

Bathymetry, sediment texture, and substrate cohesiveness; their impact on modern *Glossifungites* trace assemblages at Willapa Bay, Washington

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Abstract

Glossifungites-demarcated discontinuities have been demonstrated to have stratigraphic significance. Unfortunately, their stratigraphic utility commonly eclipses the palaeoecological information derived from such surfaces. This paper attempts to identify factors that influence the nature of trace assemblages observed in modern firmgrounds. In particular, it focuses on the causes of lateral variability and erosional topography inherent to *Glossifungites* surfaces. The extensive Pleistocene database at Willapa Bay is used to test the interpretations.

Striking heterogeneity in *Glossifungites* assemblages is documented from modern firmgrounds at Willapa Bay. This variability is related to intertidal zonation, sediment texture, the absolute firmness of the firmground, and the presence or absence of a sediment veneer. Generally, subtidal and lower- to middle-intertidal firmgrounds are colonized by crustaceans (the *Upogebia* Association) or the bivalve *Petricola* (the *Petricola* Association). These surfaces are characteristically burrowed with *Thalassinoides*- and *Gastrochaenolites*-like traces. The upper intertidal is dominated by the *Polydora* Association, the burrows of which include diminutive *Diplocraterion* and *Arenicolites*-like traces. Sandy and heterolithic substrates are avoided by burrowing crustaceans and polychaetes alike. In contrast, *Petricola* is observed in muddy, sandy-mud, and heterolithic substrates. Therefore, where colonized, sandier substrates are dominated by the clavate, *Gastrochaenolites*-like burrows produced by these bivalves. The absolute firmness of exhumed firmgrounds is quite variable. The *Upogebia* Association is absent in substrates that exceed 10⁹ Pa. *Polydora*-dominated assemblages are poorly developed in similar firmgrounds. The *Petricola* Association, however, is well-developed in relatively firm substrates.

Finally, the morphologic characteristics of exhumed (modern) firmgrounds show that the history of a *Glossifungites*-demarcated surface can be extremely dynamic. Firmground surfaces are exposed to an array of physico-chemical conditions as they are exhumed, colonized, and pass into the geological record. These surfaces are commonly re-exhumed due to auto- and allocyclic processes. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Glossifungites* Ichnocoenosis; Firmground; Ichnology; Modern; Pleistocene; Willapa Bay

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1. Introduction

The application of ichnology to the rock record focuses on using trace fossils to approximate physico-chemical parameters at the time of sediment

deposition. These variables include salinity, oxygenation, sedimentation rate, and turbidity. Ichnology has also been used to correlate sedimentary packages (Seilacher, 1970). Recently, substrate-specific trace fossil assemblages have been used to identify stratigraphically significant genetic surfaces. Such assemblages include the *Trypanites* (*Entobia* and *Gnatichnus*), *Teredolites*, and *Glossifungites* ichnofacies. *Trypanites* assemblages are specific to cemented substrates, or hardgrounds. Fürsich and Palmer (1975), working in the Jurassic of England, considered hardgrounds (and nodular lags) to be indicative of reduced sedimentation, erosion, and early cementation in carbonate substrates. Although bored and encrusted hardgrounds are most characteristic of carbonate deposits (Bromley, 1996), similar trace assemblages are observed in poorly cemented siliciclastic rocks as well. The *Teredolites* ichnofacies refers to colonized wood substrates. These include peat-grounds (Bromley et al., 1984) and log-grounds (Savrda and King, 1993), both of which have been linked to transgressive deposits (Bromley et al., 1984; Savrda and King, 1993).

This paper focuses on the *Glossifungites* ichnofacies, which consists of burrows that were emplaced in firm (compacted), siliciclastic substrates. Establishing that a depositional surface consisted of firm sediment may seem trivial to many readers. However, the very presence of a firmground implies that the sediment was either subareally exposed and desiccated, or was buried, compacted, and exhumed. Where there is no evidence of subareal exposure (i.e. an absence of desiccation cracks and salt casts, and the presence of a palimpsest assemblage of burrows) *Glossifungites* assemblages are associated with erosion. In these instances the presence of (areally significant) *Glossifungites* demarcated discontinuities can be linked to base level change in marginal marine environments and have genetic-stratigraphic significance (Pemberton and Frey, 1985; MacEachern et al., 1992; Pemberton et al., 1992; Pemberton and MacEachern, 1995; Gingras et al., 2000).

Seilacher (1964) defined the *Glossifungites* ichnofacies as a primarily littoral assemblage of trace fossils emplaced in cohesive, non-shifting, substrates. Later, Frey and Seilacher (1980) restricted the *Glossifungites* ichnofacies to include only firmgrounds present in marine environments. Modern

Glossifungites assemblages have been observed in association with wave ravinement and channel erosion (Pemberton and Frey, 1985) and are known to occur in a variety of environments, even the deep marine (Bromley and Allouc, 1992). Their research emphasized the link between ichnology and genetically significant surfaces.

Trace fossils present in *Glossifungites* assemblages have several diagnostic characteristics (Seilacher, 1964; Frey and Seilacher, 1980; Pemberton and Frey, 1985; MacEachern et al., 1992), including: (1) sharply-defined walls that are generally unlined; (2) the presence of scratch marks in the burrow walls; (3) ichnofossils that cross-cut the palimpsest trace fossil assemblage; and (4) burrow infill that consists of sediment that is texturally distinct from that which comprises the firmground (the infilling sediment is commonly identical to the sediment present in the overlying package). Also, traces in firmgrounds have simple burrow architectures including *Skolithos*, *Thalassinoides*, *Diplocraterion*, and *Rhizocorallium*.

Glossifungites-demarcated discontinuities might also impart paleoecological information. The nature of burrowing into these surfaces, which includes the type (architecture) of trace fossil, burrow density, and the depth of burrow penetration, is related to the physico-chemical conditions dominant at the time of firmground colonization. Partly due to their stratigraphic utility, this aspect of the *Glossifungites* surfaces is commonly overlooked. Modern studies at Willapa Bay, Washington indicate that the potential to develop a better understanding of these surfaces exists and, although no formal subdivisions are recommended herein, there is an opportunity to better resolve the *Glossifungites* ichnofacies.

2. Study area and geological context

Willapa Bay is located in the southwest corner of Washington (Fig. 1). The bay is separated from the Pacific Ocean by a 27-km-long spit (North Beach Peninsula). Willapa Bay is a mesotidal estuary with a tidal range of 2–3 m. The tidal prism exceeds 700,000 m³, comprising about 45% of the bay's total volume (U.S. Army Corps. of Engineers, 1975). Data for the modern component of this study were collected from three locations along the eastern margin of the bay

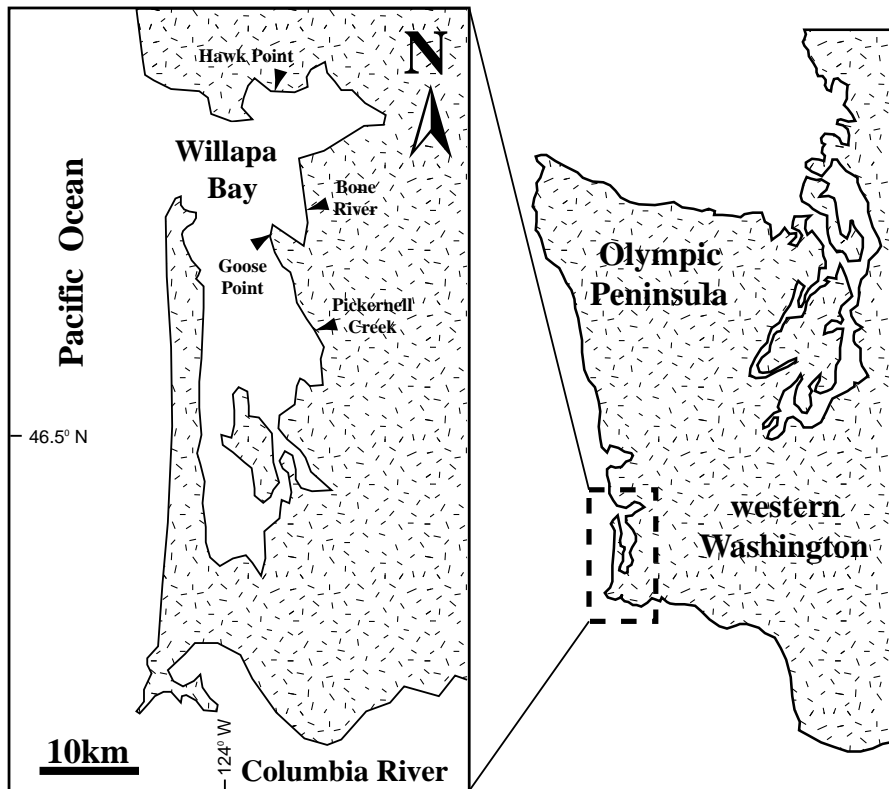


Fig. 1. Location of detailed modern and ancient *Glossifungites* studies at Willapa Bay. Goose Point, Pickernell Creek, and Bone River all exhibit examples of modern and ancient *Glossifungites* assemblages.

(Bone River, Goose Point, and Pickernell Creek; Fig. 1). Pleistocene data were collected from outcrops that rim the east and north bay margins.

At Willapa Bay, most modern occurrences of *Glossifungites* surfaces are observed in exhumed Pleistocene strata. The strata are present in at least two distinct terraces. Relatively younger Pleistocene deposits dated using amino acid racemization indicate that these strata were deposited between 100,000 and 200,000 years before present (Kvenvolden et al., 1979). The older strata have not been dated.

The Pleistocene succession is composed of mud, sand, and intercalated mud and sand. This provides an opportunity to document the development of modern *Glossifungites* assemblages in Pleistocene sediments characterized by various textures. Infaunal burrowing response to variable substrate firmness can also be assessed because the older Pleistocene deposits are much firmer than the younger Pleistocene sediment.

3. Methods

A number of methods were used to collect data from the modern, including manual coring, trenching with a shovel or grub-hoe, slabbing of samples, and X-radiographic analysis of samples. This data was supplemented with subtidal data procured with SCUBA and resin casting of burrows. Burrow densities were assessed using a 1-m grid for large diameter burrows, such as those produced by thalassinid shrimp, and a 10-cm grid for small diameter burrows (less than 2 mm in diameter). These data were plotted and contoured. Depths to sediment-veneered firmgrounds were obtained using a 1.5-m long, 10-mm diameter steel probe. These data were also mapped and contoured. Firmness profiles for exposed firmgrounds were generated using an indenter and a modified Brinell hardness test (Gingras et al., 2000). A standard Brinell configuration consists

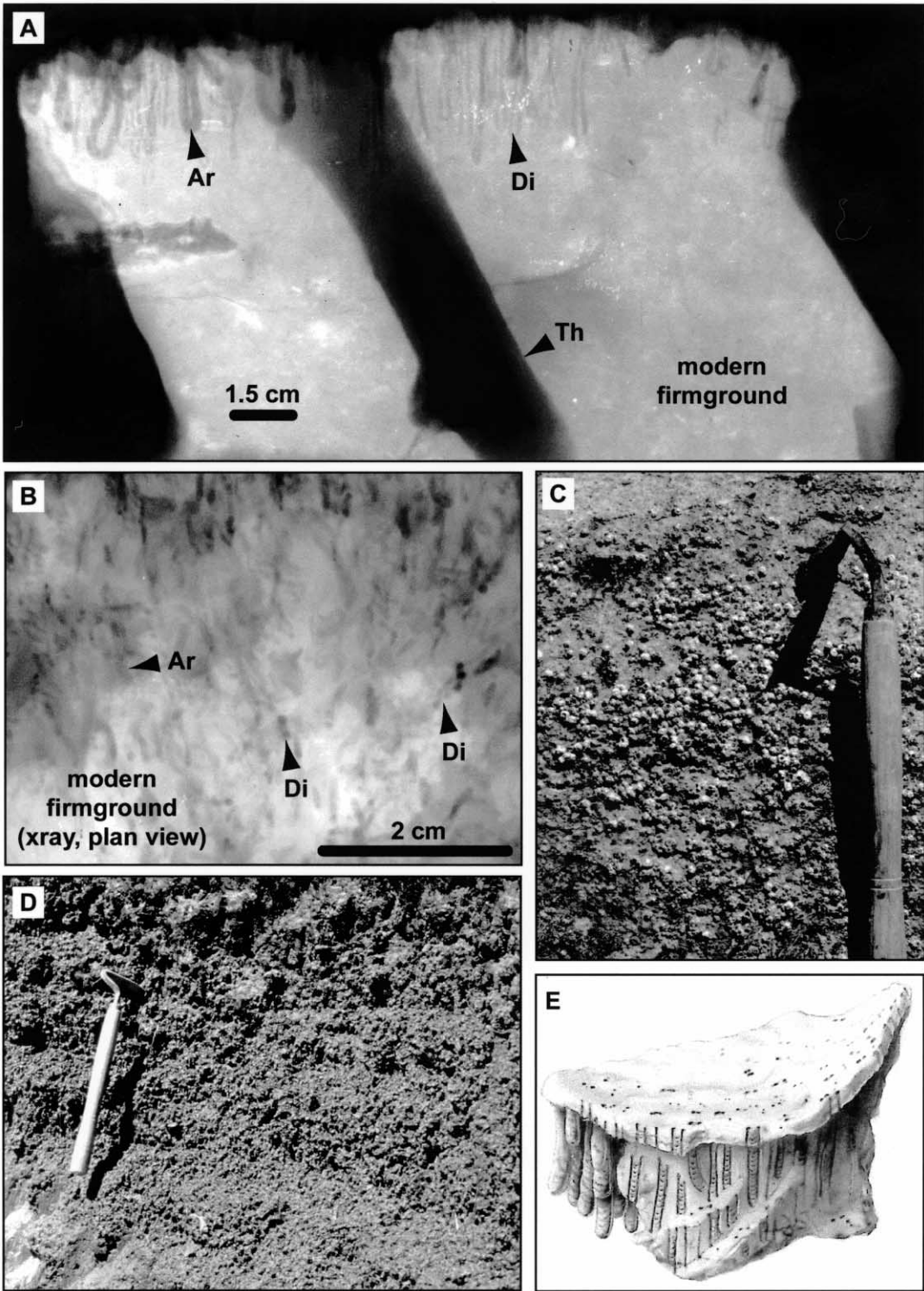


Table 1

Summary of the characteristics of the three different *Glossifungites* assemblages observed at Willapa Bay

	Substrate texture	Substrate firmness (Pa)	Occurrence	Common tracemakers	Common biogenic structures
<i>Polydora</i> Association	Primarily muddy	1×10^5 to 1×10^7	Upper intertidal	<i>Polydora</i> , <i>Corophium</i> , <i>Hemigrapsus</i>	<i>Diplocraterion</i> , <i>Arenicolites</i> , and <i>Psilonichmus</i> - like
<i>Petricola</i> Association	Muddy to sandy Mud with sandy laminae	$>1 \times 10^8$	Middle intertidal	<i>Petricola</i> , <i>Polydora</i>	<i>Diplocraterion</i> and <i>Gastrochaenolites</i> - like
<i>Upogebia</i> Association	Primarily muddy	1×10^6 to 1×10^7	Subtidal to middle intertidal	<i>Upogebia</i> , <i>Polydora</i> , <i>Corophium</i>	<i>Diplocraterion</i> , <i>Arenicolites</i> , and <i>Thalassinoides</i> - like

of a ball (the indenter), which is pressed into a deformable medium with consistent force. The force with which the substrate can resist deformation is inversely proportional to the distance the indenter penetrates the medium. Pleistocene data were obtained through the detailed logging and analysis of Pleistocene cliff exposures.

4. Results

4.1. *Glossifungites* trace associations at Willapa Bay

Three distinctive biological associations can be recognized in modern firm substrates at the bay. These are the *Polydora*, the *Petricola*, and *Upogebia* Associations. Each association exhibits a preference for specific ranges of substrate firmness and texture, and bathymetric zonation (Table 1). All three assemblages produce characteristic ichnocoenoses that are similar to ichnofacies recognized in the extensive Pleistocene record.

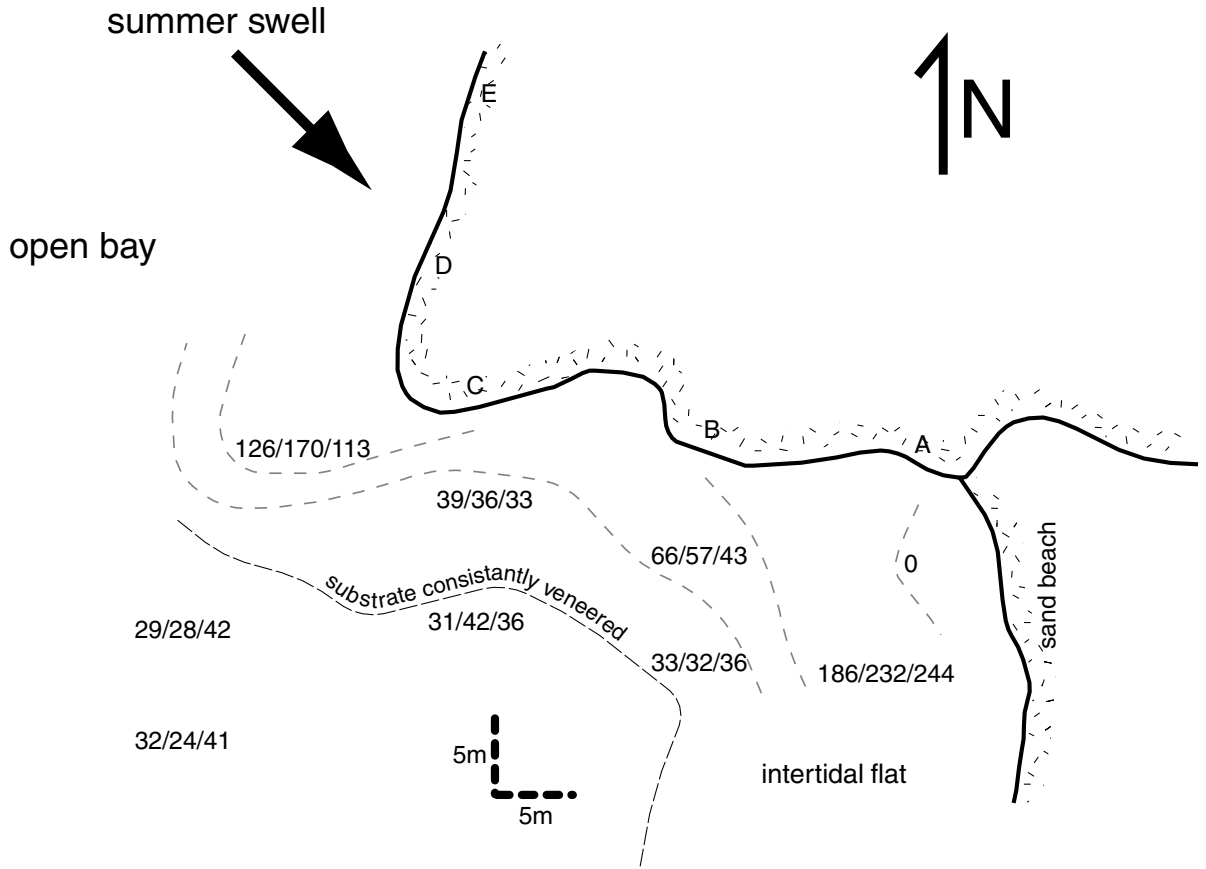
4.1.1. The *Polydora* Association

The *Polydora* Association primarily consists of small *Diplocraterion*-like traces that are produced by the spionid worm *Polydora proboscidea* (Fig. 2). The traces are generally 3–4 mm wide and have been

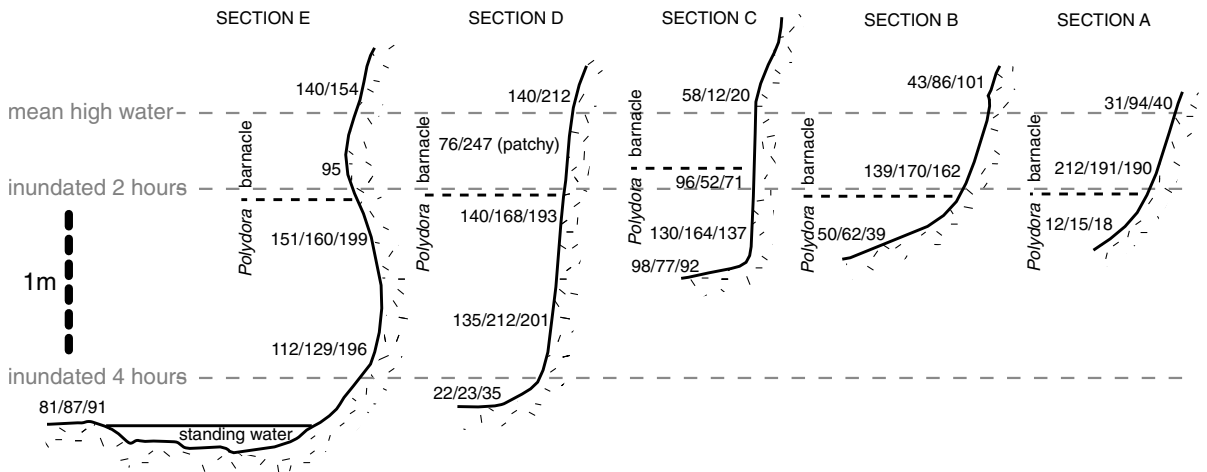
observed to descend 1–6 cm below the sediment–water interface. The causative tubes that generate these structures are approximately 1 mm in diameter. These burrows are oriented perpendicular to the firmground surface regardless of its slope. Burrow densities commonly exceed 150 individuals/100 cm², however, this value ranges from 20 to 244 individuals/100 cm² (Fig. 3). Where the burrow density of *P. proboscidea* exceeds 100 individuals/100 cm², burrows of the amphipod *Corophium volutator* are relatively common. These traces have an *Arenicolites*-like geometry, are somewhat broader than the burrows generated by *Polydora*, and have a burrow diameter of approximately 2 mm (Fig. 2A). Larger burrows are present locally, particularly those of the crab *Hemigrapsus oregonensis* and the bivalve *Petricola pholadiformis*. Their burrows are *Psilonichnus*- and *Gastrochaenolites*-like, respectively (Fig. 4).

The *Polydora* Association is most commonly observed in the upper intertidal zone (inundated 2–4 h every tide cycle; Fig. 3). Substrate that is submersed for less than 2 h or is exposed only to the spray zone, is dominated by the barnacle *Balanus glandula* (Figs. 2 and 3). Data plotted in Fig. 3 show the strong correlation between tidal zonation and the population densities of *Polydora* and *Balanus*, particularly on exposed intertidal cliff faces. Population densities plotted along the intertidal flat show a

Fig. 2. Various X-rays (A,B) and photographs (C,D) of *Polydora*-burrowed firmground. (A) Sectional X-ray of *Polydora* burrows in a compacted Pleistocene substrate. *Diplocraterion*- (Di), *Arenicolites*- (Ar), and *Thalassinoides*-like (Th) traces are indicated. These burrows were made by *Polydora*, *Corophium*, and *Upogebia*, respectively. The plate is approximately 16 cm wide. (B) Plan view of the same surface shown in A. Note the relatively high burrow density (approximately 100 burrows/10 cm square). (C) The barnacle encrusted zone in the area of brief tidal inundation. (D) Zone of intense *Polydora* colonization in firmground that is inundated for approximately 4 h. (E) Summary diagram of the *Polydora* Assemblage. Small *Diplocraterion*-like traces are the most common biogenic structure, although broader *Arenicolites*-like traces are locally common. Illustration by Tom Saunders.



exposed cliff faces



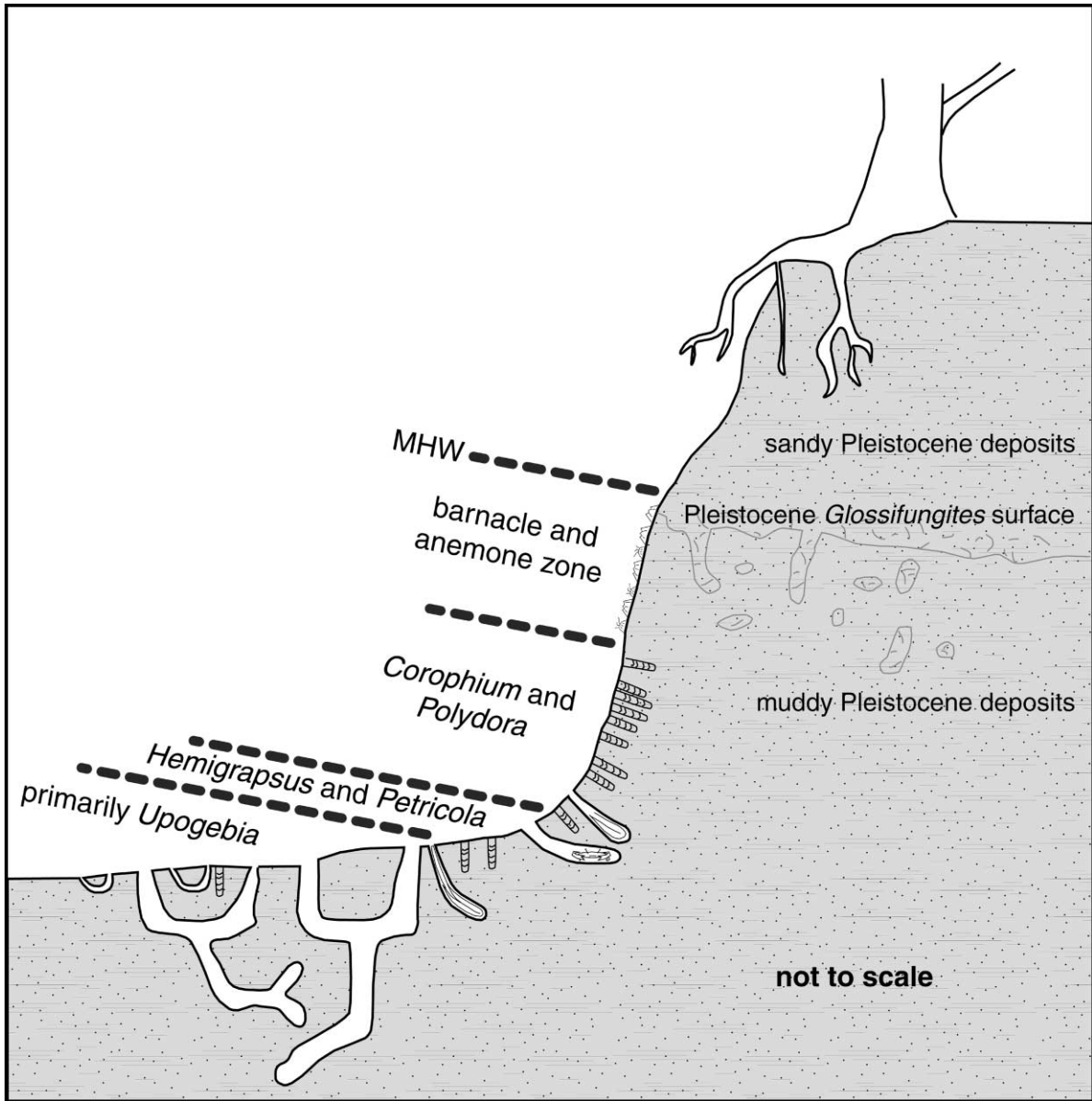


Fig. 4. Schematic of biological distribution commonly observed with the *Polydora* Association. The lowermost part of the diagram shows the location of crustacean and bivalve burrows. These grade abruptly into the *Polydora* zone. The zonation is primarily controlled by the duration of tidal inundation.

Fig. 3. Schematic plan and vertical views of *Polydora*-burrowed firmground at Goose Point. In the top plan view, burrow density is contoured. All burrow densities were approximated by counting the burrows in a 10-cm square. Three counts are shown for every data point. The plan view shows a strong shore-parallel trend in the burrow distributions. The lower portion of the diagram shows side views of burrowed cliff faces. In section, population distributions strongly correlate to the duration of tidal inundation. The zonation between barnacle and *Polydora*-dominated substrates is especially striking, as it almost perfectly correlates with the tide line. Also note the consistent population trends and their strong correlation to inundation duration.

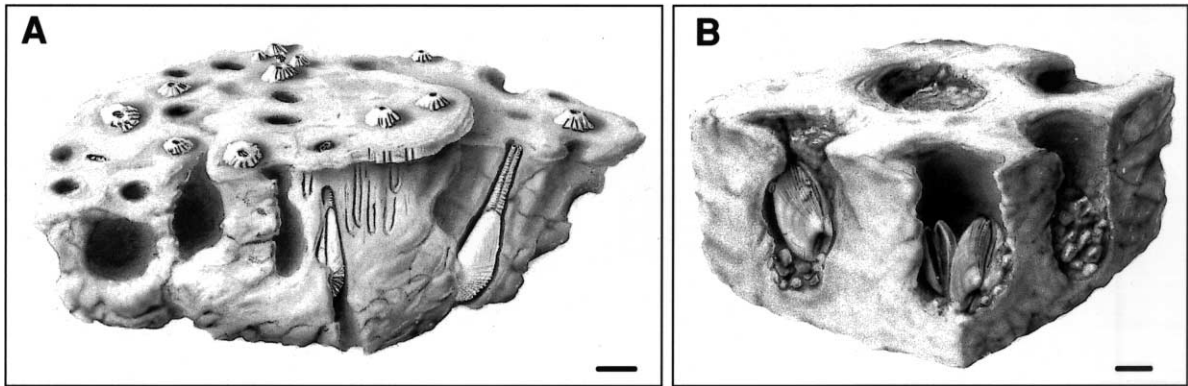


Fig. 5. (A) Summary diagram of the *Petricola* Assemblage. *Gastrochaenolites*-like traces are the most common biogenic structure. *Diplocraterion*-like traces are locally common. (B) Detail of shell nests observed locally within the *Petricola* Assemblage. The bivalves that lay at the bottom of the cup-shaped structures are *Tapes japonica* (the Japanese littleneck). It is unclear how these structures are made, however, hydraulic turbulence in conjunction with the small, thick-walled bivalves may have erosionally excavated the pockets. Illustration by Tom Saunders.

similar distribution pattern. Intertidal flat data are somewhat variable due to the sporadic presence of a veneer of unconsolidated sediment (hitherto sediment veneer) that correlates to a reduction of *Polydora* burrow density (Fig. 3).

Substrate texture and firmness are notable factors in the distribution of this association. Where the sediment firmness is approximately 1×10^9 Pa, burrow densities do not exceed 30/100 cm². In contrast, the firmness of highly populated substrates is only about 1×10^7 Pa. Extremely firm substrates ($>1 \times 10^9$ Pa) are generally unburrowed. Grain size analyses of colonized firmgrounds indicate the *Polydora* Association is most common in mud-dominated firmgrounds. These data revealed that in all *Polydora*-colonized (firm) substrates, the silt and clay fraction comprise between 81 and 96% of the sample mass (four samples measured). At the bay, sandy firmgrounds are simply not colonized by *Polydora*.

4.1.2. The *Petricola* Association

The *Petricola* Association is composed of clavate burrows produced by the bivalve *Petricola pholadiformis* (Fig. 5). These burrows normally measure 10–25 mm in diameter near the base, tapering to approximately 10 mm at the aperture. They typical range between 5 and 10 cm in length. Burrow densities range from 10 to 87 burrows/m². Sporadically distributed patches of *Polydora proboscidea* are

present as well. As with the *Polydora* Association, these trace makers generate small *Diplocraterion*-like structures, however, burrow density seldom exceeds 30 individuals/100 cm². Small cup-shaped structures are also present locally (Fig. 5). These measure between 5 and 8 cm in diameter, and are generally 8–10 cm deep. Two to three small shellfish (*Tapes japonica*) are always present at the base of these features but it is speculative to suggest these are biogenic structures. Barnacles and small anenomes are often found attached to the firm substrate, commonly in population densities less than 20 individuals/100 cm². If either type of organism is pried free, a small circular indentation is revealed. The indent is less than 1 mm deep and is normally less than 4 mm in diameter.

This ichnocoenosis is more commonly observed in the lower to middle intertidal zone and is inundated at least 4 h/tidal cycle. Kozloff (1996) noted that *Petricola* was present from the 0.0 to the 0.6 m tide line at Willapa Bay. Our observations indicate that this assemblage is locally present up to the +1.0 m tide line.

The *Petricola* Association is generally observed in comparatively firm substrates (Purchon, 1955). In situ firmness values are approximately 1×10^9 Pa, which is about one to two orders of magnitude higher than firmness values measured in intensely burrowed *Polydora*-dominated firmgrounds. The *Petricola*

Association is limited to mud-dominated substrates, and the percent fines (by mass) varies between 67 and 89%, based on three samples. These values are sand-rich compared to those generated from *Polydora*-dominated substrates. Like the *Polydora* Association, the *Petricola* Association is rarely developed in firm substrates that are characterized by heterolithic lamination (intercalated sand and mud).

4.1.3. The *Upogebia* Association

This association primarily consists of *Thalassinoides*-like burrows excavated by the mud shrimp *Upogebia pugettensis* (Fig. 6). These traces have Y-shaped architecture, although a short branch is frequently observed near the base of the burrow. Burrow cross-sections are circular and their diameters generally vary between 9 and 21 mm in diameter. Depths of penetration are variable, ranging between 40 and 60 cm. It is unknown, however, what the maximum depth of penetration into the firmground is. This is due to the difficulties associated with excavating and retrieving resin casts from these substrates.

Unlike the *Polydora* and *Petricola* Associations, the *Upogebia* Association is present in uncovered and sediment-veneered firmgrounds (Fig. 6). Where the firmground is exposed or thinly veneered, *Upogebia* burrows extend fully into the consolidated sediment. The overall architecture, size, and penetration depth of these traces are identical to *Upogebia* burrows observed in uncompacted mud. These burrows are generally observed with rare to moderately abundant burrows of *Polydora* and *Corophium*. Less commonly, *Petricola* is present, lending rare clavate burrows to this association.

Where the firmground is covered with a thicker veneer of soft sediment (>10 cm), *Upogebia* burrows are normally the only biogenic structures observed to penetrate the firmground (Fig. 6). This occurs in sediment veneer that is up to 60 cm thick, in which case only the basal terminus extends into the firmground. *Upogebia* is a persistent vertical burrower, and its burrows generally show no attempt to run horizontally along the contact between the firm and soft sediment. Removing the sediment veneer from the firmground reveals several abandoned burrows, evidencing the activities of previous (crustacean) generations. Generally, the soft sediment hosts several trace-makers that do not burrow into the firmground. Notable

burrowers include *Nereis*, *Saccoglossus*, *Heteromastus*, *Cirriiformis*, *Nephtys*, and *Corophium*. They would generate an assemblage that would be composed of *Arenicolites*-, *Planolites*-, *Palaeophycus*-, *Gyrolithes*-, *Rosselia*-, and *Diplocraterion*-like trace fossils (Fig. 6). Most of these lebensspuren bend horizontally where they encounter the firmground, although locally they reburrow abandoned shrimp traces that penetrate the firmground.

Burrow densities vary between 10 and 100 burrows/m² (Fig. 7). Like the *Petricola* Association, this association is most common in the lower and middle intertidal zones. The burrows are inundated by the high tide for at least 4 h/tidal cycle, and they are present in the highest densities where inundation exceeds 6 h (Fig. 7). Population densities are lowest where the firmground is exposed, especially at the higher tide levels (Fig. 7). The *Upogebia* Association has also been observed in subtidal channels at Willapa Bay (Gingras et al., 1999). In these instances, it resembles its intertidal counterpart in most respects.

Upogebia-colonized firmgrounds are characterized by firmness measurements similar to those measured in the *Polydora* Association (1×10^7 to 1×10^8 Pa). In fact, the *Upogebia* Association is not observed in substrates firmer than 1×10^9 Pa. Also, this association was not observed where the sand content of the firmground exceeded 10% (by mass), or where sand was interlaminated with mud.

4.2. Physical and environmental controls on the trace associations

Firmness, textural, and bathymetric data all indicate that the *Polydora*, *Petricola*, and *Upogebia* Associations each develop on substrates characterized by unique physical parameters. Each of the parameters measured presents different burrowing obstacles or stresses that the trace-maker must overcome. The duration of tidal inundation contributes a number of physico-chemical stresses that have been assessed by previous researchers. These include salinity fluctuation due to surface runoff and ground water discharge, temperature variation, desiccation, and oxygenation stress. Of these, salinity and oxygenation stresses are potentially lethal to burrowing organisms. Salinity fluctuations are effectively dampened by the substrate, however, reducing the

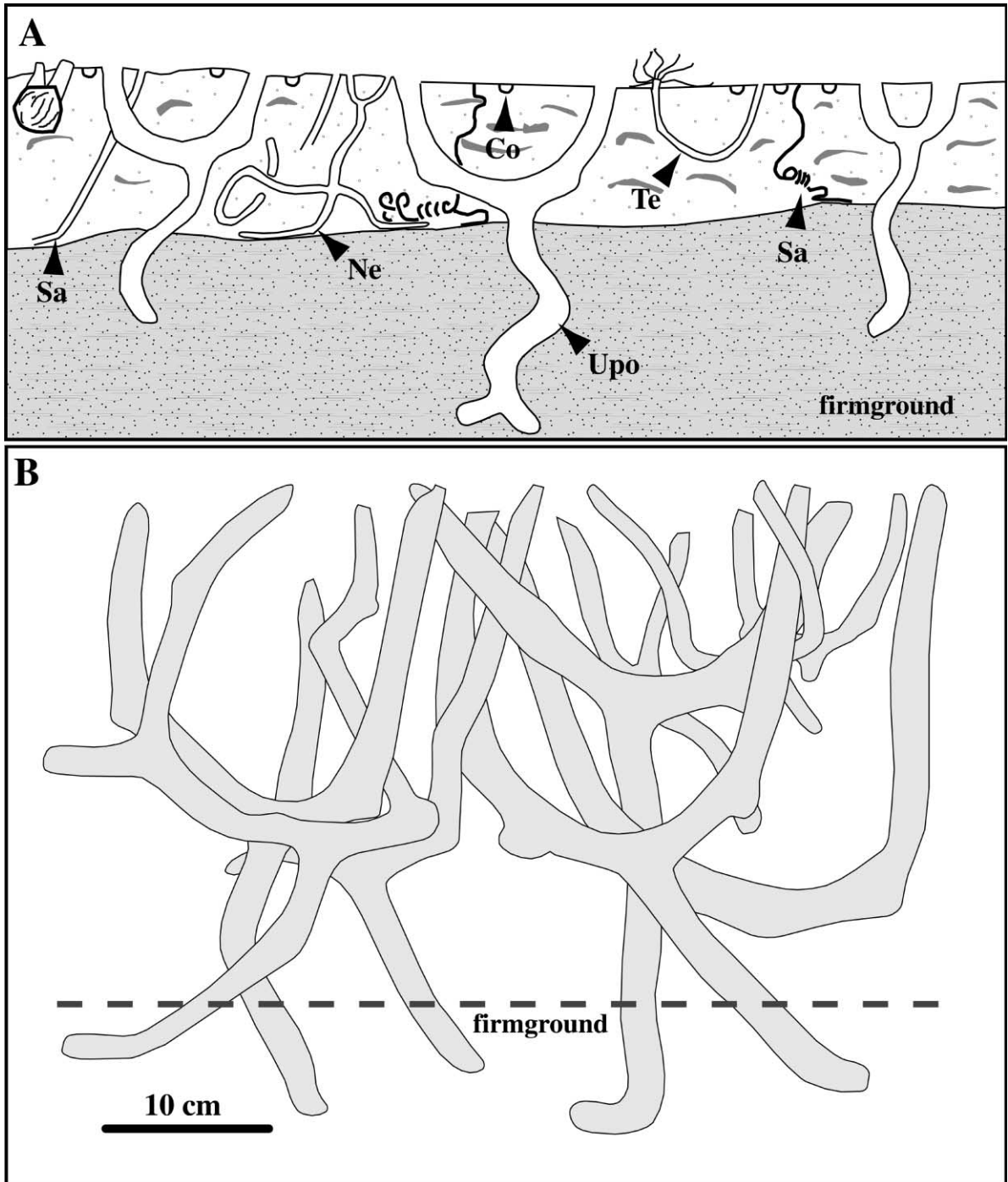


Fig. 6. Summary schematics of *Upogebia*-colonized substrates. (A) *Upogebia pugettensis* most commonly burrows into a firmground through a soft sediment veneer. Although the soft ground assemblage may be quite diverse, the only burrows that penetrate the firmground are those made by the mudshrimp. Burrows illustrated here include those constructed by *Nereis* (Ne), *Saccoglossus* (Sa), *Corophium* (Co), terrebellid polychaetes (Te), and *Upogebia* (Upo). (B) Schematic representation of *Upogebia*-burrow casts removed from the mud near Goose Point.

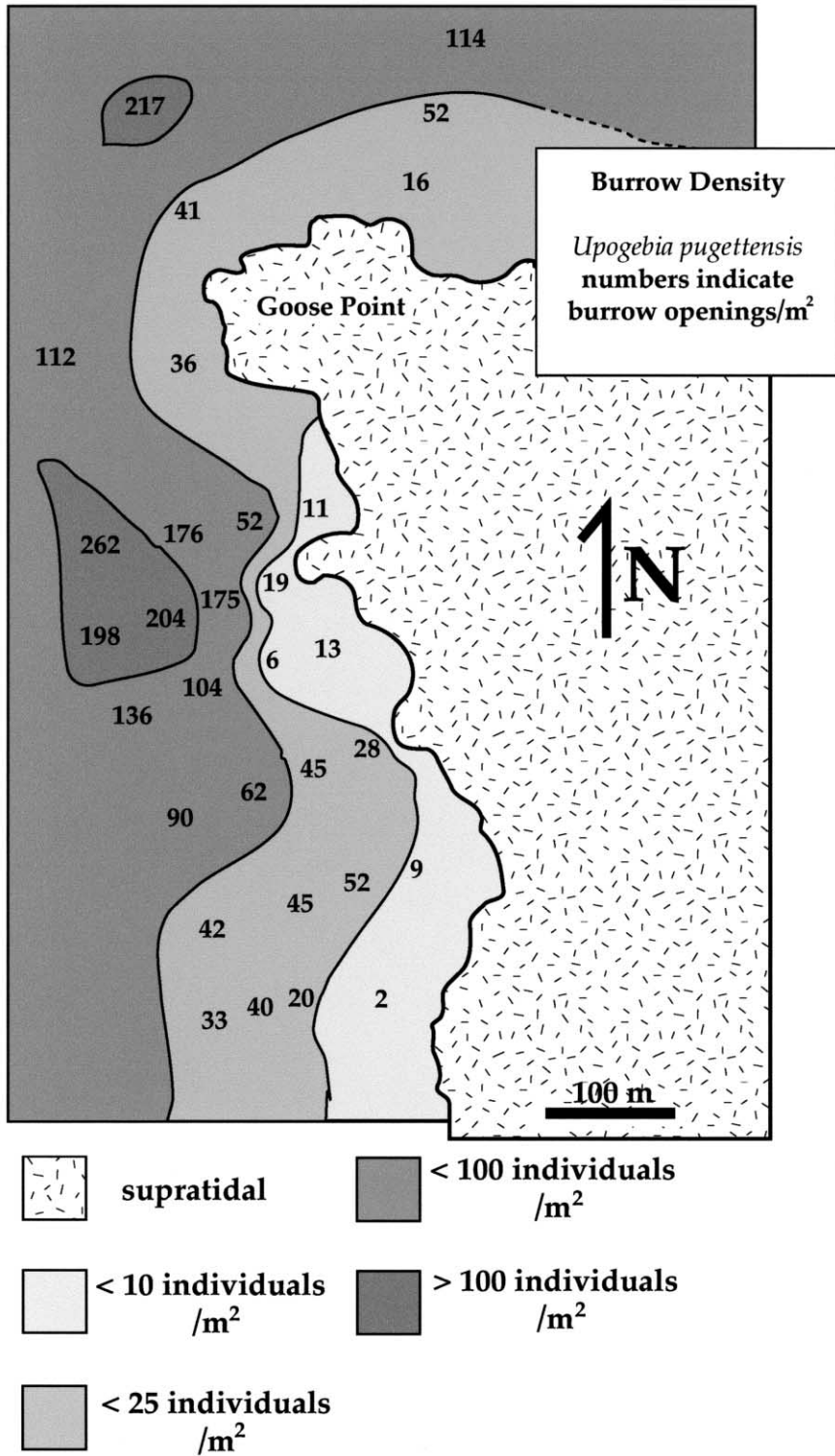


Fig. 7. Mapped burrow densities of *Upogebia pugettensis*. Note the shore-parallel trend and the mappable extent of this surface. The thickness of sediment veneer is variable, but is generally zero near the supratidal, increasing to >60 cm in the zones of highest population density.

stress on infauna (Knox, 1986). Oxygen stress has been well characterized in the literature (Rhoads and Morse, 1971; Bromley and Ekdale, 1984; Savrda and Bottjer, 1987). Generally, low oxygen levels result from aerobic respiration in the burrow during the low tide. The availability of replenishing oxygenated water is strictly a function of the time period between tidal flooding. For this reason, animals at higher tide levels are subjected to greater oxygen stress. Some animals are notably tolerant to these stresses. For example, the sand shrimp, *Neotrypaea californiensis*, has been shown to be sufficiently tolerant of low oxygen levels for up to 12–14 h (Thompson, 1967). Certain worms, such as the lug-worm *Arenicola*, are also oxygen-stress tolerant. The lug-worm enthusiastically irrigates its domicile during high tide, and, because its burrows are commonly unlined, it potentially benefits from somewhat oxygenated interstitial water during the low tide.

Stresses related to bathymetry and tidal zonation suggests that variation in the *Glossifungites* assemblages will normally occur along shore-parallel trends. Figs. 3 and 7 show that variations in population density approximate intertidal zonation. The faunal distribution represented in Fig. 4 illustrates a common firmground succession observed at Willapa Bay that is the result of intertidal zonation (Fig. 3).

Lateral variations of the ichnocoenoses reflect heterogeneity of the sediment texture and firmness. For instance, higher sand contents reduce the likelihood of colonization of that substrate. This is especially true if sand is interlaminated with mud. Heterolithic substrates require the burrower to be proficient at excavation in muddy and sandy substrates. This is exacerbated in firm substrates, as mud can be pushed aside, but sand, because it is already compacted, must be excavated. Further to this, greater energy expenditure must be associated with burrowing/boring in sandy firmgrounds.

Firmgrounds characterized by interlaminated sand and mud are rarely burrowed. Where colonized, elements of the *Petricola* Association are present. Thalassinid-shrimp burrows have not been observed in such substrates. This, however, may be idiosyncratic to Willapa Bay, as many crustaceans, notably species of *Callianassa*, burrow in sand and muddy sand. It is well established that the sediment texture strongly influences the nature of the burrowing

assemblage present in a substrate but, particularly for thalassinids, the controls are not well understood or simple (Miller and Myrick, 1992). Marine ecologists have repeatedly noted that similar groups of organisms are consistently found in texturally-specific substrates (Ricketts et al., 1983). This is due to differing requirements regarding larval recruitment, functional morphology, and behavioral ecology in different substrates (Craig and Jones, 1966). These factors are related to parameters such as porosity, permeability, oxygen content, and organic resource; all of which are passively linked to grain size (Craig and Jones, 1966). Furthermore, Peterson (1991) suggested that intertidal zonation of invertebrates was primarily related to two factors: bathymetry and texture. Although this oversimplifies the complexities of natural systems, it serves us well to consider texture and bathymetric disposition to be dominant controls in marginal marine environments.

In summary, the sediment texture and its relationship to burrowing behavior supports several conclusions: (1) boring bivalves cope with heterolithic substrates better than burrowing polychaetes or crustaceans; (2) as sand content in mud increases, the burrowing activity of crustaceans and polychaetes decreases; and, (3) polychaetes, in this case *Polydora*, are more tolerant of a higher overall sand content than *Upogebia pugettensis*.

The textural heterogeneity observed in firmgrounds is related to the ancient depositional environment. For this reason, variability in the grain size of firm substrates does not normally reflect the geometry of the modern bay. Therefore, textural changes are not necessarily shore-parallel or -perpendicular and an overprinting control, independent of tidal zonation or absolute bathymetry, may effect modern and ancient *Glossifungites* assemblages.

As with textural variation, the absolute firmness apparently plays an important role in determining what animals might exploit particular substrates. Both the *Polydora* and *Upogebia* assemblages are found in substrates less indurated than those dominated by *Petricola*. This is not surprising given that boring bivalves excavate firmer sediment primarily by drilling and rasping. Bivalve borings are, in fact, common elements of the *Trypanites* ichnofacies. In contrast, polychaetes burrow into firmgrounds

partly by advecting, or pushing aside the substrate. It is important to note, however, that spionids, which include *Polydora*, commonly bore into hard substrates (Gripp, 1967; Bromley, 1972; Guenther, 1996; Sato-Okoshi and Okoshi, 1997). Crustaceans have the ability to remove and advect firm substrate but it is unclear how effective their chelae are when burrowing into unusually firm substrates. *Upogebia operculata* is known to bore into coral by drilling with specialized mouth parts (Kleemann, 1984). Also, several examples of apparent thalassinid burrows have been associated with ancient hardgrounds (Bromley, 1967; Bromley, 1968; Fürsich and Palmer, 1975), however, these are generally interpreted as having been emplaced in the sediment prior to lithification. Although other examples of crustacean bioerosion have been cited, crustacean traces are far more common in soft and firm substrates.

At the bay no notable exceptions to the firmness relationships previously outlined have been observed. Some of the interpretations for preferential colonization of relatively softer firmgrounds are intuitive. The energy expenditure dispensed in excavating a burrow increases with firmer substrates (in already consolidated sediment). Larval recruitment may also be affected by the firmness of a substrate. These factors (energy expenditure and larval recruitment) do not necessarily explain the field observations already outlined. The apparent preference of *Polydora proboscidea* for slightly softer firmgrounds is unclear. Other species of *Polydora* (*P. giarda*, *P. convexa*, *P. pygidialis*, *P. limicola*, *P. ciliata* and *P. ligni*) have been observed in substrates that range from mud, to wood, to shell, to rock (Guenther, 1996; Sato-Okoshi and Okoshi, 1997). Sato-Okoshi and Okoshi (1997) note that in Barkley Sound (southwest British Columbia, Canada) there are boring and non-boring species of *Polydora*.

Upogebia pugettensis has been observed burrowing into consolidated mud at other locations along the coast of Washington. The earliest documentation of this is provided by Stevens (1929). Despite a number of similar reports, no database of relative or absolute firmness has been accumulated; speculation regarding global firmness preferences, if a preference exists, is therefore impossible. There are many parallels between the *Upogebia* Association described here and that by Asgaard et al. (1997) from the Mediterra-

nean. These include the shape of burrows, nature of the substrate, type of fill, their location in the shallow sublittoral, and the overall dominance of *Upogebia*. This ichnocoenosis is potentially widespread and might be compared globally.

As with the *Upogebia* Association, *Petricola* occurrences are common on the west coast. Similarly, no absolute firmness, or grain size analysis are reported.

At the bay, the cohesiveness of firmground is related to the relative age of the Pleistocene unit exposed in intertidal and subtidal zones. ‘Younger’ Pleistocene deposits (100,000–200,000 y.b.p.) are normally characterized by firmness measurements of 10^7 to 10^8 Pa. Relatively older strata (not reliably dated) commonly exceed 10^9 Pa. Other factors include the rate of erosion into Pleistocene strata and the length of exposure to modern processes. The duration of this study was not long enough to assess these factors.

Overall, the firmness measurements reflect cross-cutting relationships in the ancient strata. Like textural heterogeneity, the distribution of firmness values is not related to the geometry of the modern bay. Ichnological variability due to firmness can therefore overprint colonization patterns resulting from intertidal and bathymetric zonation.

In summary, certain associations of trace-making organisms colonize various *Glossifungites* surfaces at Willapa Bay (Table 1). Subtidal occurrences are dominated by the *Upogebia* Association. Depending on the firmness and texture of the exposed substrate, firmgrounds exposed in the lower and middle intertidal zones are characterized by either the *Upogebia* or *Petricola* Association. Upper intertidal zones are colonized by diminutive burrowers that comprise the *Polydora* Association. Intermediate between the middle and upper intertidal, a transitional *Petricola* Assemblage may be present (Fig. 4). Lateral variation overprints bathymetric and intertidal zonation and is attributed to variations in grain size and firmness. Other factors, such as wave energy, salinity and salinity fluctuations, and oxygen content must play a role as well. These parameters have not been characterized for the different associations outlined in this paper.

4.3. The geomorphology of modern firmgrounds at Willapa Bay

The topography of the firmground beneath the

sediment veneer was mapped at three locations at Willapa Bay (Bone River, Pickernell Creek, and Goose Point; Figs. 1 and 8). The veneer thickness was measured to a depth of 150 cm, which was the length of the probe. At Bone River, the firmground abruptly passes below this depth within 100 m from the shoreline (defined by Pleistocene bluffs; Fig. 8). Approximately 600 m from the shore a small pod of firm substrate was mapped at a depth of 90–150 cm. The lateral extent of this isolated firmground is unknown, but it was mapped to a length of 120 m.

At Pickernell Creek the firmground topography is characterized by two distinct steps. The first occurs about 220 m from the present shoreline, and is represented by an abrupt 50-cm drop (Fig. 8). The second step descends below 150 cm deep; it was mapped 400 m from the shore. Depth measurements from three lines of traverse indicate that these steps are laterally continuous (Fig. 8).

The firmground topography near Goose Point is similar to that observed at Pickernell Creek. Two steps are apparent at 75 and 480 m. Each step represents a drop of approximately 50 cm and is laterally continuous (Fig. 8). Around the northern tip of Goose Point, the steps are no longer evident. Here the firmground has a consistent slope in the direction of the Palix River.

At all three locations, exposed to thinly veneered firmground is present near the shoreline (defined by Pleistocene bluffs). Close to the cliffs, the firmground is generally flat to slightly undulatory, except where it slopes up to the Pleistocene outcrop.

4.4. Interpretation of the modern firmground topography

The presence of the curious, stepped topography implies that *Glossifungites* assemblages produced in intertidal environments may develop complex (ichnological) cross-cutting relationships (Fig. 9). For example, sudden subsidence (or rapid retrogradation) of the bay's shoreline, causes the sediment veneer to increase in thickness. This process subjects the firmground to different levels of burrowing activity. If the change in the sedimentary environment drastically alters the bathymetry or induces a transition from veneered to exposed firmground different trace assemblages may overprint each other. Ichnological succes-

sions generated by these auto- and allocyclic mechanisms must be considered to represent a fourth parameter that passively reshapes bathymetric, textural, and firmness trends.

The firmground morphology is indicative of larger scale processes as well. At Goose Point and Pickernell Creek, two distinct steps characterize the firmground topography. These are present below a sediment veneer and are locally mappable (Fig. 8). The origin of these steps is uncertain but two hypotheses are likely. The first suggests that the stepped topography results from changes in base level due to plate flexure associated with mega-thrust earthquakes. In subducting tectonic regimes, particularly those characterized by sporadic (sticky) plate movement, accommodation space is reduced due to upwards plate flexure. This is followed by sudden subsidence associated with mega-thrust earthquakes. These processes are evident in the modern bay (Atwater, 1987; Rogers, 1988; Atwater and Yamaguchi, 1991; Atwater and Hemphill-Haley, 1997).

A second thesis relates each successive step to different orders of tidal creek erosion. Differential depths of down-cutting may also be attributed to erosion by different orders of tidal creek down-cutting (Fig. 9B). Although this might explain the firmground topography, a number of observations do not support this concept. Firstly, there is generally little correspondence between the location of runoff channels and the location of the steps. Also, the steps tend to be more or less shore-parallel, which is best explained by wave-erosion.

Steep firmground profiles at Bone River reflect different erosional processes than those considered for Goose Point and Pickernell Creek. The abrupt passing of the firmground below 150 cm provides little information regarding the overall morphology of that surface. Therefore, no interpretation regarding its origin is divulged.

4.5. Examples of Pleistocene *Glossifungites* surfaces at Willapa Bay

Three types of *Glossifungites* surfaces have been observed in the Pleistocene outcrop at Willapa Bay. The first, and most commonly observed type of *Glossifungites* ichnofacies at the bay, consists of *Thalassinoides*-dominated horizons (Fig. 10A–D).

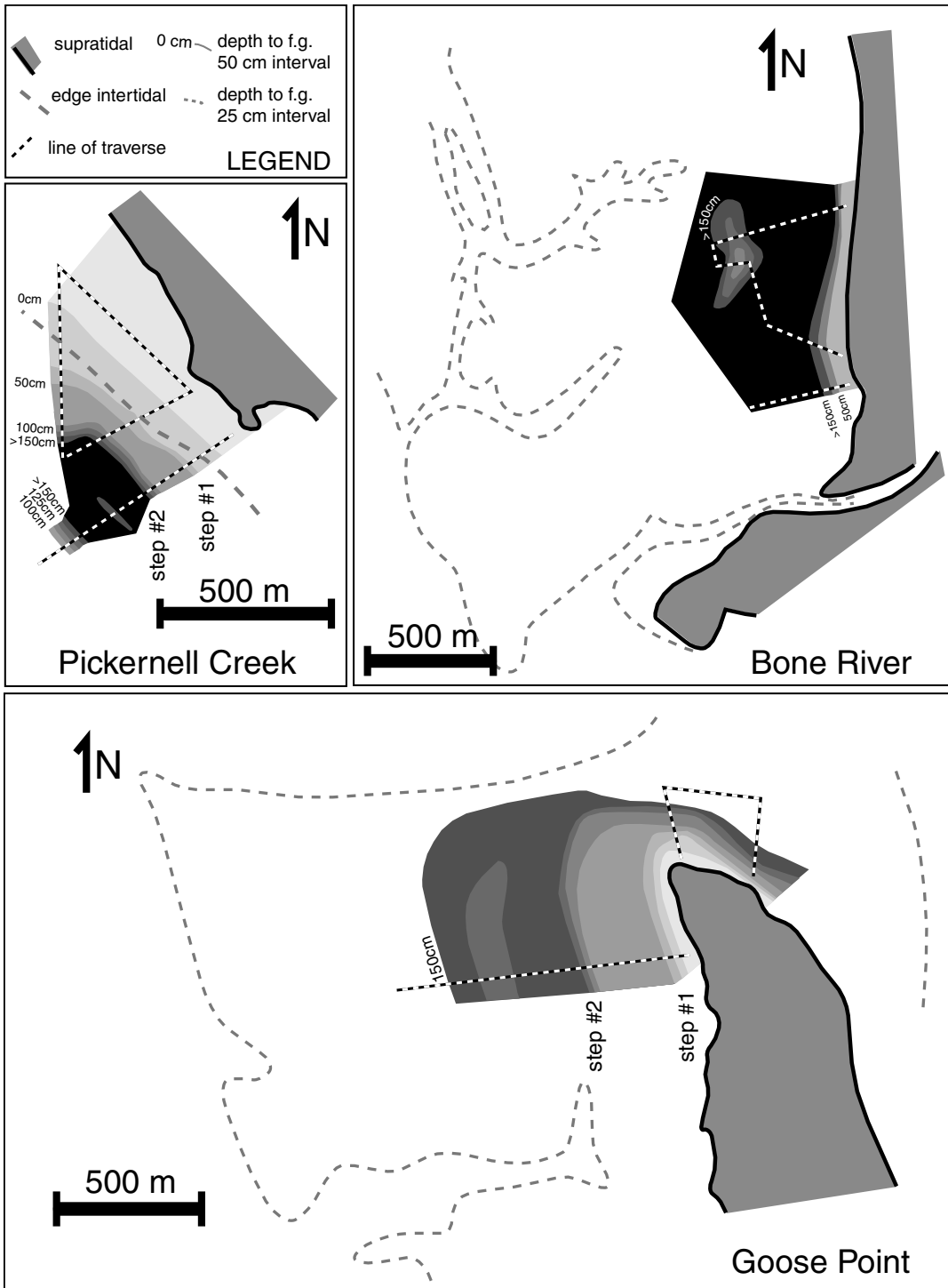


Fig. 8. Contour maps showing the topography of firmground surfaces beneath the soft sediment veneer. At Goose Point and Pickernell Creek, two steps are discernible on the surfaces. The firmground at Bone River drops off more abruptly. It is postulated that the stepped surfaces are erosionally produced, either by local tectonic events or by tidal creek migration.

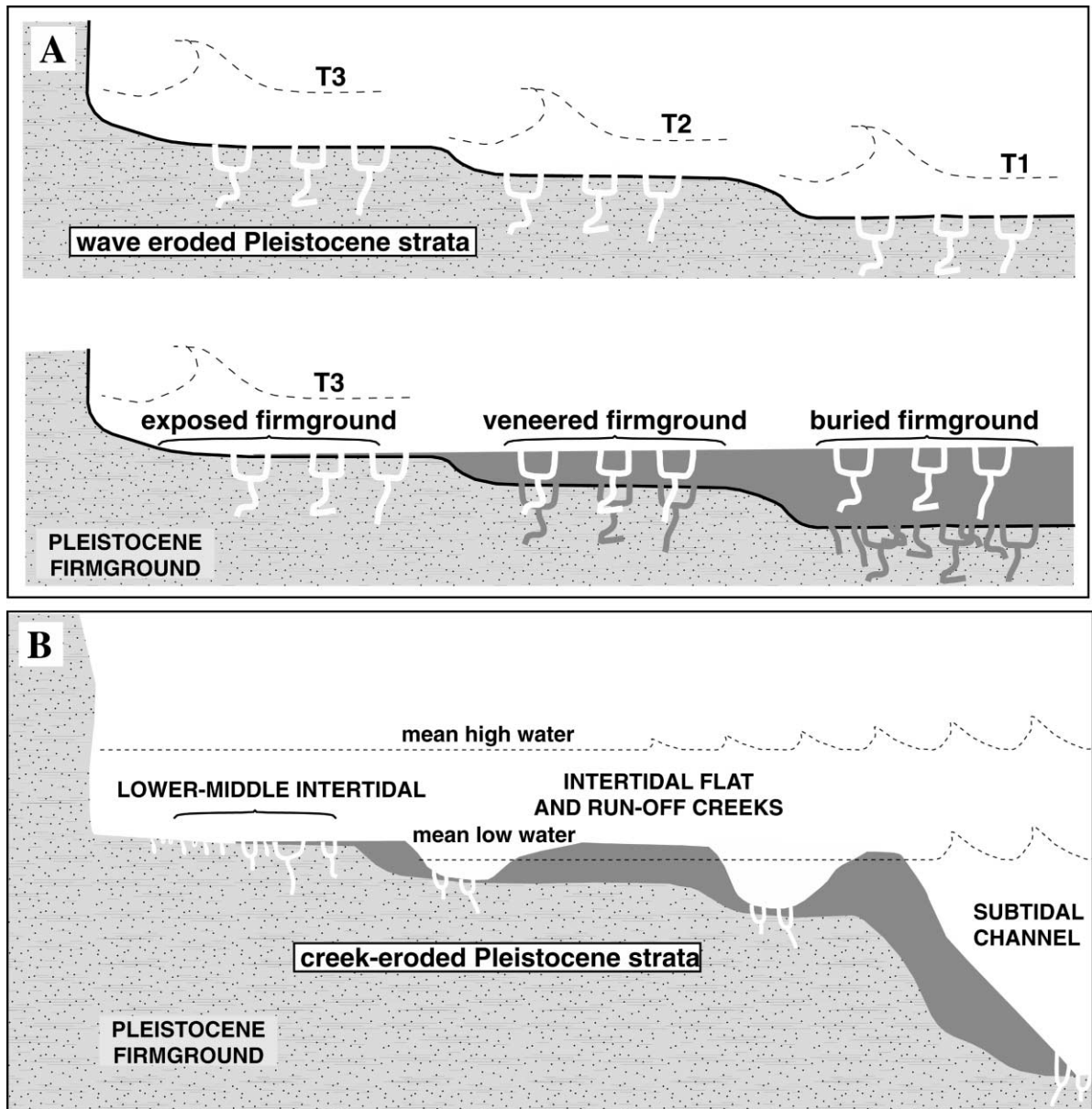


Fig. 9. (A) Schematic representation outlining the development of a stepped firmground/*Glossifungites* surface. Different base levels during T1, T2, and T3 might result from post seismic subsidence. Following each subsidence interval, Pleistocene sediment is truncated by a wave-erosion surface. Lower wave-cut notches are concurrently covered by a sediment veneer. (B) Erosion due to different orders of tidal run-off channels might also induce the stepped topography shown in Fig. 9. In this case down-cutting due to tidal channel erosion increases baywards, as the size of drainage creek also increases in that direction. *Glossifungites* assemblages are shown developing at the base of these channels. This diagram illustrates that a single *Glossifungites*-demarkated discontinuity can have an extremely complex history, and is commonly correlative to discontinuity surfaces that were exhumed by entirely different erosional processes.

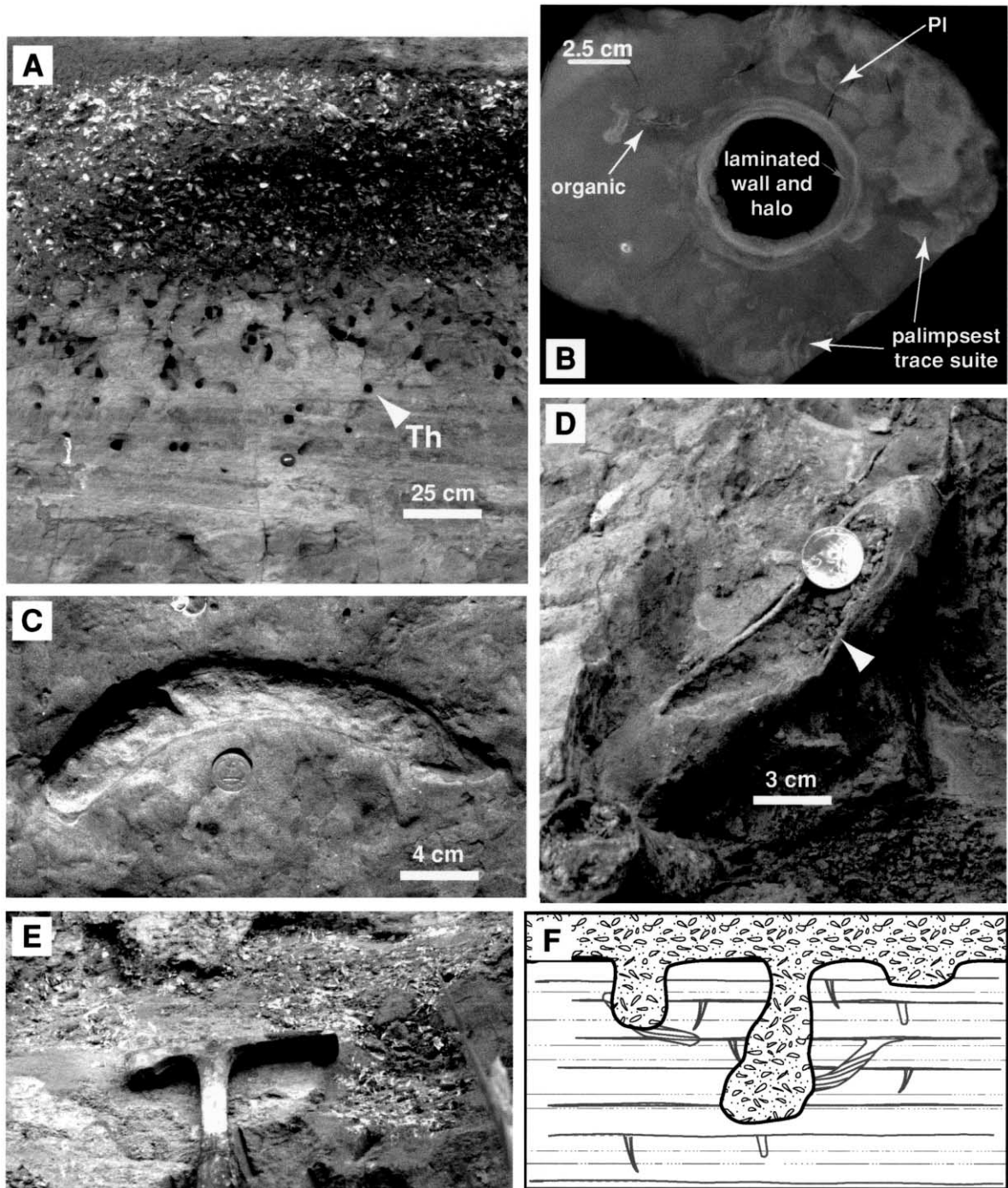


Fig. 10. Several examples of burrow fabrics observed in Pleistocene outcrop at Goose Point, Willapa Bay. (A) Large diameter *Thalassinoides* descending from a shell-lag demarcated erosional surface. The burrows descend up to 1.5 m below the erosional surface. (B) X-ray of a thin slab across a burrow excavated from A. Here an oxide halo, organic material, and a cross-cut palimpsest trace assemblage are shown. (C) Almost horizontal basal portion of the ancient shrimp burrow. An United States of America quarter provides the scale. (D) Obliquely tending *Thalassinoides*. (E) Irregular, cup-shaped structure filled with shelly debris. Photo from near Hawk Point (Fig. 1). (F) Schematic interpretation of A.

These trace fossils have a large diameter (normally exceeding 20 mm), penetrate deeply below the erosive surface, and locally branch and interpenetrate each other. The lebensspuren are typically unlined to thin walled (up to 2-mm thick), although a thick diagenetic halo composed of iron oxide cement is normally present. This assemblage is observed at the base of tidal channel and intertidal flat deposits where the underlying stratum is particularly muddy (Fig. 10).

The best examples of these surfaces are present at Goose Point. Clifton et al. (1989) commented on the stratigraphic significance of these *Glossifungites* horizons. At this location, muddy accumulations are unconformably overlain by relatively sandy strata interpreted to have been deposited in a tidal channel. A shelly layer of variable thickness (5–170 cm) lie directly on top of the erosional surface (Fig. 10). The shell deposit consists of both articulated and disarticulated oysters (*Ostrea lurida*) and has been previously interpreted as a more or less in situ bioherm (Clifton et al., 1989). Shelly sand from the channel base is present in almost all of the crustacean burrows, even those that extend 2 m below the erosional surface. This particular surface is sporadically present over 3 km and highly burrowed sections are commonly continuous for 150–200 m.

Rare shell nests are characteristic of another type of *Glossifungites* surface. These are similar to those illustrated in Fig. 5, however, the Pleistocene examples are decidedly less regular and are normally larger (up to 14 cm; Fig. 10E and F). The trace fossils have a roughly circular cross-section and normally constrict to a 10 cm diameter near the top. All the Pleistocene occurrences observed are interpreted as having an intertidal nature (i.e. highly bioturbated, thin, with evidence of rooted horizons). These surfaces have little lateral continuity, although they can be traced up to 30 m.

Finally, the least common *Glossifungites* surface observed at Willapa Bay consists of small *Skolithos* and *Arenicolites*. The burrow diameters are generally less than 2 mm and they are less than 20 mm long; they are therefore difficult to see in the weathered outcrop. This ichnological assemblage is also associated with deposits interpreted as intertidal. Their small size and extremely sporadic distribution make lateral tracing of these surfaces all but impossible.

4.6. The significance of Pleistocene *Glossifungites* surfaces at Willapa Bay

The majority of the *Glossifungites* assemblages observed in the Pleistocene deposits at Willapa Bay are composed of *Thalassinoides*. In the modern bay, similar traces are produced by *Upogebia pugettensis*. Ancient examples of similar assemblages include several Cretaceous examples from the Western Canadian Sedimentary Basin (MacEachern et al., 1992; Pemberton et al., 1992; Pemberton and MacEachern, 1995; Fig. 6.1) and occurrences of *Glyphichnus* observed at the Cretaceous/Paleocene unconformity in southern England (Bromley and Goldring, 1992). Modern intertidal analogs have been observed at Willapa Bay, Puget Sound (Stevens, 1929), in the Mediterranean (Asgaard et al., 1997), and along the Georgia coast (Pemberton and Frey, 1985).

Pleistocene *Glossifungites* assemblages (similar to the *Upogebia* Association) are generally subtidal at Willapa Bay, mostly occurring at the base of tidal channels (Fig. 10A). Intertidal examples have also been documented. Like the *Upogebia* Association, these Pleistocene *Thalassinoides* descend through a shelly sediment veneer that is situated immediately above the erosional surface. Two taphonomic biases explain the overall abundance of these ichnofossils in the rock record at Willapa Bay: (1) subtidal channels tend to migrate laterally, allowing estuarine point-bars to prograde over *Glossifungites* assemblages (Clifton et al., 1989); and, (2) large, deep-penetrating crustacean burrows are protected from complete eradication if erosional processes continue.

Glossifungites surfaces more akin to the *Petricola* and *Polydora* associations are locally present in ancient intertidal deposits at the bay. These consist of large, open excavations that are commonly filled with shelly debris, rare *Thalassinoides*-dominated assemblages, or stressed assemblages composed of minute *Skolithos* and *Arenicolites*. The more robust assemblages are interpreted to represent surfaces developed in the lower to middle intertidal, whereas the diminutive assemblages, which are analogous to the *Polydora* Association, are interpreted as being characteristic of the upper intertidal. The poor lateral continuity of these surfaces probably reflects

the firmground's susceptibility to erosion in upper intertidal zones.

In short, *Glossifungites* surfaces are commonly preserved in outcrop at Willapa Bay. Modern analogs support the paleontological and sedimentological information gathered from outcrop observations, illustrating the potential for application of this data to more ancient rocks. Taphonomic biases are also considerable, a factor that may not be uniformitarian where considering *Glossifungites* assemblages in more ancient rocks.

4.7. Implications outside of Willapa Bay

Several of the aforementioned observations have potential application to the rock record outside of Willapa Bay. Sedimentologically and ichnologically two generalizations are especially significant: (1) lateral variability in *Glossifungites* surfaces should not be immediately assigned to bathymetric factors, although texture and bathymetry appear to exert the most influence on the trace fossil assemblage; and, (2) there is great opportunity for subdivision of the *Glossifungites* Ichnofacies in the rock record. The paucity of burrowing in compacted heterolithic sediment is equally intriguing. In the modern bay, uncompacted heterolithic stratification is commonly burrowed. Why then, are compacted, intercalated sands and muds an effective burrowing barrier? This question needs to be tested against other modern and ancient examples.

Although this paper focuses on lateral variability in the modern Willapa Bay, it can be demonstrated that nearly identical trace fossil assemblages exist in sedimentologically similar Pleistocene deposits. This is not because spionid worms, upogiid shrimp, and boring bivalves *only* burrow in particular substrates. Indeed, as stated earlier spionids, crustaceans, and bivalves have been reported in an array of substrates, hard, firm and soft. It is more likely, although not substantiated here, that the organisms more successfully exploit particular substrates and physico-chemical conditions. This suggests that the colonization patterns reported herein result from competition. Furthermore, similar patterns should be observed in the ancient rock record. Clearly a great deal of research might be done in this area.

5. Conclusions

Striking variability is evident in *Glossifungites* assemblages at Willapa Bay. Variation is consistently related to intertidal zonation, sediment texture, and the absolute firmness of the firmground. The presence or absence of a sediment veneer also affects the observed assemblage. Intertidal zonation results from prolonged exposure of the substrate during low tide. Generally, subtidal and lower to middle intertidal firmgrounds are colonized by crustaceans and, more rarely, the bivalve *Petricola*. These surfaces are therefore dominated by the *Upogebia* association, and are characteristically burrowed with *Thalassinoides*- and *Gastrochaenolites*-like traces. The upper intertidal is dominated by the *Polydora* assemblage, the burrows of which include diminutive *Diplocraterion* and *Arenicolites*-like traces. Boundaries between these zones are somewhat gradational, with a poorly developed *Petricola* assemblage locally serving as a transitory element.

At the bay, sandy substrates are avoided by burrowing crustaceans and polychaetes alike, although *Polydora* is observed in deposits that are sandier than those associated with *Upogebia*. Heterolithic substrates are not burrowed by either. In contrast, *Petricola* is observed in both muddy, sandy mud, and (rarely) in heterolithic substrates. These are characterized by clavate, *Gastrochaenolites*-like burrows.

The absolute firmness of exhumed firmgrounds is quite heterogeneous. At the bay, the firmness of younger Pleistocene strata typically ranges between 10^7 and 10^8 Pa, whereas older Pleistocene strata normally exceed 10^9 Pa. The *Upogebia* association is absent in substrates that exceed 10^9 Pa. *Polydora*-dominated assemblages are poorly developed in similar firmgrounds. The *Petricola* Association, however, is common in relatively firm substrates. More robust *Thalassinoides*-like traces are absent in sediment characterized by firmness values exceeding 10^9 Pa.

Textural and firmness characteristics are inherited from other, older depositional configurations. They therefore cross-cut intertidal zonation and perturb the predictable succession attributed to the duration of tidal inundation, which normally exhibits a shore-parallel orientation.

Where sediment veneer exceeds 1 cm, it is generally detrimental to the development of a

Polydora-dominated assemblage. The *Petricola* association is generally inhibited where the veneer exceeds 3–5 cm. Only the *Upogebia* Association is unaffected by the presence of a thick sediment veneer, however, the presence of soft sediment sharply overlying firm sediment influence which part of the burrow might be preserved in the firmground. The presence or absence of certain burrow architectures in ancient firmgrounds should reveal whether or not a sediment veneer was present above that firmground at the time of burrow emplacement. Furthermore, it is worth emphasizing that the entire burrow is commonly not necessarily preserved in a fossil firmground, rather some portion of it existed in the sediment veneer above. Taphonomic considerations indicate that only the portion of the burrow that descends into the firmground might pass into the historical record.

Finally, the morphologic characteristics of exhumed firmgrounds show that *Glossifungites* surfaces are dynamic. They are exposed to different physico-chemical conditions as they are exhumed, colonized, and pass into the rock record. Also, they are potentially re-exhumed due to auto- and allocyclic processes. The small-scale topography present on a surface is related to the processes that exposed it, in this case tectonic adjustment, ravinement, and potentially channel erosion. However, a comprehensive study regarding the morphology of similar surfaces below sediment veneer is required before these data can be applied to the rock record. Such an endeavor should consider different sedimentary environments, particularly those related to shorelines and bays.

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