

PLEISTOCENE WALRUS HERDS IN THE OLYMPIC PENINSULA AREA: TRACE-FOSSIL EVIDENCE OF PREDATION BY HYDRAULIC JETTING

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ABSTRACT

Quarry walls in Pleistocene marginal-marine coarse-grained deposits adjacent to Willapa Bay, Washington, expose a contact from which unusual sedimentary structures originate. These structures have two distinct occurrences: (1) vertical-to-subvertical columns where laminae and bedding deflect downward, and (2) normally graded beds with symmetric or asymmetric U-shaped structures with flared limbs. The scale, morphology, and distribution of the features suggest these are not physical sedimentary structures. Rather, they are more akin to biogenic sedimentary structures generated by the predatory action of marine animals on deep-burrowing bivalves. Several animals are known to forage sediment: elasmobranch fishes, fish, crabs, sea stars, sea otters, whales, and walrus. In particular, walrus generate distinctive excavations on the sea floor as they root for prey with their snouts and emit a jet of water that liquefies the bottom sediments where a bivalve has burrowed. The trace fossils reported likely represent the first examples of walrus feeding from the geologic record. Documentation in recent years of sea-floor furrows and pits on the Bering Shelf and Chukchi Sea produced by the Pacific Walrus (*Odobenus rosmarus* Linnaeus) provides modern analogues for the ancient trace fossils described from Willapa Bay. We present three significant implications from this comparison: (1) The method of hydraulic jetting employed by walrus for extraction of their prey leaves a distinctive trace fossil that can be used to identify the presence and activities of foraging walrus. (2) These predation structures are temporally significant in that they provide a minimum time of exposure and corresponding rate of accretion for the ancient estuary inlet. (3) Feeding excavations in paleo-Willapa Bay, Washington, were produced by walrus herds that wandered from the northern Pacific ice front during the Pleistocene after becoming barricaded from their present habitat in the Bering Shelf and Chukchi Sea.

INTRODUCTION

This paper scrutinizes occurrences of *Piscichnus* observed crosscutting bivalve equilibria (*Siphonichnus*) in Pleistocene outcrops near Willapa Bay, Washington. The trace-fossil assemblage and its relationship to sedimentary structures is notable because (1) a potential predatory relationship is suggested by the observed trace fossils; (2) the trace-fossil occurrence can be linked to the overall rate of sediment aggradation at the time of substrate colonization; and (3) the trace fossils can be related to feeding behavior consistent with the activities of specific animals. The trace fossils are problematic in that the outcrops are not lithified, lithologic contrast is low, and the trace fossils are large, thus, making them difficult to classify (Bromley et al., 1975).

Trace fossils are used to produce paleoecologic and sedimentologic information from sedimentary deposits. The range of studies is broad and includes the evaluation of invertebrate ichnofossils to assess physical and

chemical conditions at the time of deposition; studies of invertebrate burrow, boring, and rasping structures in sediment of variable cohesiveness; and the process-sedimentological significance of trace-fossil assemblages.

Papers that assess the importance of ichnofossils associated with vertebrates are increasingly common in the recent literature. In general, these papers document the great variety of vertebrate locomotion traces and focus on ancient continental trackways (e.g., Lockley et al., 2002). The breadth of other vertebrate ichnofossils including burrows and nesting structures is also well established; these are most common in continental settings (e.g., Horner, 1982).

The trace-fossil record of marine vertebrate animals is understood poorly in comparison. The sinuous tracks of finned fishes, *Undichnia*, are the most conspicuous of the subaqueous vertebrate trails (Wood and Cameron, 1998). Another common ichnofossil is *Piscichnus waitemata*, a bowl-shaped ichnofossil, interpreted to result from biogenically induced hydraulic excavation of sedimentary substrates (Gregory, 1991). Feibel (1987) originally established *Piscichnus brownii* for a dish-shaped structure preserved in concave relief sandstones, interpreted as fish nests. Shallow-marine trackways produced by quadrupeds bound to shallow water also have been reported (e.g., Geister, 1998). These trackways are evident as swimming, bouncing, and clawing impressions. Larger structures, some of which are similar conceptually to *Piscichnus*, have been reported as animal bite marks out of the sediment. These are centimeter-to-meter scale and take on a host of morphologies (Oliver et al., 1985; Nelson et al., 1987; Pearson et al., 2007).

STUDY AREA LOCATION AND GEOLOGICAL SETTING

Willapa Bay, Washington, is a mesotidal estuary north of the Columbia River mouth (Fig. 1). Long Beach Peninsula extends 26 km northward from the river mouth and protects the bay on its western margin from the Pacific Ocean. Willapa Bay is flanked by terrace deposits of Pleistocene age on its eastern and northern periphery that have been intermittently sourced from sediments from the Columbia River mouth since at least the Pleistocene (Luepke and Clifton, 1983). Those ancient estuarine deposits have been termed the younger terrace set and older terrace set (Clifton and Phillips, 1980), corresponding to elevations of ~15 m and <50 m above sea level, respectively. Amino acid racemization age dating of shell material indicates that deposition of stratigraphic units equivalent with the younger Pleistocene strata occurred between 120 ka and 200 ka (Kvenvolden et al., 1979; Kvenvolden and Blunt, 1980). There are no dates for the older Pleistocene strata because of a dearth of dateable organic material within the deposits.

The study area is located in the vicinity of North Cove, Willapa Bay, where sand and gravel quarry operations have exposed a 30 m interval of the older Pleistocene terrace (Fig. 1). At the time the observations reported here were made, the floor of the quarry lay at about 20 m above sea level; the lateral exposure ranged from 40 m at the base to 15 m at the top of the quarry. The exposure represents the most complete and uncovered stratigraphic interval within the older terrace set (Fig. 1), other exposures of the older terrace are dispersed widely and restricted to such

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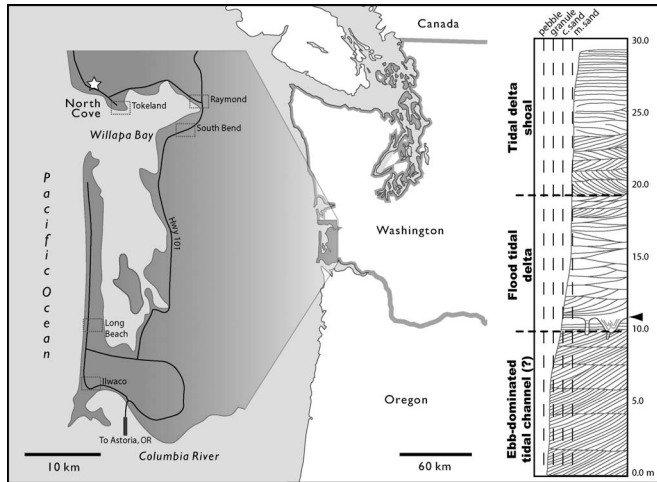


FIGURE 1—Location map of the study area with North Cove indicated on the north edge of Willapa Bay. To the right is a lithologic strip log (scale in m) of the section at North Cove with inferred depositional environments. Horizon with trace fossils indicated with an arrow.

anthropogenic excavations as road cuts and waste disposal sites. Consequently, the geology of the older Pleistocene terrace is understood poorly.

The facies succession at North Cove is interpreted to represent transgressive infilling and marine reworking of the paleotidal inlet to Willapa Bay during the Pleistocene. Disparities between provenance of the sedimentary grains and paleocurrent orientation of physical structures allow the facies succession within the quarry to be grouped into facies associations indicative of deposition in channel (0–10.3 m) and baymouth (10.3–30.0 m) settings (Fig. 1). Luepke and Clifton (1983) showed that sediments constituting the channel deposits contain a heavy mineral distribution suggesting a comparatively exotic (?Olympic Peninsula) provenance. In contrast, like the modern Willapa Bay, the overlying fine-grained, baymouth sand was probably sourced from the Columbia River drainage. Luepke and Clifton (1983) suggest that clasts within channel-fill succession were intermittently derived from a glacial source to the northeast of Willapa Bay during the Pleistocene. The contrast in grain provenance between the two facies associations is coincident with a contrast between paleocurrent orientations of physical structures within the lower and upper facies associations (Fig. 1). Measurements taken within the lowermost facies association indicate a net seaward or ebb-oriented flow (southwest), whereas paleocurrent orientations within the uppermost facies association show dipolar distributions between west northwest and east southeast. It is at the contact between these two facies associations that the sedimentary structures addressed here originate.

DESCRIPTION AND INTERPRETATION OF BIOGENIC SEDIMENTARY STRUCTURES

Two distinct morphologies are distinguished along the contact between the gravel-rich spit platform and overlying sand-rich, flood-tidal-delta deposits. The first is made up of approximately 4–16 cm wide by 26–55 cm tall, vertical-to-subvertical columns constituting crudely defined, concave-upward laminae (Fig. 2; yellow arrows), and the second is made up of 20–35 cm wide by 10–40 cm tall, upright-to-slightly reclined bowl-shaped structures, which contain a poorly graded fill that coarsens toward the center of the bowl (Fig. 2; black arrows). The columnar structures are discrete fossils that do not normally interpenetrate each other (Fig. 2). Bowl-shaped trace fossils are more commonly amalgamated and crosscut each other. The bowl-shaped structures often truncate the uppermost portion of the columnar structures (Figs. 2–3).

Both kinds of ichnofossils crosscut the primary depositional fabric of sediments underlying the gravel-sand contact. The biogenic structures are

differentiated on the basis of distribution, sorting, orientation of constituent sedimentary grains, and dimensional characteristics.

Biogenic Sedimentary Structures: Description

We describe 15 columnar trace fossils in detail, including truncated occurrences, at or near the sand-gravel contact (Fig. 3; 19 others have since been observed (M. Gingras, personal observation, 2007)). The trace fossils are composed of a pebbly, fine-grained sandstone core surrounded by an adjacent zone containing crudely imbricated pebbles (Fig. 2B, yellow arrow; Fig. 4C, white arrows). Bedding planes peripheral to the columns commonly show subtle downward deflection near the outer edge of the columnar structures (Fig. 2B, orange arrow). The cross-sectional width and height of the columnar structures is between 4.4–15.6 cm and 26.1–54.5 cm, respectively. Mean dimensional values for nontruncated columns are 8.6×40.1 cm. Excavation of two of the ichnofossils show that they are ovoid to tubular in plan view.

The columns can be divided into an upper and lower portion. The upper segment is dominated by massive-appearing sand, whereas the lower part generally contains imbricated pebbles that define concave meniscas.

With respect to the columnar traces, bowl-shaped structures are present in greater abundance along the gravel-sand contact (12 m; see Fig. 1 inset). This is a consequence of the columnar traces being deeper penetrating and the prevalent coincidence of bowl-shaped trace fossils cross-cutting columnar artifacts. Maximum cross-sectional widths of the bowl-shaped structures varies from 20 cm to 35 cm, whereas height varies between 10 cm and 40 cm. Variability of maximum height and width measurements is far greater in the concave structures than in the columns. Excavation into the outcrop reveals that the bowl-shaped structures have a circular cross section; thus, the maximum measured widths referred to above are apparent widths that represent the minimum diameters of the structures observed.

The bowl-shaped structures contain poorly sorted, locally granular gravel that commonly displays crude, normal grading (Fig. 2A, upper left; Fig. 4A, upward from yellow arrow; Fig. 4C, upward from yellow arrow). Upright occurrences of the U-shaped structures dip inward at 40° – 45° . Inclined or recumbent occurrences typically contain one side that dips at a shallow angle (30°), whereas the opposing side is steeply inclined to near vertical (60° – 85° ; Fig. 2C inset). Several examples coarsen toward the center of the bowls, but sediment grading is strictly restricted to occurrences of the structures that penetrated more than 20 cm beneath the contact into the underlying gravel-rich unit (Fig. 4A, black arrow).

Near the central axis of many of the observed bowls, a tubular, vertically oriented, sandy gravel core is present (Fig. 4A, black arrow). In such examples, the gravel adjacent to the sandy core is void of matrix. Moreover, adjacent prolate (rare), oblate, and bladed clasts are oriented concordantly with the sandy core. Away from the core, imbrication is bowl-parallel or defines curvilinear surfaces suggestive of flow convection, which we discuss below (Fig. 4A, white arrow).

The bowl-shaped structures are most common where the columnar structures are present. In fact half of the bowls—7 of a reported 14—are coincident with the biogenic columns (Fig. 3).

Biogenic Sedimentary Structures: Interpretation

Despite the absence of shell material or a preserved steinkern, the columnar ichnofossils described here are most similar to trace fossils ascribed to deep-burrowing bivalves at other locales. Similar structures in the rock record include *Siphonichnus*, *Conichnus*, and fugichnia (Stanistreet et al., 1980; Savrda, 2002), all of which represent the efforts of an animal to maintain its connection to the sediment-water interface (Fig. 5A). In the case of *Siphonichnus*, the connection is maintained using a prehensile siphon, which in some species of clam can extend several times the valve length and can generally be retracted to very near the shell (Zaklan and Ydenberg, 1997). Notably, many bivalves also have a foot that is capable of moving the shellfish up and down in the sediment

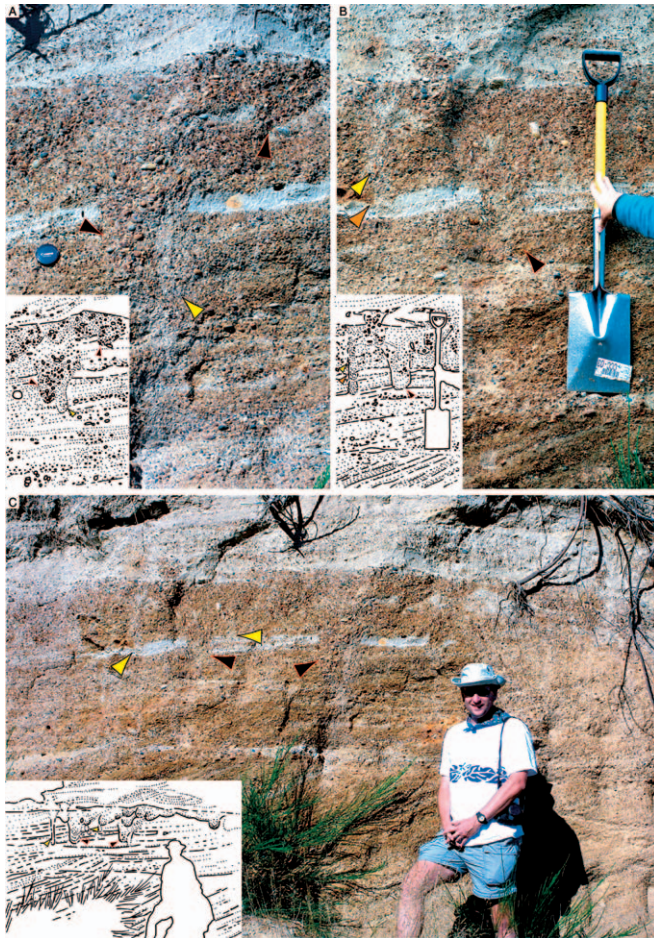


FIGURE 2—Occurrence and details of biogenic sedimentary structures. A) Close-up of trace fossils with interpreted schematic inset. Black arrows indicate positions of two bowl-shaped structures (*Piscichnus*); the yellow arrow indicates a truncated columnar trace fossil (*Siphonichnus*). B) A larger *Piscichnus* (black arrow) with schematic interpretation. An almost complete *Siphonichnus* indicated by the yellow and orange arrow. C) Larger view of the outcrop shows *Piscichnus* (black arrows) and *Siphonichnus* (yellow arrows). The interpreted inset shows some recumbent bowl structures in upper third of the sketch.

that result in equilibrichnia—stacked meniscae. Together, the siphon and the foot represent the primary means of sediment reworking.

The upper, sandy part of the burrow is probably the result of fine sand piping down from the depositional surface during passive infilling and partial collapse of the open burrow (Figs. 4C–D). Ultimately, the sand is incorporated into the burrow by constant reaming of the burrow wall by the itinerant bivalve's siphon. Deformation of the sediment marginal to the burrow and weak imbrication of rod- and disc-shaped pebbles also result from reworking of the burrow periphery by persistent siphonate reaming. Such behavior produces trace-fossil morphologies characteristic of the ichnogenus *Siphonichnus* (Stanistreet et al., 1980). The basal zone of the structure is composed of stacked meniscae, that is, granular and pebbly stringers probably produced by rotational movements of the mollusk's valves, which accompanied limited vertical adjustment upward through the substrate (Fig. 2B, yellow arrow; Fig. 5).

A wide array of sedimentary processes produce sedimentary structures that possess at least a gross physical similarity to the concave structures discussed here. These include fluid- or gas-escape structures (e.g., King and MacLean, 1970; Nelson et al., 1979), current or whirlpool scouring (Dionne and Laverdiere, 1972), contact with moving ice (e.g., Barnes and Lein, 1988), or various mechanisms of sediment loading and subsequent instability that might lead to localized soft-sediment deformation. No physical sedimentary process, however, is consistent with (1) the imbric-

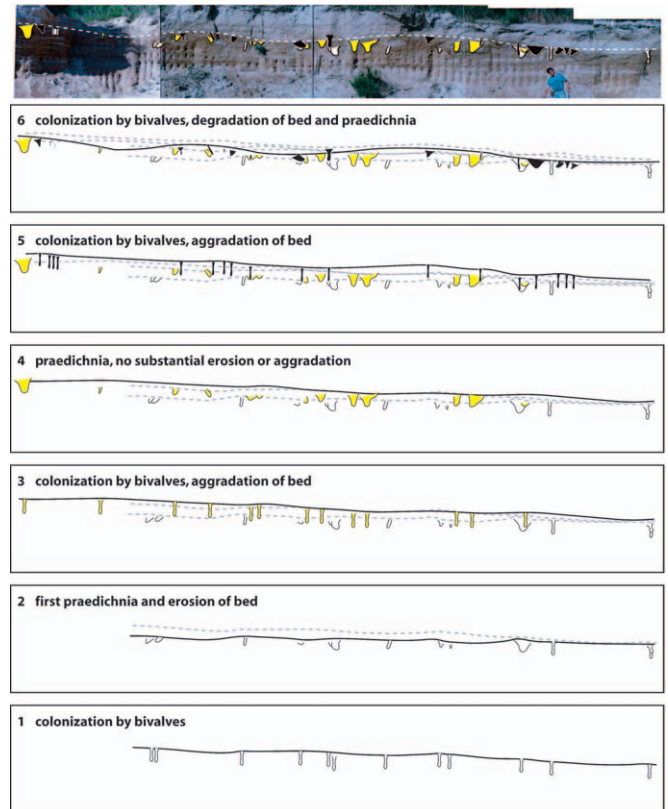


FIGURE 3—The Willapa Bay outcrop (photo on top) is the result of several phases of bioturbation and hydraulic erosion. Successive inferred depositional surfaces shown as dashed lines: (1) earliest phase of colonization by bivalves from a relatively stable sedimentary surface; (2) bivalve traces crosscut by the traces of foraging walruses and minor erosion occurred; (3) another phase of bivalve colonization descends from a slightly aggraded sedimentary surface—this phase is less penetrative and ultimately only small basal portions are preserved; (4) walrus traces crosscut the bivalve traces; (5 and 6) final recorded phase of bivalve colonization and walrus predation with minor aggradation then erosion.

ation patterns observed within the biogenic sedimentary structure, particularly those that apparently reveal convective flow patterns, and (2) the association of the bowl structures with the bivalve-generated trace fossils.

The range of potential animal predators that dig for worms or bivalves in intertidal and subtidal settings is surprisingly broad. Detailed in Table 1 are grizzly bear excavations, dolphin traces, eagle-ray traces, raccoon-feeding pits, sea-otter pits, sturgeon traces, whale furrows, and walrus pits. Table 1 is divided into three major categories of feeding activity: mechanical excavation, biting and removal of the sediment, and fluid jetting to penetrate sediment. Bears (M. Gingras, personal observation, 2001), raccoons (M. Gingras, personal observation, 1997, 1999, 2004), sea otters (Shimeck, 1977; Calkins, 1978; Hines and Loughlin, 1980), various fishes (Cook, 1971), and dolphins (Fothergill, 2002) use mechanical excavation (i.e., digging into the sediment) to feed. Biting of the sediment is a habit of sturgeon (Armitage and Gingras, 2003) and whales (Nelson et al., 1981; Nelson and Johnson, 1987; Klaus et al., 1990). Eagle rays and walruses use hydraulic jetting (Howard et al., 1977; Gregory et al., 1979; Kastelein et al., 1989; Gregory, 1991). Both mechanical excavation and sediment biting result in irregular to bowl-shaped structures that are at least partly filled with massive-appearing sediment because the resultant pit margins collapse inward. Internal lamination, if present, is probably derived passively, and thus can be regular, organic rich, and drape the trace concordantly without laminations that dip greater than the angle of repose. These characteristics are not observed in the Willapa Bay ichnofossils.

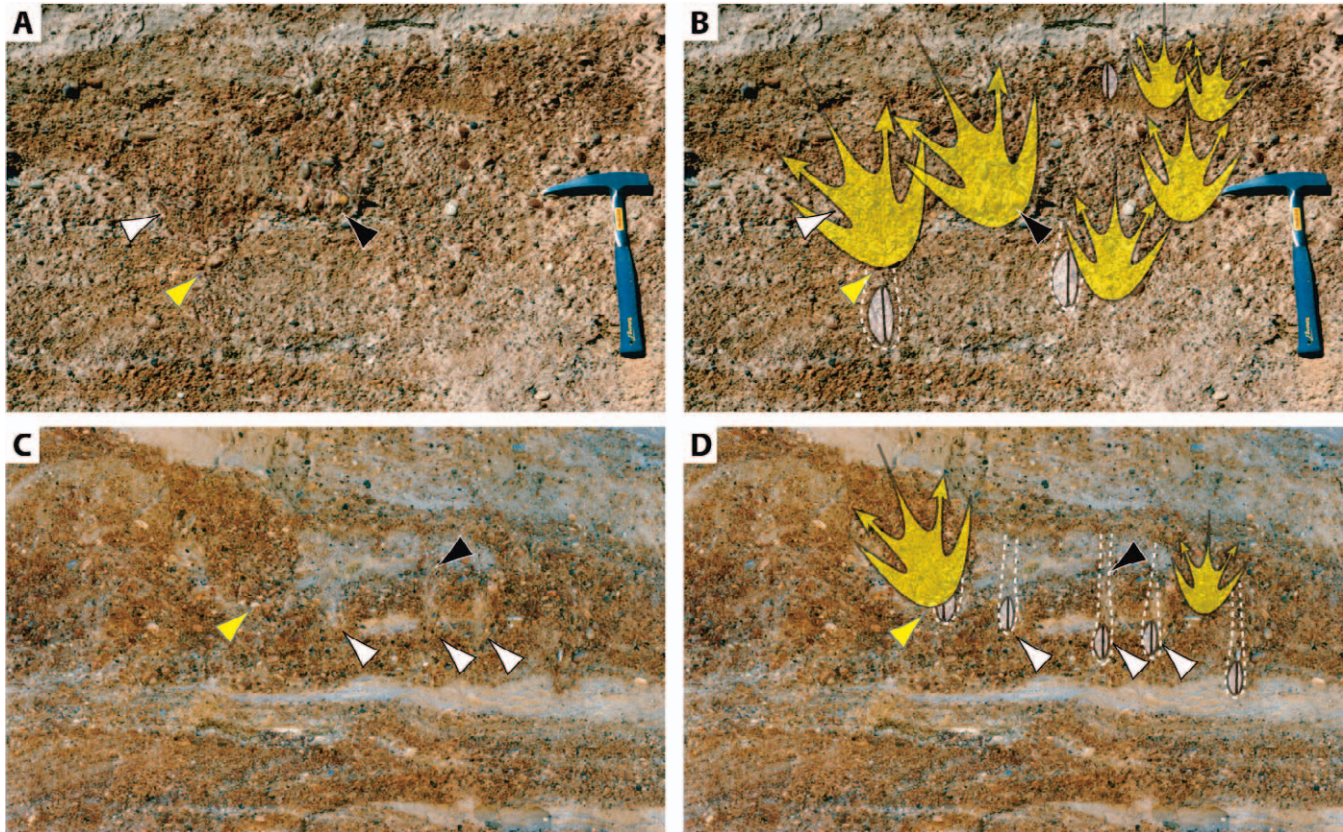


FIGURE 4—Occurrence and details of the biogenic sedimentary structures. A) Close-up of trace fossils. White and black arrows indicate positions of two bowl-shaped structures (*Piscichnus*), and yellow arrow indicates location of a truncated columnar trace fossil (*Siphonichnus*). White arrow shows hydraulically imbricated pebbles associated with biogenically injected water. Black arrow indicates zone where coarser grains accumulated near the base and center of the injected structure. B) Schematic interpretation of A showing location of jetted substrate and position of the now-absent bivalves at the base of their burrows. Bivalve trace fossils are outlined in white dashed lines. C) Close-up of outcrop where a large *Piscichnus* (yellow arrow) and several *Siphonichnus* (white arrows) are present. Black arrow shows a sandy infill where the bivalve's siphon once reworked the sediment. D) Schematic interpretation of C interpreted as in B.

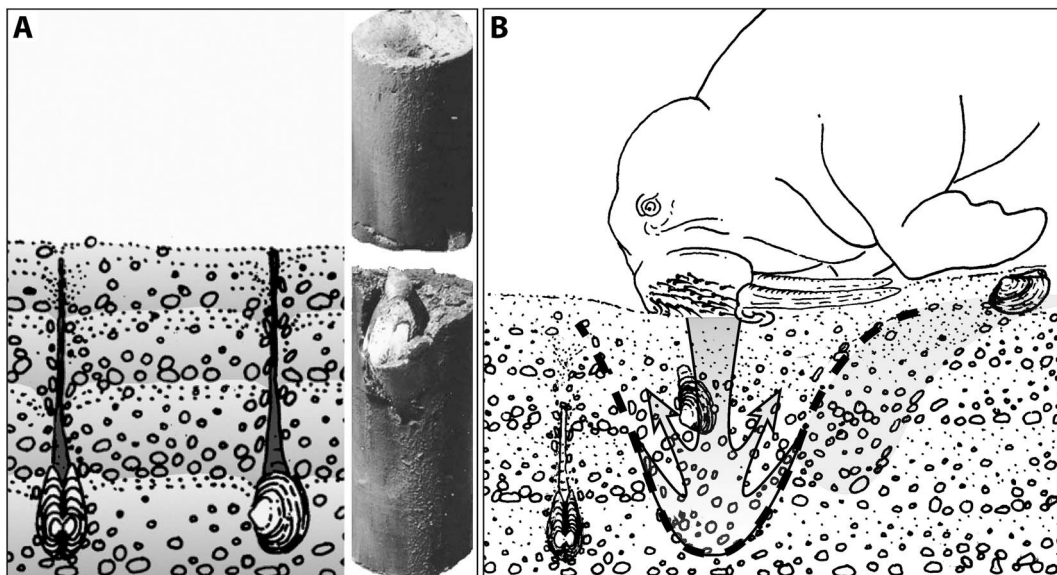


FIGURE 5—Behaviors represented by trace fossils. A) Schematic interpretation showing relationship between columnar trace fossils and bivalve lifestyle. Core on the right is a modern example of *Mya arenaria* taken from a sandy deposit at Willapa Bay. B) Schematic interpretation showing relationship between bowl-shaped trace fossils and walrus-feeding behavior.

TABLE 1—Range of animals that make bowl-shaped traces in marginal-marine settings and the physical characteristics of those structures.

Animal	General description of behavior	Morphology of excavation
<i>Mechanical excavation (Digging)</i>		
Grizzly Bear <i>Ursus ursus</i>	Grizzly bears are known to forage intertidal flats for bivalves—most commonly the razor clam <i>Siliqua patula</i> . The bear's efforts result in large excavations into sandflats that extend down to the burrow depth of the bivalve.	Irregular pit, 20–60 cm diameter. The depth should be variable, but 30 cm, which is typical for razor clams, should represent a reasonable mean.
Raccoon <i>Procyon lotor</i>	Raccoons commonly hunt for bivalves on intertidal flats in eastern and western North America. Their preferred prey is <i>Mya arenaria</i> , but shell debris derived from <i>Macoma</i> species have also been observed.	Round and slightly irregular in plan view, ranging between 5–30 cm in diameter. In general, the animal digs to the depth of smaller bivalves (10–25 cm). Massive fill.
Sea Otters <i>Enhydra lutris</i>	Sea otters exhibit foraging preferences similar to raccoons. But because otters are capable of hunting underwater, they can focus on prey that is more accessible and more shallowly burrowed. Thus, this is a subordinate behavior.	Similar to raccoon pits, but with a crudely laminated fill (hydraulically reworked).
Dolphins <i>Lagenorhynchus</i> (for example)	Dolphins dig underwater—especially for sediment-dwelling fish. Dolphin excavations leave a conical surface crater and may disrupt sediment to a depth exceeding 40 cm. The general cross section of these traces is indeterminate; current reworking would be absent.	Circular in plan view, but with an irregular cross section. Soft sediment deformation common near the burrow margins. Has a massive to crudely laminated infill.
<i>Substrate biting</i>		
Grey Whale <i>Estrichtius robustus</i>	Grey whale traces are meter scale troughs that represent a combination of sediment biting and mandibular reworking. The troughs are thought to be primarily filled with massive appearing sediment. The whale's quarry is typically sand shrimp.	Large (2–3 m X 1 m), with an elliptical plan view. Broad troughs up to 40 cm deep with massive, soft-sediment deformed, or laminated infill.
Sturgeon <i>Acipenser oxyrhynchus</i> (for example)	Sturgeon use a strongly overting mouth to punch into sediment and mechanically remove short cylinders of sediment—like a cookie cutter. The diet of sturgeon largely comprises amphipods, crustaceans, and polychaetes. Small bivalves (<i>Macoma balthica</i>) are potential prey.	Cylindrical excavation 8 to 16 cm in diameter. The bite may extend to a depth of 20 cm, but usually falls between 5–15 cm deep. Massive to laminated fill.
<i>Hydraulic jetting</i>		
Eagle Rays <i>Aetobatus narinari</i> (for example)	Rays have the capacity to jet fluid into sediment substrates and suspend food into the immediate water column. Then the rays ingest the food. Ichnofossils attributed to this behavior have been identified in sand substrates in the rock record.	Variable morphology that is usually deep (20–40 cm). The trace has a somewhat variable diameter to the terminal depth. Trace can be filled with jetted laminae.
Walrus <i>Odobenus rosmarus</i> (for example)	Walruses exhibit a behavior similar to rays but have the capacity to generate higher current velocities. In modern settings, walrus traces have been observed in a range of sediments, including gravels, and are normally associated with bivalves as prey.	Vertically oriented and deep (25–55 cm) with a hydraulically sorted core, especially in coarse-grained sediments. Inclined or dipping examples locally common.

Notably, elasmobranch- and walrus-feeding traces are bowl shaped and can be filled with massive-to-laminated sediment infill: these traces, referred to as *Piscichnus* (Gregory, 1991), are similar to the large, concave trace fossils reported here. Until now, *Piscichnus waitemata*, which is interpreted generally to represent jetting of the bottom sediment to suspend and then ingest food, and *Piscichnus brownii*, thought to represent fish nests, have only been identified in sandstone and mudstone (Feibel, 1987; Gregory, 1991). The occurrence of *Piscichnus* in gravel sediment is surprising, as the water velocities required to move pebbles are very high. Yet the organized fill of the Willapa *Piscichnus* show that hydraulic currents generated the fabric therein.

Of walruses and rays, only the former has a mouth that is capable of producing the high-current velocities and holding, in its mouth, the large volumes of water (more than 2 L, estimated from walrus skulls) required to suspend gravel and expose infaunal prey. Moreover, bivalves and bivalve siphons represent an important food resource for walruses, and such predation traces juxtaposed with bivalve traces are expected (Oliver et al., 1983; Fukuyama and Oliver, 1985).

Observation of walruses indicates that they locate prey by using visual methods as well as touch by using vibrissae (Oliver et al., 1985). Where a potential meal is identified, the walrus roots with its snout and subsequently jets water into the seafloor at an incident angle of 45°–90° to the horizontal plane. The mollusk's siphon is thus exposed or, alternatively, the shellfish is propelled upward nearer the sediment-water interface by dispersion pressure resulting from grain-grain collisions within the sediment boil induced by the hydraulic jet (Fig. 5). During jetting, sand-sized grains are partly winnowed from bottom sediments, probably resulting in the cleaner gravel infill (see Figs. 2 and 4).

Once the mollusk reaches the sediment-water interface within the sediment boil, it is extracted from the liquefied sediment slurry, and the soft parts are sucked from the valves of the mollusk. With walruses, this is done using the same muscles employed during jetting (Fay, 1981). The

suctioning of valves by walruses is supported by three common observations reported from the modern record: (1) uncrushed valves devoid of soft fleshy material located commonly adjacent to the excavation pits on the seafloor (Oliver et al., 1983; Nelson et al., 1987); (2) apparently whole, nonmasticated soft parts recovered commonly from the gut contents of slaughtered walrus; and, (3) an absence of whole or crushed shells in the gut contents of slaughtered walrus. The walrus does not have to exhume the entire bivalve to achieve success: biting off a large portion of the prey's siphon is a common result of the walrus' activity (Welch and Martin-Bergmann, 1990).

DISCUSSION

We interpret the trace fossils at the North Cove outcrops to represent the activities of infaunal bivalves and foraging walruses. Their co-occurrence represents a predator-prey relationship between the two animals. Although other predators of bivalves are common, only walruses are known to use very high-energy jets to attack their infaunal prey. The use of hydraulic jetting, indicated by the internal fabric of the concave ichnofossils, excludes most other large animals as potential tracemakers.

Sedimentological Significance

Many deep-burrowing bivalves possess a longevity unmatched by any other noncolonial invertebrates. Analytical methods of molluscan growth structures used in conjunction with radiometric-dating techniques have established that the minimum ages of such larger bivalves as *Mya arenaria*, *Tresus nutalli*, and *Panope generosa* extend beyond 30 years and, in some instances, to 150 years (Jones, 1989). Bivalve longevity results in part through deep-burial depths in coarse-grained sediments that are well armored against predation. Deep-burrowing bivalves have few predators that can effectively excavate to the depths necessary for their capture. Beyond a certain depth and grain-size threshold, many of the ex-

cavation mechanisms utilized by invertebrates are ineffective and detrimental to the predator's foraging strategy. This is particularly true for such invertebrates that have long been recognized as common predators of bivalve mollusks as crabs and sea stars. Profitability—energy intake per unit handling time—of bivalve predation by crabs is influenced by burial depth of prey (Zaklan and Ydenberg, 1997; Smith et al., 1999) and by the grain-size of bottom sediments (Ansell, 1962; Arnold, 1984, Alexander et al., 1993; Smith et al., 1999). Coarse sediment, however, can be detrimental to pelecypod colonization and growth (Swan, 1952; Pratt, 1953; Ansell, 1962).

Approximate ages for bivalves provide minimum times of stability for the contact along which the traces at North Cove are preserved. Notably, many deep-burrowing bivalves are not exceptionally mobile, and they live in one burrow for their entire life cycle (Armstrong, 1965). In the outcrop studied here, the size and depth of the bivalve structures are typical of large, adult bivalves, and their occurrence in gravelly bottom sediments is consistent with modern occurrences of *Tresus nutalli* and *Panope generosa* (Stanley, 1970; Zwarts and Wanink, 1989). Thus—at least for a time of 2–4 decades—the gravelly sand-sand contact in the Pleistocene terrace is interpreted to have experienced little sediment aggradation or degradation while the surface was exposed to marine waters. This temporal scale is consistent with internal baymouth dynamics of the modern Willapa Bay, in which large tidal channels migrate northward across the 5-km-wide inlet and then avulse across the inlet to the south through time periods of 40–100 years (Clifton and Gingras, 1997).

Paleoecological Significance

Absolute-age dating of bones recovered from sedimentary deposits throughout North America provides a chronological basis from which to map the paleogeographic distribution of Pacific and Atlantic walrus herds, as shown by Harrington and Beard, (1992), Bouchard et al. (1993), and Dyke et al. (1999). In those studies it has been shown that within the Late Wisconsinian (29 ka) and throughout the Holocene, walrus herds have wandered from their northern latitudes to as far south as San Francisco Bay, California, and Kitty Hawk, North Carolina. These displacements of the walrus herds from their present distributions in the Bering and Chukchi Seas and Canadian Arctic Archipelago coincide with glacial maxima and correspond to advances of oceanic ice flows southward. Trace-fossil evidence of walrus feeding in and around paleo-Willapa Bay provides physical evidence of similar southerly displacements prior to the Holocene epoch. Relative age comparisons made between the younger and older Pleistocene terraces indicate that the trace fossils described here represent the earliest presence of walrus herds along the Pacific coastline of North America (>190 ka).

Although paleoecological information from body fossils may be limited by uncertainties associated with their taphonomic history, the sedimentologic nature of trace fossils is such that they are generated in situ and are not subject to posthumous transport. As such, trace fossils accurately record the spatiotemporal context in which the tracemaker generated the structure in response to imposed environmental conditions. Praedichnia or biogenic predation trace fossils preserve the unique paleoecological predator-prey interactions and can provide additional information about the paleoenvironmental contexts in which the trace fossils were produced (Harper, 2005).

SUMMARY

Walrus herds are likely to have produced the feeding excavations at paleo-Willapa Bay, Washington. The herds presumably wandered from the northern Pacific ice front during the Pleistocene. This was likely the result of the walruses becoming barricaded from their present habitat in the Bering Shelf and Chukchi Sea during glacial maxima. In general, walruses require ice as a medium for leaving water to rest and breed; today, they are principally restricted to moving ice pack (Fay and Ray, 1968; Fay, 1981). Lateral movement of the ice pack and, hence, walrus

habitat was affected greatly by continental glaciations during the Late Wisconsinian and Holocene (Dyke et al., 1999); this is confirmed independently by the presence of walrus traces in southern Washington. Such data independently confirm the presence of ice pack in lower latitudes—at least down to approximately 47°N—and demonstrate climate-induced migration of walruses.

Sedimentary structures documented from a Pleistocene-age stratum at Willapa Bay, Washington, are best explained by biological interactions with sedimentary media than by physical sedimentary processes. This interpretation depends on the physical characteristics of columnar structures (*Siphonichnus*), including poorly defined spreite and evidence of repeated reaming and reworking, both of which are associated commonly with bivalve behavior. Moreover, the size and general morphology of the structures are typical of modern and ancient bivalve traces. Large bivalve traces indicate long periods (probably decades) of sea-floor colonization and can thus be linked to dynamic processes associated with the bay-mouth. Larger bowl-shaped structures (*Piscichnus*) are discounted as strictly hydraulic artifacts because they are commonly coincident with the bivalve structures, and the interred grain fabric is best explained by fluid jetting into the sea floor—a behavior exhibited by some marine vertebrates, including walruses.

The co-occurring trace fossils, whereby *Piscichnus* generally crosscuts *Siphonichnus*, indicate a predator-prey relationship and are thought to represent walruses foraging on bivalve siphons. Insofar as the morphology of the ichnofossils fits, we base our interpretation on the powerful jetting that walruses are capable of producing—sufficient to fluidize gravelly sediments—and on the knowledge that bivalves are a favored staple of walruses.

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