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Sedimentology and taphonomy of the Early to Middle Devonian plant-bearing beds of the Trout Valley Formation, Maine

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ABSTRACT

The Trout Valley Formation of Emsian–Eifelian age in Baxter State Park, Maine, consists of fluvial and coastal deposits that preserve early land plants (embryophytes). Seven facies are recognized and represent deposits of main river channels (Facies 1, 2), flood basin (Facies 4), storm-influenced nearshore shelf bars (Facies 3), a paleosol (Facies 5), and tidal flats and channels (Facies 6, 7). The majority of plant assemblages are preserved in siltstones and are allochthonous and parautochthonous, with only one autochthonous assemblage identified in the sequence above an apparent paleosol horizon. Taphonomic analysis reveals that plant material within allochthonous assemblages is highly fragmented, poorly preserved, and decayed. Plant material within parautochthonous assemblages shows evidence of minimal transport, is well preserved, and shows signs of biologic response after burial. The one autochthonous assemblage contains small root traces. Trimerophytes (*Psilophyton* and *Pertica quadrifaria*), rhyniophytes (cf. *Taeniocrada*), and lycopods (*Drepanophycus* and *Kaulangiophyton*) are the most common taxa in estuarine environments. *Psilophyton* taxa, *Pertica*, cf. *Taeniocrada*, and *Drepanophycus* are found also in fluvial settings. The presence of tidal influence in deposits where parautochthonous and autochthonous assemblages occur shows that these plants occupied coastal-estuarine areas. However, the effects on the growth and colonization of plants of the physical conditions (e.g., salinity) that exist in these settings in the Early to Middle Devonian are unknown.

Keywords: sedimentology, plant taphonomy, paleobiology, paleobotany, Emsian, Eifelian.

INTRODUCTION

The Devonian marked a time of rapid diversification of vascular land plants. According to Beerbower (1985) and DiMichele and Hook (1992), increased root and rhizoid activity that accompanied

vascular land-plant diversification stabilized Devonian substrates, increased both physical and chemical weathering, and increased nutrient availability. The spread of vascular land plants also has been proposed to account for the decreased atmospheric concentration of CO₂ at the end of the Paleozoic (Berner, 1997; 1998;

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Elick et al., 1998) and the initiation of Carboniferous glaciation. Major Middle to Late Devonian marine-bottom anoxic events also are considered to be, in part, the result of Devonian land-plant radiation (Algeo and Scheckler, 1998; Algeo et al., 2001).

Despite the importance of early land plants, there have been few studies that detail their ecologic setting (e.g., Andrews et al., 1977; Gensel and Andrews, 1984; Edwards and Fanning, 1985; Griffing et al., 2000; Hotton et al., 2001). The wetland environments in which these Early Devonian land plants grew have been interpreted to range from coastal lowland marshes to terrestrial freshwater settings such as stream banks, exposed bar forms, and backwater swales (Edwards, 1980; Gensel and Andrews, 1984; Beerbower, 1985; DiMichele and Hook, 1992). On the basis of these studies, Early Devonian land-plant communities have been interpreted as consisting of an array of vegetational patches, where each was dominated by a single taxon (DiMichele and Hook, 1992). Plants in this low-diversity, patchy landscape developed a space-occupation pattern referred to as "turving in," allowing them to control access to limited nutrients and water (DiMichele and Hook, 1992).

The Trout Valley Formation has been the focus of numerous paleobotanical studies since Dorf and Rankin (1962) first described its fossiliferous character and geologic setting. They described the Trout Valley Formation as a heterogeneous mix of light-blue, gray-to-black shale, siltstone, sandstone, and conglomerate, with minor sideritic sandstone and ironstone. Fossilized plant remains occurred in thin zones of limited lateral extent. Dorf and Rankin (1962) interpreted the depositional environment as a shallow, brackish-water setting on the slope of a volcanic island.

Previous to the present work, studies focused on the morphology and anatomy of the fossil plants recovered from these rocks (Andrews et al., 1968; Gensel et al., 1969; Kasper and Andrews, 1972; Kasper et al., 1974; Andrews et al., 1977; Kasper and Forbes, 1979; and Kasper et al., 1988). Two new genera and six new species of early vascular and nonvascular land plants were identified. Locality data were given as collections along Trout Brook and, in most accounts, the actual lithology in which the specimen was preserved was not identified. The depositional context of the plant fossils was based upon Dorf and Rankin's (1962) interpretation.

The details surrounding the depositional context of the Trout Valley plant fossils must be understood because these assemblages have been used, in part, to reconstruct the stereotypical Early to Middle Devonian plant community. Without an integrated sedimentologic and taphonomic analysis, paleoecologic interpretations cannot be substantiated. Plant fossil assemblages may be preserved in both their growth position and habitat (autochthonous), in their growth environment but not in situ (parautochthonous), or as transported material out of their growth environment (allochthonous) (Gastaldo, 2001). This information is pivotal for interpreting the paleocommunities in which these fossil plants lived. There is, however, no indication in the published literature whether a certain assemblage horizon represents an allochthonous accumulation of detritus that was transported or an autochthonous assemblage that was buried in situ. Plant taphonomic studies were not envisioned when the collections

were made, and the foci of the published studies were biological, not geological. Fully integrated studies of pre-Carboniferous plant assemblages have only recently been conducted (e.g., Scheckler, 1985; Powell et al., 2000; Jarvis, 2000; Griffing et al., 2000; Hotton et al., 2001).

The project goal was to conduct an integrated examination of the sedimentologic, stratigraphic, and plant taphonomic character of the Trout Valley Formation to test the hypotheses that (1) the depositional setting of the formation was a terrestrial brackish marsh and (2) the fossil plant assemblages are autochthonous as suggested by Andrews et al. (1977).

REGIONAL GEOLOGIC SETTING AND AGE

The strata of the Trout Valley Formation are part of a thick succession of clastic rocks deposited in a foreland basin northwest of the Acadian orogen (Bradley et al., 2000). The paleolatitude was $\sim 20^{\circ}$ – 30° S in the Emsian (Scotese and McKerrow, 1990); hence, climate was presumably subtropical with pronounced wet/dry seasonality. The aerial distribution of the formation truncates major tectonic structures in the Traveler Rhyolite, and Rankin (1968) placed an unconformity between these units. The Trout Valley Formation is of latest Emsian to earliest Eifelian age based on plant fossils (Kasper et al., 1988) and palynomorphs corresponding to the *douglastownese-eurypterota* spore assemblage zone (McGregor, 1992).

STUDY AREA

The Trout Valley Formation is located in the northwest section of Baxter State Park in northern Maine, located in T6 R9, T5 R9, and T5 R10 (Frost Pond and Wassataquoik, Maine, USGS 7.5' quadrangles; Fig. 1). The present study was conducted in agreement with park officials; any and all material collected from the Trout Valley Formation is the sole property of the Baxter State Park Authority. Unauthorized collecting in the park is strictly prohibited.

The outcrop localities of Dorf and Rankin (1962) and Andrews et al. (1977) were used in field reconnaissance, and several additional outcrops not reported previously were found and described (Fig. 1). Strata are exposed along Trout Brook and South Branch Ponds Brook, and dip to the NW at 15° (Bradley et al., 2000). The longest outcrop exposure is 100 m in length. The maximum vertical extent of any particular outcrop is 7.1 m in height. Three normal faults, with a maximum displacement of 1.3 m, have been observed along Trout Brook.

METHODS

Detailed measured sections were logged and photomosaics were taken of all exposed outcrops to describe bed geometries and interpret depositional environments. Hand samples of all sedimentological and plant-bearing facies were collected for laboratory analysis. Sedimentologic analysis included standard lithologic

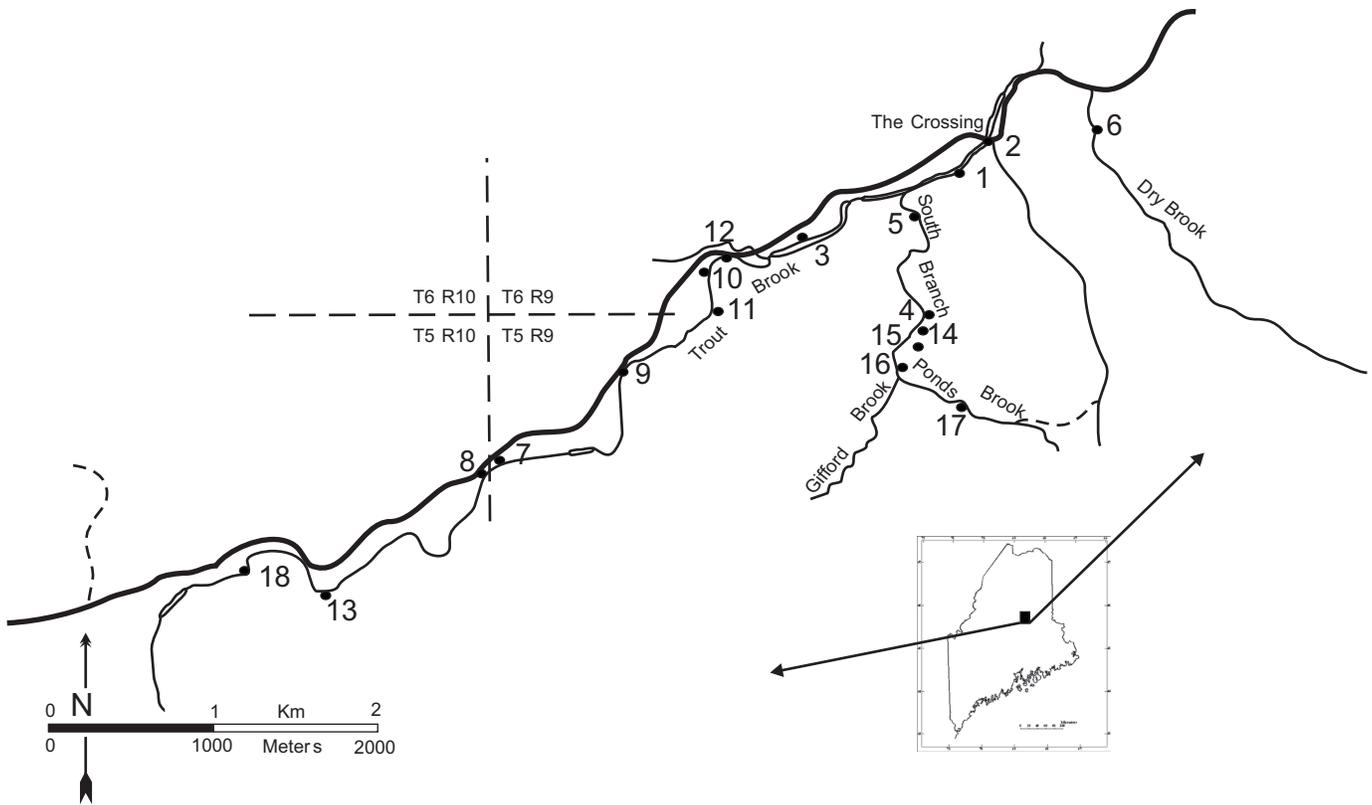


Figure 1. Map of the Trout Valley Formation and all sections in the present study (T6 R9, T5 R9, and T5 R10, Frost Pond and Wassataquoik, Maine, USGS 7.5' quadrangles). Note that minor faults have not been mapped.

identification and description of primary sedimentary structures, presence or absence of bioturbation, and thin section evaluation.

Fossil-bearing samples were split along bedding planes for taphonomic analyses using modified methods of Krassilov (1975). These include the relationships between plant material and sediments, arrangement of axes in sediment (prostrate or erect, flat-lying or dispersed three-dimensionally), concentrated or dispersed assemblages, isomeric (plant parts of one type) versus heteromeric (an array of different plant parts) part composition, ordered (plants have a “dynamic” orientation; e.g., parallel arrangement) versus disordered (plants are oriented randomly on bedding planes), examination of crosscutting relationships (between the plant parts and the matrix in outcrop and thin section), and sediment fining/coarsening sequences relative to plant axes. Thin section analysis also was used to evaluate the microstratigraphic relationships between organic debris and the entombing sediments, using both petrographic and binocular stereo microscopes.

SEDIMENTOLOGY

Seven facies are recognized in the Trout Valley Formation. Details of these facies and their depositional interpretations are given in Table 1, and their relative vertical and lateral variations are provided in Figure 2.

Facies 1—Conglomerate

Description

Facies 1 consists of an extraformational clast-supported conglomerate of ~155 m in thickness. Clasts range in size from 3 to 15 cm, are poorly sorted, subrounded to rounded, ovate to platy in shape, and entirely rhyolite in composition. The conglomerate unconformably overlies the Traveler Rhyolite (Rankin and Hon, 1987). The base of the conglomerate appears massive; however, crude meter-scale trough cross-bedding is observed in the upper part of the facies (Fig. 3). The upper portion also exhibits northwardly oriented clast imbrication.

Interbedded, lenticular dark-gray sandy siltstone occurs in the upper portion of this facies. These beds are restricted laterally and are in sharp erosional contact with overlying conglomerate beds. Siltstone lenses are 15–80 cm thick with centimeter scale undulose/wavy bedding in which plant fossils assigned to cf. *Taeniocrada* (ribbon-like axes with wavy margins) are preserved. The contact with Facies 2 is abrupt and erosional.

Interpretation

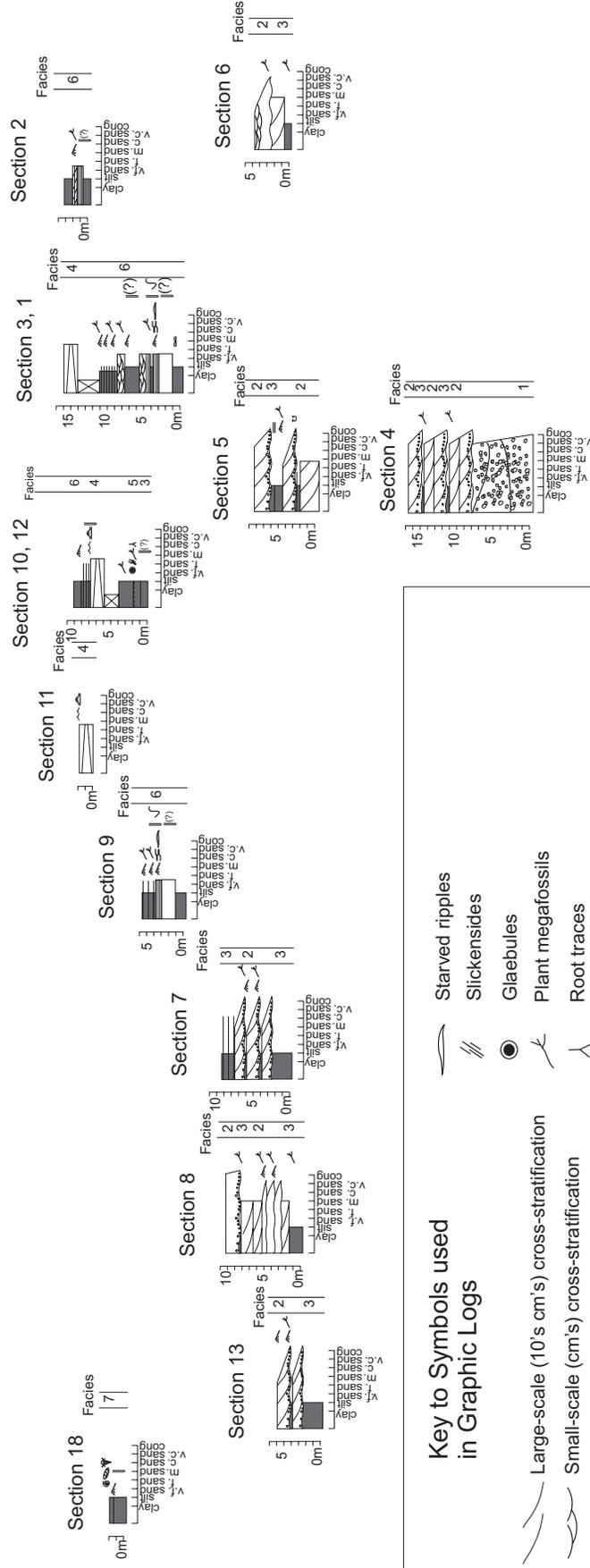
This facies is either alluvial fan or fluvial in origin. In the context of the original Dorf and Rankin (1962) interpretations, the conglomerate could represent braided channel systems

TABLE 1. SUMMARY OF LITHOLOGIC, SEDIMENTOLOGIC, AND BIOGENIC FEATURES, AND INTERPRETED DEPOSITIONAL ENVIRONMENTS OF THE TROUT VALLEY FORMATION

Facies	Lithology	Locality	Sedimentary characteristics	Fossils	Trace fossils	Depositional environment
1	Clast-supported, poorly sorted, pebble-cobble extraformational rhyolite conglomerate, upward fining with interbedded siltstone lenses	14, 15, 16, 17	Massive or crudely developed cross-bedding or horizontal stratification, imbricated clasts, siltstone lenses truncated by successive conglomerate beds.	Plant debris	N/A	Braided fluvial or alluvial fan
2	Poor-moderate sorted, sub-angular-sub-rounded, coarse-fine lithic arenites and wackes, fining-upward units <2m thick	4, 5, 6, 7, 8, 13	Channel geometries, trough cross-bedding, planar bedding, ripple cross-lamination, loading, reactivation structures	Plant axes and debris	N/A	Migrating braided channels
3	Very coarse-fine siltstone	4, 5, 6, 7, 10, 13	Laterally continuous beds, massive bedding, laminated bedding	Plant axes	N/A	Flood basin/overbank
4	Fine-medium grained quartz arenites and wackes	2, 11, 12	Lenticular geometries, ripple laminated, current modified wave ripples, hummocky cross-stratification	N/A	(?) <i>Skolithos</i> , (?) <i>Helminthopsis</i> , meniscate burrows	Storm-influenced nearshore shelf sand bars
5	Pedogenically altered medium siltstone	10	Planar bedding, slickensides, sideritic glaebules	Plant axes, apparent root traces	N/A	Protosol (incipient wetland soil horizon)
6	Interbedded fine sandstone and siltstone	1, 2, 3, 9, 10	Sheet and channel geometries; trough cross-bedding; planar bedding; climbing, wave, and starved ripples; ripple cross-lamination; low-angle cross-stratification; herringbone cross-stratification; mud cracks	Plant axes	(?) <i>Skolithos</i> , (?) <i>Helminthopsis</i> , (?) <i>Diplocraterion</i> , meniscate burrows, fecal pellet aggradations	Estuarine/tidal flats and channels
7	Coarse siltstone	18	Lenticular bedforms	Bivalves, gastropods, ostracods, a single eurypterid	N/A	(?) Tidal channels

SW

NE



Key to Symbols used in Graphic Logs	
	Starved ripples
	Slickensides
	Glaebules
	Plant megafossils
	Root traces
	Vertical (Skolithos-type, Diplocraterion) burrows
	Helminthopsis
	Gastropods
	Bivalves
	Eurypterid

Figure 2. Graphic logs of measured sections for the Trout Valley Formation based on outcrop exposures along Trout Brook, South Branch Ponds Brook, and Dry Brook, Baxter State Park, Maine. Graphic logs detail the relative stratigraphic positioning and lateral variation of outcrops. Due to the limited exposure, physical correlation is not possible except at certain locations along Trout Brook.



Figure 3. Upper portion of Facies 1—conglomerate. Arrow points to crudely developed trough cross-bedding. The best examples of this feature occur in the upper part of this facies.

entrenched in an alluvial fan complex. Modern alluvial fan channels are characterized by thick deposits in which imbricated clasts define crude bedding (Steel and Thompson, 1983; Nemeč and Steel, 1984). Vos and Tankard (1981), López-Gómez and Arche (1997), and Yagishita (1997) have described similar conglomerates as proximal fan deposits. The poor sorting and well-rounded, oblate to prolate clast shapes are features of shal-

low, gravel braided channels (Pettijohn et al., 1987; Miall, 1996), which are indicative of a braided fluvial influence.

These deposits could have been deposited in braided stream channels, alluvial fan channels, or mass flows; however, in the overall context that these were deposits from eroding highlands, a braided stream channel environment seems likely.

Facies 2—Trough Cross-Bedded Lithic Sandstone

Description

Facies 2 is in sharp, erosional contact and consists of beds of very coarse sandstone with granule clasts at the base fining upward to medium- to fine-grained sandstones. Sand clasts are sub-angular to sub-rounded and are poorly to moderately sorted. Compositionally, these sandstones are lithic arenites or wackes (depending on section), with abundant quartz and rhyolite. Interbedded siltstones are common within fining-upward cycles.

Sandstone beds are typically 1–2 m in thickness and sheetlike in overall geometry. Beds have sharp erosional bases that display loading, and are channel-form in some cases (Fig. 4). Upper contacts, where preserved, may be either a gradational or sharp contact with siltstones of Facies 3 (see description below). The fine-grained sandstone and siltstone of the overlying facies commonly are truncated by a successive fining-upward sandstone body. Locally, flame structures penetrate material overlying the upper contact.

Trough cross-bedding is the dominant internal sedimentary structure within sandstone bodies, with sets typically 0.1–0.5 m in thickness. Fossiliferous coarse siltstone displaying lenticular bedding, similar to that of Facies 1, commonly occurs in the troughs. Small-scale sedimentary structures, including trough cross-bedding (centimeter-scale), planar bedding, and ripple cross-lamination, are common at the tops of beds. Reactivation surfaces at the upper contact with Facies 3 are observed locally. Paleocurrent orientations measured from cross-beds are to the northwest (Fig. 5). Plant remains are preserved within the medium- and fine-grained sediments of Facies 2.

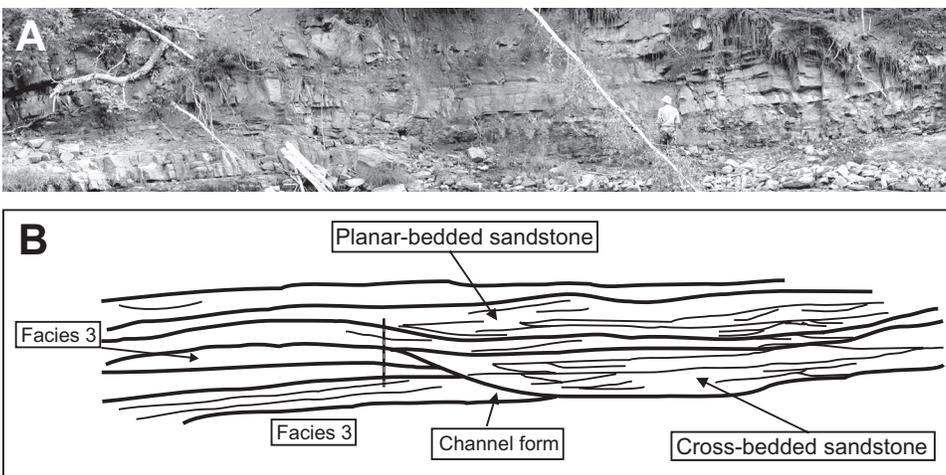


Figure 4. Typical unit of Facies 2—trough cross-bedded lithic sandstone. (A) Photomosaic showing one channel form that truncates a fining-upward sequence of cross-bedded and planar sandstone and siltstone (Facies 3—massive siltstone) along Trout Brook (section 8). (B) Line drawing illustrating bounding surfaces that are difficult to discern because of similar weathering patterns between lithotypes. Scale = 2 m.

Interpretation

The trough cross-bedded lithic sandstone represents migrating braided fluvial channels. The dominance of granule clasts within channel-form geometries indicates a high proportion of fluvial channel-lag and bar deposits similar to those described in time-equivalent settings from Schoharie Valley, New York (Bridge and Jarvis, 1998), the Battery Point Formation, Quebec (Griffing et al., 2000), and other localities (Miall, 1977, 1996).

The coarse-grained nature and low paleocurrent variance are similar to modern shallow braided channel systems (Nyambe, 1999). According to Rust (1978), the dominance of framework-supported grains is a key diagnostic feature for distinguishing braided from meandering systems. In addition, the lithic components of Facies 2 are of the same mineralogy as the clasts of the conglomerate facies, which suggests continued mechanical weathering and accumulation within a more mature braided environment than the underlying conglomerate (Facies 1). Nyambe (1999) reported a similar association in which the dominant clasts within a coarse sandstone were derived from a micro-conglomerate, indicative of a braided fluvial influence.

The relatively low variance in paleocurrent direction also is more indicative of a braidplain channel as opposed to a meandering system (Miall, 1978). This is because channel migration in the latter results in highly variable paleocurrent orientations reflecting the degree of channel sinuosity. Paleocurrent direction has been inferred to reflect mean channel direction (Rust, 1972; Chakraborty, 1999) and, as such, inferred channel axes, based on trough cross-bed measurements in this facies, were to the northwest. This orientation is toward the inferred paleoshoreline (Bradley et al., 2000). Ripple cross-lamination directed to the northwest also supports this interpretation.

Reactivation surfaces occur in the upper part of Facies 2 and may represent evidence for change in direction of discharge or environments influenced by other processes (McCabe and Jones, 1977; Weimer et al., 1982). Also, the juxtaposition of this facies fining upward into bioturbated siltstone suggests that these channels were in a coastal plain, and possibly within an estuarine-fluvial setting. Hence, this part of the interval may be transitional between fluvial and tidal environments.

Facies 3—Massive Siltstone

Description

Facies 3 consists of massive medium- to dark-gray siltstone/sandy siltstone and locally thinly interbedded very fine to fine-grained sandstone. In some instances, it is intercalated with medium-grained sandstone. Its massive appearance is attributed to the nature in which it weathers, because locally it is thinly laminated and millimeter-scale, fining-upward sequences are observed in thin section. This facies can be at least 2 m in thickness but, in many instances, it is truncated erosionally by channel-fills of Facies 2 (Fig. 4). Plant fragments are preserved throughout this lithofacies.

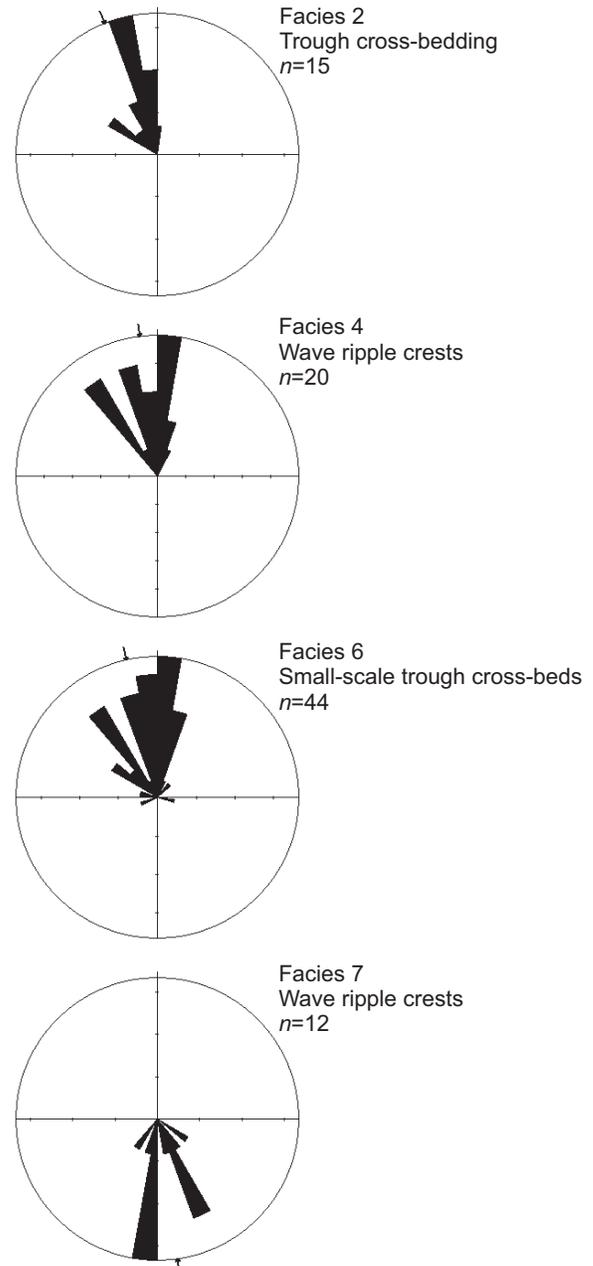


Figure 5. Rose diagrams summarizing paleocurrent data for several facies of the Trout Valley Formation. Facies 2 orientations measured from trough cross-beds; Facies 4 orientations based on measurements of wave ripples; Facies 6 orientations based on measurements from small-scale trough cross-beds; and Facies 7 orientations measured from ripple crests.

Facies 3 has either gradational or sharply bounded bases where it overlies Facies 2 (Fig. 2), as noted above, and where it is overlain by Facies 5 (section 10; see below). This facies occurs as discrete lenses in cross-bed troughs of Facies 1 and 2, but it is predominantly laterally continuous and displays a sheetlike geometry in the study area.

Interpretation

The massive siltstone is interpreted as an overbank (flood basin) environment. On the basis of its association with Facies 2 and a sheetlike geometry, these sediments were deposited in a non-channel setting. The presence of intercalated sand indicates that these clasts were deposited proximal to channel margins. The occurrence of Facies 3 as lenses in which plant fragments are preserved may represent either overbank deposits along the margin of the channel or abandoned scours of channel-fill sequences.

Facies 4—Lenticular Quartz-Rich Sandstone

Description

Facies 4 consists of subrounded to rounded, well-sorted, medium- to fine-grained quartz arenites (section 1 and 12) and wackes (section 11) that weather to a pale brown. Sandstone beds are sharply bounded, lenticular in geometry, range in thickness from 0.8 to 2.5 m, and thin laterally (Fig. 6). Beds exhibit low-angle trough forms, with ~16 m between troughs. Several troughs are filled with dark-gray siltstone preserving fragmentary remains of *Psilophyton*.

Internal structures are absent; however, the tops of these sandstone beds are ripple laminated and locally contain current-modified wave ripples and *Skolithos*-like trace fossils. Hummocky cross-stratification also is observed locally with wavelengths on the order of 10 cm between swales. Paleocurrents, based on measurements taken from wave ripples, are to the north, but vary from the northwest to the northeast (Fig. 5).

Interpretation

These quartz-rich sandstones are interpreted as nearshore storm-influenced shelf sand bars. Their thin lenticular nature, lithologic composition, bioturbated bed tops, minimal amount of terrestrial detritus, and *en echelon* arrangement are consistent with reported nearshore deposits (Reineck and Singh, 1980; McCubbin, 1982; and others). Measured paleocurrents toward the north and northeast differ from the underlying lithic sandstone facies and indicate sediment transport parallel to the inferred shoreline (Bradley et al., 2000). Northeast paleocurrents suggest that these sand bars migrated laterally across the shelf and possibly shoreward. However, the absence of shoreface deposits precludes an interpretation of onshore sand-wave migration.

These sandstones are compositionally more mature and better sorted than others in the formation, which suggests that the depositional environment was exposed to wave reworking. The absence of internal bedding structures, the presence of modified ripples at bed contacts, and hummocky cross-stratification at the upper bed contacts are consistent with storm deposition above wave base (Dott and Bourgeois, 1982; Aigner, 1985; Nottvedt and Kreisa, 1987; Collinson and Thompson, 1989; Duke et al., 1991).

Facies 5—Pedogenically Altered Siltstone

Description

Facies 5, present only at section 10 (Fig. 2), consists of 10 cm of dark-gray siltstone. This lithology is similar to Facies 3; however, there are several important differences. Pedogenic features, including slickensides, and thin, organic structures oriented vertically downward, are present. Aerial debris of *Psilophyton* is concentrated within the upper few centimeters of the bed. Petrographic analysis shows the presence of geopodally oriented organic structures and sideritic glauconites, ranging from 0.5 to 1.5 mm in diameter (Fig. 7). These features have been observed only within this facies.

Interpretation

The slickensides, sideritic glauconites, concentrated plant debris, and vertically oriented axes, possibly roots, are indicative of a paleosol. Sideritic nodules are characteristic of permanently waterlogged soils (Altschuler et al., 1983; Moore et al., 1992). The presence of iron carbonates is a potential product of original soil formation (Ludvigson et al., 1998) and, as such, this paleosol is best described as a protosol (Mack et al., 1993) based on the characteristic features and poorly developed horizonation (see Plant Taphonomy).

Facies 6—Bioturbated Interbedded Sandstone and Siltstone

Description

This facies consists of coarse siltstone and interbedded fine- to very fine grained sandstone. Siltstones are heavily bioturbated, with *Helminthopsis*-like traces preserved within the upper portions as well as burrows and fecal pellets observed in thin section. Locally, the upper 18–30 cm are massive siltstone alternating

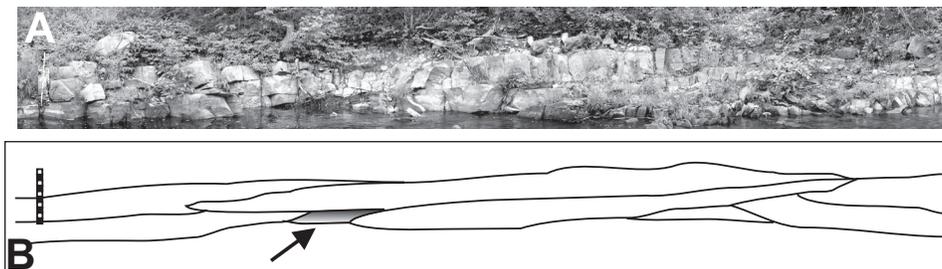


Figure 6. Photomosaic of section 11 where Facies 4 (lenticular quartz-rich sandstone) is best exposed. This lithofacies consists of *en echelon* stacked lenticular bodies of quartz arenites (section 11) or quartz wackes (section 10). Arrow points to a siltstone lens. Scale at left = 1 m.

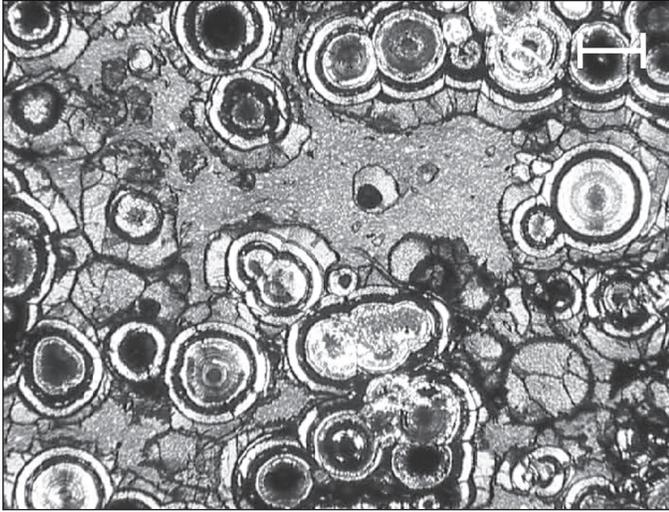


Figure 7. Sideritic glauconites, 0.5–1.5 mm in diameter, occur in Facies 5 (pedogenically altered siltstone; section 11). These structures are indicative of original reducing conditions. Scale = 1 mm.

with ripple cross-stratified siltstone (1–6 cm thickness). Mud-cracks also are preserved at one locality.

The contacts with sandstone beds are sharp and bed thickness ranges from 0.2 to 1 m. Sandstones are heavily bioturbated and structureless, planar bedded, or trough cross-bedded. Their upper surfaces display ripple cross-lamination, symmetrical ladder ripples, starved ripples, and climbing ripple stratification (Fig. 8). Trace fossils are also common at the tops of planar-bedded sandstone. Traces (Fig. 9) include vertically compressed burrows averaging 5 mm in diameter (?*Skolithos*) and, in some instances, appear paired (cf. *Diplocraterion*). Burrow densities are high, with an average of 120 burrows per 10 cm². Horizontal traces, ~2 mm in diameter (?*Helminthopsis*), are less common in mud drapes.

These rocks typically display a sheetlike geometry that is laterally continuous over at least 100 m. At several sections (1, 3), this facies occurs in channel-forms (Fig. 10). Channel geometries measure 6 m in width and 0.5 m in depth, and are stacked *en echelon*. Here, bioturbated siltstone is overlain by low-angle cross-stratified (~10°) sandstone and interbedded ripple cross-laminated siltstone. A fossiliferous rippled siltstone of variable thickness occurs at the top of these channel fills (Fig. 11). Fossils are restricted to the rippled siltstone and include cf. *Taeniocrada*, *Psilophyton forbesii*, *P. princeps*, *P. sp.*, and *Kaulangiophyton akantha*. Possible herringbone cross-stratification is present at one locality; however, it is truncated by an overlying sandstone bed, making identification of this structure equivocal. Due to reworking of ripples and obfuscation of ripple crests, only one paleocurrent measurement to the southeast was taken. Overall paleocurrent direction for this facies, based upon small-scale trough cross-beds, varies from northwest to northeast (Fig. 5).

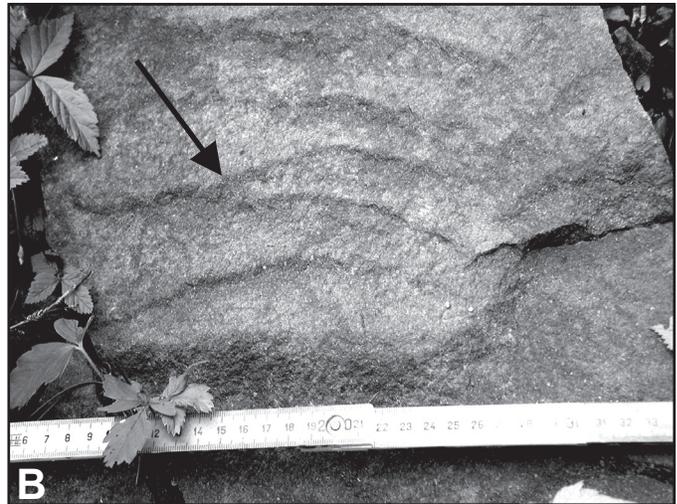
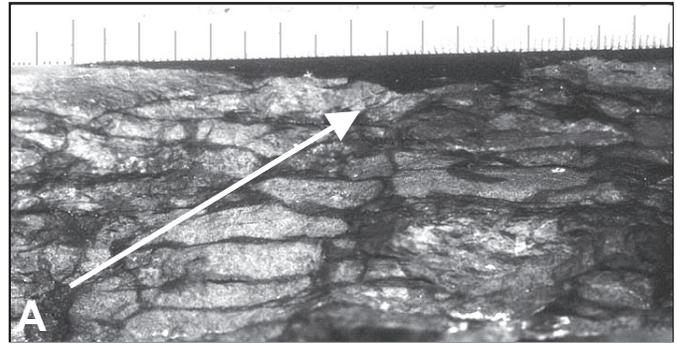


Figure 8. Sedimentological features of Facies 6—bioturbated interbedded sandstone and siltstone. (A) Cross section of siltstone in which climbing ripples can be seen. Arrow points to the direction of climb. Scale in cm. (B) Bedding surface exposure of very fine sandstone/coarse siltstone showing ladder ripples. Arrow shows “Y” split. (section 9); scale in cm. (C) Thin section in which micro cross-stratification is preserved in very fine sandstone to coarse siltstone. Scale = 1 mm.

Interpretation

This bioturbated and interbedded facies is interpreted as a coastal setting, probably within an estuarine intertidal flat. The sediments are fine grained, including very fine sand and coarse silt. Primary and biogenic structures and the lateral extent of beds are similar to intertidal deposits reported from the North Sea (Weimer et al., 1982) and other areas (van Straaten, 1954;

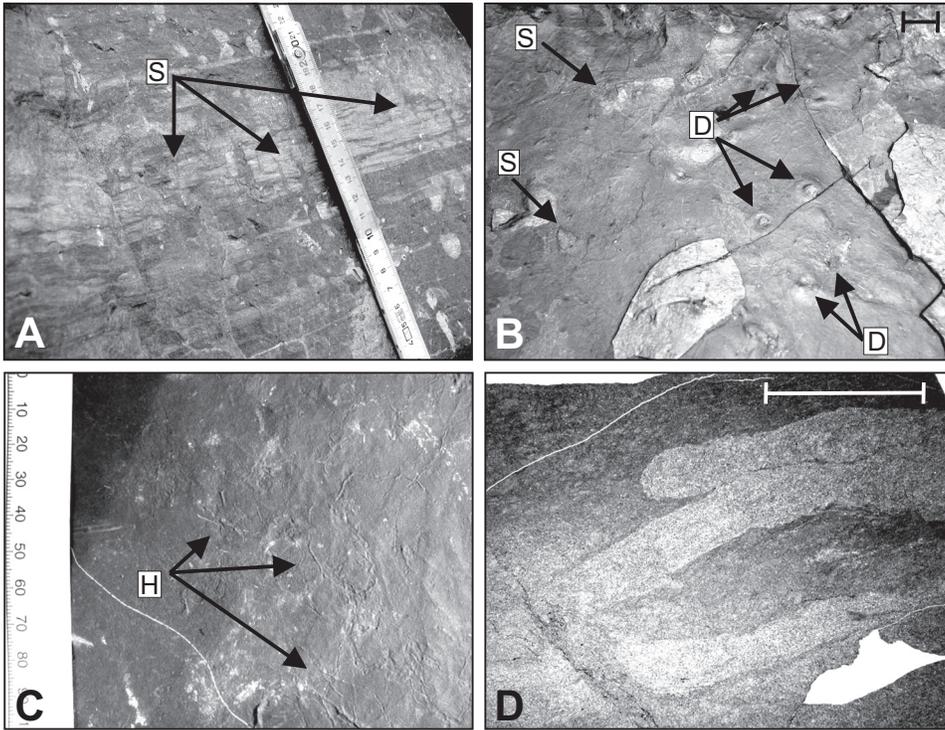


Figure 9. Trace fossils within Facies 6—Bioturbated interbedded sandstone and siltstone. (A) *Skolithos* (S) on vertical surface exposure at section 1. Scale in cm. (B) *Skolithos* (S) and ?*Diplocraterion* sp. (D) on bedding surface of a homogenous siltstone, section 9. Scale = 1 cm. (C) Horizontal traces, ?*Helminthopsis* (H), on bedding surface of homogenous siltstone, section 9. Scale in mm. (D) Thin section of homogenous siltstone in which infilled burrow system can be seen. Scale = 1 cm.

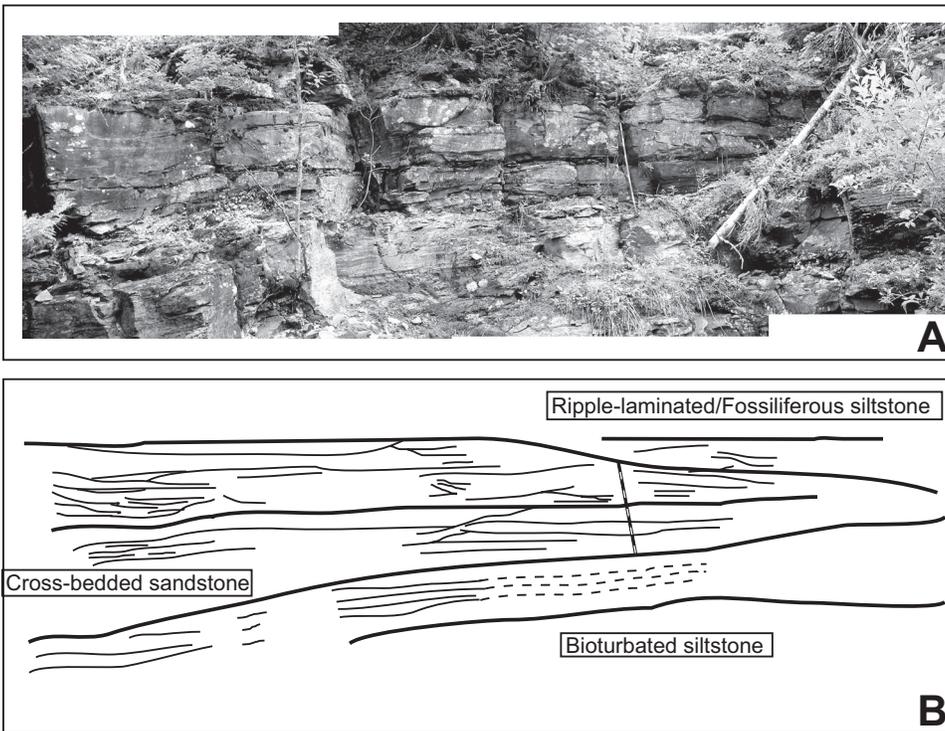


Figure 10. Facies 6—bioturbated interbedded sandstone and siltstone. (A) Photomosaic of this facies occurring as channel geometries (section 1). (B) Line drawing interpretation detailing the characteristic broad and shallow channel geometries. Scale = 1 m.

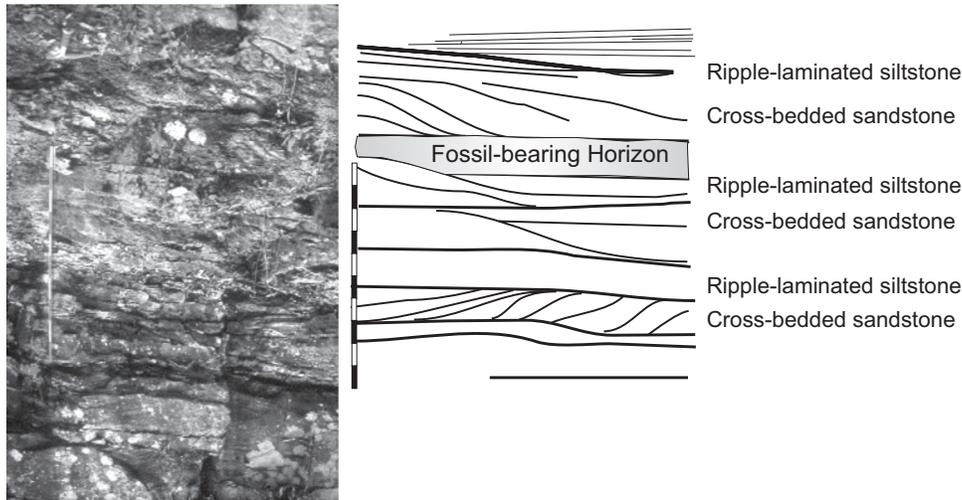


Figure 11. Alternating beds of cross-stratified sandstone and ripple-laminated siltstone in Facies 6 channel fills (section 1). Plant-bearing horizons occur within ripple-stratified beds found at the top of channel-fill sequences. Scale = 1 m.

Baldwin and Johnson, 1977; Reineck and Singh, 1980; Clifton, 1982; Terwindt, 1988). The absence of a macrofauna, the high degree of bioturbation, and dominance of *Skolithos*-type ichnofacies in the coarse siltstone/fine sandstone are typical of deposits in coastal areas such as tidal flats (Miller 1984; Miller and Woodrow, 1991; Bridge and Jarvis, 1998; Griffing et al., 2000).

Parallel and tabular cross-stratified beds adjacent to channel forms are interpreted as channel-bank deposits associated with shallow migrating tidal channels. In turn, these structures are overlain by tidal-flat deposits. Other evidence supporting a tidal-flat setting includes the presence of starved ripples (Singh and Singh, 1995) as well as ladder and wave-modified ripples, indicative of sedimentation during tidal slack water.

A tidal channel environment is interpreted for Facies 6 where channel-form features are found. Channel-form geometries characterized as broad (up to 6 m) and shallow (0.5 m) and *en echelon* stacked, as well as possible herringbone cross-stratification indicating bi-directional flow, is evidence for this type of setting (Boothroyd, 1985; Singh and Singh, 1995). The alternating nature of parallel-bedded siltstone, grading into alternations of cross-stratified sandstone and rippled siltstone from channel to channel, represents the changes in hydrodynamic conditions from higher flow velocities and open channels to lower flow velocities following channel filling. The presence of well-preserved plant axes, ranging from small (1–2 mm) fragments to large (19 cm) entire plants in the ripple-laminated, final stages of channel fill suggests detritus originated via erosion of the tidal channel margin during bank undercutting (see discussion).

Facies 7—Bioturbated Siltstone

Description

Facies 7 is restricted to one isolated locality exposed only at low water (Figs. 1, 2). It consists of dark-gray bioturbated coarse siltstone/very fine sandstone. Beds are lenticular in geometry

with wavelengths of 6 m and a maximum thickness of 17 cm. Beds thin laterally and wave ripples are preserved at the contact between beds. Numerous dispersed macroinvertebrates, including bivalves, gastropods, ostracods, and a eurypterid, are preserved as impressions beneath bed-form crests. Paleocurrents measured from the wave-ripple crests are oriented to the south (Fig. 5).

Interpretation

The bioturbated siltstone facies records the migration of megaripples within a tidal channel. Megaripples are a common structure within tidal or tidally influenced channels (Boersma et al., 1968; Reineck and Singh, 1980; Terwindt, 1981). The presence of marine and brackish macroinvertebrates, including *Phthonia sectifrons* and the eurypterid cf. *Erieopterus* sp., in the crests of ripples indicates that these animals were transported into these channels and concentrated at megaripple crests (Selover et al., 2005). The concentration of shelly detritus within megaripple crests, rather than in the troughs, supports an interpretation emplacement during a high-energy event. Southward-directed paleocurrents are opposite to those measured in the underlying facies, and suggest a flood-dominated or possibly storm-influenced depositional event(s). The transition from this fossiliferous, megarippled siltstone into overlying bioturbated siltstone records the transition from high- to relatively low energy deposits (Miller and Woodrow, 1991). The bioturbated siltstone may have been reworked at the margins of these channels.

PLANT TAPHONOMY

Twelve plant taxa are reported from the Trout Valley Formation (Table 2). Megafossils are preserved in all facies, with concentrated assemblages occurring within Facies 2 (trough cross-bedded lithic sandstone), 4 (lenticular quartz-rich sandstone), and 6 (bioturbated interbedded sandstone and siltstone). Trimerophytes (*Pertica* and *Psilophyton*) are the most common components of all

TABLE 2. ASSOCIATION OF PLANT REMAINS AND FACIES IN THE TROUT VALLEY FORMATION BASED ON RESULTS OF ANDREWS ET AL. (1977), KASPER ET AL. (1988), AND THIS STUDY

Plant Megafossils	Facies						
	1	2	3	4	5	6	7
	Fluvial			Estuarine			
Thallophytes							
<i>Prototaxites</i> sp.*	X*						
Embryophytes							
<i>Sciadophtyon</i> sp.*						X*	
Bryophytes							
<i>Sporongonites</i> sp.*						X*	
Rhyniophytes							
<i>Taeniochrada</i>	X	X				X	
Trimerophytes							
<i>Pertica quadrifaria</i>		X	X			X	
<i>Psilophyton dapsile</i>						X	
<i>P. forbesii</i>		X	X		X	X	
<i>P. microspinosum</i> *						X*	
<i>P. princeps</i>		X					
<i>Psilophyton</i> sp.		X	X		X	X	
Lycophytes							
<i>Drepanophycus gaspianus</i>		X				X	
<i>Drepanophycus</i> sp.		X					
<i>Kaulangiophyton akantha</i>						X	
<i>Kaulangiophyton</i> sp.						X	
<i>Leclercqia complexa</i> *		X*				X*	
<i>Leclercqia</i> sp.			X			X	
						X	
Unidentified		X	X				X

*Reported by other authors, but not found in present study.

plant assemblages. Associated floristic elements, such as rhyniophytes and lycophytes, either constitute a minor component (a few fragmented individuals) of any one assemblage or are absent. As a result, assemblage characteristics and the following discussion are focused mainly on trimerophytes.

Facies 1

Plant-bearing intervals occur in the upper part of the conglomerate facies where fine-grained deposits are found near the contact with the overlying trough cross-bedded lithic sandstone (Facies 2; Fig. 2). Plant remains occur in the troughs of cross-beds preserved in lenticular bodies of dark-gray, coarse siltstone that pinch out laterally across a distance of a few meters (Fig. 12A). Compressions of cf. *Taeniochrada* sp. dominate at section 4 (Fig. 12B) with *Psilophyton* sp. and cf. *Taeniochrada* on some bedding planes. Both homogeneous and heterogeneous assemblages occur in these channel fills. Plants are moderately well preserved fragments, ranging in size from 5 to 20 mm on the

surface of bedding planes. Axes are oriented randomly and concentrated at the base of siltstone lenses (~15 cm in larger lenses) and become increasingly dispersed upward.

Facies 2

Plant assemblages are preserved in coarse-to-medium sandstone that fines into siltstone and can be traced laterally for meters across outcrop at sections 5, 7, 8, and 13. Different taxa are preserved at different stratigraphic horizons. *Pertica quadrifaria* is common at the base of plant-bearing intervals. Fragments average 13 cm in length, but axes as much as 50 cm in length have been collected (Fig. 13A). Plants consist of both main and lateral axes (some specimens display second-order dichotomizing branching) that occur parallel to bedding. Primary axes of *Pertica* from a single locality are preserved in random orientations (Fig. 13B). The concentration and diversity of axes increases upward as the sediment fines to medium-fine sandstone. *Psilophyton* sp., *P. princeps*, and, to a lesser degree, *P. forbesii* dominate the upper

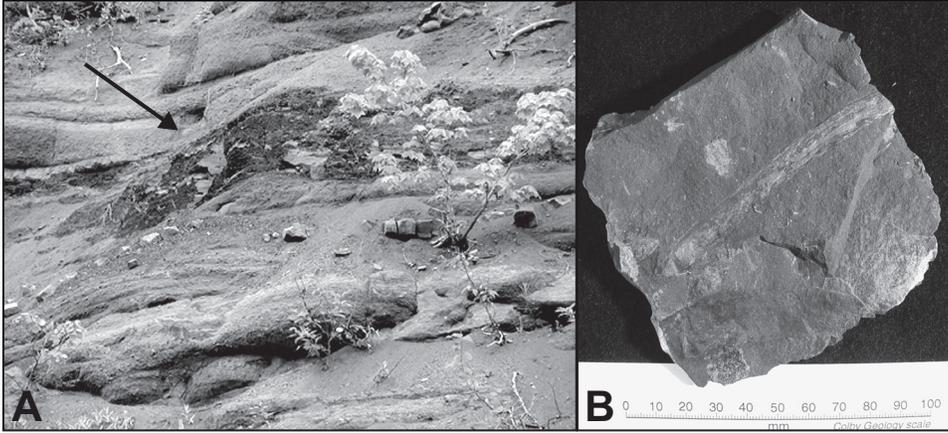


Figure 12. Plant fossil assemblages of Facies 1—conglomerate. (A) Fossiliferous siltstone lens (15 cm in thickness) intercalated within the conglomerate. Picture occurs in the upper part of this facies. Note overlying conglomerate truncates siltstone lens at arrow. (B) Typical feature of cf. *Taeniocrada*-dominated assemblages recovered from siltstone lens. Scale in mm.

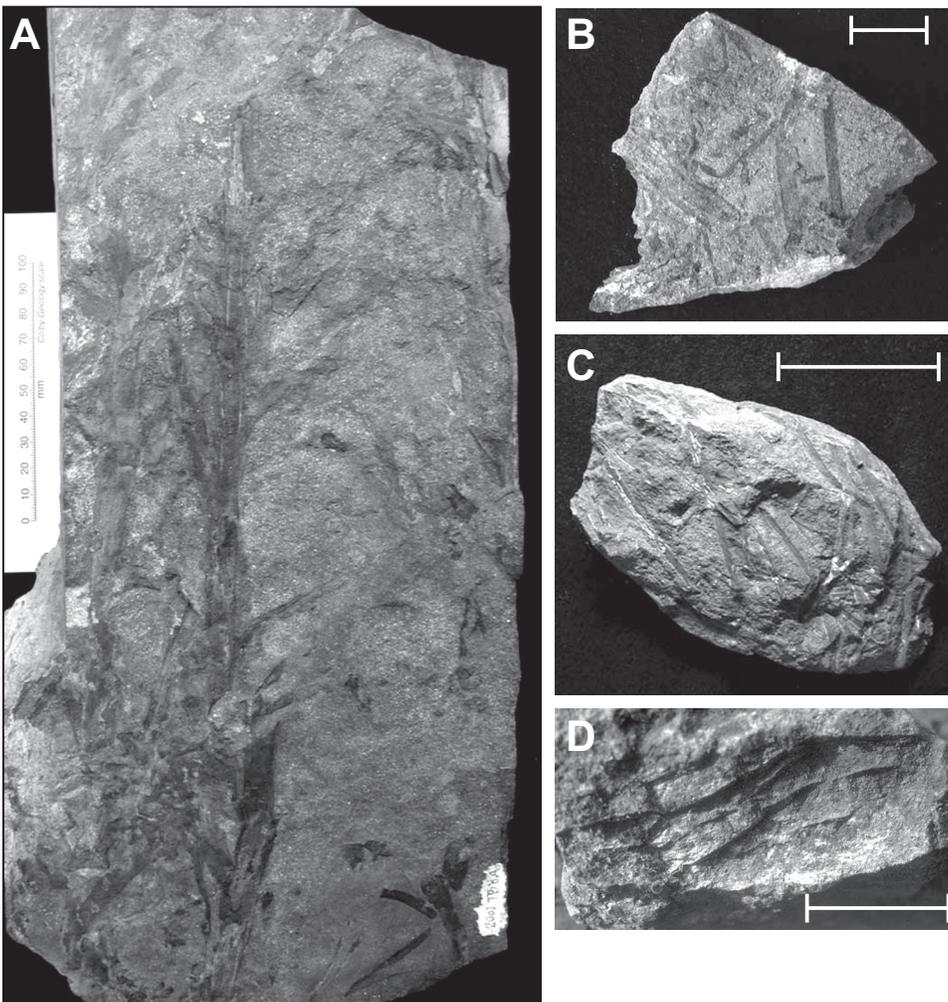


Figure 13. Plant macrofossils from fluvial facies (Facies 2, 3). (A) Large main axis with lateral axes assigned to *Pertica quadrifaria* preserved in fine sandstone (locality 12). Scale in mm. (B) Fragmented main axes and laterals of *P. quadrifaria* in very fine sandstone/coarse siltstone intercalated with medium sandstone. These features are typical of assemblages found at the base of plant-bearing intervals. Scale = 2 cm. (C) Fragmentary nature of most plant axes recovered from fluvial facies. Scale = 2 cm. (D) Axes of *Psilophyton* sp. that crosscut bedding in upper part of plant-bearing fluvial intervals. Inclined axes are not indicative of in situ burial (see text for explanation). Scale = 2 cm.

portions of plant assemblages within this facies (*Drepanophycus* sp. at section 5), and are best preserved in medium-fine sandstone. Axial fragments, 1–13 cm long, occur as disordered assemblages and are restricted to bedding planes (Fig. 13C). Sandstones fine upward into siltstones of Facies 3 where the number of *Pertica quadrifaria* and *Psilophyton* sp. axial remains decreases.

Facies 3

Plant assemblages in the massive siltstone facies typically are disordered and consist of fragmented *Psilophyton* sp. axes. However, dense, matlike concentrations of *Pertica* and *Psilophyton* axes occur in coarse siltstone intercalated with medium-fine sandstone ~40 cm above a non-fossiliferous interval (section 5). Here, axes are concentrated, disordered, heteromeric, and typically flat-lying. However, some axes crosscut bedding at angles ranging from 10° to 35° (Fig. 13D). This interval is truncated by

a coarse channel sandstone of Facies 2. *Pertica quadrifaria* is preserved parallel to bedding above these matlike concentrations, similar to assemblages previously described from the trough cross-bedded lithic sandstone (Facies 2).

Millimeter-scale plant fragments are dispersed throughout the matrix, with orientations ranging from horizontal to sub-vertical in thin section. Plant material is typically concentrated in medium-to-fine sandstone and coarse siltstone, but in thin section occurs in both the coarse and fine fractions of micro-fining-upward sequences. Plant detritus overlies the contact between fine and coarse sediments (Fig. 14A, 14B). In several thin sections, sediment grains are observed to have migrated within bedload over flat-lying plant material, creating a scour surface on the down-current side of plant detritus that was filled subsequently with finer sediment (Fig. 14C). Plant material also is observed as casts, with axes filled with fine mud and silt (Fig. 14D). Several axes are contorted and overlie ripple crests (Fig. 14E).

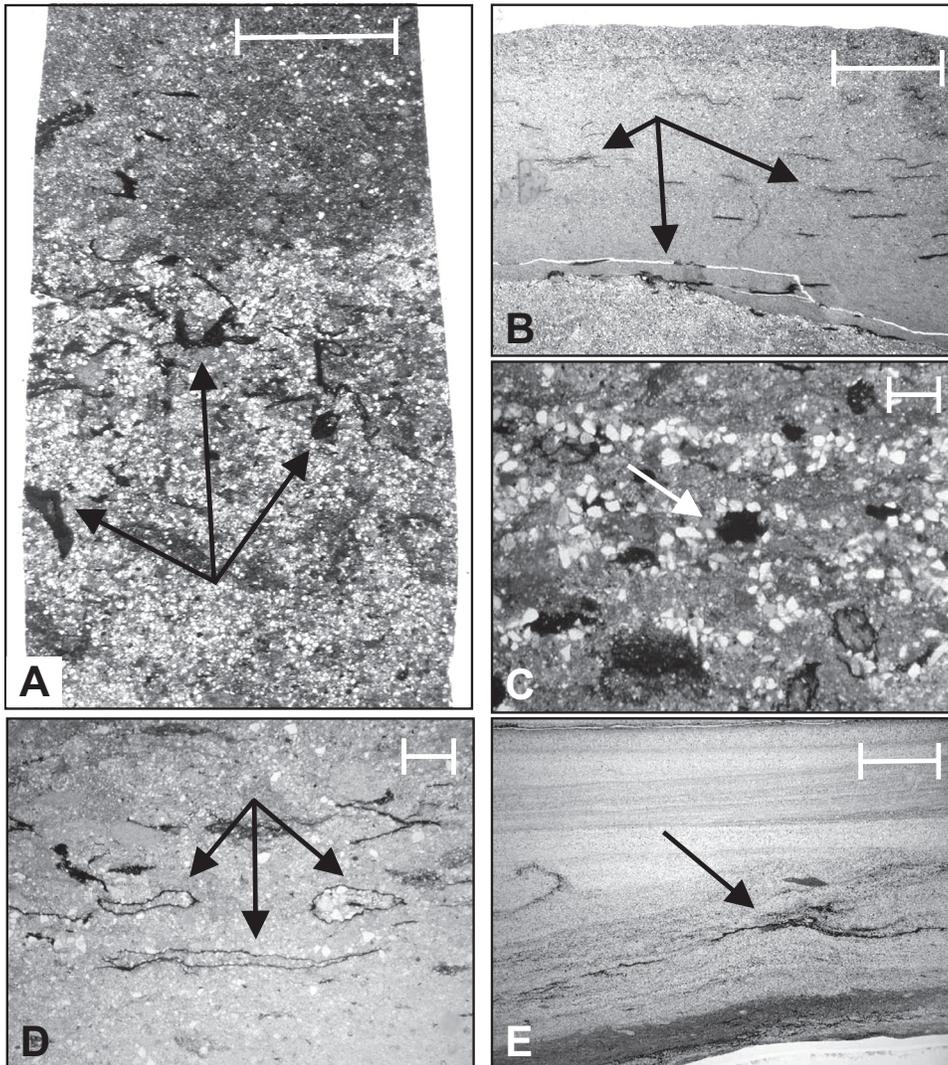


Figure 14. Photomicrographs of plant-bearing intervals in fluvial assemblages. (A) Dispersal and arrangement of plant matter in fining-upward sequence typical of Facies 3. Plant material (arrows) are oriented variously within both the coarse and fine sediment intervals. Scale = 1 cm. (B) Plant debris (arrows) oriented parallel to bedding and concordant with the contact between the coarse and fine sediments. Plant axes also are oriented parallel within the fine sediment interval. Scale = 1 cm. (C) Axis at arrow shows individual silt clasts that were transported over the plant material, scouring the downstream side. Scale = 1 mm. (D) Plant axes of *Psilophyton* sp. (arrows) that are infilled with coarse silt, indicating that axes decayed and were hollow prior to deposition and burial. Scale = 1 mm. (E) Contorted plant axis (arrow) that overlies a primary ripple structure, indicating settling from suspension load following a decrease in discharge. Scale = 1 cm.

Facies 4

Plant remains occur as sparse, fragmentary, disordered axes of *Psilophyton* sp. preserved within one lens of siltstone of the lenticular, quartz-rich sandstone. This assemblage is not mentioned in the later generalized taphonomic discussion.

Facies 5

Plant-bearing horizons at section 11 are similar to those at section 2 (Facies 6; Fig. 1). Plant remains are very concentrated, disordered, and isomeric within a 25 cm interval. The assemblage is dominated by *Psilophyton* sp. (?*P. princeps*), with minor contributions from *P. forbesii*. Aerial axes are inclined upward and crosscut bedding, whereas positively geopedal, vertically oriented structures, smaller in size than associated axes, crosscut the siltstone. These are interpreted as rooting structures (see Discussion), and this is the only location where possible original (primary) rooting is observed (recent roadwork near Trout Brook has exposed another paleosol horizon which has not been evaluated, to date. R.A. Gastaldo, September 2005, personal observation). Aerial detritus overlies this possible rooting horizon. The megaflores are associated with sideritic glauabules (Fig. 7) in the upper part of this plant-bearing interval. Several positive geopedal structures, also interpreted as roots, occur in oriented thin section and crosscut bedding into the subjacent coarser sediment (Fig. 15).

Facies 6

Here, plant remains occur in coarse siltstone that underlies planar-bedded, very coarse siltstone or very fine sandstone. Plant intervals vary in thickness, ranging from 10 to 40 cm. *Psilophyton forbesii* and cf. *Taeniochrada* axes are preserved at the base of these beds and are dispersed within the matrix. Axes are primarily in random orientations and several *Taeniochrada*-like axes, restricted to the basal intervals of the siltstone, show three-dimensional curvature. *Psilophyton microspinosum*, although not abundant, occurs in association with cf. *Taeniochrada* in the coarse siltstone. Axes are dispersed at the base of the beds and become more concentrated upsection, with fragments parallel aligned and restricted to bedding planes.

Plants occur in planar siltstone below tabular cross-stratified beds at section 2 (Figs. 1, 2). Above the contact, *Psilophyton* sp. occurs as relatively sparse, flat-lying axes in an interval ~14 cm in thickness. A maximum of four, dense matlike intervals overlie this dispersed assemblage and consist of axial concentrations of *P. forbesii*, *P. dapsile*, *P. princeps*, and *Pertica quadrifaria*. Each interval varies from 1.5 to 3 cm in thickness and preserves a disordered plant assemblage. Each layer, however, is separated from the overlying assemblage by 2–7 cm of non-fossiliferous siltstone. Inclined axes (10° to 45°) originate from flat-lying axes and can be traced across bedding for several centimeters (Fig. 16A). Axes also vertically crosscut bedding and, in some instances, small axes (0.2–1.5 mm in width) crosscut bedding in

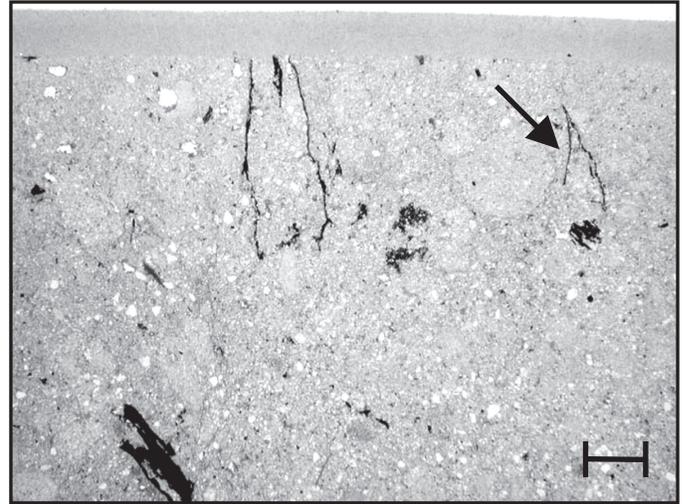


Figure 15. Geopedally oriented rootlike axes in estuarine Facies 5. Apparent roots on right display well-defined bifurcation and are similar to those illustrated in Figure 16. Scale = 1 mm.

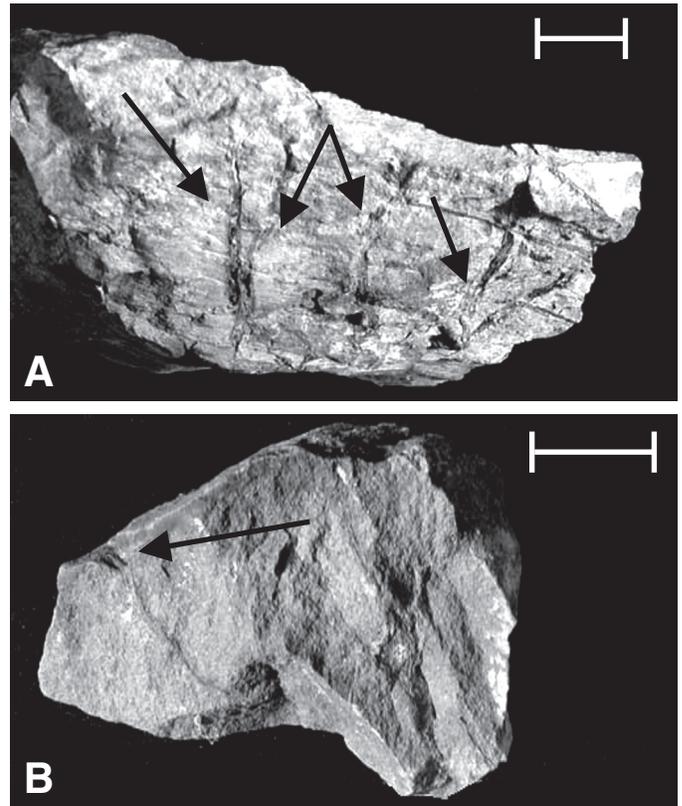


Figure 16. Plant macrofossils from estuarine Facies 6—bioturbated interbedded sandstone and siltstone. (A) Oblique view of inclined *Psilophyton* axes penetrating bedding. (B) Naked, sigmoidal small axis extending down from bedding surface. Scales = 2 cm.

a sigmoidal orientation (Fig. 16B). *Pertica quadrifaria* is concentrated at the base of the matlike accumulations without preferential orientation; this taxon becomes rare in stratigraphically higher beds. Orientations of *Psilophyton forbesii* and *P. dapsile* become more ordered in the uppermost matlike accumulations and approach parallel orientation. Axial orientations range from 50° to 266°, with predominant north and northwest directions. These vectors are similar to paleocurrent measurements based on trough cross-beds within this facies (Fig. 5).

In thin section, plant material is scattered within the coarser silt with up to several millimeters of matrix separating stratigraphically successive axes. Plant material is relatively concentrated in the fine silt where less than 15 mm of sediment is found between overlying axes. Plant material is parallel to bedding, and generally parallels the bedding contact between the coarse and fine silt in millimeter-scale fining-upward sequences (Fig. 17A). Several axes appear to be sub-horizontal relative to bedding, although they overlie small-scale, poorly defined cross-lamination (Fig. 17B). Contorted axes occur in both coarse and fine intervals.

Remains of *Psilophyton forbesii* are well preserved in concentrated, monotypic, isomeric assemblages in channel-form geometries, where observations were limited to bedding surface exposures on 0.5 m² float blocks. Axes are concentrated throughout the rippled siltstone intervals of channel fills and occur parallel to each other on every bedding surface (Fig. 18), although successive bedding surfaces display different axial orientations. Each plant-bearing interval, generally 2–3 cm in thickness, is

overlain by barren ripple-laminated siltstone that is 3–5 cm in thickness. Primary structures in these unfossiliferous intervals include bi-directional, ladder, and current-modified ripples. Plant-bearing beds are restricted to the troughs of meso-scale bedforms on the order of 30 cm in wavelength with no indication that plants extend into waveform crests. While *P. forbesii* is the dominant, and at times the only, taxon present, *Psilophyton* sp., *P. princeps*, cf. *Taeniochrada* sp., and *Kaulangiphyton akantha* also occur (Table 2).

Thin section analysis of samples from section 1 shows plant axes in various orientations. Plant material may be distorted and recurved, and associated with soft-sediment deformation. Detritus typically occurs at the top of fining-upward sequences. There is evidence of coarse silt migration over several plant axes (? lateral axes), creating a scour surface on the down current side of the organic remains (similar to Facies 2). Apparent rooting structures, originating from flat-lying axes, vertically crosscut bedding, and these organically stained structures disrupt bedding (Fig. 17C). Three different horizons of possible rooting structures occur in a series of fining-upward sequences, with each originating from the top of the sequence (Fig. 17D).

Facies 7

Plant remains in the bioturbated siltstone facies are small, <1 cm in greatest dimension, and occur only as isolated fragments. Because of their fragmentary nature and poor preservation, systematic identification is not possible. Axes show no preferential

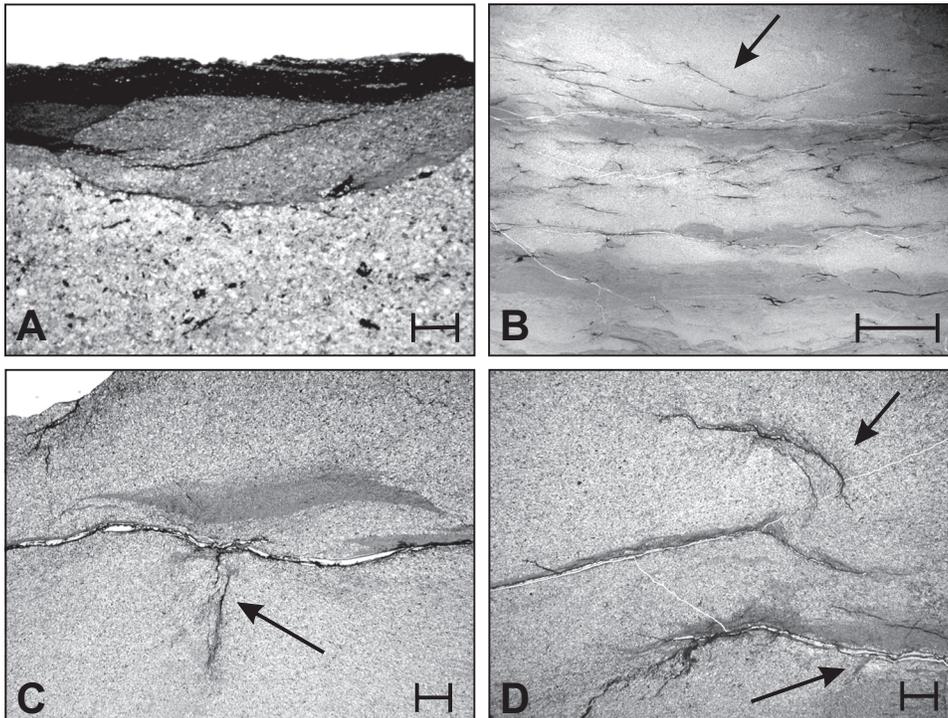


Figure 17. Photomicrographs of plant-bearing intervals in estuarine Facies 6—bioturbated interbedded sandstone and siltstone. (A) Plant material paralleling bedding contact between coarse and fine silt fraction. Scale = 1 mm. (B) Sub-horizontal axes (arrow) overlying poorly defined ripple-lamination. Scale = 1 cm. (C) Possible rooting structures originating from flat-lying aerial axes of *Psilophyton*. Rooting structures (at arrow) disrupt bedding below a starved ripple. Scale = 1 mm. (D) Three fining-upward sequences in which possible rooting structures can be seen originating from flat-lying aerial axes (at arrows). Scale = 1 mm.

orientation, are parallel to bedding, and are found only beneath the crests of bedforms that constitute the major geometry of this unit.

DISCUSSION

From the extensive investigation of plant morphology and anatomy (Andrews et al., 1968; Gensel et al., 1969; Kasper and Andrews, 1972; Kasper et al., 1974; Kasper and Forbes, 1979; and Kasper et al., 1988), Andrews et al. (1977) interpreted the Trout Valley plant assemblages as having been preserved in a terrestrial brackish or freshwater marsh setting surrounded by modest elevation. Using the dense, parallel-aligned assemblages of *Psilophyton* in the bioturbated interbedded sandstone and siltstone (Facies 6, this study), the dominance of a single taxon in many collection sites with relatively few accessory taxa, isolated pockets of single taxa, the high preservational quality of plant remains, and modern (marsh) analogues, Andrews et al. (1977) concluded that these Early to Middle Devonian assemblages represented monotypic, low-diversity wetland communities. The presence of parallel-aligned axes was used to interpret dense stands of plants that periodically were flattened and preserved in situ by floodwaters (Andrews et al., 1977). This interpretation has been propagated as an archetypical model for plant burial in the Devonian, and has been cited by various authors when interpreting the paleoecological significance of early land plants (Edwards, 1980; Gensel, 1982; Gensel and Andrews, 1984; Edwards and Fanning, 1985; Gensel and Andrews, 1987; Kasper et al., 1988; DiMichele and Hook, 1992; Hotton et al., 2001).

The present study has identified a range of continental to nearshore marine environments wherein well-preserved plant debris was restricted primarily to two environments: fluvial (Facies 2, 3) and estuarine/tidal (Facies 6) settings. Within these settings, only one interpreted autochthonous assemblage is identified (Facies 5). Nevertheless, many in situ plant communities must have been present to have supplied abundant axes preserved in these rocks.

Plant Taphonomy in Fluvial Assemblages

The plant taphonomic data indicate that all plant assemblages within fluvial environments are allochthonous. The quality of preservation, degree of fragmentation, and arrangement of axes are all characteristic of transported plant assemblages (Bateman, 1991; Behrensmeyer and Hook, 1992; Gastaldo et al., 1995, 2005).

The plant-bearing intervals within fluvial facies are thin (a few centimeters in thickness), laterally continuous over several meters, and stratified with respect to plant size. Larger plant fragments occur at the base of the assemblages and decrease in size upward through the plant-bearing interval. Plants are found primarily flat-lying, with few axes oriented at some angle to bedding. This stratification is a reflection of settling characteristics of the various-sized plant detritus from suspension during waning flow. As overbank velocity decreased, the larger and denser detritus, such as *Pertica quadrifaria* axes, settled first; these were followed



Figure 18. Parallel-oriented axes of *Psilophyton forbesii* in estuarine Facies 6—bioturbated interbedded sandstone and siltstone. These plants are typical of previously reported collections (e.g., Andrews et al., 1977). Plant fossil assemblages are restricted to the ripple-laminated intervals in the uppermost parts of interpreted tidal channel fills (see Fig. 10). Scale in cm.

by the smaller *P. quadrifaria* and *Psilophyton* sp. axial fragments. Plant parts are parallel to bedding unless the axes retained their structural fidelity and three-dimensional architecture. In the latter case, axes then may be oriented subhorizontal to bedding.

The presence of interbedded medium sandstone throughout these plant intervals, occurring with both large and small axes, indicates that flood-stage velocities fluctuated. Plant assemblages are dominated by axial components deposited within both channels and overbank settings during high-flow events.

The orientation of plant material that crosscut bedding is not believed to be a response to burial of autochthonous communities. No evidence has been observed for subjacent rooting structures or pedogenic alteration. The plants that crosscut bedding are generally fragments, ~5–6 cm in length, and originate from flat-lying axes; these fragments crosscut bedding at low angles. Hence, these assemblages are interpreted as transported (allochthonous). Inclined axes in this setting represent plants that maintained their structural integrity following deposition and burial, rather than exhibiting a biological response to burial.

An interpretation of allochthony also is supported by the microstratigraphic relationships between plant material and their entombing sediments. Plant fragments are scattered in random orientations within the matrix, suggesting that individuals were disarticulated before transport and deposition. If plants were buried in place, plant material would be expected to be concentrated at the contacts of a rich organic horizon with downward-projecting roots anchoring them in place. Additionally, the plants are preserved as casts rather than adpressions. Hence, axes underwent decay and hollowing, and subsequently were infilled with coarse silt and mud (e.g., Gastaldo et al., 1989). Decay is consistent with deposition in channels and overbank deposits (Kosters, 1989;

Alexander et al., 1999). Plant debris introduced from the floodplain would be entrained directly into the floodwaters and incorporated into the suspended load of the channel. Following decay, axes settled to the bedload and the hollow void was infilled by migrating bedload sediment (Degges and Gastaldo, 1989). Under high-discharge conditions, these small sediment-filled axes could be re-entrained and transported into overbank settings. Infilled axes, as well as other flat-lying detritus, are contorted and overlie primary ripple structures, which indicates settling from suspension load transport to bedload where hydrodynamic processes were in flux. Scouring on one side of plant material has been observed, implying a baffling effect that deflected sediments over the top of the plant fragment (see Rygel et al., 2004). Scouring on the down-flow side resulted in subsequent infill by finer-grained sediment and burial. This evidence points toward allochthonous accumulations in this setting (Gastaldo, 2004).

Plant Taphonomy in Estuarine/Tidal Assemblages

Fluvial and marine processes may affect estuarine environments, and plant assemblages preserved in these Trout Valley Formation regimes span the spectrum of possible preservational modes. Most assemblages are interpreted as parautochthonous, with only one allochthonous assemblage identified (Facies 7—bioturbated siltstone facies) and only one autochthonous assemblage encountered (Facies 5—pedogenically altered siltstone).

Autochthonous Facies 5

The presence of geopedally oriented structures that crosscut bedding within an inferred protosol suggests that the plants in the pedogenically altered siltstone were buried in situ. It may be argued that the geopedal structures are laterally forked branches of *Psilophyton* that were oriented downward during burial. However, if these were lateral axes emplaced when the plant fell over, more of these structures would be expected in this horizon owing to the organization and architecture of these taxa (e.g., Andrews et al., 1968; Kasper et al., 1974). A forked, lateral, aerial axis would have been deformed when emplaced into soft mud (Gastaldo, 1984), yet no such deformation is observed; the structures in the facies are straight and unkinked (Fig. 15). These structures are smaller in diameter than the other axial *Psilophyton* fragments observed within this facies (and the formation as a whole), as well as having features similar to other structures identified as roots in coeval floral assemblages (Griffing et al., 2000; Hotton et al., 2001). These lines of evidence lead to the conclusion that these structures are roots. Roots originate from an organic-rich horizon (poorly developed O-horizon) consisting of concentrated axial fragments that crosscut into the subjacent coarser sediment. Aerial plant remains preserved above the organic-rich horizon are similar in arrangement and preservation to axes in Facies 6 (bioturbated interbedded sandstone and siltstone). These are oriented subvertical to vertical, crosscut bedding, and are adpressions. Axes were neither hollowed nor infilled, as in the fluvial assemblages, indicating that individuals were not decayed prior

to burial. This is the only locality where rooting structures are present and, thus, the only locality where an autochthonous assemblage is preserved.

Parautochthonous Facies 6

Here, plant assemblages are characterized by concentrated, well-preserved axial fragments, in both random and preferred orientations, and may be flat-lying, inclined, or vertically cross-cut bedding. These accumulations are interpreted as parautochthonous assemblages. The relative size sorting seen in the fluvial assemblages with the larger plants (e.g., *Pertica quadrifaria*) concentrated at the bottom and smaller plants (e.g., *Psilophyton*) concentrated at the top of the plant-bearing intervals also is seen in the bioturbated interbedded sandstone and siltstone. This arrangement indicates settling in decreasing flow velocities. The small angle between dichotomizing branches noted in *Psilophyton microspinosum*, which is not typical of the plant (Andrews et al., 1977), is also attributed to transport and grounding processes.

Axes are found in three-dimensional arrangement throughout Facies 6 assemblages, where they crosscut bedding. However, bedding is neither interrupted nor disrupted by any inclined axis. This condition indicates that axial orientation occurred during burial, and was not a subsequent biological response by the plant to burial (regeneration and/or positive phototropic response). Plant response to burial was reported in several assemblages from the Battery Point Formation (Hotton et al., 2001) and observed in other Trout Valley Formation localities. Hotton et al. (2001) used re-anchorage, preservation of complete axes in fine detail (although an equivocal criterion as demonstrated by the present study), and axes oblique or perpendicular to the bedding plane as evidence for plant response to burial.

The assemblages preserved in interpreted tidal channels are characterized by concentrated, well-preserved axial segments with lateral axes in sub-parallel to parallel-aligned orientations. Several lines of evidence suggest that the alignment is a result of transport and not in situ burial as previously interpreted (Andrews et al., 1977). The presence of barren siliciclastic intervals between each plant-bearing horizon is evidence that these are not in situ assemblages. A basal layer of organic detritus (incipient or actual O-horizon) from which positive geopedal structures originate generally characterizes in situ assemblages. Although the assemblage mat could be such an organic layer, there is no macroscopic or microscopic evidence for primary rooting originating from these horizons. Each bedding surface on which large fragments are preserved is underlain by coarser clastics in which neither rhizomes nor rhizoids exist. Aerial axes are found in three-dimensional arrangement throughout the plant-bearing interval, where inclined axes are both sub-horizontal and vertical. These plant parts are in their original burial orientation rather than indicative of a later biological response to burial.

The presence of barren intervals above and below each assemblage, in which wave and tidally modified primary structures are preserved, also indicates transport before emplacement. Aerial plant detritus occurs only in the troughs of large-scale

ripples, indicating a relationship between transport and settlement as the current velocities decreased (Gastaldo, 2004). Although these assemblages occur within interpreted tidal channel deposits and may have represented colonization of adjacent incipient wetlands, the absence of rooting horizons, the multiple stratified assemblages intercalated with barren intervals, and restriction of plant axes to ripple troughs are indicative of some degree of transport.

However, these plants probably were not transported out of their habitat to the burial sites. The plants in these assemblages apparently were neither dead nor decayed at the time of transport and burial. Nearly all the plants retain their three-dimensional architecture along with the presence of epidermal features (e.g., spines), intact terminal and lateral sporangia, and complex lateral branching. The primary sedimentary structures indicate a transported assemblage, but microstratigraphic analysis suggests that these plants were still alive when buried. Infrequent, forked, possibly root-like structures that appear to originate from flat-lying aerial axes suggest regeneration. Although regeneration has not been observed in other Devonian plant assemblages, it has been documented in Carboniferous *Calamites* (Gastaldo, 1992a).

There is a possibility that the plant material was transferred from inland sites into the nearshore setting and reworked into tidal channels. In general, such freshwater-discharged plant material gets entrained within tidal cycles and degraded, chemically and physically, to fragmentary materials before burial in tidal flats and channels (Gastaldo et al., 1987; Gastaldo, 1994; Gastaldo et al., 1993). Rarely do aerial architectures remain intact following tidal and wave activity. Rather, well-preserved and entire aerial plant debris is found where tidal channels have been occluded or blocked (e.g., Gastaldo and Huc, 1992). The presence of nearly complete, well-preserved plant axes up to 30 cm in length in these channel forms negates the possibility of long-distance fluvial transport and reworking into a coastal, estuarine channel system. Thus, these plants are interpreted as having lived close to the depositional setting, possibly on the margins of tidal channels and/or intertidal flats. Channel erosion during high-velocity spring flood or tidal cycles enhanced by storm processes would have undercut channel bank margins, allowing sediments and plant material to be incorporated into the adjacent channel.

Allochthonous Facies 7

The poorly preserved nature of the plant remains, their random orientations, and the concentration of material only in bedform crests in the bioturbated siltstone facies, along with their association with marine and brackish-water macroinvertebrates, indicate that this is an allochthonous assemblage (Selover et al., 2005).

Taphonomic and Paleoecologic Implications

The occurrence of trimerophytes in both fluvial assemblages and estuarine/tidal assemblages suggests that these plants occupied a range of habitats. Larger trimerophytes, such as *Pertica*

quadrifaria, are found in the coarser sediments, indicating that they grew near the margins of active channels and were transported during flood events. Smaller trimerophytes (e.g., *Psilophyton*) also occur in channel margin settings, especially those of Facies 6 (bioturbated interbedded sandstone and siltstone; see below). However, their occurrence within finer sediments above an interpreted rooting horizon suggests that they may have also colonized coastal flood basin and wetland (marsh) settings.

There is no evidence in any of the Trout Valley Formation plant assemblages for rhizomes attached or associated with any aerial axes in the present or in previously reported studies (Andrews et al., 1968; Gensel et al., 1969; Kasper and Andrews, 1972; Kasper et al., 1974; Kasper and Forbes, 1979). Therefore, there are two ways to account for this observation. The first is that rhizomatous specimens have not been collected, because of limited exposure and a Park rule that prohibits extensive excavation of outcrops. The other explanation to account for the presence of large, well-preserved, monopodial sporophyte axes with sterile and/or fertile laterals, but lacking rooting parts, in transported assemblages is that individuals were uprooted by some physical mechanism associated with a hydrological event (wind-derived traumatic events would rip and fragment individual plants; Gastaldo, 1992b) prior to burial. This is particularly true of assemblages in the bioturbated interbedded sandstone and siltstone (Facies 6). Here, plants are preserved within the final stages of tidal channel infill (the origin of many previously reported taxa; Table 2), and this is the interpretation in the present study. Hence, these plants represent initial, r-strategist juveniles/adults established on tidal channel margins and intertidal flats that were subjected to channel-margin erosion as each tidal channel migrated across the transitional zone. Bank undercutting would have been effortless because of the shallow rooting horizon that developed following colonization, introducing aerial biomass into the channels. Plants are restricted to the uppermost part of each channel fill within troughs of meso- to macro-scale ripples (developed during bedload clastic transport) following suspension-load transfer. Individual plants may have originated from other areas within the tidal flat and not immediately adjacent to their preservational site.

Trout Valley Formation plant assemblages are very low in diversity, with one or two taxa dominating any assemblage (Table 2). This condition reaffirms earlier conclusions that early land plants “turfed in” as monodominant stands (DiMichele and Hook, 1992; Hotton et al., 2001). Where plants occur within estuarine/tidal settings, no clear marine indicators are present, suggesting that these plants lived in primarily freshwater habitats. However, the associations with nearshore sand deposits (Facies 4) both above and below estuarine/tidal deposits suggest that part of this section was within the marine-influenced zone where the plants may have been exposed to saline (fully marine or brackish water) conditions. However, due to a lack of data, such as halite pseudomorphs in the siltstones, there is no direct evidence to suggest that these plants either were tolerant of or were killed by brackish-water conditions.

Comparison with Other Devonian Plant Localities

Several time-equivalent Devonian plant localities have been reported from northern Maine, New Brunswick, and Quebec. However, only the Cap-aux-Os Member floral assemblage of the Battery Point Formation from Gaspé Bay, Quebec, has been studied in detail (Griffing et al., 2000; Hotton et al., 2001). Both the Trout Valley and Cap-aux-Os localities are interpreted as fluvial channels that migrated across coastal plains. The Trout Valley Formation and Cap-aux-Os Member floras are very similar floristically, but there are significantly more autochthonous assemblages preserved in the Cap-aux-Os Member. There, plant megafossils occupy specific areas of the landscape, which are inferred to represent clade-related niche partitioning (Hotton et al., 2001). Trimerophytes and rhyniopsids occupied fully fluvial ephemeral, near-channel environments, whereas monotypic zosterophyll assemblages occur in mud-dominated wetlands such as backswamps and marshes (Griffing et al., 2000; Hotton et al., 2001). In the Trout Valley Formation trimerophytes also are interpreted as having occupied fully fluvial environments, similar to the Cap-aux-Os assemblages, as well as coastal flood basin and wetland tidal-flat settings. *Prototaxites*, an enigmatic fungus (Hueber, 2001), is reported to occur exclusively in terrestrial fluvial environments within both the Trout Valley Formation and the Cap-aux-Os.

SUMMARY AND CONCLUSIONS

The Trout Valley Formation of north-central Maine was deposited initially in a relatively steep alluvial fan complex with high-velocity channels flowing to a coastal plain setting in which estuarine environments dominated. The presence of nearshore shelf sands, in addition to the increasing proportion of fine clastics upsection, is indicative of increasing marine influence in the area.

Trimerophytes are preserved in both fluvial and estuarine settings, suggesting that these plants probably occupied a wider range of habitats than previously interpreted. The plant assemblages consist of monodominant stands that occupied fluvial and estuarine/tidal channel margins, as well as coastal flood basin and wetland settings, that were primarily freshwater hydrological regimes. These conclusions reaffirm similar observations on early land plant habitats (DiMichele and Hook, 1992; Griffing et al., 2000; Hotton et al., 2001). The question of whether these plants were tolerant of brackish water conditions common in coastal areas (e.g., sea spray, storm-generated marine incursions) remains elusive due to a lack of sedimentologic and taphonomic evidence. The effect(s) of such physical conditions on early land plants only can be answered by further paleoecological studies based on other Early-Middle Devonian land-plant localities.

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