadworm burrows attached to the crab traces, for example, it is conceivable that as the sediment filled in the crab burrow, the threadworm-squatters were compelled to adjust to the new sediment level (Fig. 4). As filling continued, the threadworms would keep up to the continuously aggrading sediment-water interface. The infauna would be progressively concentrated into the larger burrow's steadily shrinking volume as a result of this activity (Fig. 4). The product of this behavior is a burrow fill that is similar to those that are described as 'reburrowed.' In fact, it is difficult to consider the *Psilonichnus*-like traces reburrowed if they are more or less contemporaneous with the threadworm burrows. In any case the connotation relating the actual process of burrow emplacement is lost.

A relationship that merits closer attention is that presented by the twinned bivalve trace (Fig. 3). The bivalves may have shared the siphon trace until one out-competed the other for resources. One trace will therefore be infilled while another was still active. The net fabric would comprise a bivalve trace neatly cross-cut by another (Fig. 3). It is difficult to say how common this relationship may be in the historical record at Willapa Bay. It is not likely, however, that the resin cast fortuitously captured the only pair of bivalves using the same siphonate shaft in the Willapa Bay mudflats.

Criteria for identifying coeval, interpenetrating burrow relationships may be difficult to evolve and may require the systematic re-evaluation of several curated ichnofossil specimens. Some obvious criteria that can be derived from the resin cast documented here are: (1) interpenetrating trace fossils are generally perpendicular to the larger burrow's margins; (2) the interpenetrating ichnofossil chang-

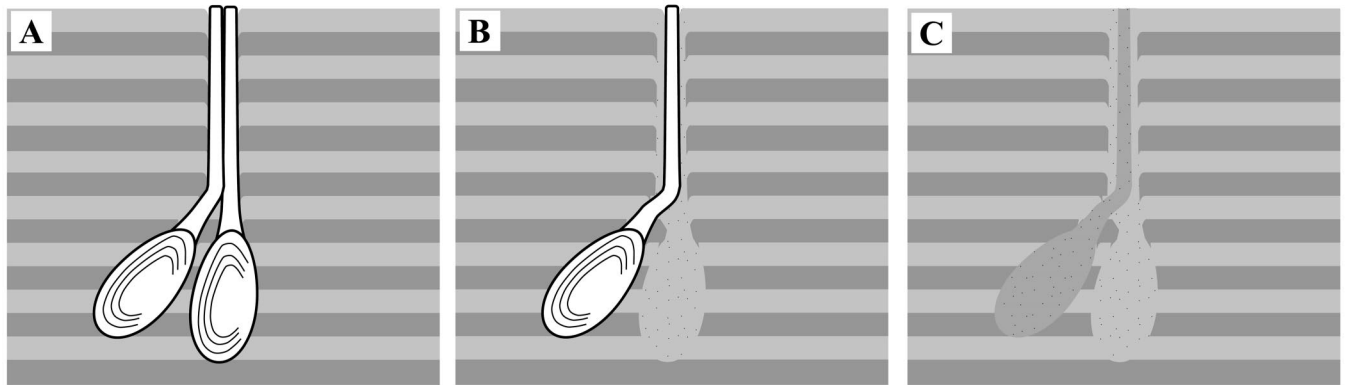


FIGURE 3—Proposed means of generating a contemporaneous, composite trace fossil. (A) Two bivalves advantage themselves of the same siphon passage. (B) Resource competition causes one bivalve to die while the other continues to use the burrow. (C) The composite relationship is preserved following the death of the second animal.

es direction inside the larger trace fossil as a result of worms crowding to use a shrinking sediment-water interface (Fig. 4); (3) burrow terminations are observed inside the larger trace fossil where passive, infilling laminae were colonized (Fig. 4; not documented in the resin cast but observed in burrow excavations); and, (4) traces that are of similar size and architecture interpenetrate each other due to crowding within the burrow as it fills. None of these criteria are without exception.

SUMMARY

The examined resin cast is informative in that it reveals much of the architecture of the infaunal community present in this part of the Willapa Bay mudflat. The trace assemblage comprises *Psilonichnus*-, *Skolithos*-, *Trichichnus*-, *Chondrites*(?)-, *Palaeophycus*-, and *Arenicolites*-like burrows. These represent a mixed suite of behaviors that are not easily summarized with archetypal (Seilacherian) ichnofacies. Threadworms (mostly *Heteromastus*) are the most common burrowers and their traces dominate the ichnofabric.

Important coeval, composite traces are noted: (1) siphon shafts of *Mya arenaria* descending from crab domiciles; (2) a pair of *Mya arenaria* sharing a single siphon shaft; (3) threadworm burrows that connect to crab and bivalve burrows; and (4) *Nereis* burrows that are mostly connected to the crab traces. These relationships are potentially important as they may strongly influence an interpretation of ti-

ering relationships in a substrate. Furthermore, they show that the term 're-burrowed' is not always appropriately applied to interpenetrating ichnofossils. Although a thorough evaluation of composite burrows in the rock record is required to confirm some of the derivations herein, the preponderance of composite traces in this resin cast hint at how common these behaviors are in modern organisms.

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FIGURE 4—Proposed means of generating a contemporaneous, composite trace fossil. (A) Threadworms use the inner surface of the crab burrow as an extension of the sediment-water interface. (B) Occupation of the burrow by the crab ceases and the burrow begins to infill with sediment. The worms follow the changing sediment-water interface and focus their activity into the volume of the crab burrow. (C) The burrow fills, and the worms establish themselves at the sediment surface. Parts of this sequence were observed by the authors in the modern setting of Willapa Bay (while trenching and excavating).

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