

# The Significance of Pleistocene *Psilonichnus* at Willapa Bay, Washington

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*Two types of ichnofossils from Pleistocene outcrop at Willapa Bay are described. Because both trace fossils are characterized by an inclined to horizontal tunnel, are unlined, have an exaggerated J-shaped morphology, rarely branch, and have an unconstricted apertural opening, they have been classified as Psilonichnus upsilon Type A and B.*

*Psilonichnus upsilon Type A is generally 1 to 3 cm in diameter and is infilled with laminated sediment. In general, P. upsilon Type A is observed in ancient point-bar deposits. It has an extremely simple architecture that is almost identical to that produced by the crab Hemigrapsus oregonensis in modern tidal flats at Willapa Bay. Psilonichnus upsilon Type B normally exceeds 10 cm diameter and is infilled with laminated sediment. The passive infill commonly is deposited in couplets and may be delivered to the burrow network by tide-generated currents. Psilonichnus upsilon Type B is observed in intertidal flat deposits. The overall morphology of this trace fossil is most similar to burrows generated by large crustaceans such as crabs, stomatopods, and lobsters.*

*The occurrence of these traces leads to four findings: (1) Psilonichnus upsilon has a more variable architecture than discussed in the literature. The size and angle of the tunnel are variable, and Psilonichnus may aggrade, forming Teichichnus-like structures. (2) In the modern bay, burrowing shrimp dominate subtidal, point-bar, and intertidal deposits. The Pleistocene record indicates that burrowing crabs sometimes occupied similar niches in the ancient bay. (3) Laminated, heterolithic burrow fills provide evidence of rhythmic sedimentation. These laminae represent tidal or episodic sedimentation and provide the only evidence of such processes in otherwise muddy deposits. (4) A large burrowing crab that might make P. upsilon Type B may not be present in the modern bay. However, such a trace maker was present when these Pleistocene deposits accumulated.*

## INTRODUCTION

Studies of modern burrows associated with the activities of crabs are numerous (e.g., Rice and Chapman, 1971; Hill and Hunter, 1973; Allen and Curran, 1974; Katz, 1980; Robertson and Pfeiffer, 1982), and the environmental significance of these burrows is largely understood (e.g., Chakrabarti, 1981; Frey et al., 1984; Duncan, 1986; Frey and Pemberton, 1987). Studies of modern burrowing activity have helped develop a general understanding of the paleoecology of ancient deposits marked by the presence of crab burrows (e.g., Stephenson, 1965; Frey and Mayou, 1971; Curran and Frey, 1977; Humphreys and

Balson, 1988; Pemberton and Jones, 1988; Curran and White, 1991).

Crab burrows and trace fossils resulting from the activities of crabs have been described in numerous deposits from a wide range of depositional settings, most commonly marginal marine and quasimarine (Frey et al., 1984). Trace fossils recognized as crab domichnia have been reported in backshore deposits (Curran and Frey, 1977; Howard and Frey, 1980; Curran and White, 1991), beach rock (Curran and White, 1991), subtidal marine sands (Humphreys and Balson, 1988), coastal plain deposits (Williams, 1965; Frey and Mayou, 1971; Allen and Curran, 1974), and intertidal marine environments (Fürsich, 1981). Modern occurrences of crab burrows also have been noted in a wide diversity of depositional environments that include salt marshes (Allen and Curran, 1974; Edwards and Frey, 1977; Letzsch and Frey, 1980), backshore (Frey and Mayou, 1971; Allen and Curran, 1974), beach/foreshore (Stephenson, 1965; Chakrabarti, 1980, 1981; Hill and Hunter, 1973), intertidal bar (Chakrabarti, 1993), shoaling estuaries (Williams, 1965), and interdune flats of barrier islands (Hill and Hunter, 1973).

In this report, two trace fossils are described from Pleistocene deposits at Willapa Bay, Washington (Fig. 1). These ichnofossils are interpreted to represent crab domiciles. Although they are observed normally in intertidal-flat and subtidal point-bar deposits, the lebensspuren also are present in central-bay deposits (Gingras et al., 1999). The aim of this study is to characterize these trace fossils and describe their paleoecological and sedimentological significance.

## WILLAPA BAY

Willapa Bay is located in the southwestern corner of Washington (Fig. 1). It measures approximately 38 km in length and 8 km in width. The bay is sheltered from the open Pacific Ocean by a 30-km-long barrier spit called Long Beach Peninsula. The spit is derived from sediments that were discharged by the Columbia River and subsequently redistributed by longshore currents (Ballard, 1964).

Pleistocene deposits outcrop along the modern bay's eastern and northern margins. These strata are interpreted to have been deposited in an estuarine environment similar to that of the modern bay (Clifton et al., 1976; Clifton and Phillips, 1980; Clifton et al., 1989; Gingras et al., 1999). Previous researchers at Willapa Bay have characterized the sedimentology and stratigraphy of both the modern and Pleistocene sediments (Clifton, 1983; Luepke and Clifton, 1983; Clifton and Phillips, 1980; Anima et al., 1989).

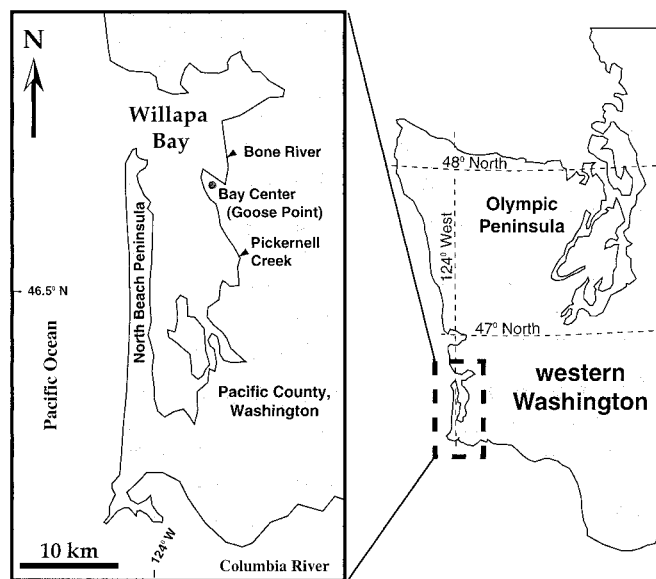


FIGURE 1—Location map of Willapa Bay, Washington. *Psilonichnus upsilon* A and B commonly are observed in outcrop at Bone River and between Goose Point and Pickernell Creek.

### PSILONICHNUS FROM WILLAPA BAY

Two types of *Psilonichnus upsilon* (Type A and B) have been observed in Pleistocene strata at Willapa Bay. Both occur in unlithified sands and muds that are interpreted to represent deposits similar to those present in the modern bay (Clifton and Phillips, 1980; Clifton et al., 1989). Outcroppings of consolidated Pleistocene sediments are exposed by scraping the outcrop face to a flat surface. Trace fossils are seldom weathered out three-dimensionally. This is primarily due to a lack of cement, which causes the outcrop to weather more or less evenly. *Psilonichnus upsilon* Type A and B both are most common in muddy deposits. Type A is associated with subtidal point-bar deposits. Type B is observed typically in intertidal-flat and subtidal bay deposits. Both types of lebensspuren have a characteristic infill and possess a distinctive architecture.

#### Description of Burrows

##### *Psilonichnus upsilon* Type A

Examples of *Psilonichnus upsilon* Type A are found almost exclusively in mud-dominated units with common sand laminae. Physical sedimentary structures observed in the deposit include lower flow-regime planar, starved ripple, and current-ripple lamination. In some instances, the bedding is comprised of inclined heterolithic strata. Organic detritus is present locally, most commonly as disseminated flakes of terrestrial plant debris; wood clasts are normally present. Fossil remains of bivalves are absent to moderately abundant. The Pleistocene strata are uncemented and, other than iron oxide staining, no diagenetic processes are evident. These accumulations previously have been interpreted as having a point-bar affinity (Clifton et al., 1976; Clifton and Phillips, 1980; Clifton et al., 1989; Gingras et al., 1999).

*Psilonichnus upsilon* Type A are typically unbranched, unlined, and have an oval cross-section (Fig. 2A–C). An iron-oxide halo less than a millimeter thick is commonly present. Burrow diameters range between 1.5 and 3.5 cm. The orientation of the tunnel is horizontal to slightly inclined with respect to bedding. Tunnel length ranges between 12 and 25 cm. The burrow aperture, which is usually less than 10 cm long, is more steeply inclined than the tunnel and shows little or no constriction (Figs. 2, 3). Passively deposited, laminated infills are commonly present (Fig. 2A,C). In contrast to the primarily muddy matrix, the fill is comprised of fine to medium sand intercalated with mud. Sand laminae within the fill are between 1 and 5 mm in thickness, whereas muddy laminations are approximately 1 mm thick. Laminae clinof orm obliquely into the burrow (Fig. 2A,C).

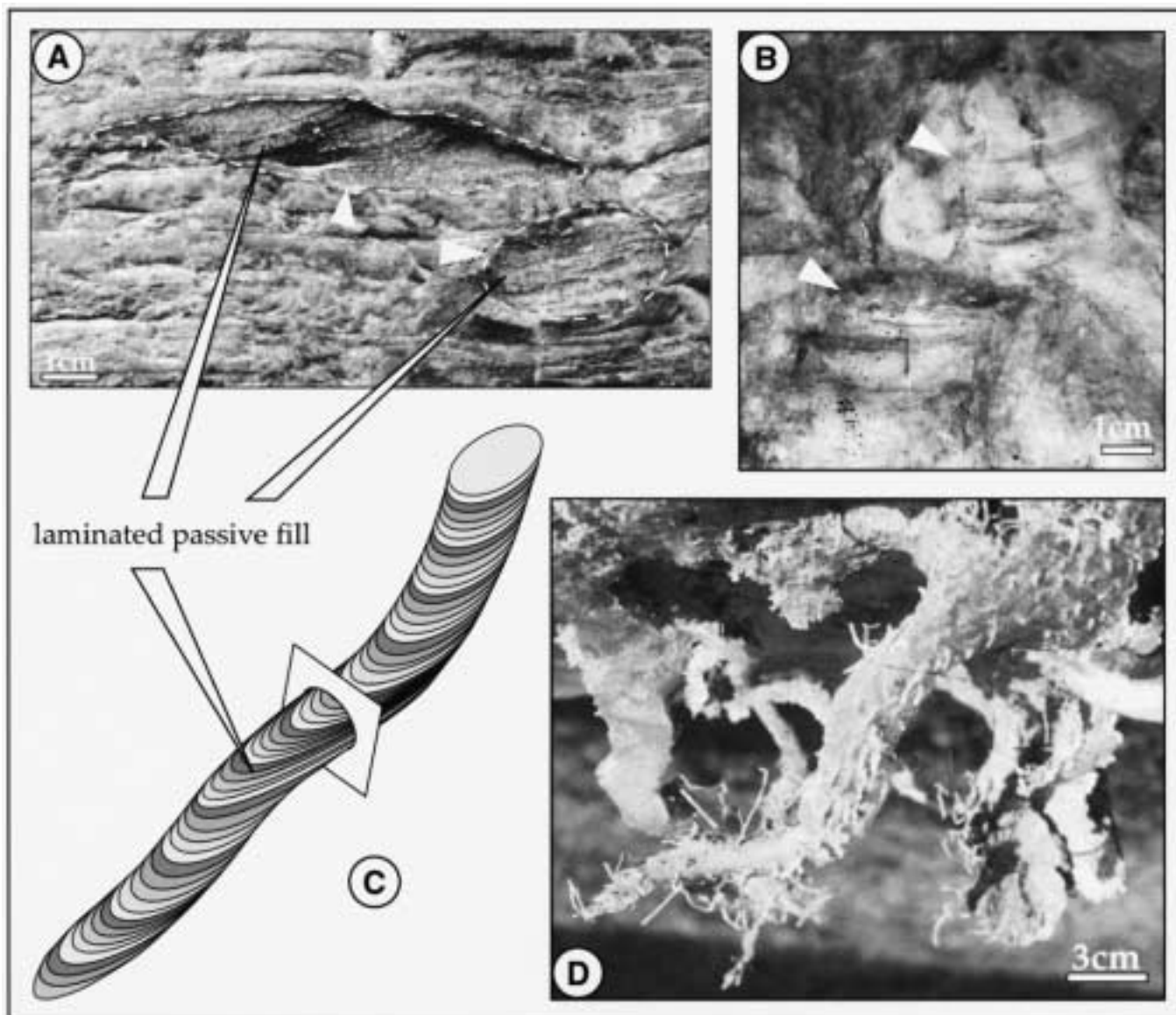
##### *Psilonichnus upsilon* Type B

*Psilonichnus upsilon* Type B is observed consistently in highly bioturbated (ichnofabric index, i.e., of 4 or 5), muddy deposits. Although many of the trace fossils are obscured due to the high degree of bioturbation, *Gyrolithes*, *Planolites*, *Palaeophycos*, *Cylindrichnus*, *Thalassinoides* (rare), and *Ophiomorpha* (rare) have been observed. Physical sedimentary structures typically are eradicated. However, rare wavy lamination, ripple lamination, and decimeter-scale scour and fill structures are present locally. Terrestrial organic detritus is common and woody debris is observed locally. Low-relief runoff channels are dispersed sporadically throughout the outcrop. These deposits have been interpreted as muddy intertidal deposits (Clifton et al., 1976; Clifton and Phillips, 1980; Clifton et al., 1989; Gingras et al., 1999).

*Psilonichnus upsilon* Type B also has been observed in quiescent subtidal deposits. These deposits are sedimentologically similar except that the ichnofabric index of the background fabric is generally higher (i.e. 5), vestigial sedimentary structures are rarer, and organic detritus is less abundant. A more comprehensive comparison of intertidal and subtidal deposits at Willapa Bay is provided by Clifton (1983) and Gingras et al. (1999).

*Psilonichnus upsilon* Type B is notably larger than Type A (Fig. 4). Like Type A, it contains a fill composed of inter-laminated mud and silt/sand. The burrows typically have diameters that range between 10 and 12 cm, and lengths that exceed 50 cm. They are J-shaped, with a long horizontal to slightly inclined, unbranched tunnel. Some burrows (approximately 30% of the specimens) have a "notch" protruding from the roof of the burrow. Notches average 2.5 cm in width and 2 to 2.5 cm in height (Fig. 4A,B). The unlined burrows commonly are rimmed by an iron oxide halo (Fig. 4A,D).

Laminae in the lower portion of the trace fossil are typically spreiten-bearing, lending the appearance of a large *Teichichnus*-like burrow in cross section (Fig. 4C). These laminations are considered to be spreite in that they represent sequential demarcations of the burrow wall (albeit the floor). This terminology is consistent with earlier applications (Frey and Seilacher, 1980; Ekdale et al., 1984; Bromley, 1996). The spreite are defined lithologically by thin mud laminae (up to 4 mm in thickness), and coarser-grained fill that is composed of fine- to medium-grained sand and wood fragments (up to



**FIGURE 2**—Details of *Psilonichnus upsilon* Type A and a similar modern trace. (A) Transverse and oblique sections of *P. upsilon* Type A from muddy point-bar deposits in Pleistocene strata at Willapa Bay. Note the passive infill lamination. (B) X-radiograph of *P. upsilon* Type A from Pleistocene intertidal deposits. In this example, the background fabric is completely obliterated (i.i. 5). (C) Schematic of *P. upsilon* Type A laminae as interpreted from outcrop observations. (D) Resin cast of a crab burrow made by *Hemigrapsus oregonensis* taken from a modern tidal flat at Willapa Bay. The small casted tubes radiating from the *Psilonichnus* were made by the threadworm *Heteromastus*.

2 cm in thickness). The spreite are crudely defined, concave upwards, slightly wavy, and non-parallel within this portion of the burrow. They typically are disrupted by walking traces (*Repichnia*), and represent successive (aggrading) floors of the tunnel. Overlying the spreite are planar parallel laminations, 1 to 10 mm in thickness, that are defined by variations in grain size and lithology. These laminae are commonly paired, and locally develop into rhythmic couplets (Fig. 4A,B).

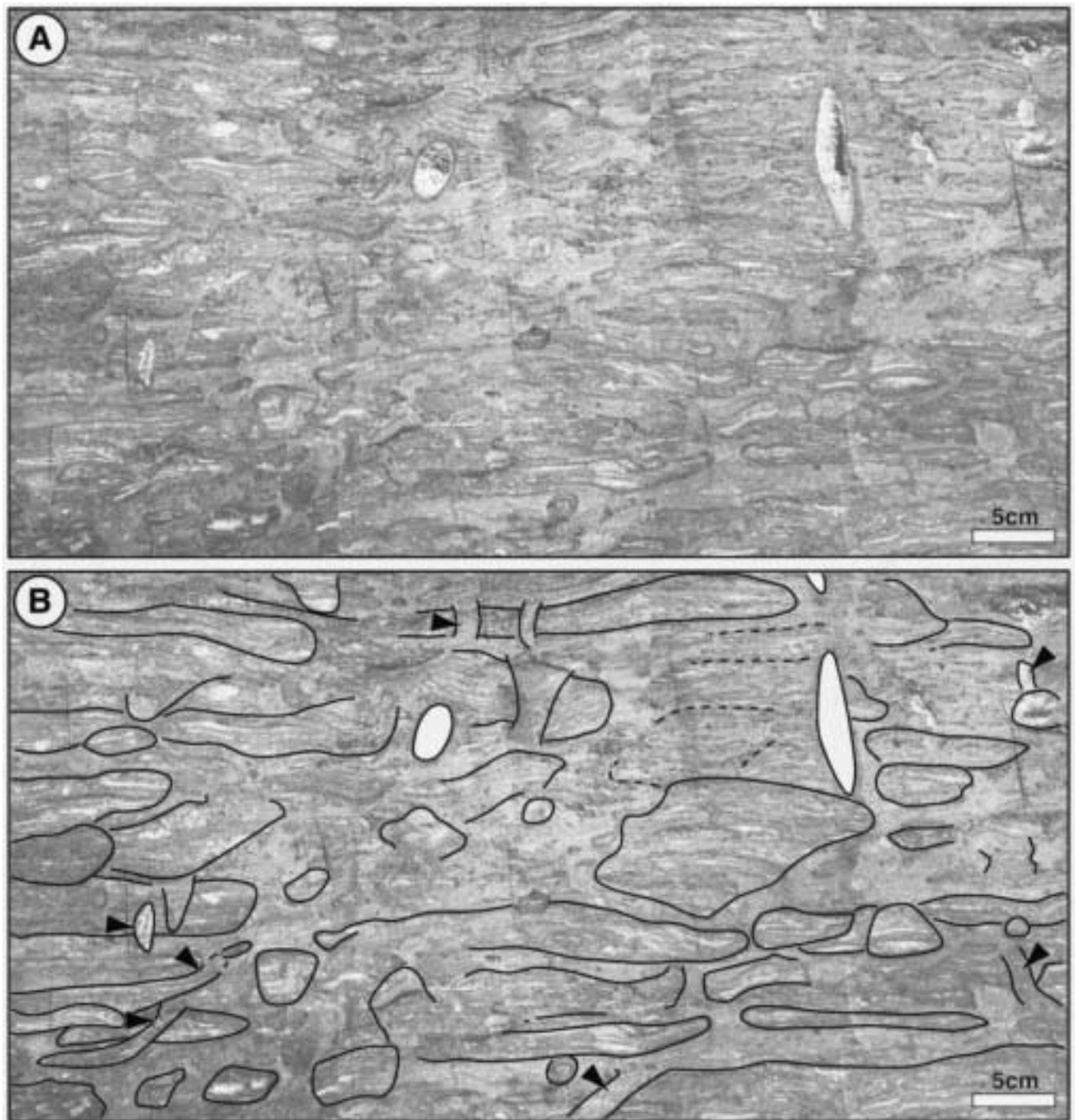
In intertidal-flat to shallow subtidal deposits, this ichnofossil is rare to moderately abundant; it is less common in sheltered subtidal deposits. The degree of bioturbation and the trace fossil diversity of the associated ichnofossil assemblage is notably higher than those associated with *Psilonichnus upsilon* Type A. Both *P. upsilon* Type-A and -B cross

cut the burrowed fabric and apparently represent the deepest burrow tier or the final stage of substrate colonization.

## Interpretation and Discussion

### *Psilonichnus upsilon* Type A

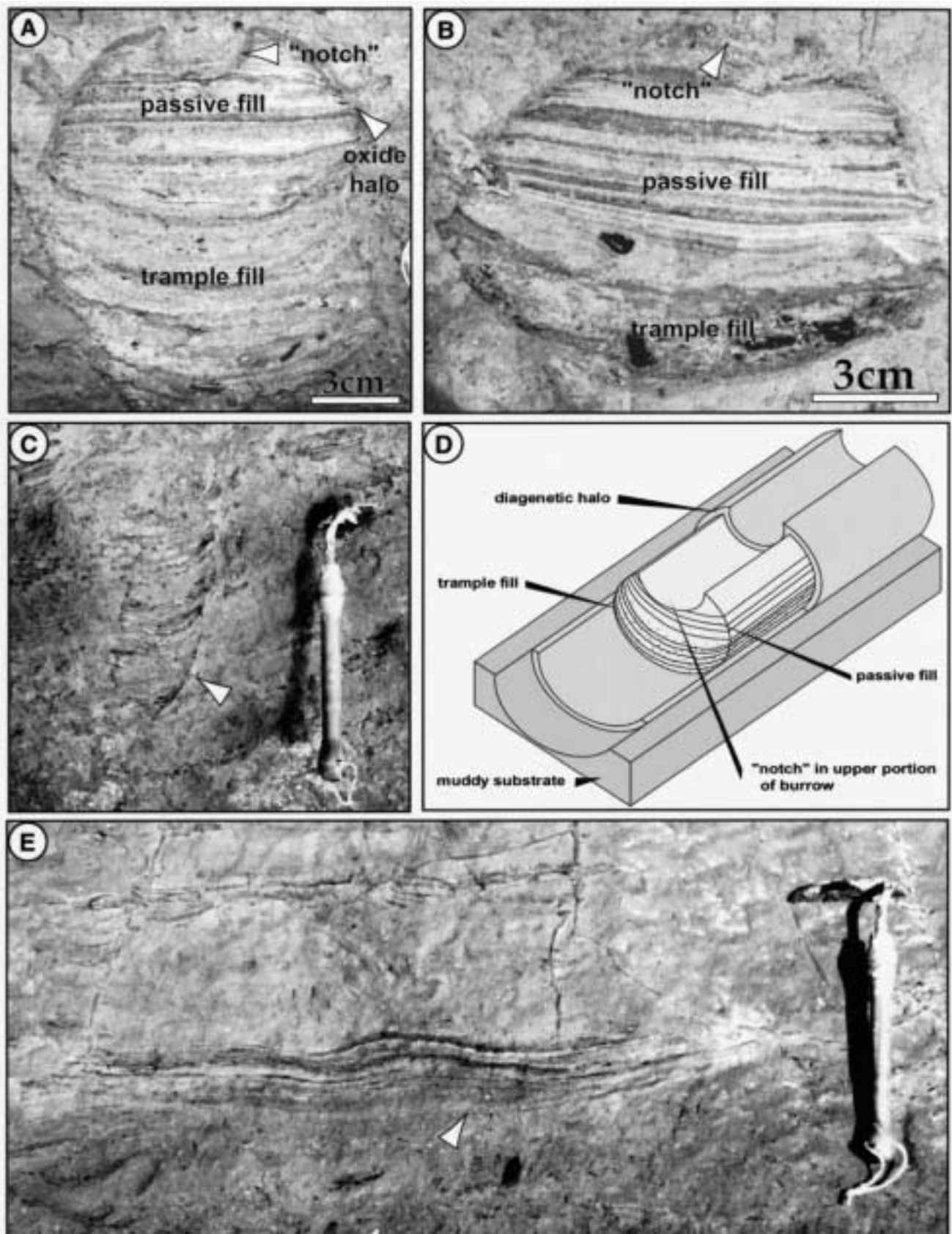
Physical sedimentary structures, such as starved ripple and current-ripple lamination, are indicative of intermittent bedload transport. Fine-grained laminae and lower flow-regime planar lamination represent sedimentation primarily from suspension. Episodic alternation from mud to sand deposition may be related to meteorological events, tidal cyclicity, or seasonal shifts of the turbidity maximum. Based upon comparisons to modern point bars



**FIGURE 3**—Outcrop photograph and interpretation of a subtidal point-bar deposit highly bioturbated with examples of *Psilonichnus upsilon* Type A. (A) *Thalassinoides* (rare) and *Psilonichnus* (abundant) represent the dominant trace assemblage at this location. Fabrics comprised of both these traces are comparatively rare at Willapa Bay. In this photo the high degree of bioturbation, combined with the laminated burrow-fill, make it difficult to discern primary sedimentary structure from the burrow fabric. (B) Solid black lines indicate the location of *P. upsilon* Type A. Dashed black lines show interpretations that are less certain. Burrow apertures are indicated by black arrows, and *Thalassinoides* are represented by black lines with white fill.

at Willapa Bay, the deposition of mud versus sand has been interpreted to largely reflect seasonal variation in sediment supply and stream discharge (Clifton et al., 1989). Undoubtedly, storm events and extreme tides overprint the seasonal record locally.

The absence of common branches and the primarily oblique to horizontal orientation of *Psilonichnus* Type A suggest it is best classified as a variation of *Psilonichnus upsilon* (Table 1; Figs. 2, 3). Other criteria, such as an irregular to ovate cross section, the absence of a lining, and



**FIGURE 4**—Outcrop examples of *Ppsilonichnus upsilon* Type B. (A, B) Cross section of *P. upsilon* Type B detailing the trample fill, passive fill, diagenetic halo, and notch. (C) *Ppsilonichnus upsilon* Type B that has aggraded approximately 25 cm (outcrop trowel is approximately 30 cm long). (D) Schematic interpretation of the burrows illustrated in 4 A, B. (E) Longitudinal section of *Ppsilonichnus upsilon* Type B.

**TABLE 1**—Table comparing *Thalassinoides suevicus*, *Psilonichnus tubiformis*, *Psilonichnus upsilon*, and the traces described in this paper. The different trace fossils are compared on the basis of the diagnosis, their occurrence, and potential tracemakers.

	<i>Thalassinoides suevicus</i> (Rieth, 1932)	<i>Psilonichnus tubiformis</i> (Fürsich, 1981)	<i>Psilonichnus upsilon</i> (Frey et al., 1984)	<i>Psilonichnus upsilon</i> Type A (this study)	<i>Psilonichnus upsilon</i> Type B (this study)
Diagnosis	<ul style="list-style-type: none"> <li>• 3-dimensional networks</li> <li>• smooth-walled</li> <li>• cylindrical section</li> <li>• Y- to T-shape branches</li> </ul>	<ul style="list-style-type: none"> <li>• upper Y- or U-component</li> <li>• predominantly vertical</li> <li>• straight to slightly curved shaft</li> <li>• irregularly spaced, horizontal to oblique dead-end branches</li> </ul>	<ul style="list-style-type: none"> <li>• gently inclined</li> <li>• rarely branched</li> <li>• J- or Y-shaped</li> <li>• inclined shafts that are straight to curved</li> </ul>	<ul style="list-style-type: none"> <li>• gently inclined to horizontal</li> <li>• rarely branched</li> <li>• J-shaped</li> <li>• almost horizontal tunnels that are straight to curved</li> </ul>	<ul style="list-style-type: none"> <li>• gently inclined to horizontal</li> <li>• never branched</li> <li>• recumbent J-shape</li> <li>• tunnels that are straight to slightly curved</li> </ul>
Possible Tracemakers	<ul style="list-style-type: none"> <li>• thalassinid shrimp</li> </ul>	<ul style="list-style-type: none"> <li>• thalassinid shrimp (?) similar to <i>Upogebia</i></li> </ul>	<ul style="list-style-type: none"> <li>• ghost crab (<i>Ocy-pode quadrata</i>)</li> <li>• shorecrab (<i>Hemigrapsus oregonensis</i>)</li> </ul>	<ul style="list-style-type: none"> <li>• shorecrab (<i>Hemigrapsus oregonensis</i>)</li> </ul>	<ul style="list-style-type: none"> <li>• <i>Cancer magistar?</i></li> <li>• mantis shrimp?</li> </ul>
Occurrence	<ul style="list-style-type: none"> <li>• silts, sands, limestones</li> <li>• common in sheltered bays</li> <li>• common on proximal offshore deposits</li> </ul>	<ul style="list-style-type: none"> <li>• marginal marine to terrestrial</li> <li>• low energy, brackish</li> <li>• intertidal, near shoreline</li> </ul>	<ul style="list-style-type: none"> <li>• foreshore to back-shore</li> <li>• intertidal to shallow subtidal in brackish, sheltered bays (this study)</li> </ul>	<ul style="list-style-type: none"> <li>• sibtidal point bar</li> <li>• rarely in intertidal-flat deposits</li> </ul>	<ul style="list-style-type: none"> <li>• intertidal to shallow subtidal in brackish, sheltered bays</li> </ul>

the presence of an open aperture support this interpretation.

The most distinctive characteristic of *P. upsilon* Type A is its passively laminated fill. Where burrow density is high, the infill laminae dominate the observed fabric and the original sedimentary fabric is all but obliterated. In such instances the perceived fabric appears to represent bedding (Fig. 3). On closer inspection, however, it is apparent that coarser clastic laminae (fine to medium sand) are only present within the burrow fill. The horizontal nature of the laminated burrow fill is partly due to the presence of an unconstricted burrow aperture (Fig. 3). The infill is well-laminated and undisturbed (Figs. 2A, 3), suggesting that the burrows were filled following abandonment. It is probable that the interlaminated nature of the infill is due to deposition under tidal influences. This is important because in many instances, the fill of *P. upsilon* Type A provides the only evidence of rhythmic sedimentation at a particular location (Fig. 3). Fluctuations in sediment transport related to meteorological events cannot be discounted, however. These processes, in conjunction with passive fill laminae up to 0.5 cm thick, suggest that the burrows filled rather quickly.

An important consideration is the simple burrow architecture typical of this trace fossil. The oblique to horizontal, unbranching tunnel is typical of modern crab domiciles (Fig. 5). Normally, *Psilonichnus upsilon* Type A is present in low-diversity assemblages. Furthermore, in any particular bed, burrow diameters do not vary appreciably (2.0 to 3.4 cm). Although little can be said regarding the population dynamics of the trace-maker, a lack of variation in burrow diameter elucidates certain potential behavioral patterns. Sudden abandonment, coupled with a lack of size variability suggests the traces were evacuated on a seasonal (or at least episodic) basis. This argument is

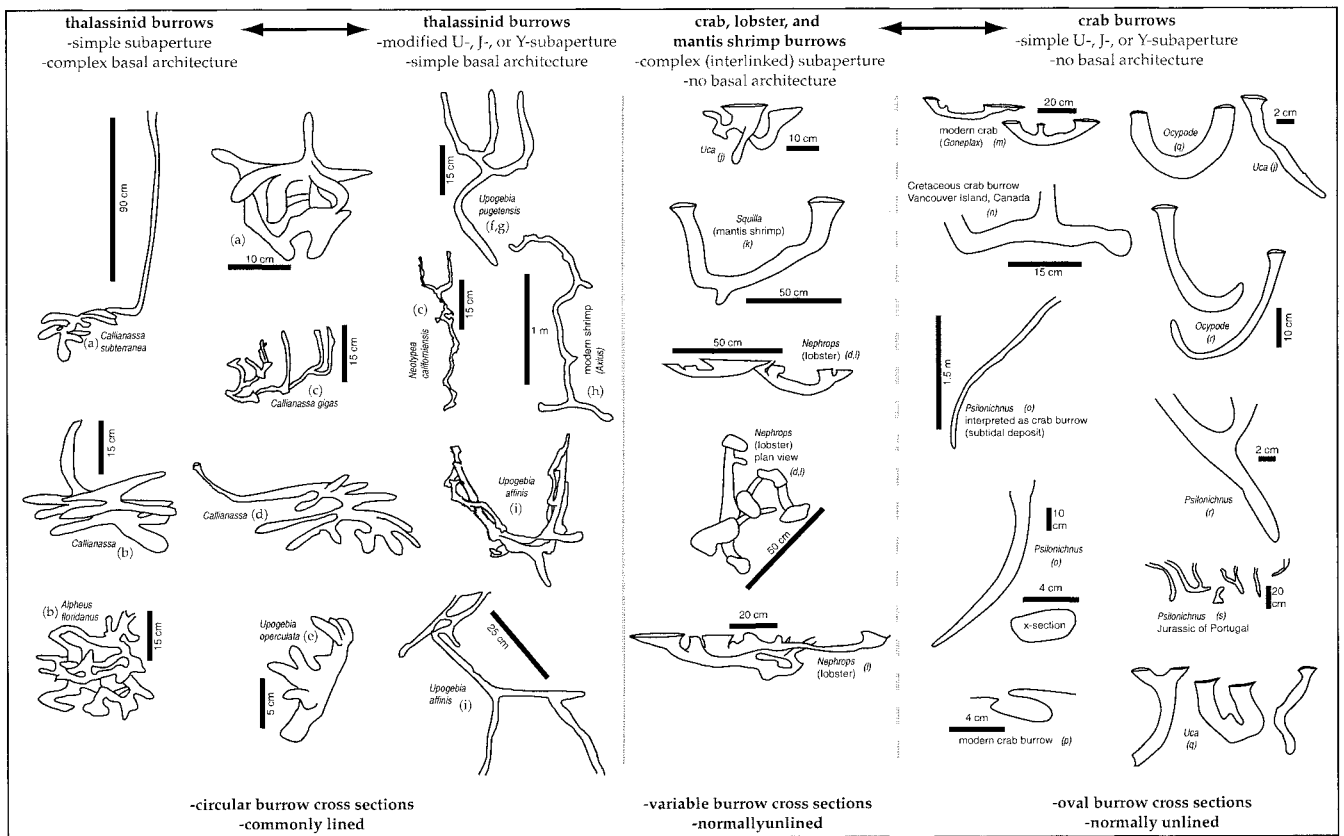
strengthened by the fact that the ichnofossils are dominantly sand-filled, and appear to record intervals of changing hydraulic conditions.

The burrowing crab, *Hemigrapsus oregonensis* makes similar traces in the modern bay. Burrows of *H. oregonensis* are typically horizontal to oblique, and they incline upwards toward the aperture (Fig. 2D). These burrows are typically unbranched, but short branches are present locally near the tunnel opening. The burrow walls are unlined, and passively, crudely laminated fill is sometimes present. Where observed, *Hemigrapsus* burrows normally range from 1 to 3 cm in diameter (Fig. 2D). Juvenile *H. oregonensis* excavate burrows smaller than 1 cm in diameter.

At Willapa Bay, *H. oregonensis* is commonly observed in the intertidal realm, particularly in muddier deposits. They commonly inhabit cut banks of intertidal-runoff creeks where the substrate is partially dewatered. Unfortunately, the preservation potential of burrows deposited in such a setting is very low, and this relationship is not observed in the Pleistocene record at Willapa Bay. Less commonly, similar traces are observed on modern intertidal pointbars, intertidal flats, and muddy subtidal point bars. These traces possess a much greater chance of passing into the historical record, and are considered analogous to the Pleistocene trace fossils described herein.

#### *Psilonichnus upsilon* Type B

Higher degrees of bioturbation associated with this ichnofossil suggest that sedimentation rates were comparatively low. In fact, unlike *Psilonichnus upsilon* Type A, Type B is absent in point-bar deposits, which are interpreted to have been deposited under relatively higher sedimentation rates. It appears that the tracemaker could not



**FIGURE 5**—Schematic diagrams of resin casts of crustacean burrows and various trace fossils. Thalassinid, lobster, and crab burrows are illustrated, primarily from left to right. Important physical characteristics, such as the shape of the burrow cross-section, the absence or presence of a lining, and the overall architectural arrangement, are detailed across the bottom of the diagram. Note the overall higher complexity of the basal portion of thalassinid burrows compared to lobster and crab burrows. Lobster burrows demonstrate more complex branching in the subaperture portion of the burrow. Crab burrows commonly display the simplest architectures. Sources are indicated by letters beside the burrow schematics and are as follows: (a) Atkinson and Nash, 1990; (b) Shinn, 1968; (c) Griffis and Chavez, 1988; (d) Rice and Chapman, 1971; (e) Kleeman, 1984; (f) Dworschak, 1982; (g) Stevens, 1929; (h) Pemberton et al., 1976; (i) Frey and Howard, 1975; (j) Basan and Frey, 1977; (k) Myers, 1979; (l) Farmer, 1974; (m) Atkinson, 1974; (n) Richards, 1975; (o) Humphreys and Balson, 1988; (p) Savazzi, 1982; (q) Farrow, 1971; (r) Frey et al., 1984; (s) Fürsich, 1981.

cope with higher sedimentation rates and/or high turbidity. Also, the large diameter of *P. upsilon* Type B would make the burrow prone to collapse in the thixotropic sediments associated with depositional surfaces on point bars.

As with *Psilonichnus upsilon* Type A, slightly inclined to horizontal tunnels, an overall J-morphology, and an absence of branching, confirm that ichnofossil Type B is best defined as *Psilonichnus upsilon* (Table 1). Furthermore, the burrows are unlined, oval in cross section, and have no complex basal architecture (compare to Fig. 5). They share little in common with thalassinid burrows, and lack the shallow networking evident in many lobster burrows (Fig. 5).

A distinctive characteristic of these burrows is the association of the shifting-upwards burrow floor (forming spreite) and the terminal, passive fill (Fig. 4). Retrusive spreiten are common in the lower portion of the burrow fill. Disruptions, interpreted as trample markings (Repichnia), indicate that the spreiten represent a sporadically aggrading tunnel floor. Intermittently, the roof of the burrow presumably collapsed. The tracemaker subsequently re-excavated the domicile in an attempt to maintain a suitable burrow architecture. Alternately, a stable depth in the substrate may have been maintained by

scraping material from the burrow roof. These two processes created the series of concave upwards, quasi-parallel laminations observed in the bottom portion of the burrow. The presence of several trampled layers (Fig. 4A) indicates several re-excavations were required to maintain the burrow. This, along with significant sediment aggradation, suggests these burrows were permanent domiciles that were inhabited for longer time spans than *Psilonichnus upsilon* Type A. Differences in substrate cohesiveness also might account for this observation. Frey and Seilacher (1980) observed similar spreite associated with *Thalassinoides* burrows from the Eocene of Georgia (they noted the same burrow was taxonomically *Teichichnus* in cross section).

The upper portion of the ichnofossil was filled passively after the tracemaker abandoned the burrow. The planar parallel laminations within the upper part of the trace fossil provide no evidence that this occurred while the inhabitant was still residing in the structure. Similar to the infill present in the smaller *Psilonichnus upsilon* Type A, this fill consists of interbedded sand and mud, reflecting alternating bed load transport and deposition from suspension. Well developed mud couplets (Fig. 4A,B) suggest

that the burrow fill was deposited under tidally-influenced conditions. As with *Psilonichnus upsilon* Type A, the laminated fill provides the only evidence for rhythmic sedimentation in its associated deposits (Fig. 4B).

The genesis of the roof notch observed in some *P. upsilon* Type B is not clear. It may, however, reflect the functional morphology of the tracemaker. The preservation of the notch above the passive fill indicates that the notch was present at the time of burrow abandonment. Close scrutiny of Figure 4A reveals that the passive-infill laminae terminate against the protrusion and confirms that the portion of the burrow that is passively filled represents the morphology of the open portion of the burrow as it migrated upwards.

Specimens of *Psilonichnus upsilon* Type B are significantly larger than many *Psilonichnus* that have been described previously (Frey and Mayou, 1971; Allen and Curran, 1974; Frey et al., 1984; Curran and White, 1991). Due to the large size of *Psilonichnus upsilon* Type B and its morphological similarities to modern crab burrows, it is postulated that these structures were constructed by a large crab, shrimp, or similar crustacean. Burrowing crustaceans common in the modern bay include the shrimp *Callinassa californiensis* and *Upogebia pugettensis*, and the crabs *Hemigrapsus oregonensis* and *Cancer magister*.

In the case of *P. upsilon* Type B, thalassinid shrimp have been discounted as potential tracemakers. This is because thalassinid shrimp (especially *Upogebia* and *Callinassa*) generally are capable of producing burrows with circular cross-sections. Furthermore, their burrows are dominantly vertical, with branching subapertural or basal architectures (Fig. 5). In contrast, crab burrows are normally oval in section (Fig. 5). This reflects the crab's flattened body and the awkward positioning of its front chelae. With certain species, *Cancer magister*, for instance, their chelae can barely touch to the front of the crab, a situation that is exacerbated when reaching upwards. Of the animals that inhabit the modern Pacific coast, a crab-like morphology is best reconciled with the elliptical cross section and the presence of a notch.

*Cancer magister* is large enough to produce a burrow of this size. Also, *C. magister* is known to burrow backwards into sandy substrates, producing temporary resting burrows (Kozloff, 1996). This activity, however, would not produce a trace favorably comparable to *P. upsilon* Type B. It is possible that *C. magister* burrows into the substrate during the winter. Overwintering has been observed with the american lobster, *Homarus americanus* (Thomas, 1968; Cobb, 1971), but this behavior is poorly documented with crabs. Fossil crab burrows, interpreted as subtidal, have been documented from Cretaceous strata on Vancouver Island (Richards, 1975). However, no examples of subtidal crab burrows are known from the Pleistocene record along the west coast of North America.

Another potential tracemaker for these large *lebensspuren* is the mantis shrimp, *Hemisquilla ensigera californiensis*, which is found in shallow coastal waters off the coast of southern California (Ricketts et al., 1985). Caldwell and Dingle (1976) observed these stomatopods occupying simple subtidal burrows in the Gulf of California. The range of these shrimp, however, is presently far south of Washington. Furthermore, burrows of mantis shrimp are commonly circular in cross-section (Fig. 5).

#### THE ICHNOGENUS *PSILONICHNUS* AND ITS RELATIONSHIP TO CRAB AND OTHER CRUSTACEAN BURROWS

Fürsich (1981) first described *Psilonichnus tubiformis* from the Upper Jurassic (Kimmeridgian/Portlandian) of the Lusitanian Basin in Portugal. He considered the ichnofossil to be related to the ichnogenus *Thalassinoides*, differing primarily in that *Psilonichnus* was considered to be dominated by vertical elements, and characterized by a simpler branching pattern (Table 1). Fürsich (1981) noted that the upper portion of *P. tubiformis* was frequently Y-shaped, and that the form was intermediate between the simpler J- and Y-shaped burrows of modern crabs and *Thalassinoides*. Another crustacean ichnofossil, *Psilonichnus upsilon*, was described by Frey et al. (1984). In contrast to *P. tubiformis*, *P. upsilon* was originally defined as consisting of an inclined, branched or unbranched, J- or Y-shaped burrow system (Table 1). These trace fossils were attributed primarily to the activities of burrowing crabs (Frey et al., 1984).

Modern and ancient crab burrows have many characteristics that generally are not shared by other crustaceans (Fig. 5). These have been discussed previously and include comparatively simple architectures, open apertures, and ovoid cross sections (Fig. 5). Notably, linings vary appreciably in shrimp burrows. These include pellet-, mud-, and mucous-lined shafts and tunnels (Pemberton et al., 1976; Frey et al., 1978). Crab burrows (and *Psilonichnus*) normally are unlined (Atkinson, 1974; Frey et al., 1978; Curran and White, 1991). Finally, thalassinid-shrimp burrows may display complex basal structures (Fig. 5). These include tiered and boxworked networks. Because crab burrows normally represent domiciles as opposed to combined feeding structures, complex basal geometry is absent. Although the architectures observed in crab traces are more similar to those of lobster traces, lobster burrows normally display more shallow, sub-apertural branching (Rice and Chapman, 1971; Farmer, 1974).

In summary, the salient physical characteristics of crab burrows include: a vertical to gently dipping J-, U-, or Y-shape; open burrow apertures; a paucity or absence of branches; an oval cross section; unlined burrow walls; and an absence of complex basal architecture. *Psilonichnus upsilon* documented from Pleistocene outcrops at Willapa Bay display all of these characters.

#### CONCLUSIONS

Two different varieties of *Psilonichnus upsilon* have been observed in Pleistocene strata at Willapa Bay. Each has a distinct fill that provides information about the burrow's history of habitation and the conditions under which they were filled. *Psilonichnus upsilon* Type A is interpreted to have been abandoned seasonally and filled shortly thereafter. *Psilonichnus upsilon* Type B, which is significantly larger than Type A, is characterized by aggraded tunnels that passively filled following abandonment.

Four notable conclusions are deduced: (1) *Psilonichnus upsilon* has a more variable architecture than previously discussed in the literature. Both the size and angle of the tunnel vary appreciably. Also *Psilonichnus* may aggrade, forming *Teichichnus*-like structures. (2) In the modern



bay, burrowing shrimp dominate quiescent subtidal, point-bar, and intertidal deposits. The Pleistocene strata, however, indicate burrowing crabs sometimes occupied similar ecospace in the ancient bay. Their presence suggests physico-chemical parameters, or competition dynamics, unlike that of the modern bay (the nature and magnitude of these differences was not characterized). (3) Laminated, heterolithic burrow fills provide evidence of rhythmic sedimentation. These laminae represent tidal or episodic sedimentation and provide the only evidence of such processes in otherwise muddy deposits. (4) A large burrowing crab that might make *P. epsilon* Type B may not be present in the modern bay. However, such a trace-maker was present when these Pleistocene deposits accumulated. Whether it was an extinct or extant species is not known.

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