

A NOVEL CONTEMPORARY FLUVIAL ICHNOCOENOSE: UNIONID BIVALVES AND THE SCOYENIA–MERMIA ICHNOFACIES TRANSITION

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ABSTRACT

A transitional *Scoyenia*–*Mermia* ichnocoenose from the Saint John River, Fredericton, New Brunswick, Canada, is dominated by elements of the *Mermia* ichnofacies, with traces comparable to *Curvolithus*, *Helminthopsis*, *Gordia*, *Spirophycus*, and *Lockeia*. Environmental characteristics are, however, more typical of the *Scoyenia* ichnofacies, with an emersion event providing conditions favorable to viewing traces preserved in a sand-softground substrate. Observation of *in situ* trace-making behavior allowed traces to be attributed to their progenitors, which include unionid and sphaeriid bivalves. An omission assemblage of vertebrate tracks also was present, comprising gull, raven, and mink. *Oichnus*-like borings were observed in some unionid shells. The shallow-tier trace assemblage created in a high-energy river channel may be expected to have a poor preservational potential, with loss of trace definition observed at the water margin during emersion and subsequent deterioration by eolian sediment transport.

INTRODUCTION

Over the previous two decades, there has been a burgeoning interest in the field of continental invertebrate ichnology, with the well-established Seilacherian *Scoyenia* ichnofacies (Seilacher, 1967, 1978; Frey et al., 1984; Bromley, 1996) characteristic of periodically emergent lacustrine, sheetflood, or fluvial situations, being amended and complemented by the lacustrine *Mermia* (Buatois and Mángano, 1995, 1998) and non-aquatic *Termitichnus* (Smith et al., 1993) and *Coprinisphaera* (Genise et al., 2000) ichnofacies (see Keighley and Pickerill, 2003; Buatois and Mángano, 2004, for recent reviews). Additionally the *Skolithos* ichnofacies, typically more characteristic of marine situations, may be encountered in the high-energy setting of active fluvial channels and within high-energy zones in lakes (Buatois and Mángano, 1998, 2004). Despite the relative abundance of fluvial compared to lacustrine successions, the fluvial realm remains relatively underrepresented in both the modern and ancient ichnological record, with few described localities (e.g., Thoms and Berg, 1985; Sarkar and Chaudhuri, 1992; Pickerill, 1992) and no exclusive recurrent ichnofacies comprising fluvial-channel facies. This largely is a function of taphonomic bias and cannot be taken to indicate the absence of trace-making organisms and structures formed by them within rivers. The majority of described fluvial traces, both modern and ancient, have been described from sheetflood, overbank, or abandoned-channel deposits because continued reworking of active channel sediment generally precludes preservation in this setting. Despite a long-running occupation of freshwater settings, few known fluvial trace assemblages have been attributed to a molluscan progenitor—bivalve traces being identified reliably from Devonian localities in New York and possible sites in New Jersey, Wales, and Ireland (Bridge et al., 1986; Chamberlain, et al., 2003, 2004). The trace-making activity of a modern bivalve and

gastropod assemblage inhabiting a point-bar setting was documented by Pryor (1967).

This paper documents a modern example of a fluvial trace assemblage recorded from a sandbar adjacent to Jewett Island (45°58'N, 066°42'W), in the Saint John River, immediately upstream of Fredericton in New Brunswick, Canada (Fig. 1). The assemblage displays features characteristic of both the *Scoyenia* and *Mermia* ichnofacies, and, as such, demonstrates their ethological continuity. Active trace-making behavior was observed in a unionid-bivalve-dominated benthic molluscan community, after an environmentally stressful emersion event created conditions favorable for observation of the trace-making organisms.

STUDY AREA

The Saint John River originates in the Maine Appalachians before flowing through Quebec and New Brunswick, eastern Canada, to the Bay of Fundy (Fig. 1). The river has a low gradient (0.03% below the Mactaquac Dam, 13 km west of the study site), and, along most of its course, consists of a single, low-sinuosity channel. Immediately upstream of Fredericton, however, the river displays an anastomosing aspect. To the west and upstream of the study site (Fig. 2), the Mactaquac Dam creates an effective ecological barrier and sediment trap in addition to blocking tidal influence above the dam. Saline influence in the river is attenuated by the Kennebecasis Bay and Reversing Falls bedrock sills, located 110 km and 120 km, respectively, downstream from the study area. The river has a mean annual discharge of 1110 m³/s, peaking during the April and May snow melt, despite evenly distributed precipitation (Cunjak and Newbury, 2005). The locality described herein represents a relatively high latitude assemblage (45°58'N, 066°42'W), with a humid continental climate exhibiting pronounced seasonality. Daily mean air temperatures range between –9.3°C in January and 19.2°C for July (Wikipedia, 2006). It should be noted that most descriptions of fluvio-lacustrine trace assemblages rarely take into account the paleolatitude and paleoclimatic range of the settings they describe, although Good (2004) attempted a climatic reconstruction based on bivalve growth bands.

OBSERVATIONS

Trace Assemblage

An abundant and moderately diverse (trace morphologies resembling six putative invertebrate ichnogenera, together with tracks attributable to three vertebrate genera) trace suite was observed on an emergent sand bar. The traces were produced in a sandy substrate and exhumed by a one-meter fall in the river water level. The unconsolidated coarse-grained sediment is mature compositionally, moderately sorted, and exhibits a range in grain size between fine-grained sand and granules. Locally, pebble and cobble lags are present downstream of the study site. The sediment contains little apparent organic matter. The siliciclastic sands are dominated by quartz (80%), but also include phyllite and mafic igneous lithoclasts (10%), feldspars (5%), and micas (5%).

The trace assemblage was formed by a molluscan fauna (Fig. 3) consisting of gastropods, including *Campeloma decisum* (Say), and

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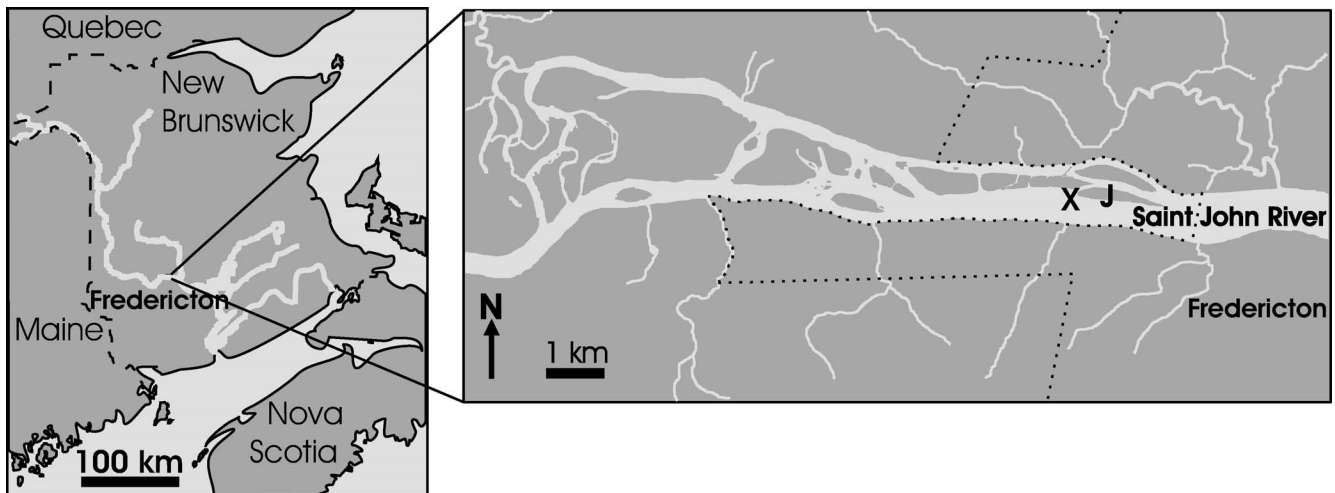


FIGURE 1—Locality map, depicting the study site (X) and Jewett Island (J) on the Saint John River, immediately west of Fredericton, New Brunswick, eastern Canada. The Mactaquac Dam occurs 2 km beyond the western figured limit of the main river channel. Dotted line=Fredericton city limits.

an abyssate, vagile epifaunal- to semi-infaunal- bivalve fauna consisting of undifferentiated members of the Sphaeriidae family, together with the unionids *Lampsilis radiata* (Gmelin) and *Anodonta cataracta* (Say). During emersion, the molluscan trace makers generally were arrested at the end of the traces, either at the sediment surface, or, occasionally, in the case of the bivalves, in shallow, vertical terminal burrows.

The trace assemblage consisted of modern traces exclusively. A pre-omission softground suite (Fig. 4), with geometries that would be attributable to the ichnogenera *Curvolithus* (gastropod-produced), *Helminthopsis* and *Gordia* (unionid and sphaeriid produced), and *Spirophycus* and *Lockeia* (unionid-produced), was preserved in concave and convex semirelief (epirelief) in a sandy substrate, together with examples of the ichnogenus *Oichnus* formed in a molluscan substrate. Additionally, track patterns and probing traces attributable to *Larus* (gull), *Corvus* (raven), and *Mustela* (mink) activity were observed, comprising an omission suite (Fig. 4).

Unionid Taphonomy

All observed unionid shells (both live and dead) displayed some degree of loss of external, umbonal shell material (Fig. 3.). This is assumed to be predominantly a consequence of chemical dissolution from the oldest part of the shell, but may have been hastened by gastropod-induced *Oichnus*-like boring, or chlorophyte-, cyanophyte-, or fungal-mediated decay. Schäfer (1972) reported complete dissolution of a *Cardium* shell

placed in distilled water within 208 days. Carbonate shell dissolution also was observed by Chamberlain (2004) and Chamberlain et al. (2004), which was attributed to acid dissolution. Dissolution by purely chemical means may have been hastened by the low water temperatures that occur for much of the year. Water-chemistry analysis from the ice-free period yielded an average pH of 7.7 and alkalinity in the range of 25–102 mg CaCO₃/L (R.A. Curry, cited in Cunjak and Newbury, 2005). Disarticulation and comminution were noted less frequently, although these states



FIGURE 2—Study site, with the vegetated Jewett Island composed of stable Pleistocene sediment distal to a recently exposed sand bar on which traces were observed.

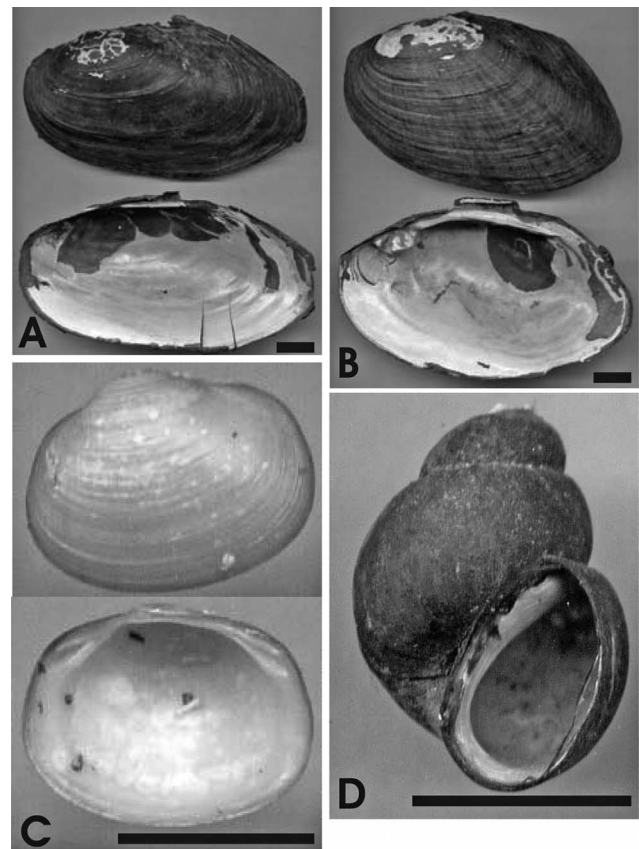


FIGURE 3—Photographs of the molluscan assemblage; scale bar=1 cm for A, B, D; scale bar=5 mm for C. (A) *Anodonta cataracta*. (B) *Lampsilis radiata*. (C) Un-differentiated Sphaeriidae. (D) *Campeloma decisum*.

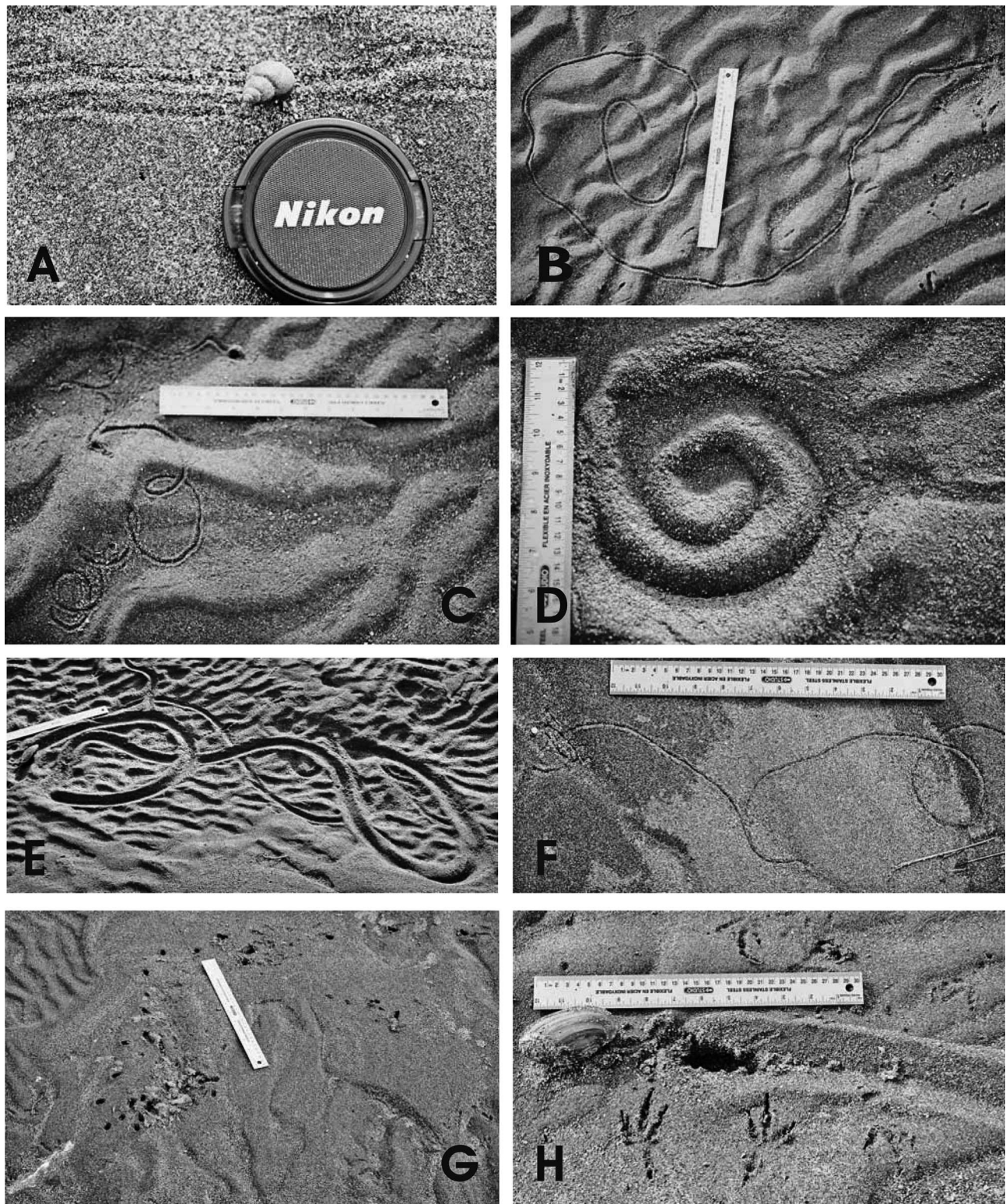


FIGURE 4—Trace-assemblage examples. Except for A, scale bar=30 cm, fine gradations in cm. (A) *Cameloma decisum* producing *Curvolithus*-like trace; lens cap=55 mm diameter. (B) Sphaeriidae-produced *Helminthopsis*-like trace, illustrating dextral coiling and terminal burrowing. (C) Sphaeriidae-produced *Gordia*-like trace, displaying sinistral coiling and terminal burrowing. (D) Unionid-produced *Spirophycus*-like trace, exhibiting sinistral coiling and terminal burrowing. (E) Unionid-produced *Gordia*-like trace overlying a *Helminthopsis*-like trace. (F) Sphaeriidae-produced *Gordia*-like trace, illustrating sinistral coiling and erratic terminal behavior; interpreted to be omission. (G) Gull-probing trace. (H) Raven excavation trace.

were apparent in a molluscan thanatocoenosis viewed several hundred meters downstream of the study site, from which dead shells displayed marked shell-carbonate dissolution. Although not apparent in this study, Good (2004) described a locally transported assemblage of disarticulated Jurassic bivalves, deposited in a fluvial channel, in which material is preserved by silica replacement. However, silica replacement would appear to be atypical, with carbonate dissolution in the vadose or phreatic zone generally prevailing (e.g., Bridge et al., 1986).

DISCUSSION

Unionid Ethology

From their Devonian origins (Chamberlain, 2004), unionid bivalves have been an integral part of freshwater ecosystems. They currently dominate fluvial benthic biomass, providing nutrient coupling between the benthic and pelagic realms (Vaughn et al., 2004). Their longevity (>25 years) and slow growth are characteristic of a K-selected strategy, contrasting with the R-selected communities previously associated with the *Scoyenia* ichnofacies (Buatois and Mángano, 1998). Their lifecycle incorporates an obligate ectoparasitic larval glochidial stage, supported by fish requiring perennial water bodies (Vaughn and Taylor, 2000).

Vertical burrowing activities are more frequent among endobenthic juveniles as opposed to the dominantly epibenthic summer-season behavior exhibited by adults. Burrowing is carried out as a response to temperature extremes, to avoid desiccation, predation, displacement, or other environmental stresses, and is observed more frequently in soft (silt-clay size) sediments (Amyot and Downing, 1997; Nichols, 1997). Burrowing has been shown to be more rapid and deeper among smaller, thinner-shelled, more motile individuals and species (Nichols, 2002; Saarinen and Taskinen, 2003). Surface-crawling behavior has been attributed to food, oxygen, or spatial-competitive environmental stresses, although reproductive, pedal-grazing, and trematode-parasite-induced behavioral abnormalities all may play a part (Saarinen and Taskinen, 2003).

Feeding activities of juvenile unionids and sphaeriids are based upon pedal-deposit feeding, a bias that is retained in many adult unionids (80% of consumption), although siphonal-suspension feeding takes on an increasing role in some species (20% of consumption; Raikow and Hamilton, 2001). Different habitats may be exploited with different feeding strategies among the same species, with bacteria comprising an increasing food component in shaded, turbid, or low-productivity rivers, where feeding may be observed continuously. This contrasts with the plankton-dominated diet of lake-dwelling species, whose feeding activity is diurnal (Vaughn and Hakenkamp, 2001).

Trace Taphonomy

While observations immediately after the emersion event revealed an abundant and relatively diverse trace suite, the preservational potential of the assemblage is poor. The high-energy river, with shifting sand bars in an area of net sediment transport, would create a generally harsh taphonomic regime both for the traces and for the associated molluscan assemblage. The traces were seen to post-date wave ripples, and active trace making was observed in shallow (<0.5 m) water. A receding shoreline led to pronounced deterioration in trace definition, with subaqueous reworking observed at the water margin, and saturated, wave-agitated sediment forming a softground unable to retain well-defined trace margins. Bivalve-trace production ceased upon subaerial exposure, with the bivalves' trace-making behavior becoming erratic before being replaced by upending that led into vertical burrowing as emersion occurred. Subsequent deterioration of the traces was apparent in those subaerially exposed, with desiccation allowing eolian transport of sand that removed material from ridges and infilled furrows.

The surface-dominated, shallow-tier nature of the trace assemblage contributes to their poor preservational potential, and while "No biogenic structure can be said to have zero preservation potential" (Bromley, 1996,

p. 146), the authors know of no instances of a similar occurrence from the rock record (the only described fluvial bivalve-trace assemblages being characterized by deeper-tier activity; Chamberlain et al., 2003).

The research supports the well-established ichnological principles (Bromley and Fürsich, 1980; Ekdale et al., 1984) that one trace maker may produce a diverse trace assemblage (e.g., unionid-generated *Helminthopsis*, *Gordia*, *Spirophycus*, and *Lockeia*), and conversely that different organisms may create identical traces (e.g., unionid- and sphaeriid-generated *Helminthopsis*).

Fluvial Settings and the *Mermia*-*Scoyenia* Ichnofacies Models

Miller et al. (2002) documented the delayed colonization of freshwater as opposed to marine substrates throughout the Phanerozoic, additionally documenting the predominantly horizontal and surficial rather than vertical nature of traces in lacustrine settings, which are bioturbated most frequently. The paucity of trace observations in fluvial-channel settings was attributed to erosion. Floodplain settings demonstrated degrees of colonization intermediate between the fluvial and lacustrine end-members.

Limitations for the application of the existing terrestrial ichnofacies model have been discussed by Hasiotis (2004). Hasiotis documented a diverse trace assemblage (including bivalve-generated traces) within the Jurassic Morrison Formation of the U.S. Rockies, which "could occur in any one of the proposed *Scoyenia*, *Termitichnus*, and *Coprinisphaera* ichnofacies based on their broad and ambiguous definitions" (Hasiotis, 2004, p. 182-183). Hasiotis (2004) emphasized the prominent role played by geographic and temporal variability in hydrologic conditions from intermediate settings between aquatic and non-aquatic.

Variations within the fluvial realm appear to be particularly difficult to encapsulate adequately. Zonneveld et al. (2000) exercised a three-fold subdivision of the fluvial system, consisting of: (1) flood-basin or alluvial-plain (*Planolites*, rare *Skolithos*, meniscate burrows); (2) crevasse-splay (*Arenicolites*, *Skolithos*, vertical shafts, *Camborygma/Thalassinoides*, *Scoyenia*, *Rusophycus*, *Taenidium*, *Planolites*, *Palaeophycus*); and (3) fluvial-channel (vertically oriented burrows with *Camborygma*, cf. *Ophiomorpha*, *Spongeliomorpha*, *Thalassinoides*) divisions. These divisions were distinguished based on their distinctive trace assemblages in conjunction with physical sedimentary structures. In his discussion of the *Scoyenia* ichnofacies, Hasiotis (1997) proposed a four-fold subdivision of the alluvial environment, with channel, levee and proximal-floodplain, crevasse-splay, and distal-floodplain ecological and depositional sub-environments. The channel environment contained a dominantly horizontal-trace assemblage recording the activity of gastropods, nematodes, bivalves, crayfish, crabs, insect larvae, beetles, and oligochaetes. Ethologically, the burrows are constructed for shelter, deposit feeding, and locomotion. Gastropod and clam grazing, feeding, and aestivation burrows also are reported from distal-floodplain subenvironments, together with the permanent benthos sub-environment of lakes. Despite this partitioning, the trace assemblage reported here would suggest that the assemblage is from a lacustrine setting if it were to be encountered in the rock record, with elements including *Gordia*, *Helminthopsis*, and undifferentiated gastropod trails.

Buatois and Mángano (2002) discussed floodplain deposits and their implications for continental ichnofacies models, identifying two discrete assemblages. Desiccated floodplain assemblages were attributed to the *Scoyenia* ichnofacies, with a low diversity of invertebrate and higher diversity of vertebrate ichnofossils. The assemblages included backfilled, meniscate, and bilobate traces, with scratch marks and arthropod and tetrapod tracks. Floodplain assemblages represented an impoverished *Mermia* ichnofacies, and contained a low-diversity assemblage of shallow to surficial grazing, locomotion, and dwelling trails and burrows, with poor preservation as a consequence of a water-saturated substrate. Floodplain water bodies are ephemeral and unstable, and required more rapid colonization than permanent lakes; thus, these ichnofacies reflect envi-

ronmental factors rather than purely sedimentary environments, as stressed by Buatois and Mángano (2002) in their discussion of the breadth of environments in which the *Skolithos* and *Cruziana* ichnofacies are encountered. They noted that the *Scoyenia* ichnofacies indicates periodic inundation or exposure, characteristic of lake-margin, floodplain, or wet-interdune settings, while “the *Mermia* ichnofacies indicates permanently subaqueous freshwater conditions” (Buatois and Mángano, 2002, p. 83), conditions that occur in lacustrine basins, fjords, and water bodies formed in floodplain basins. Buatois and Mángano (2004) noted the presence of *Skolithos* ichnofacies in lacustrine settings, specifically within active-channel and wave-dominated lake shorelines or lacustrine delta-mouth-bar settings. The *Skolithos* ichnofacies assemblage includes both vertical burrows and escape traces. The presence of an assemblage, including rare *Skolithos* traces within a braided-fluvial system, was discussed by Hiscott et al. (1984), whose interpretation invoked marine incursions to explain the presence of *Skolithos*. Buatois and Mángano (2004) described the *Scoyenia* ichnofacies from abandoned or inactive channels and low-energy lake margins, where the trace assemblage included a low diversity of meniscate traces. Within floodplain settings, the *Scoyenia* ichnofacies contained abundant arthropod and vertebrate tracks, meniscate traces, ornamented burrows, and bilobate traces with scratch marks. The *Mermia* ichnofacies, found within permanently subaqueous floodplain (impoverished) or lake settings, was comprised of simple grazing trails, locomotion trails, and horizontal dwelling burrows. While emphasizing that “ichnofacies are not indicators of particular sedimentary environments but reflect sets of environmental factors instead” (Buatois and Mángano, 2004, p. 315), Buatois and Mángano (2004) also pointed out the importance of sediment water content and substrate consolidation in determining ichnofacies.

Other authors have worked on fluvial ichnological assemblages outside the ichnofacies paradigm. Pryor (1967) described recent point bars with bivalve and gastropod trails migrating downslope, produced when the animals maintained their position relative to a falling shoreline. Trails and burrows exhibiting random orientations also were encountered in flooded back-bar pools. Bridge et al. (1986) also undertook work on a bivalve assemblage, with an association being observed between *Archanodon* bivalves and meniscate traces in overbank and channel-bar settings of Devonian age. These traces had a predominantly vertical alignment, and were interpreted as escape burrows. The assemblage presented here would appear to be atypical with regard to the complete absence of meniscate burrows. Several authors (e.g., Zonneveld et al., 2000) have recorded vertical crayfish burrows in fluvial-channel deposits. However Gingras et al. (2005) reported that crayfish burrows were conspicuously absent, because they “are dug deeply only in subaerial settings” (Gingras et al., 2005, p. 340), while Hasiotis (2004) only documented their occurrence in settings subjected to subaerial exposure.

Should the observed trace suite be preserved, it would include elements transitional between the *Mermia* and *Scoyenia* ichnofacies, as described by Buatois and Mángano (1995, 1998). The pre-omission trace assemblage consists of traces typifying the *Mermia* ichnofacies (e.g., *Gordia*, *Helminthopsis*, *Lockeia*), while the post-omission suite vertebrate tracks are associated with the *Scoyenia* ichnofacies exclusively.

The described assemblage was observed in a sandy substrate from a periodically emergent fluvial area, most closely paralleling the environmental interpretations for the modified *Scoyenia* ichnofacies of Buatois and Mángano (1995). However, if the assemblage were to be encountered in the rock record, the majority of traces would place the assemblage firmly in the *Mermia* ichnofacies, whose environmental interpretation suggests an exclusively low-energy, permanently subaqueous lake environment with fine-grained sedimentation. An impoverished equivalent to the *Mermia* ichnofacies (including both *Helminthopsis* and *Lockeia*) has been described from overfilled overbank deposits, which “tend to dominate in proximal overbank settings and/or temperate and humid settings” (Buatois and Mángano, 2004, p. 319); however, this setting still implies a permanently subaqueous condition. These observations provide a cau-

tionary note against a perhaps too-rigid application of some ichnofacies models, and stress the importance of supporting trace-fossil-based interpretations with appropriate sedimentological observations (Frey et al., 1984). If sufficient occurrences of this and similar ichnocoenoses were to be observed in the sedimentary record, then the formulation of a fluvial-channel ichnofacies may be warranted, as originally proposed in Buatois and Mángano (1995).

While most emphasis within this contribution is placed on the invertebrate component of the trace assemblage, which, because of physiological constraints, has the greatest significance for paleoenvironmental reconstruction (Hasiotis, 2004), it should be noted that vertebrate tracks were prominent in the original diagnosis of the *Scoyenia* ichnofacies (Seilacher, 1967). Structures produced by aquatic or semi-aquatic terrestrial vertebrates have been reported throughout the preserved sedimentological record (e.g., Miocene *Diamonelix* burrows attributed to *Palaeocastor*; Martin and Bennett, 1977). Although their utility and applicability have been called into question (see Hunt and Lucas, in press, for a recent review), a number of vertebrate ichnofacies and ichnocoenoses have been proposed for environmental settings that overlap the environments with which the *Scoyenia* and *Mermia* ichnofacies are associated. These include the shore-bird ichnofacies (Lockley et al., 1994), subsequently amended to the *Avipeda* ichnocoenose (Hunt and Lucas, in press). This ichnocoenose, together with mammal tracks and other components, forms part of the amended *Grallator* ichnofacies that is found in lacustrine-margin environments (Hunt and Lucas, in press). The vertebrate traces described herein might be ascribed to an impoverished example of the amended *Grallator* ichnofacies.

ACKNOWLEDGMENTS

We would like to thank Don McAlpine, the curator of Zoology at New Brunswick Museum, for his kind assistance with the identification of the molluscan fauna, together with Donovan Blissett for his general support. The Small Craft Aquatic Centre of Fredericton provided the kayak used to access the study area. The research was funded by an NSERC Discovery Grant. An initial draft of this manuscript benefited from the constructive reviews of Gabriela Mángano and Tony Martin.

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ACCEPTED JANUARY 30, 2006

