

An Estuarine Assemblage from the Middle Devonian Trout Valley Formation of Northern Maine

ROBERT W. SELOVER, ROBERT A. GASTALDO,* and ROBERT E. NELSON

Colby College, Department of Geology, 5800 Mayflower Hill, Waterville, Maine 04901, Email: ragastal@colby.edu

PALAIOS, 2005, V. 20, p. 192–197 DOI 10.2210/palo.2004.p04-16

*The Middle Devonian (Emsian / Eifelian) Trout Valley Formation is exposed in the northeastern corner of Baxter State Park, Maine, and is noted for its abundant plant-fossil assemblages. However, to date no invertebrate macrofaunal assemblages have been reported in this fluvial-to-marine sequence; only isolated eurypterid parts have been reported. A previously undescribed outcrop of coarse- to medium-grained siltstone characterized by megariipples preserves a restricted, transported invertebrate assemblage. The macrofossils are randomly oriented and concentrated in the ripple crests. Similar sedimentological features in other parts of the stratigraphic section indicate an estuarine, tidally influenced depositional regime. The fossil assemblage is dominated by *Phthonia sectifrons*—an uncommon Devonian bivalve known previously from open-marine deposits. Few other fossil taxa occur. Typically associated with deep-shelf brachiopods, the presence of *P. sectifrons* in these estuarine deposits indicates that this taxon occupied a wider range of habitats, extending from the shallow silty shelf facies to more transitional settings. The facies associations in the Trout Valley Formation suggest that Devonian near-shore communities resembled modern bivalve-dominated near-shore communities.*

INTRODUCTION

Few Middle Paleozoic faunas are known from the Maritimes and northern New England (Nova Scotia, New Brunswick, Quebec, Maine), with most reports focused on Ordovician–Silurian occurrences from fully marine strata (e.g., Neuman 1987, 1994; Bradley et al., 2000). To date, few macrofaunal assemblages have been recovered from transitional and/or estuarine settings (McKerrow 1978; Boucot, pers. comm., 2003). Such assemblages are significant because of their rarity, and because they help complete a picture of a Middle Paleozoic ecosystem that is not well documented. Without closely investigating strata and environments of deposition previously considered barren of fossils, it is impossible to gain an understanding of the spatial distribution of various taxa in context. This study expands upon previous knowledge of transitional environments, and suggests that further study of such paleoenvironments may help complete our understanding of Paleozoic marine communities.

*Corresponding Author

Strata of the Trout Valley Formation are part of a thick succession of siliciclastic rocks deposited from early erosional stages in a foreland basin northwest of the Acadian orogen (Bradley et al., 2000). These are of Late Eifelian to Early Emsian age and unconformably overlie volcanoclastics of the Traveler Mountain Rhyolite (earliest Emsian; Bradley et al., 2000). The Trout Valley Formation is restricted to Maine's Baxter State Park and consists of basal conglomerates overlain by non-marine sandstones and siltstones. The sequence is interpreted to represent a transition from braidplain to intertidal facies (Allen and Gastaldo, in press). Although ostracodes, ?estherids, and eurypterid scales were noted previously from plant-rich intervals (Dorf and Rankin, 1962), the rocks were not reported to preserve shelly invertebrates. A previously undescribed locality in Baxter State Park provides further insight into Devonian invertebrate assemblages in the Maritimes and northern New England. This report documents the first invertebrate fauna to be discovered in this terrestrial and transitional sequence. The fauna is dominated by bivalves, particularly *Phthonia sectifrons*, a taxon reported in New York and Illinois that is, otherwise, relatively unknown. Small, unornamented gastropods and a small, butterflyed ostracode are found in association as well as a juvenile eurypterid, which is the first nearly complete specimen described from Maine. In addition, plant fragments are preserved including a reproductive structure and other, poorly preserved aerial parts.

MATERIALS AND LOCALITY

The fossil assemblage occurs in one locality, in a bed that is aerially restricted. The strata are exposed in the bed of Trout Brook only during periods of low water flow, which may be the result of the recent construction of a beaver dam upstream (USGS 15' Wassataquoik Quadrangle, Maine, T5 R10; Fig. 1). Details on the collection site can be obtained by contacting the Baxter State Park Commission; collection in the park is controlled by permit, and application must be made to the Baxter State Park Research Committee for access. The fossil assemblage is preserved in a coarse- to medium-grained gray (N3) siltstone characterized by megariipples. The macrofauna is concentrated and oriented randomly within ripple crests, rarely within ripple troughs.

The siltstone is heavily bioturbated, quartz rich, siliceous, and carbonaceous. The megariipples are approximately 17.0 cm thick at the crest and 3.0 cm thick in the troughs. Megariipples have a wavelength of 6.0 m, and are offset stratigraphically. Ripple orientations indicate paleocurrent was to the south ($n = 12$), which is opposite to paleocurrents observed in other parts of the section (Allen and Gastaldo, in press). Reineck and Singh (1980) noted that fossil deposits are common in tidally influenced channels, but caution that shell concentrations also may be formed by the erosion of tidal-flat surfaces. Such assemblages are comprised of concentrated shells in lenticular beds or geometries. The shells in these concentrations may or may not be broken. Paleocurrents in tidal flats are highly variable (Reineck and Singh, 1980), which is due to the influence that wind can have on wave direction. Although the observed paleocurrent is different from the remainder of the Trout Valley section (Allen and Gastaldo,

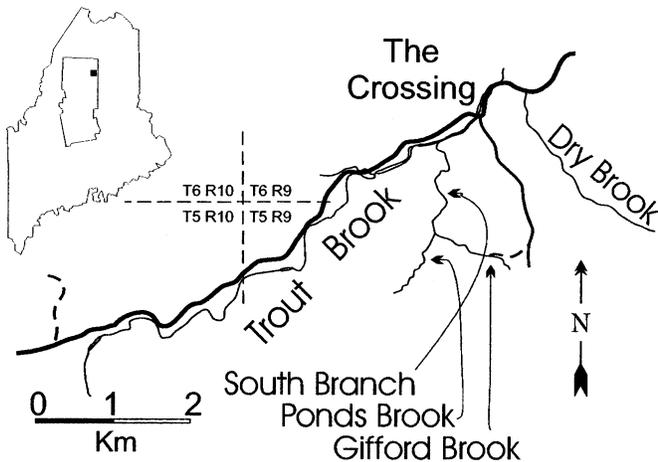


FIGURE 1—Generalized locality map of collection site in Baxter State Park, Piscataquis County, Maine. The site is exposed at low water in the bed of Trout Brook (USGS 7.5' Wassataquoik Lake Quadrangle). Details of the exact locality are available from the Baxter State Park Commission; collection within the Park is restricted, and permit access must be obtained through the Baxter State Park Research Committee.

in press), the presence of large fossiliferous megaripples suggests a high-flow event. Furthermore, megaripples are a common component of tidal channels rather than tidal flats (Reineck and Singh, 1980)—an observation that may preclude multi-directional waves as a cause for the anomalous paleocurrent. These observations and assemblage characteristics are consistent with a storm-deposit origin, although limited observation of bedform geometry precludes further interpretation.

INVERTEBRATE ASSEMBLAGE

The assemblage consists of a single species of bivalve, small spiral and planispiral gastropods, a small, poorly preserved, butterflyed ostracode, and a juvenile eurypterid. These specimens have been repositated at the Maine State Museum (MSM-IP). Most bivalves are disarticulated or preserved in an open, butterflyed position, whereas the gastropods often are fragmented with the aperture end commonly preserved. The small eurypterid is nearly complete, with only a few legs disarticulated. Several concentrations of shells and shell fragments occur within the crests of the megaripples; however, most fossils are dispersed and randomly oriented parallel to bedding. There is an average of five fossils per 10 cm^3 in the crests, whereas the number of fossils in the troughs averages 0–2/ 10 cm^3 . There is approximately one gastropod for every 20 bivalves, with other taxa rare (1 or 2 for the whole assemblage; Fig. 2). The macrofauna consists, in rank order abundance, of bivalves, spiral and planispiral gastropods, and an eurypterid.

Bivalves

The primary taxon ($n = 151$, 74% of assemblage) is *Phthonia sectifrons* (Fig. 3), an elliptical bivalve with a short anterior end and concentric growth lines. The growth lines (radii of Shimer and Shrock, 1944) are most pronounced on the umbonal ridge and anterior end. Indi-

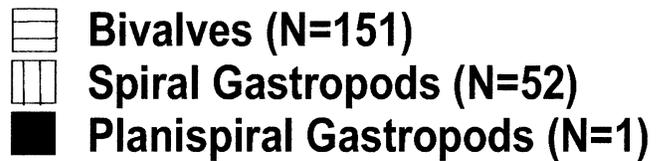
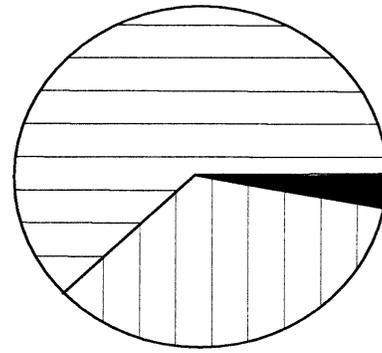


FIGURE 2—Pie diagram showing proportion of bivalves, spiral gastropods, and planispiral gastropods within the collection.

vidual shells range in size from 3.0 to nearly 40.0 mm, with a mean length of 14.2 mm (± 9.2 mm). This taxon is distinguished from other Devonian bivalves by its small size, elliptical shape, and radiating striae.

Gastropods

Small, high-spired gastropods are common ($n = 52$, 25% of assemblage), while planispiral gastropods are rare ($N = 1$). Both morphotypes are ~ 2 mm in length and are unornamented (Fig. 4). High-spired gastropods often are fragmented and are found represented by the largest basal-most whorl. While only one complete planispiral gastropod was encountered, it is highly likely that they are better represented in concentrations of shell fragments in the megaripple crests. However, because many shell frag-

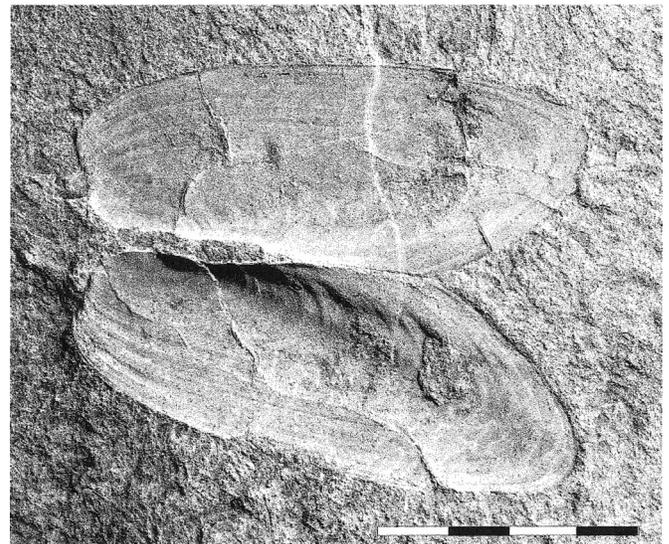


FIGURE 3—Butterflyed specimen of *Phthonia sectifrons* (MSM-IP 1002) preserved as an impression in coarse siltstone, showing concentric growth lines originating from umbonal region. Scale = 2 cm.

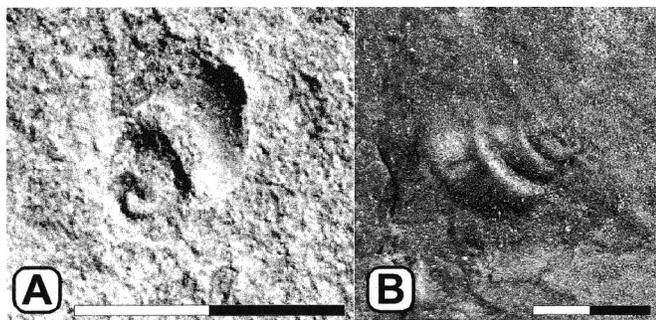


FIGURE 4—Gastropod casts from the Trout Valley Formation. (A) Unidentified, poorly preserved high spired gastropod (MSM-IP 1006). Scale = 2 mm. (B) Unidentified, poorly preserved planispiral gastropod (MSM-IP 1017) Scale = 2 mm.

ments lack the diagnostic features (texture and shape) that help to identify planispiral gastropods, it is not possible to attribute any single shell fragment to this morphology.

Eurypterid

Eurypterid classification generally is based on the shapes of three features: the prosoma, metasoma, and the telson (Tollerton, 1989). Additional adult ornamentation and morphology often are used to further distinguish species. The Trout Valley eurypterid is a juvenile, and exhibits characteristics of several different genera. These include *Jaekelopterus*, *Lanarkopterus* (a Late Silurian taxon), *Stylonurella*, and *Tarsoptrella*; however, Tollerton (pers. comm. 2002) suggested that it is *Parahughmilleria*, and may not be identifiable beyond genus because it is immature. Isolated graphitized fragments assigned to the Hughmilleridae were reported previously from this deposit by Terkla et al. (2002).

The Trout Brook specimen is 30 mm in length by 12 mm in width at the base of its prosoma. It is nearly complete, with the prosoma, metasoma, and opisthoma preserved (Fig. 5A, C, D). Several of its appendages also have been preserved, including 3–4 walking legs and 1–2 swimming legs (Fig. 5B). One major feature missing is the telson, which could not be exposed from the matrix. The prosoma is trapezoidal to sub-quadrate, whereas the metasoma is cardioid in shape. Additional ornamentation is preserved, and includes *Erieopterus*-type spiniferous walking legs, reniform eyes, and centrimedial eye placement. However, juvenile morphology may not be the same as its adult counterpart, on which generic classification is based (Tollerton, 1989). Hence, assignment cannot be made beyond genus, and even this is ambiguous.

Ostracode

The ostracode is butterflyed and preserved on the upper-right corner of the eurypterid metasoma (Fig. 5E). It is small and unornamented.

Plants

Limited in occurrence and fragmentally preserved, the dispersed, randomly oriented plant fossils are not concen-

trated as are the shells. Rather, they occur in equal quantities in both the megaripple crests and troughs. Plant macrofossils in other estuarine deposits that are stratigraphically higher are concentrated on bedding surfaces (Allen and Gastaldo, in press). The poor preservational quality at this locality prevents identification even to genus; however, one fragment may be either a reproductive structure or macroalgae (Fig. 6). The low abundance of highly fragmentary plant remains may be related to the high-energy regime responsible for generation of the shell concentrations in the megaripple crests.

DISCUSSION

Middle Devonian estuarine strata are stratigraphically scarce in the Maritimes and northern New England and, to date, there have been few reported invertebrate assemblages from transitional environments during the early Paleozoic (Boucot, pers. comm., 2003). Instead, brachiopod-dominated, deep-water faunas typify Maritime and northern New England fossil assemblages (e.g., Neuman, 1994, and references therein). Boucot and Perry (1981) suggested that a combination of erosion and dolomitization were mechanisms that removed or altered shoreline deposits, and this stratigraphic bias may lead to a possible misinterpretation of the overall Early Middle Devonian paleocommunity. Because of the relative scarcity of fossiliferous estuarine deposits in the Devonian (e.g., Wehrmann et al., 2005), any new information gained greatly augments our understanding of Paleozoic biodiversity as a whole.

The presence of a low-diversity assemblage devoid of brachiopods suggests that these organisms lived in an environment that was either too shallow or turbulent for filter feeding, or the physiochemical conditions were beyond the limits of brachiopod tolerance. Infaunal bivalves and gastropods are, however, typical faunal components of tidal flats and channels (McKerrow, 1978). Furthermore, there is sufficient evidence to suggest that the fossils in this assemblage had not been transported extensively. Because bivalves are known to butterfly hours to days after death (Schäfer, 1972), it is highly unlikely that the butterflyed shells could have been transported intact. The butterflyed orientation of *Phthonia* implies that the organisms were transported alive with closed valves and subsequently died after deposition. To be transported alive, the organisms must have lived within a short distance of the depositional site, thereby implicating a tidal-flat or tidal-channel fauna. The gastropods occur in random orientations, and often are fragmented, implying that, unlike the bivalves, these shells did not survive the depositional event intact.

Eurypterids commonly are found in freshwater to estuarine settings (McKerrow, 1978). Furthermore, it is common for marine and freshwater organisms to travel to the nutrient-rich waters of an estuary to reproduce. Thus, the presence of a juvenile eurypterid in the assemblage also implicates a distinct estuarine component to this assemblage. In addition, because the specimen is nearly complete, it is unlikely that it traveled far before deposition. Finally, because terrestrial plants dominate the Trout Valley Formation (Andrews et al., 1977; Kasper et al., 1988; Allen and Gastaldo, in press), the occurrence of sub-

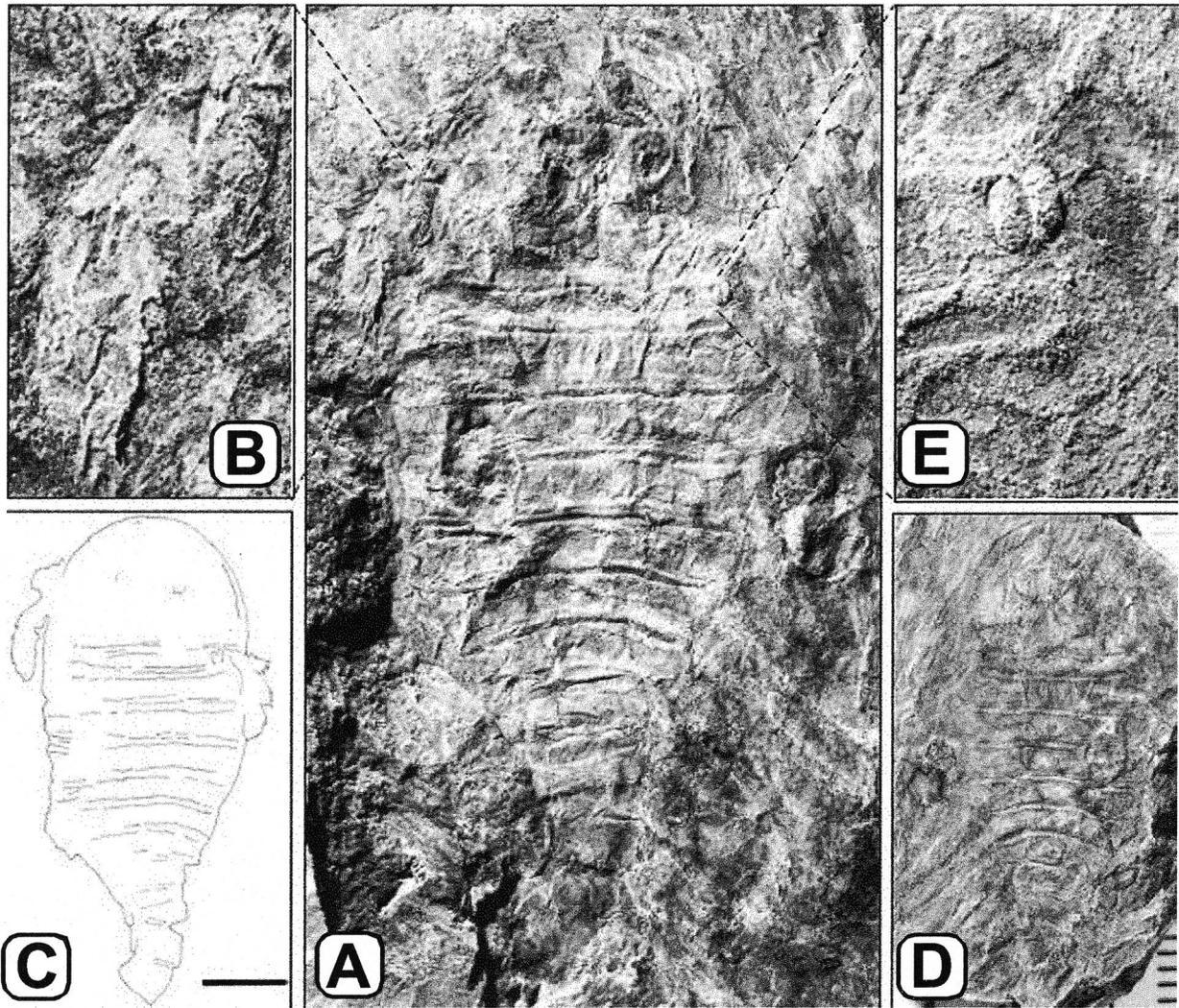


FIGURE 5—Juvenile eurypterid, questionably assigned to cf. *Parahughmilleria*, on which an ostracode of unknown affinity is preserved; A, B, C, E—MSM-IP 1065; D—MSM IP 1064. (A) Body fossil impression in coarse siltstone showing prosoma, metasoma, opisthoma, and *Erieopterus*-style swimming arm; $\times 3.5$. (B) Enlargement of *Erieopterus*-style swimming arm; $\times 10.5$ (C) Line drawing of body fossil figured in A. Scale = 0.5 cm. (D) Counterpart of eurypterid body fossil. Scale in mm. (E) Unidentifiable butterfly-shaped ostracode preserved on the metasoma; $10.5\times$.

aerial plant fragments ties this assemblage to nearshore-barrier or marginal-estuarine settings. The scattered nature of these fossils shows that they were deposited following a high-energy depositional event, during a period of calm or low water.

Estuaries are generally low-energy, low-flow environments (Reineck and Singh, 1980), making it difficult to size-sort while simultaneously transporting material into the depositional site. The size range of the fossil taxa in this assemblage (2-mm gastropods to 40-mm bivalves), combined with the presence of the eurypterid, suggests that little transportation occurred outside of the mechanism responsible for concentrating the fossils in the crests of the mega-ripples. Bioturbation in the siltstones directly overlying the assemblage destroyed any potential for preservation of megafauna or megafloora.

The assemblage is interpreted to represent deposition as the result of a high-energy storm. The south-oriented paleocurrent at this locality is opposite to the predominant

NW flow direction documented in fluvial and estuarine tidal channels (Allen and Gastaldo, in press). As such, it indicates a higher energy event directed landward, which supports Baird's (pers. comm., 2003) observation that *Phthonia sectifrons*, although rare, is associated commonly with storm deposits, probably occupying either a benthic-epifaunal or shallow-infaunal niche that was easily disturbed when wave base was lowered. The small size of all taxa and the tendency of the bivalves to be butterflyed within this assemblage place a limit on the distance this assemblage could have been transported and the energy involved in the transportation. Furthermore, the presence of the eurypterid, which is constrained typically to estuarine deposits, suggests that this assemblage had been moved minimally only. Because the plant fossils are not preserved preferentially in either the crests or the troughs of the megaripples, their presence suggests deposition during periods of lower energy either during or following the depositional event.

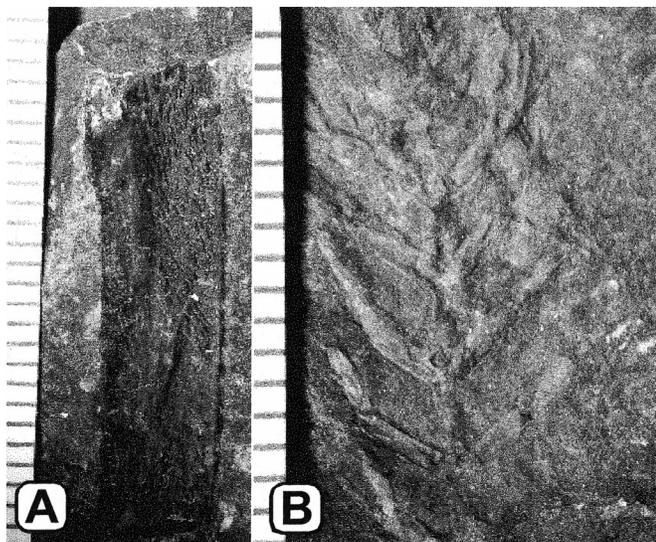


FIGURE 6—Fragmentary, detrital plant material preserved in association with the invertebrate fauna. (A) Unidentifiable degraded axis (MSM-IP 1030). Scale in mm. (B) Unidentifiable axis with lateral appendages (MSM-IP 1114). This may be a reproductive structure or fragment of a noncalcified dasycladaceous alga (e.g., *Chaetocladus*). Scale in mm. Lighting from lower left.

Brachiopod dominance is well documented throughout the Paleozoic marine record (Stempien et al., 2003). However, the present study suggests that this trend may be a product of stratigraphic bias. The Trout Valley assemblage is devoid of brachiopods—instead consisting of a bivalve-dominated, parautochthonous assemblage, which suggests that a transitional boundary existed for the brachiopod biozone in the Devonian. The nature of estuarine deposits prevents extensive transportation of deeper water shelly animals into tidal flats or tidal channels because of the existence of geomorphic barriers that commonly are associated with estuaries (see Reineck and Singh, 1980). Furthermore, if transfer of offshore shells to transitional estuarine settings were to occur, the predicted preservational mode of fossil shells would be more fragmented and damaged than the observed butterfly condition of the bivalves. In addition, the generally rare taxon *Phthonia* is associated with several brachiopods, including *Tropidoleptus*, *Mucrospirifer*, and *Nucleospira* (C. Brett, pers. comm., 2003). These taxa inhabited shallow to moderately deep, offshore, silt and muddy silt bottom conditions, and are known from nearshore facies. The taxa generally are found in deposits indicative of high sedimentation rates and/or turbidity. *Phthonia* also commonly is associated with rapidly emplaced sediments, including turbidites and storm deposits (Vogel et al., 1987; C. Brett, pers. comm., 2003). Under these conditions, the bivalve typically is associated with the *Tropidoleptus* biofacies (C. Brett, pers. comm., 2003), which is restricted to aerobic, muddy to silty ocean floors (Vogel et al., 1987).

The Trout Valley locality differs from that reported by Wehrmann et al. (2005) in which a higher diversity assemblage, including brachiopods, bivalves, eurypterids, tentaculitids, merostomes, and fragmentary plants, is preserved in nearshore, intertidal settings. The nearshore environment at Alken consisted of periodically emergent tid-

al channels and tidal flats into which the fossils were transported. Most plants in both assemblages are considered to be of terrestrial origin, with occasional fragments of marine algae. The macroinvertebrates are small, similar to those in the present study, with both brackish and fully marine taxa present. In some instances, monotypic lingulid assemblages and terebratulids indicate a restricted-marine environment, probably with reduced salinity. Other invertebrates, including the arthropods, are considered to have lived in freshwater. The limited macroinvertebrate assemblage from Maine is the result of bedload transport within a tidal channel during a higher-energy event associated with a storm. Its very low diversity probably is the result of a culling process only from the intertidal zone during the event, rather than an amalgamation of invertebrates from the regional ecosystem.

The distribution of Holocene muddy estuarine shores is a function of sediment supply and hydrodynamic processes operating within the transitional zone. Of importance is the tidal energy per unit area in the system, which establishes the overall geomorphology of the tidal flat and estuary (Pethick, 1996). Rapid variation in wave energy, due to short-term perturbations or adjustments, results in periodic erosion and deposition, exposing parts of the shoreline and burying others. Wave and wind processes control the extent, location, and depositional morphology of the intertidal mudflats (Pethick, 1996), with storm-induced events providing the mechanism to excavate, transport, and deposit infauna. A low macroinvertebrate diversity exists in these environments, and their systematic affinities depend upon latitude. Temperate muddy intertidal flats are dominated by polychaetes, crustaceans, and molluscs (e.g., Howard and Döriges, 1972; Daiber, 1982; Santelices, 1991), whereas brachiopods (i.e., *Glottidia*) are found occasionally in the tropics (Vargas, 1996). In the former region, this substrate supports large numbers of benthic invertebrates whose average body sizes are small when compared with animals in sandy substrates (Orth et al., 1991), whereas densities in tropics are much lower (e.g., Caribbean; Dawes et al., 1991). The small size of shelly invertebrates in the Trout Valley Formation may reflect this size-substrate relationship. The absence of brachiopods in the assemblage may be a function of collection and locality size, the original sampling of the coastal ecological mosaic, the timing of storm events relative to changes in seasonal population densities (e.g., Vargas, 1996), climate, or the true absence of these animals in the coastal regime.

CONCLUSIONS

The low-diversity, bivalve-dominated assemblage in estuarine deposits of the Trout Valley Formation mirrors the distribution of faunas observed today. Single-species assemblages are noted from as early as the Ordovician (Ross, 1981), and are thought to represent success of a guild in establishing itself in a particular environment. The predominance of *Phthonia sectifrons* and the complete absence of any brachiopods in this assemblage suggest that a similar situation developed in the proximal regions of the Devonian coast. Furthermore, the gastropods are dominated by one morphotype, indicating that this trend exists for different taxa as well. These two examples hint

at a clustering of species, similar to other environments seen in the Recent and fossil record. The appearance of a parautochthonous assemblage, including *Phthonia sectifrons*, in an estuarine tidal-channel deposit suggests that previous reports of the bivalve in offshore deposits may represent displacement of the taxon in response to storms, or fossil communities on the deeper end of the *Phthonia sectifrons* biozone.

ACKNOWLEDGEMENTS

The authors would like to thank the Baxter State Park Commission for permission to conduct research in the park. In addition, special thanks go to Jean Hoekwater, whose expertise was extremely helpful in the field. Many thanks go to David and Paula Work of the Maine State Museum for their help with photography. Arthur Boucot, Gordon Baird, Lisa Churchill-Dickson, Robert Neuman, Roy Plotnick, and Victor Tollerton all helped with locating references and identifying specimens. Carl Brett and Patrick Racheboeuf are thanked for reviews of the manuscript. The National Science Foundation (NSF EAR 0087433) and a grant from Howard Hughes Medical Institute supported this research project; and the Colby College Dean of Faculty provided travel funds for the authors to attend the national GSA meeting in 2002.

REFERENCES

- ALLEN, J.P., and GASTALDO, R.A., in press, A sedimentologic and plant taphonomic evaluation of the early Middle Devonian Trout Brook Formation, Maine: in DiMichele, W.A., and Greb, S., eds., *Wetlands Through Time*: Geological Society of America, Special Publication.
- ANDREWS, H.N., KASPER, A.E., FORBES, W.H., GENSEL, P.G., and CHALONER, W.G., 1977, Early Devonian flora of the Trout Valley Formation of northern Maine: Review of Palaeobotany and Palynology, v. 23, p. 255–285.
- BOUCOT, A.J., and PERRY, D.G., 1981, Lower Devonian brachiopod dominated communities of the Cordilleran region: in Gray, J., Boucot, A.J., and Berry, W.B.N., eds., *Communities of the Past*: Hutchinson Ross Publishing Company, Stroudsburg, p. 185–222.
- BRADLEY, D.C., TUCKER, R.D., LUX, D.R., HARRIS, A.G., and MCGREGOR, D.C., 2000, Migration of the Acadian Orogen and foreland basin across the Northern Appalachians of Maine and adjacent areas: United States Geological Survey Professional Paper v. 1624, p. 1–49.
- DAIBER, F.C., 1982, *Animals of the Tidal Marsh*: Van Nostrand Reinhold Company, New York, 422 p.
- DAWES, C.J., MCCOY, E.D., and HECK, K.L., JR., 1991, The tropical western Atlantic including the Caribbean Sea: in Mathieson, A.C., and Nienhuis, P.H., eds., *Ecosystems of the World, Intertidal and Littoral Ecosystems*: Elsevier, Amsterdam, p. 215–233.
- DORF, E., and RANKIN, D.W., 1962, Early Devonian plants from the Traveler Mountain area, Maine: *Journal of Paleontology*, v. 36, p. 999–1004.
- HOWARD, J.D., and DÖRGES, J., 1972, Animal-sediment relationships in two beach-related tidal flats, Sapelo Island, Georgia: *Journal of Sedimentary Petrology*, v. 42, p. 608–623.
- KASPER, A.E., GENSEL, P.G., FORBES, W.H., and ANDREWS, H.N., 1988, Plant paleontology in the state of Maine: a review: Maine Geological Survey, *Studies in Geology*, v. 1, p. 109–128.
- MCKERROW, W.S., ed., 1978, *The Ecology of Fossils*: MIT Press, Cambridge, Massachusetts, 384 p.
- NEUMAN, R.B., 1987, Type section of the Early Ordovician Shin Brook Formation and evidence of the Penobscot orogeny, northern Penobscot County, Maine: in Roy, D.C., ed., *GSA Centennial Field Guide Volume 5—Northeastern Section*, Geological Society of America, Boulder, p. 307–309.
- NEUMAN, R.B., 1994, Late Ordovician (Ashgill) *Foliomena* fauna brachiopods from northeastern Maine: *Journal of Paleontology*, v. 68, p. 1218–1234.
- ORTH, R.J., HECK, K.L., JR., and DIAZ, R.J., 1991, Littoral and intertidal systems in the mid-Atlantic coast of the United States: in Mathieson, A.C., and Nienhuis, P.H., eds., *Ecosystems of the World, Intertidal and Littoral Ecosystems*: Elsevier, Amsterdam, p. 193–214.
- PETHICK, J.C., 1996, The geomorphology of mudflats: in Nordstrom, K.F., and Roman, C.T., eds., *Estuarine Shores: Evolution, Environments and Human Alterations*: John Wiley & Sons, New York, p. 185–211.
- ROSS, J.R.P., 1981, Ordovician environmental heterogeneity and community organization: in Gray, J., Boucot, A.J., and Berry, W.B.N., eds., *Communities of the Past*: Hutchinson Ross Publishing Company, Stroudsburg, p. 1–33.
- REINECK, H.E., and SINGH, I.B., 1980, *Depositional Sedimentary Environments with Reference to Terrigenous Clastics*: Springer-Verlag, New York, 549 p.
- SANTELICES, B., 1991, Littoral and sublittoral communities of continental Chile: in Mathieson, A.C., and Nienhuis, P.H., eds., *Ecosystems of the World, Intertidal and Littoral Ecosystems*: Elsevier, Amsterdam, p. 347–369.
- SCHÄFER, W., 1972, *Ecology and Paleocology of Marine Environments*: The University of Chicago Press, Chicago, 568 p.
- SHIMER, H.W., and SHROCK, R.R., 1944, *Index Fossils of North America*: John Wiley and Sons, New York, 837 p.
- STEMPIEN, J.A., KRAUSS, R.A., MILLER, A.I., and KOWALEWSKI, M., 2003, Body size variation in Early Paleozoic bivalves and brachiopods: assessing environmental effects: *Geological Society of America, Abstracts with Program*, v. 35, p. 317.
- TERKLA, M.G., ALLEN, J.P., NELSON, R.E., and GASTALDO, R.A., 2002, Lower Middle Devonian eurypterid remains from the Trout Valley Formation of north-central Maine: *Geological Society of America, Abstracts with Program*, v. 34, p. A-72.
- TOLLERTON, V.P., JR., 1989, Morphology, taxonomy, and classification of the Order Eurypterida Burmeister, 1843: *Journal of Paleontology*, v. 63, p. 642–657.
- VARGAS, J.A., 1996, Ecological dynamics of a tropical intertidal mudflat community: in Nordstrom, K.F., and Roman, C.T., eds., *Estuarine Shores: Evolution, Environments and Human Alterations*: John Wiley & Sons, New York, p. 355–371.
- VOGEL, K., GOLUBIC, S., and BRETT, C.E., 1987, Endolith associations and their relation to facies distribution in the Middle Devonian of New York State, U.S.A.: *Lethaia*, v. 20, p. 263–290.
- WEHRMANN, A., HERTWECK, G., BROCKE, R., JANSEN, U., KÖNIGSHOF, P., PŁODOWSKI, G., SCHINDLER, E., WILDE, V., BLIECK, A., and SCHULTKA, S., 2005, Paleoenvironment of an Early Devonian land–sea transition: a case study from the southern margin of the Old Red Continent (Mosel Valley, Germany): *PALAIOS*, v. 20, p. 101–120.

ACCEPTED JULY 30, 2004

