Modern Perspectives on the *Teredolites* Ichnofacies: Observations from Willapa Bay, Washington

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This study details occurrences of Teredolites ichnocoenoses from modern bay-margin settings in Willapa Bay, Washington. In particular, the paper scrutinizes in situ loggrounds from two intertidal zones situated immediately seaward of low-lying, supratidal, forested marshlands that are fed by small streams. Vestiges of remnant marshes and streams are preserved on intertidal flats as in-situ roots, broken stumps, strewn logs, abundant organic detritus, and organic sandy mud. Xylic material and organic sediment were deposited in the supratidal marshes: tide and wave processes truncated the swamps, exposing in situ treeroot networks and the lowermost supratidal sediments. Stream and swamp deposits overlie and incise older Pleistocene strata. Both units are overlain by discontinuous, modern intertidal deposits.

The intertidally exposed stumps and logs support a diverse community of animal and plant life. Boring organisms, encrusters, and refugium seekers are found on and within the xylic substrates. Some encrusting animals and all of the boring fauna produce traces that are comparable to ichnofossils reported by palichnologists. Wood-boring traces reported in this study are similar morphologically to the ichnogenera Caulostrepsis, Entobia, Meandropolydora, Psilonichnus, Rogerella, Teredolites, Thalassinoides, and Trypanites. Most of these ichnogenera have not been reported from rock-record examples of the Teredolites ichnofacies.

The stratigraphic and environmental significance of the reported (modern) locales is consistent with previous studies that associate Teredolites ichnofacies with base-level rise in marginal-marine environments. At Willapa Bay, bored xylic media form a coeval surface with adjacent, burrowed firmgrounds as well as softgrounds.

INTRODUCTION

The *Teredolites* ichnofacies comprises borings that penetrate xylic substrates. The most common element of the ichnofacies is *Teredolites longissimus*, although typically, *Teredolites clavatus* Leymerie also is present. These ichnofossils are normally considered to be indicators of mar-

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ginal-marine or marine conditions (Bradshaw, 1980; Bromley et al., 1984; Urreta, 1987; Arua, 1991; Savrda, 1991; Mikulás, 1993; Savrda et al. 1993; Mikulás et al., 1995; Lavigne et al., 1998; Pirrie et al., 1998; Obata, 2000). Some researchers have linked *Teredolites*-bored woodgrounds to marine transgression (e.g., Panos and Skacel, 1966; Bromley et al., 1984; Savrda, 1991; Savrda et al., 1993).

Two occurrences of *in situ* log-grounds at Willapa Bay, Washington, provide an ideal opportunity to assess the overall significance of the *Teredolites* ichnofacies. As detailed below, the *in situ* xylic media support diverse boring communities that thus far have not been accounted for in rock-record examples. Observations made at these locations potentially can enhance our understanding of fossil occurrences of the *Teredolites* ichnofacies.

STUDY AREA AND GEOLOGICAL CONTEXT

Willapa Bay is a mesotidal estuary situated near the southwest corner of Washington, USA (Fig. 1). Outcropping Pleistocene terraces, which have been the focus of intense scientific scrutiny, rim the bay on its east and north margins. The Pleistocene deposits represent ancient bay accumulations that reflect similar, but not identical, depositional conditions. It is the similarity of the ancient strata to the modern bay sediments that has inspired much of the previous geological investigation (Clifton and Phillips, 1980; Smith, 1989; Gingras et al., 1999). Additionally, Willapa Bay is reasonably well known because of its association with megathrust earthquake studies (Atwater, 1987) and ecological studies pertaining to diatoms (Atwater and Hemphill-Haley, 1997), thalassinid shrimp, and various fisheries.

Willapa Bay is considered to represent a relatively pristine west-coast embayment (Clifton and Phillips, 1980). However, anthropomorphic influences, including local logging since the late 1800s, a diverse and enduring oyster industry, shrimp-bait harvesting, salmon and crab fishing, and bay invasion by exotic flora and fauna (i.e., *Spartina* (cord grass) and the Japanese littleneck clam, *Tapes japonica*), have shaped the modern bay. Moreover, efforts to maintain the bay as a navigable waterway have led to repeated dredging of active (inlet) tidal channels.

Following the most recent continental de-glaciation, the

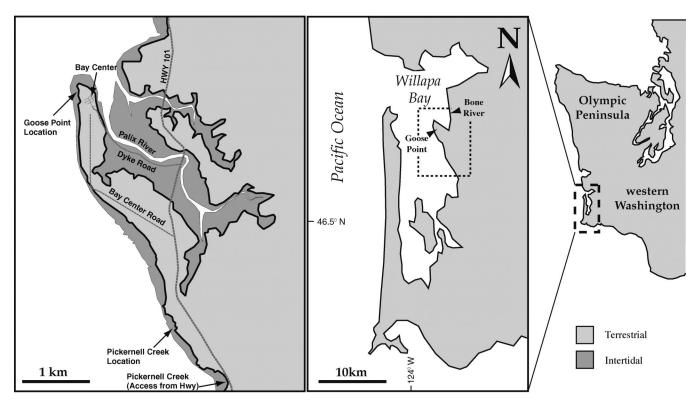


FIGURE 1—Location map of the study areas. Goose Point and Pickernell Creek locations are easily accessed: Goose Point is accessed from Bay Center, while the Pickernell Creek location is best reached by walking (at low tide) from Pickernell Creek, on Highway 101, northwards along the outcrop. Rising tide inhibits exit from the Pickernell area approximately 3 hours before high water is reached.

modern bay has maintained a state of sediment infilling. Although presently it is filling, the eastern and northern bay margins are clearly in a state of erosion. Bay widening is associated with wave- and tidal-ravinement processes that are disjointed from the initial lowstand and transgressive erosion that shaped the valley in which the bay now resides. Modern erosion is most evident on the east side of the bay near Goose Point and Pickernell Creek (Fig. 1). At these locations, Pleistocene strata form prominent bluffs that abruptly break slope into gently, bayward-dipping surfaces that coincide with the upper intertidal zone. The firm, ancient substrate extends tens of meters from the outcrop at Goose Point, and as much as 260 m at Pickernell Creek (Fig. 1). Locally, the eroded Pleistocene unit has a curiously stepped morphology that has been attributed to wave or tidal-creek erosion (Gingras et al., 2001), but may also be related to post-seismic subsidence (Gingras et al., 1999). The nature and form of these erosional surfaces are discussed in detail in Gingras et al. (2001).

Modern creeks and swamp/wetlands occupy topographic lows in the Pleistocene strata. Where the creeks and swamps meet the tidal flats, the wetlands generally have eroded back with the outcrop. Two excellent examples of this—an eroded swamp at Goose Point and an exhumed creek bed near Pickernell Creek (Figs. 1–3)—are present at Willapa Bay. At Goose Point, the truncated swamp is manifested by *in situ* stumps that are immersed during high tide and occupy an 80 x 100 m area. The logs are bored by a diverse marine fauna; the intensity of boring increases towards the bay. The occurrence of woodground at Pickernell Creek results from an eroded creek and marsh, the remains of which can be traced across the tidal flat for over 260 m. Trees, generally fir and cedar, once resided near the low-energy channel and are preserved as *in situ* stumps that follow a long meander of exhumed creek bed. As with the Goose Point locality, the Pickernell stumps provide a xylic substrate for marine organisms. This study concentrates on the ichnology and sedimentology of these two locations to generate perspectives on their applications to the rock record.

METHODS

Key aspects of this study included: (1) observation and identification of borings in wood and burrows in soft- and firm-clastic sediment, (2) characterization of sediment distribution, (3) documentation of the colonization patterns on the *in situ* tree stumps, and (4) mapping the distribution of bored stumps.

Borings in wood were observed, photographed, and documented by sawing or breaking the wood and exposing the inner, bored portions. Several examples were cut by saw, photographed, and x-rayed. Wood x-ray slabs were cut to a thickness of 2.5 cm. X-ray exposures were 60MVp for 50 seconds at approximately 3.0 mA, using a Hewlett-Packard Faxitron portable x-ray unit. Burrows in the sedimentary substrates were exposed by trenching, using box cores, and by x-raying slabbed sediment samples. Sedimentary slabs generally were 2 cm thick. X-ray parameters were approximately 75MVp for 110 seconds at about 2.9 mA.

Sixty-eight logs and stumps were described at both lo-

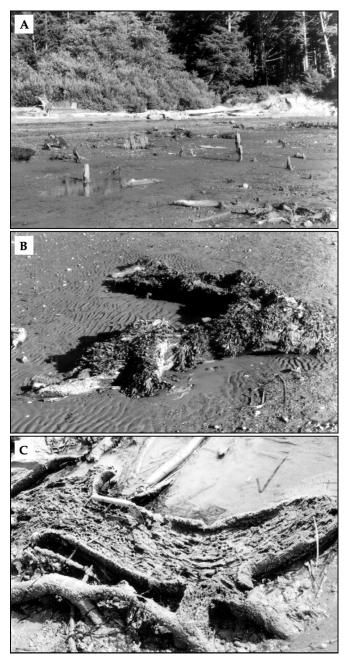


FIGURE 2—Settings and occurrences of the bored xylic substrate. (A), (B) Goose Point locality. (A) Overall view of study area. Note wood clasts and *in situ* stumps are present throughout study area. The low-lying temperate, wooded wetland from which the wood is derived is visible in the background. Field of view in foreground is 10 m. (B) A kelp-encrusted, *in situ* root system that was partly exhumed from the clastic substrate. Field of view is 2.5 m. (C) Pickernell Creek locality. A beveled, laterally extending, extensively bored basal root with teredinid domiciles. Field of view is 2.5 m.

cations. Organism and boring distributions on larger stumps and wood clasts were assessed using 100 cm^2 counts around the object. The counts were accomplished by placing a 10×10 cm wire and string grid directly on the wood or sediment substrate. Smaller wood samples were assessed with total counts of borings and encrusting organisms. Stumps and logs were plotted on plan-view

sketches of the study areas. Surveying of the areas was conducted with large tape measures, compass and pacing, and by a portable GPS system.

OBSERVATIONS

Distribution of Substrates

The immediate study area consists of exhumed Pleistocene strata, discontinuously superposed by recent marsh and creek deposits and even younger tidal-flat sediments (Fig. 3). Thus, sediment parameters at the surface, such as cohesiveness, grain size, and organic content, are markedly heterogeneous.

In the study areas, the tidal flats lie on, or comprise exhumed Pleistocene strata. At both locales, the strata are interpreted to have accumulated between 100,000 and 200,000 years before present (Kvenvolden et al., 1979). The Pleistocene unit is eroded flat and dips at a low angle away from the upper intertidal edge. At this point, either the slope breaks upwards into steep bluffs that locally form the bay margin, or the intertidal flat grades into supratidal, marshy lowlands. The ancient sediment is very firm, indicating previous burial and dewatering (Gingras et al., 2000, 2001).

Organic-rich, muddy, Recent sands locally overlie the firm Pleistocene strata. The organic deposit encompasses occurrences of *in situ* stumps, wood clasts, and logs. Wood fragments, seeds, fir cones, and flakes of terrestrial organic debris are disseminated throughout the sediment. The contact between the firm and soft substrates is sharp and occurs on either side of the wood-rich deposit, suggesting the muddy sands have accumulated in an incised channel. This is particularly obvious at the Pickernell Creek location, where a channel meander can be traced for 260 m across the tidal flat. Marshy lowlands, fed by small creeks, back both localities. It is inferred that the organic substrate represents the remnants of the eroded marsh and creek that previously occupied the tidal flat, albeit in a supratidal location.

Modern intertidal sediments are patchily distributed across both the firmground and the organic substrate. The thickness of this sediment is variable, up to 15 cm, and ranges texturally from muddy sand to sandy mud. The sediments become an even, overlying blanket that thickens significantly baywards. At Goose Point, the modern tidal-flat deposits exceed a meter in thickness approximately 100 m from the bay margin. Pickernell Creek has a shallower grade adjacent to the outcrop; thus, sediment veneer does not exceed a meter in thickness until well past the 260 m mark from the pocket beach, where the eroded creek bed originates.

Because there is a wide range of substrates presently available in the study areas, a variety of modern burrowing and boring behaviors are observed. In general, the trace assemblages are characteristic of particular substrates. The most important characteristics of woodground, firmground, and softground trace-making communities (ichnocoenoses) are outlined below.

Woodground Ichnocoenose

At both locations, woody substrates, although sporadically distributed, exhibit the most diverse faunal commu-

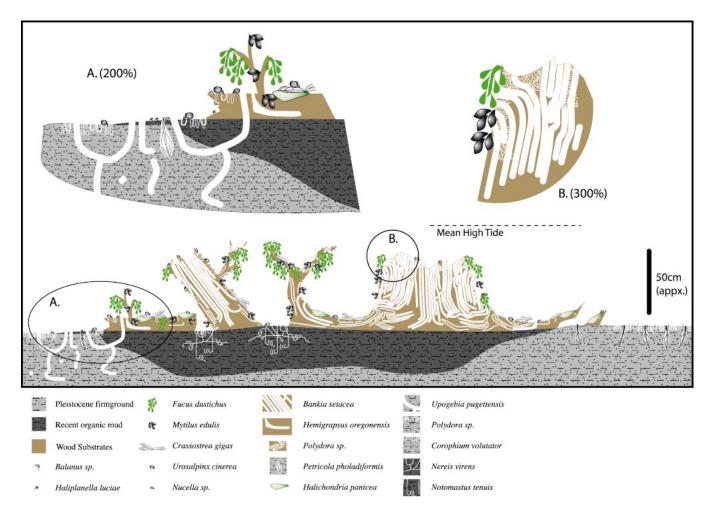


FIGURE 3—Schematic diagram of the burrowing, boring, and encrusting community associated with *in situ* log- and stump-grounds and underlying sediments at Willapa Bay. Stumps and wood clasts primarily are found in firm, organic to sandy mud that overlies firmer Pleistocene substrates. Large, Y-shaped burrows of the mud shrimp, *Upogebia pugettensis*, are most abundant in the firm Pleistocene stratum at Goose Point. Locally, they penetrate the organic sediment and are undeterred by wood fragments. *Psilonichnus*-like borings, emplaced by *Hermigrapsus oregonensis*, also are present. Although these borings may reflect re-excavation of teredinid borings, their overall geometry is very similar to excavations made by the same animal in softer substrates. Xylic substrates host a diverse community of boring, encrusting, and squatting organisms. Borings of spionid polychaetes (*Polydora* sp.) are present as U-shaped to meandering borings near the surface of stumps and wood clasts. Locally, these smaller borings are cut by, or intersect larger teredinid borings. The most conspicuous organism in xylic substrates is *Bankia setacia* (Inset A). U-shaped burrows of polychaetes and isopods also penetrate xylic substrates (Inset B).

nities (Figs. 2–4). Several encrusting organisms, including sponges (*Halichondria panicea*), mussels (*Mytelus edulus*), barnacles (*Balanus glandula*), small anemones (*Haliplanella luciae*), oysters (*Crassostrea gigas*), and rock kelp (*Fucuc dustichus*), cover stumps, logs, and exposed roots. Encrusting animals are unevenly distributed about the stumps and root systems (Figs. 2B, C, 3). However, those organisms clearly prefer wood that is continuously exposed to standing water. In such instances, the surfaces of the wood substrates are completely covered by encrusting animals. Small anemones and sponges dominate these aqueous refugia.

Boring activities in the woody substrates largely reflect the activities of three animals, namely shipworms (*Bankia* setacea), spionid polychaetes (*Polydora* proboscidea=Boccardia proboscidea; henceforth Polydora), and boring isopods (*Limnoria lignorum*, also known as gribbles). Shipworms emplace long, tubular, *Teredolites*-like borings in the wood that originate perpendicular to the wood surface and ultimately bend, becoming grain-parallel, and generally parallel to each other (Figs. 5, 6). Teredinid borings range between 3 and 16 mm in diameter, and are up to 28 cm in length. Tight turns are observed where available substrate is restricted (Fig. 5B, C). Interpenetrations are rare. Boring activities can be so intense that up to 92% of the original xylic material is removed. Typically, a calcite tube surrounds the entire boring. Calcite linings are lacking in abandoned teredinid borings.

The spionid, *Polydora* is the second most common borer in these woody substrates. Generally, it emplaces smalldiameter (< 2 mm), U-shaped tubes that have a decidedly *Caulostrepsis*-to *Meandropolydora*-like morphology. *Polydora* borings initiate perpendicular to the wood surface, and commonly veer parallel to the wood-grain where it is encountered. Notably, where *Polydora* boring densities are high, the borings develop into a complex antler-form

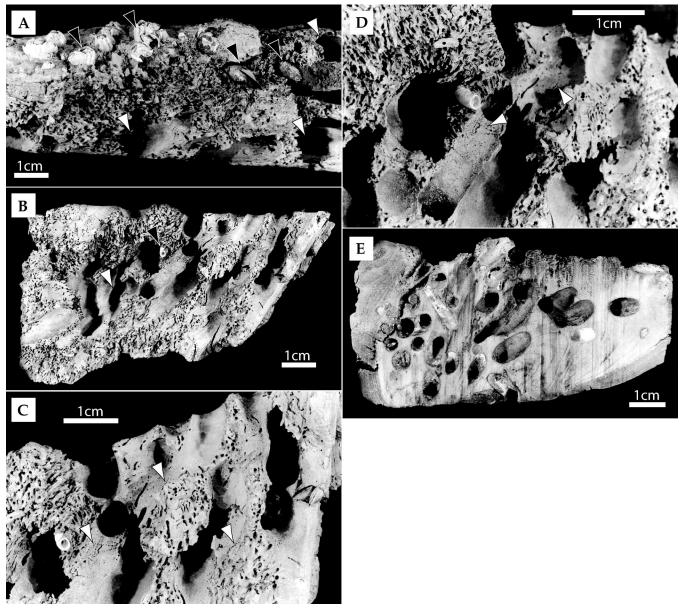


FIGURE 4—Conspicuous borings and encrusters from xylic substrates in the study areas. (A) Intensely *Polydora*-bored branch cut from an *in situ* stump at Goose Point. *Polydora* borings meander about each other, forcing departure from simple U-shaped geometries. Also present are larger teredinid borings (white arrows) and encrusting barnacles and mussels (black arrows). (B) Bored wood fragment from the Pickernell Creek location. As with (A), this sample is bored by *Polydora* and *Bankia* (white arrow). A raised tube, possibly a raised extension of a *Bankia* tube, is indicated by the black arrow. (C) Close-up of the wood fragment shown in (B), indicating the locations of various sponge borings (white arrows). (D) Close-up photograph of the clast shown in (B) emphasizing the intense amount of substrate removal that is common with the clasts. Sponge borings are labeled with white arrows. (E) In slabbed samples, the wood grain-parallel nature of the teredinid borings is most obvious. Here, the borings radiate with wood grain.

(*Meandropolydora*) (Figs. 4, 5B). As with teredinid borings, ecospace utilization is locally very high, such that very little original substrate remains.

Boring isopods (*Limnoria lignorum*) introduce 2–3 mm diameter tunnels into the woody substrate. The tunnels are long (up to 10 cm) and tend to be arranged en echelon. The borings loosely follow the grain of the wood either until another boring is encountered or until the tunnel returns to the wood-water or wood-air interface. The traces ultimately resemble *Trypanites* or *Teredolites*; however, the animal also constructs crude U-shaped forms that are better compared to broad *Caulostrepsis*. The overall form of these latter borings is not eurythmically proportioned as those induced by *Polydora*. It is also evident that the amphipod *Corophium volutator* Pallas squats in abandoned *Polydora* borings. The isopod renovates the initial gracile structure by increasing its diameter and extending its length.

Other borings observed more rarely in the wood substrates include *Psilonichnus*-like excavations of the intertidal crab, *Hemigrapsus oregonensis*, and large-diameter (24 mm), *Thalassinoides*-like borings emplaced by the

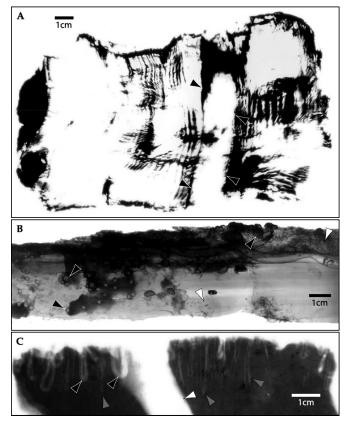


FIGURE 5—X-rays of specific borings observed in woodground and firmground substrates at Willapa Bay. (A) Wood clast with an extension of a shrimp burrow. In this case, *Upogebia pugettensis* was recovered from the domicile. The edge of the burrow is marked with black arrows. (B) Complex fabric composed of *Caulostrepsis* and *Meandropolydora*-like borings (white arrows). These borings are primarily the work of *Polydora*. Also present are various encrusting or ganisms. Barnacles (black arrows) produce a small divot beneath them (not visible on x-ray), which is likened to *Rogerella*. (C) Slab of firmground with *Thalassinoides* (white arrow), *Arenicolites* (black arrow), and *Diplocraterion* (gray arrow). These were made by *Upogebia pugettensis*, *Corophium volutator*, and *Polydora* sp., respectively.

mud shrimp, *Upogebia pugettensis* (Figs. 3, 5A). These typically are associated with xylic substrates at the Goose Point locality. The sponge *Halichondria panicea* Pallas is rarely present. Where sponges have fastened to the wood, small *Entobia*-like traces are developed. Barnacles, although quite common, leave only shallow indentations that are not always discernible. These are most similar to the trace fossil *Rogerella*.

Besides the array of encrusting and boring organisms occupying the woody substrates, a host of squatters and refugia seekers are present in the borings as well (Figs. 2, 3, 4, 5B). These include the Japanese littleneck clam (*Tapes japonica*), mussels (*Mytilus edulis*), amphipods (*Corophium volutator*), polychaetes (*Neries virens* = *Neanthes virens*), ligiad isopods, Pacific whelks (*Urosalpinx* sp.), and periwinkles (*Nucella* sp. and *Littorina keenae*).

Based on the 68 logs and stumps described from both locations, the distribution of boring, encrusting, and squatting organisms is variable. *In situ* stumps that are exposed in middle-intertidal zones (submerged for 4–8 hours every flood tide) contain as many as 48 borings of *Bankia* in a



FIGURE 6—X-rays of teredinid bivalve borings that represent a variety of population densities and space-utilization strategies. (A) Two isolated borings penetrating a branch taken from Goose Point. The bivalve that produced the boring is visible in the right-hand example. (B) Moderate to high burrow densities that follow convolute wood grain at a branch junction. (C) Densely emplaced, grain-parallel borings. Note the squatters (white arrows) and the wood grain (black arrows).

100-cm² area. Other extremes are 198 *Corophium* and 82 *Polydora* in 100 cm². Crab and shrimp borings are rare and only occur in the middle-intertidal zone. Barnacles are present in numbers up to 139 individuals/100 cm². Anemones (*Haliplanella luciae*), oysters, mussels, snails, and kelp holdfasts approach 20, 3, 14, 21, and 73 individuals/100 cm², respectively. Sponges are present only in the middle-intertidal zone, where standing water remains around the wood.

Stumps present in the upper-intertidal portions of the exposure (submerged for 2–4 hours every flood tide) have lower maximum boring densities, but about the same quantity of encrusting organisms. Here, the teredinid bivalve, *Bankia* is generally absent. Occurrences of *Polydora* and *Corophium* range between 0 and 40 individuals/100 cm². However, unbored wood is most common. Anemones,

oysters, mussels, snails, and kelp holdfasts approach 4, 3, 5, 37, and 22 individuals/100 cm², respectively.

Firmground Ichnocoenose

Three distinctive biological associations are recognized in the firmground substrates at Willapa Bay: the *Polydora*, the *Petricola*, and the *Upogebia* associations. Each association exhibits a strong preference for substrate firmness, substrate texture, and bathymetric zonation. Animal responses to these substrate parameters are detailed in Gingras et al. (2001).

Polydora and *Petricola* associations characterize the study area (Fig. 5C). *Polydora*-dominated assemblages primarily consist of small *Diplocraterion*-like traces, which are produced by the spionid worm *Polydora*, and *Arenicolites*-like traces emplaced by *Corophium*. The traces consist of 1 mm diameter, 3–4 mm wide U-shaped tubes that descend 1 to 6 cm below the surface of the firmground. Burrow densities range locally between 0 and 128 individuals/100 cm². Population densities plotted along the intertidal zone also show a sporadic distribution pattern. Intertidal data are somewhat variable, due to the sporadic presence of a veneer of tidal flat sediment that correlates to a reduction of *Polydora* burrow density (Gingras et al., 2001).

Along with *Polydora*, burrows of the amphipod *Corophium volutator* are common. These traces have *Arenicolites*- and *Diplocraterion*-like geometries (Fig. 5C), and are broader than the burrows generated by *Polydora*. Larger burrows of the crab *Hemigrapsus oregonensis* and the bivalve *Petricola pholadiformis*, whose burrows are *Psilonichnus*- and *Gastrochaenolites*-like, respectively (Fig. 3), are rare.

In contrast, *Petricola*-dominated assemblages comprise clavate burrows produced by the bivalve *Petricola pholad-iformis* (Fig. 3). These burrows normally measure 10 to 25 mm in diameter near the base, taper to approximately 10 mm at the aperture, and range between 5 and 14 cm in length. Burrow densities range from <10 to 87 burrows/ m^2 . This ichnocoenosis is observed more commonly in the lower to middle intertidal zone, and is inundated at least 4 hours per tidal cycle.

Other trace fossils include rare, *Thalassinoides*-like burrows excavated by the mud shrimp *Upogebia pugettensis*. These traces have a Y-shaped architecture (Figs. 3, 5C). Burrow cross-sections are circular and their diameters vary between 9 and 21 mm. Depths of penetration are between 40 and 60 cm. Locally, these traces are observed to translate from firmground to softground, and then into xylic media, without any perturbation of the burrow morphology.

Softground Ichnocoenose

Generally, soft sediments host several tracemakers that do not burrow into the firmgrounds. In sediment veneers overlying the firmgrounds, notable burrowers include the worms *Nereis*, *Saccoglossus*, *Heteromastus*, *Cirriformis*, and *Nephtys*, and the amphipod *Corophium*. These animals generate, respectively, *Arenicolites-*, *Planolites-*, *Palaeophycus-*, *Gyrolithes-*, *Rosselia-*, and *Diplocraterion-*like trace fossils. Most of these traces veer from and parallel the firmer substrate where they encounter the firmground.

Soft, organic-rich substrates that contain the bored stumps and wood clasts host an entirely different ichnocoenosis. In these sediments, the redox discontinuities are at, or very near the sediment-water interface. Thus, animals that live within the anaerobic media irrigate their burrows with open connections to the surface. The burrows themselves also are maintained as open structures. The burrowing community is sparse and sporadically distributed. In general, it only includes the polychaete *Neries*, which persists in branching *Palaeophycus*-like burrows, and the threadworm, *Heteromastus*, which constructs small-diameter, incipient *Skolithos*, *Trichichnus*, and even small *Gyrolithes*.

INTERPRETATIONS AND DISCUSSION

Woodground Boring Assemblage

Perhaps the most striking feature of these present-day woodground ichnocoenoses is the high diversity of boring and encrusting organisms comprising the faunal and floral community. In contrast, most rock-record occurrences of woodgrounds display a low diversity of trace fossils (Bromley et al., 1984; Plint and Pickerill, 1985; Savrda et al., 1993; Mikulás et al., 1995; Pirrie et al., 1998). Although these low-diversity suites are dominated by the ichnofossil Teredolites longissimus, Bromley et al. (1984) presented an excellent example of a woodground dominated by Teredolites clavatus. Woodground trace assemblages commonly are monospecific, however, size-class variations have been observed in some of the boring assemblages. For example, several *Teredolites clavatus* detailed by Bromley et al. (1984) appear to represent animals at different stages of maturity. This is more evident with examples figured in Savrda et al. (1993), where two sizes of Teredolites longissimus are present. This bimodal size distribution is best attributed to successive colonization events or the presence of different species of boring shipworms (see Singh and Sasekumar, 1996).

Notably, the diversity of traces observed in this study has not yet been recognized in the rock record. Although Teredolites is the common boring observed in xylic substrates of our study areas (Figs. 2, 4, 5, 6), structures akin to Caulostrepsis (Fig. 5B), Meandropolydora (Fig. 5B), and *Rogerella* (Fig. 5B) also are observed, as are less-common Entobia (Fig. 4C, D) and Trypanites, and rare Psilonichnus and Thalassinoides (Fig. 5A). Considering the abundance of animals that squat in, encrust, or bore into the woody haven, it is apparent that in situ occurrences of the Teredolites ichnofacies can represent a great diversity of organisms living in small bioherms. This is certainly true of potential bivalve diversity. Singh and Sasekumar (1996), for instance, showed that destruction of (test) wood panels was primarily the work of several organisms, including Martesia striata (the wood-boring piddock) and the various shipworms Lyrodus pedicellatus, Bankia campanellata, Teredo furcifera, and Teredo bartschi.

Nevertheless, fossilized examples of the *Teredolites*bored woodgrounds that include *Thalassinoides*, *Trypanites*, *Entobia*, *Rogerella*, *Psilonichnus*, *Caulostrepsis*, and/or *Meandropolydora*, as well as *Teredolites*, are unknown to

us. It is likely that taphonomy has played a major role in biasing our understanding of the Teredolites ichnofacies. Smaller burrows and surficial markings, particularly borings akin to Entobia, Rogerella, Caulostrepsis, and Meandropolydora, generally penetrate only up to 20 mm into xylic substrate. Because wood is susceptible to abrasion during hydraulic transport, it is hardly surprising that such less-penetrative borings are absent on wood clasts. Even *in situ* stumps are in a continual state of exfoliation, providing they are exposed to even mild current and wave energy. In most cases, woodgrounds represent relict as opposed to well-preserved substrates (sensu Savrda et al., 1993). Thus, deep-penetrating borings are commonly all that remain of the boring community. Still, it should be expected that more diverse Teredolites assemblages have been interred in the rock record. Moreover, closer inspection of known occurrences of the Teredolites ichnofacies may reveal more similarities to the modern than has been realized previously. One must also consider differences in depositional environments: many studied fossil loggrounds are subtidal and may host a different suite of borings. Because most examples of *Teredolites* assemblages in the fossil record reflect a preservational bias that favors penetrative borings, *Teredolites* commonly is listed as the only notable component of wood-boring assemblages (e.g., Bradshaw, 1980; Bromley et al., 1984; Plint and Pickerill, 1985; Urreta, 1987; Savrda, 1991; Mikulás, 1993; Savrda et al., 1993; Lavigne et al., 1998; Pirrie et al., 1998).

Thalassinoides is also a rare but persistent component of the *Teredolites* ichnofacies. James Howard informally, and with good humor, referred to such occurrences as "coal worms" (George Pemberton, pers. comm., 2002). Thalassinoides in xylic substrates are common in the Miocene Pebas Formation of Amazonia (Gingras et al., 2002). In the Upper Cretaceous Blackhawk Formation of Utah, Kamola (1984) reported a channel-floor xylic substrate dominated by *Thalassinoides* preserved as exichnia. Although the surface is otherwise unbored, wood clasts interred in associated sedimentary media reportedly were bored with Teredolites, and abundant trace fossils (Ophiomorpha, Piscichnus, Pholeus, Arenicolites, and Skolithos) were observed in surrounding sand and mud beds. Considering the evidence supporting the presence of a diverse biota, it is reasonable to suggest that the bored surface hosted a dynamic biome more like the Willapa Bay examples.

Depositional and Stratigraphic Significance

Erosion on the bay margin and back stepping of intertidal sediments indicates that the study area is undergoing transgression. This is congruent with Savrda's (1991) and Savrda et al.'s (1993) interpretation that bored wood clasts of the Paleocene Clayton Formation (Alabama) may have been concentrated following an influx of xylic clasts into a marginal-marine setting. However, that study focused on wood clasts that suffered notably more transport and input energy than the largely *in situ* specimens scrutinized herein. Savrda et al. (1993) also noted the presence of reworked *Teredolites*—a phenomenon not manifested in the study areas of Willapa Bay.

The present study is more analogous to Bromley et al.'s (1984) report of a bivalve-bored xylic peatground from the Cretaceous Horseshoe Canyon Formation of southern Al-

berta. There, *Teredolites clavatus* dominate a coalified peat horizon that is taken to represent colonization following tidal-creek incision into coastal-plain sediments. None of the reported observations suggests that a diverse animal community colonized the surface (the trace-fossil assemblage is monospecific). However, dissolution of the boring infills reveals various plant seeds, fish teeth, foraminifers, wood fragments, and rare bone fragments, all of which indicate that the depositional environment was not sterile. Again, the taphonomic characteristics of individual ichnotaxa censor the interpretations derived from the bored media.

Another similar fossil example has been described from near Beloslav, in northeastern Bulgaria (Panos and Skacel, 1966). There, the petrified remains of an Eocene forest records similar encroachment of marginal-marine environments over coastal lowlands. In this case, transgression of the Lutetian Sea exposed tree trunks to the boring activities of teredinid bivalves.

As the above examples and this study imply, exposure to marginal-marine conditions and subsequent colonization of *in situ* tree trunks by marginal-marine to marine organisms require an increase of relative sea level. Thus, as previous researchers have suggested, the *Teredolites* ichnofacies is strongly associated with transgressive settings.

Substrate-controlled ichnofacies commonly are used to enhance genetic stratigraphic models. Glossifungites-demarcated discontinuities, for instance, have been demonstrated to have sequence stratigraphic significance (MacEachern et al., 1992; Pemberton and MacEachern, 1995). This understanding comes from the realization that exposure of widely distributed, firm-sediment substrates normally is the result of a local base-level change (Pemberton and Frey, 1985). Furthermore, the process of sediment dewatering due to compaction has been shown to represent century- to millennia-scale temporal significance (Pemberton and Frey, 1985; Gingras et al., 2000). Because marginal-marine organisms typically thrive under increasingly marine conditions, the Glossifungites ichnofacies, like the Teredolites ichnofacies, develops preferentially in transgressive settings.

Gingras et al. (2001) discuss the genetic and biological significance of *Glossifungites*-demarcated discontinuities. Therein, they failed to address the possible link between *Glossifungites* and *Teredolites* ichnofacies: namely, that discontinuities may be demarcated by discontinuous and sporadically distributed firmground and woodground assemblages (Fig. 3). This study demonstrates that transgressive surfaces may be demarcated not only by the *Teredolites* and *Glossifungites* ichnofacies, but also by coeval softground assemblages (Fig. 3). Thus, a single discontinuity may translate from softground- to firmground- to woodground-associated ichnofacies. This conceptualization is especially disconcerting if one considers the difficulties inherent to subsurface correlation with a limited core database.

Taxonomic Considerations

In this study, the reported biogenic structures generally are borings in that the borings cut wood grains (cells). Several of the incipient ichnotaxa described in this study previously have not been reported from xylic substrates, and given ichnotaxonomic nomenclatural dilemmas and/or taphonomic considerations (e.g., MacNaughton and Pickerill, 2003), perhaps understandably so. The ichnogenera *Trypanites, Entobia, Rogerella, Caulostrepsis,* and *Meandropolydora* are normally assigned to borings in hard shelly substrates or hardgrounds. Thus, their assignment to borings in a xylic substrate is dubious by convention. *Thalassinoides* and *Psilonichnus,* which originally were described from softgrounds and firmgrounds, represent burrowing activities, not boring behaviors. Thus, the taxonomic affinity of those dwelling structures is likewise unclear.

It has been shown that organisms are capable of transposing ethology from substrate to substrate. *Polydora* sp., which is ascribed above to *Caulostrepsis* and *Meandropolydora*-like borings, make almost identical borings in shell, wood, and firmground (Sato-Okoshi and Okoshi, 2000). Likewise, although certain species of *Polydora* only colonize specific substrates, the borings are very similar from species to species.

The dilemma of classifying morphologically similar biogenic structures that occur in markedly dissimilar substrates has previously posed similar ichnotaxonomic difficulties. Bromley et al. (1984) upheld Leymerie's (1842) distinction between the two ichnogenera for club-shaped borings: *Teredolites clavatus* in woody substrates and *Gastrochaenolites* in lithic substrates. Further complicating the issue, *Teredolites longissimus* clearly represents a distinct behavior that is not known in cemented substrates. Our observations in the modern suggest that *Teredolites clavatus* represents a behavior that is almost identical to that represented by *Gastrochaenolites*. In contrast, *Teredolites longissimus* represents a different boring habit and merits its separate classification.

More fundamentally, the distinction between Trypanites in hardgrounds versus Skolithos or Trichichnus in softgrounds is not, strictly speaking, based entirely on the morphology of the different ichnogenera. Rather, there has been a preference to employ the trace fossil-encompassing substrate as a taxonomic character of the trace fossil itself. In the context of xylic versus cemented substrates, it is not clear that differentiation warrants assigning a unique ichnotaxon to borings that occur in wood. Because ichnological classification is used primarily to communicate morphological information of a trace fossil, inferred behavioral characteristics are not required and are potentially incorrect. Moreover, because it is uncertain exactly how boring in xylic substrates differs from similar behaviors in cemented substrates, taxonomic discrimination may be futile.

SUMMARY AND CONCLUSION

This study has presented field-based observations from modern bay-margin settings in Willapa Bay, Washington. In particular, it has focused on the development of *in situ* log-grounds from two intertidal areas that are situated seaward of low-lying marshes dissected by small streams. The vestigial swamps and streams remain imprinted upon the intertidal zone as *in situ* root networks, broken stumps, strewn logs, and abundant organic detritus that are preserved in organic-rich, sandy muds. The organic sediment represents detrital material that accumulated in the swamps before it was transgressed and truncated by tide and wave processes. The low portions of the swamps superpose, and lie adjacent to, older Pleistocene strata, which now form a cohesive intertidal firmground.

Scrutiny of the in situ root networks and stumps and their associated sediments reveals that the stumps and logs maintain the highest diversity of animal and plant life. Several boring organisms, squatters, and encrusters enjoy the refugia that the xylic material provides. Although animal squatters do not necessarily leave any evidence of their stay in the bioherm, some encrusters, and all of the boring fauna indelibly alter the substrate in that incipient trace fossils are carved into the wood. The traces reported in this study include: Teredolites, Thalassinoides, Trypanites, Entobia, Rogerella, Psilonichnus, Caulostrepsis, and Meandropolydora. Most of these ichnogenera have not been reported as wood borings, indicating that either they are commonly overlooked or taphonomic bias within wood substrates is extreme. Most importantly, the observations reported in this study suggest that similar ichnofossil assemblages might exist in the rock record.

Notably, the occurrence of a diverse boring community within xylic substrates generates potential taxonomic difficulties. It is suggested that xylic versus cemented or firm substrates should, in general, not be given taxonomic consideration, despite the fact that both the *Teredolites* and *Trypanites/Glossifungites* ichnofacies are firmly entrenched in the literature.

The stratigraphic implications of this Willapa Bay ichnocoenosis are consistent with previous studies that suggest the *Teredolites* ichnofacies and/or isolated bored loggrounds typically are associated with relative sea-level rise. This is particularly true if it can be shown that the log- or stump-ground is more or less *in situ*. Notably, the xylic media forms a coeval substrate with adjacent softgrounds and firmgrounds, all of which maintain distinctive trace-making communities. This study thereby underscores the potential complexity of bay-margin diastems in the rock record and, consequently, their correlation.

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