

ICHOLOGY OF DELTAS: ORGANISM RESPONSES TO THE DYNAMIC INTERPLAY OF RIVERS, WAVES, STORMS AND TIDES

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ABSTRACT: Analyses of deltaic facies successions highlight recurring ichnological patterns that reflect a variety of physicochemical stresses imposed upon infaunal organisms by the interaction of various delta-front processes. Analysis of numerous ancient deltaic deposits in Canada, the United States, Australia, and offshore Norway persistently show reductions in bioturbation intensity and impoverishment in ichnological diversity, compared to those of nondeltaic shorelines. Some facies locally demonstrate sporadic colonization and recolonization of substrates left denuded by episodic depositional conditions. Deltaic ichnological suites also locally display size reductions of ichnogenera and a paucity of suspension-feeding ethologies. Resulting trace-fossil suites are overwhelmingly dominated by deposit-feeding behaviors, even in sandy facies.

Such ichnological characteristics largely reflect increased sedimentation rates and heightened fluvial discharge, which serve to impede infaunal colonization. River-derived stresses are profound: salinity changes, hypopycnal-flow-induced water turbidity, distributary flood discharges with accompanying phytodetrital (comminuted plant debris) pulses, hyperpycnal-flow-induced sediment gravity flows, and fluid-mud deposition all conspire to produce the overall depauperate nature of the ichnological assemblage. Freshet-discharge events during river floods, accompanied by hyperpycnal conditions, may lead to the episodic introduction of reduced-salinity waters immediately above the sediment-water interface in delta-front and prodelta depositional settings. Such conditions may facilitate development of syneresis cracks and promote reductions in infaunal populations.

Wave energy generally buffers fluvial effects, by dispersing suspended sediment offshore and encouraging the thorough mixing of waters of contrasting salinity. High mud concentrations near the delta front damp wave energy, however, limiting its effectiveness in remediating the benthic ecosystem, particularly immediately following distributary flood discharges and storm events. In wave-dominated settings, strong alongshore drift also operates to extend river-derived stresses considerable distances downdrift from distributary mouths. Where asymmetric deltas are formed, markedly different ichnological expressions are expressed on either side of distributary-channel mouths. Updrift settings typically retain classic shoreface assemblages, whereas downdrift environments commonly acquire markedly stressed suites. Storm energy may be effective in dispersing mud and mixing waters, but it also results in erosion and episodic sediment deposition. Concomitant precipitation induces river floods, returning river-derived stresses to the delta front. Tidal energy and its effects on the infaunal communities of deltas are poorly documented. Tidal flux may trap mud plumes against the delta front, elevating water turbidity. Pronounced mud flocculation coupled with increased settling velocity associated with tidal mixing also leads to rapid deposition of thick fluid muds, particularly in low-lying areas, hampering or precluding colonization. Tidal energy also leads to marked changes in energy and salinity near the sediment-water interface at several time scales.

Deltaic ichnological suites are characterized by structures of opportunistic trophic generalists, though mainly those of facies-crossing deposit feeders. High water turbidity, particularly near the sea floor, precludes most suspension-feeding behavior, and suppresses the development of the *Skolithos* ichnofacies, even in many proximal delta-front deposits. Ichnological characteristics record the dynamic interplay and relative importance of these different processes, both temporally and spatially, on delta systems.

INTRODUCTION

Although general concepts of deltaic sedimentation are generally well understood, the specific details of the accompanying ichnology are not. Many recent studies of modern deltaic systems, including many in this volume, emphasize the physical sedimentology. Measured sections through cores typically depict sedimentary structures, textures, grain size, body fossils, microfossils, geochemical analyses, and age dating. Although most descriptions note that burrows are present, detailed analysis of the ichnology, such as assessment of the Bioturbation

Index (BI; Figure 1) and its distribution, identification of ichnospecies, ichnogenera, and general information on the diversity, abundance, and ethological groupings of the trace-fossil suite are almost totally lacking. Consequently, there is a paucity of work addressing the potentially unique characteristics of those ichnological suites, which may be critical in identifying various deltaic subenvironments. Some of the ichnological terms used in this paper are included in a glossary following the references.

Many sedimentary processes (e.g., formation of ripples or dunes) are not especially sensitive to the environment of deposition. Dunes, for example, can be formed in deserts, rivers,

Grade	Classification	Visual Representation
0	Bioturbation absent	
1	Sparse bioturbation, bedding distinct, few discrete traces	
2	Uncommon bioturbation, bedding distinct, low trace density	
3	Moderate bioturbation, bedding boundaries sharp, traces discrete, overlap rare	
4	Common bioturbation, bedding boundaries indistinct, high trace density with overlap common	
5	Abundant bioturbation, bedding completely disturbed (just visible)	
6	Complete bioturbation, total biogenic homogenization of sediment	

FIG. 1.—Schematic representation of bioturbation index (BI) values. The BI classification was originally modified after Reineck, 1963 (cf. Taylor and Goldring, 1993, and Taylor et al., 2003) and was based on broad ranges of percentage of burrow overlap. This has been modified since to dispense with the time-consuming and largely inaccurate semiquantitative estimation of percent (after Bann et al., 2004).

shorefaces, and shelves, and observation of cross bedding is not diagnostic of any particular environment. Organisms, in contrast, are extremely sensitive to the environment (Pemberton et al., 1992a, 2001). Environmental factors such as energy conditions, substrate consistencies, depositional rates, oxygenation, salinity, and other physicochemical conditions all lead to discrete biological communities (Ekdale et al., 1984; Bromley, 1990; Pemberton et al., 1992a). These faunal communities yield recurring, strongly facies-controlled groupings of trace fossils that reflect specific combinations of organism behaviors (ethology). Such recurring groupings have been designated “ichnofacies”. The environmental factors that control organism distributions and their traces only *tend* to change in response to changes in water depth, and consequently, trace-fossil groupings typically display, at most, a passive relationship to paleobathymetry (Frey et al., 1990). This paradigm lies at the heart of ichnology and ichnofacies analysis.

Various general models and approaches for using trace fossils in the identification and interpretation of specific sedimentary environments have been developed (e.g., Seilacher, 1967; Howard and Frey, 1984; Savrda and Bottjer, 1989; MacEachern and Pemberton, 1992; Pemberton et al., 1992a; Pemberton et al., 1992b; Pemberton and Wightman, 1992; Gingras et al., 1999; MacEachern et al., 1999a, Taylor et al., 2003; Bann et al., 2004, among others).

Animal–sediment interactions are well documented from the more uniform conditions associated with strandplain shorefaces, and the shoreface ichnofacies model is robust (Fig. 2) (e.g., Howard and Reineck, 1981; Howard and Frey, 1984; Pemberton and Frey, 1984; Frey, 1990; Vossler and Pemberton, 1989; MacEachern and Pemberton, 1992; Pemberton and MacEachern, 1995; MacEachern et al., 1999b; Bann and Fielding, 2004). Likewise, ichnological models are well established for inshore tidal settings, on the basis of studies of modern environments (e.g., German and Dutch North Sea; Schäfer, 1956; 1962; Reineck, 1958; Reineck et al., 1967; et al., 1968; Dörjes, 1970; Hertweck, 1970; the Normandy coast of France; Larssonneur, 1975; the Georgia coast of the United States; Frey and Howard, 1972; Hertweck, 1972; Dörjes and Howard, 1975; Howard and Frey, 1973, 1975; Howard et al., 1975; and Majou and Howard, 1975; the tidal flats of Taiwan; Dörjes, 1978; Reineck and Cheng, 1978; and Willapa Bay, Washington; Gingras et al., 1999). This paper reviews and integrates what is known from the ichnological and biological literature with sedimentological studies of both modern and ancient delta deposits, in order to develop a more robust framework for understanding the ichnology of deltaic depositional systems.

In deltaic settings, the effects of faunal responses and therefore of animal–sediment characteristics are typified by the dynamic interplay of fluvial influx, fluvial discharge types, tidal energy, wave action, and storms (see Tables 1 and 2). Such interactions, at least as they affect infaunal diversity, abundance, feeding strategy and overall behaviors, are poorly understood. Moslow and Pemberton (1988) presented a preliminary assessment of deltaic ichnology, based on a single core each of the Lower Cretaceous Cadotte Member and Bluesky Formation of the Western Interior Seaway of Alberta. Raychaudhuri and Pemberton (1992) and Raychaudhuri (1994) summarized the ichnological characteristics of the Lower Cretaceous Bow Island Formation of south-central Alberta. Gingras et al. (1998) conducted a preliminary ichnological study of the wave- and river-influenced delta lobes in the Upper Cretaceous Dunvegan Formation in west-central Alberta, building on the detailed stratigraphic analysis and mapping of the depositional systems of Bhattacharya (1989) and Bhattacharya and Walker (1991a, 1991b). This preliminary ichnological work was expanded upon by Coates and MacEachern (1999, 2000), Coates (2001), and MacEachern and Coates (2002), who also included a comparison with the more mixed-influence (fluvial–wave) deltaic deposits of the Upper Cretaceous Basal Belly River Formation. Siggerud and Steel (1999) presented an integrated ichnofabric and sedimentological assessment of the coarse-grained Eocene Sant Llorenç del Munt fan-delta complex of SE Ebro Basin, Spain.

The ichnology of ancient deltaic intervals has become increasingly studied in recent years. Howell et al. (2004) and Gani et al. (2004) have concentrated on ichnological signals in deltaic strata of the Upper Cretaceous Wall Creek Member, Powder River Basin, Wyoming. Soegaard and MacEachern (2003) carried out a detailed ichnological and ichnofacies treatment of coarse-grained fan-delta lobes in the Upper Jurassic Oseberg Formation of the Norwegian Shelf. MacEachern and Løseth (2003) addressed the ichnological characteristics of the more storm-dominated deltas in the Upper Jurassic Tarbert Formation of the Norwegian Shelf. Bann and Fielding (2004) have recently addressed the ichnological characteristics of several Permian units in the Denison Trough of the Sydney–Bowen Basin, Eastern Australia. McIlroy (2004) presented an ichnofabric–sedimentological appraisal of the tide-dominated Ile Formation delta in offshore mid-Norway. These studies, coupled with the aforementioned studies on the Upper Cretaceous Dunvegan, Basal Belly River, and Bow Island formations of the Alberta Basin are summarized in Tables 1 and 2, and

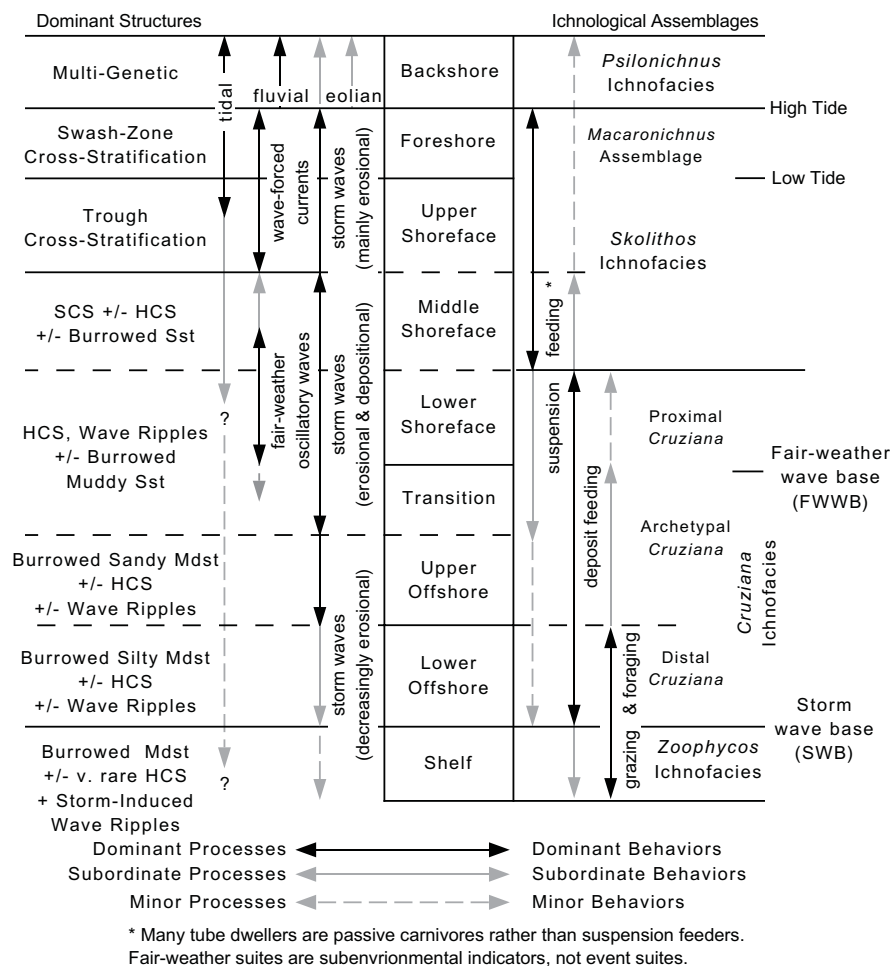


FIG. 2.—An integrated ichnological-sedimentological model of strandplain shorefaces and their various subenvironments, based on datasets of the Cretaceous Western Interior Seaway of North America (modified after MacEachern et al., 1999b).

constitute virtually all of the detailed ichnological assessments of delta systems. Clearly there is a long way to go.

This previous work necessarily constituted local case studies and attempted to delineate criteria for the recognition of deltaic sedimentation, and the characterization of the deposits with respect to the relative influences of river, wave, and tide processes. Despite this, these results are rarely applied to the description and analysis of cores taken in modern deltas. It is, therefore, timely to summarize the results of these studies in an attempt to present a more integrated framework for interpreting the ichnology of deltaic depositional systems. This paper addresses the current state of affairs in deltaic ichnology, outlines some of the current that attempt to explain empirical observations in the rock record, and suggests some future avenues of research that will be necessary in order to carry the study of deltaic systems to the more robust level presently enjoyed by estuarine incised-valley and strandplain shoreface/strandplain settings.

FLUVIAL INFLUX

The most distinctive aspect of the deltaic shoreline is the influence of fluviially derived discharge and sediment influx (Figs. 3–5). Fluvial discharge may range from hypopycnal, through homopycnal, to hyperpycnal; such changes may be temporally

variable, especially seasonally. Fluvial discharge also has a marked impact on deposition rates.

Hypopycnal Conditions: Sedimentation Rates and Water Turbidity

In hypopycnal settings, suspended mud is typically carried significantly above the sea floor as a buoyant plume (e.g., Nelson, 1970). Mixing of salt and fresh water occurs at the boundary between the salt wedge and the overlying sediment-laden plume. As the plume widens and slows, mixing of water may enhance clay flocculation, and eventually the suspended material falls onto the bed. Plumes may be severely deflected by waves. Infauna may not experience significant salinity fluctuations in hypopycnal settings, although the overriding plumes tend to block sunlight. Eventually, suspended sediment is deposited on the bed, although rates of sedimentation are generally significantly lower than in hyperpycnal settings.

Higher fluvial discharge, in general, is characterized by heightened sedimentation rates in proximal positions, resulting in lowered bioturbation intensities. Extremely rapid deposition, more characteristic of homopycnal and hyperpycnal settings, commonly shows abundant soft-sediment deformation features and formation of extensive fluid mud that forms soupground

TABLE 1.—Case-study examples that address the ichnological characteristics of river-dominated delta deposits and their subenvironments. Ichnological abbreviations are: An/Ph, *Anconichnus*/*Phycosiphon*; Ar, *Arenicolites*; As, *Asterosoma*; Au, *Aulichnites*; Be, *Bergaueria*; bivalve e/a, bivalve equilibrium adjustment structure; Ch, *Chondrites*; Cy, *Cylindrichnus*; Co, *Conichnus*; D, *Diplocraterion*; fu, fugichnia; Gy, *Gyrochorte*; Gyr, *Gyrolithes*; H, *Helminthopsis*; Lo, *Lockeia*; Ma, *Macaronichnus*; Mo, *Monocraterion*; O, *Ophiomorpha*; P, *Planolites*; Pa, *Palaeophycus*; Pho, *Phoebichnus*; Phy, *Phycodes*; Pi, *Piscichnus*; Pk, *Polykladichnus*; Ps, *Psammichnites*; Ro, *Rosselia*; Rh, *Rhizocorallium*; Sc, *Scolicia*; Sch, *Schaubcylindrichnus*; Sk, *Skolithos*; Si, *Siphonichnus*; T, *Terebellina* (*sensu lato*); Ta: *Taenidium*; Te: *Teichichnus*; Ter: *Teredolites* (allochthonous); Th: *Thalassinoides*; Tri: *Trichichnus*; Z, *Zoophycos*.

Unit	Prodelta	Distal Delta Front	Proximal Delta Front
Palo Pinto Deltas (Pennsylvanian) Texas, USA Outcrop Data	BI 0-3; typically \leq BI 2. Traces sporadically distributed. Suite: P, T, Lo, An/Ph, Ch. <i>Cruziana</i> ichnofacies.	BI 0-2. Traces sporadically distributed. Suite: Ta, Ps, Au, P, Sk, Lo, fu. <i>Cruziana</i> ichnofacies.	Not reported
Ivishak Fm (Triassic) Prudhoe Bay, Alaska, USA Core Data	BI 0-2. Sporadic distribution. Suite: Te, P, Th. All forms are facies crossing; no ichnofacies identifiable	Not reported Wave-influenced along strike: Suite Ma, Pa, Te, Sk, Ar.	Not reported
Oseberg Fm (M. Jurassic) Norwegian shelf, Norway Core Data	BI 0-4; \leq BI 3. Sporadic distribution. Suite: An/Ph, H, P, Te, Cy, Ta, Si, Th, A, As. Rare O, Pa, fu. Some units unburrowed. Distal expression of the <i>Cruziana</i> ichnofacies.	BI 1-3. Traces very sporadically distributed. Suite: Cy, As, Ch, Pa, Ro, Te, Sk, O, Ar, fu. Archetypal <i>Cruziana</i> in mixed <i>Skolithos-Cruziana</i> ichnofacies.	BI 0-3; \leq BI 2. Sporadic distribution. Suite: Ro, Cy, O, Ma, fu, bivalve e/a. Rare Sk, Pa, D (<i>D. habichi</i>), As. Proximal expression of <i>Cruziana</i> in mixed <i>Skolithos-Cruziana</i> ichnofacies.
Wall Creek - Frontier Fm (U. Cretaceous) Wyoming, USA (Raptor Ridge) Outcrop & Core	BI 1-3; rare bands of BI 4. Traces are sporadically distributed. Suite: P, Th, O, Pa, T, An/Ph, Te, bivalve e/a, fu. Archetypal <i>Cruziana</i> ichnofacies.	BI 1-3; rare bands of BI 3-4. Sporadic distribution. Suite: P, Pi, Cy, Ch, Ar, Sc, As, D, O, Th, Ter, Ma, An/Ph, Te, bivalve e/a, fu. Proximal expression <i>Cruziana</i> ichnofacies	BI 0-2; mainly \leq BI 1. Sporadic distribution. Suite: Pa, O, As, fu, Ch, H, P, Sk, Ma. Facies-crossing elements; ichnofacies uncertain.
Wall Creek - Frontier Fm (U. Cretaceous) Wyoming, USA (Murphy Reservoir) Outcrop Data	BI 0-3; mainly BI 1-3; bands of BI 4-5 along strike. Sporadic distribution. Suite: P, Th, T, Te, Ch, H, As, P, bivalve e/a, An/Ph. Facies-crossing <i>Cruziana</i> ichnofacies elements.	BI 0-3; mainly \leq BI 2; bands BI 4-5 along strike. Sporadic distribution. Suite: Pi, O, Th, Ro, Cy, As, P, Lo, Ch, H, bivalve e/a, D, Ar, Ter, Mo, Sk, fu. Archetypal to proximal expression <i>Cruziana</i> ichnofacies.	BI 0-3; mainly \leq BI 1. Traces more sporadically distributed. Suite: Pi, P, Th, O, fu, Mo, Sk, Ro, Cy. Facies-crossing elements in proximal expression of <i>Cruziana</i> ichnofacies.
Dunvegan Fm (Alloember E) (U. Cretaceous) Alberta, Canada Core Data	BI 0-2. Traces sporadically distributed and diminutive. Suite: P, Te, An/Ph, H, T, Z, fu. Facies-crossing elements of <i>Cruziana</i> ichnofacies.	BI 0-2. Traces sporadically distributed and diminutive. Suite: Te, P, Cy, An/Ph, H, Z, As, Th, T, Rh, Pa, O, D, fu. Archetypal <i>Cruziana</i> ichnofacies.	BI 0-1. Traces sporadically distributed and uncommon. Suite: Isolated O, Te, P. Facies-crossing forms. Ichnofacies uncertain.
Panther Tongue (U. Cretaceous) Utah, USA Outcrop Data	BI 1-3; highly sporadic intensity and distribution. Suite: P, An/Ph, H, O, Ch, Pa, As, T, Cy, Mo, bivalve e/a, Th. Archetypal <i>Cruziana</i> ichnofacies	BI 0-3, highly sporadic intensity and distribution. Suite: O, Cy, Ro, Cy, Pa, fu, Ar, Lo, Ta, Gy, Th, Te, Sch, Ter, bivalve e/a. Proximal expression of <i>Cruziana</i> ichnofacies	BI 0-2, sporadic distribution. Suite: O, Cy, Ar, Ter (<i>T. longissimus</i>) fu, Sch, D. Facies-crossing elements; proximal expression of <i>Cruziana</i> ichnofacies.
Belly River Fm Allomember D & E (U. Cretaceous) Alberta, Canada Core Data	BI 0-2; Traces sporadically distributed; diminutive. Suite: H, An/Ph, P, Te. Lesser Ro, As, Th. Very rare Z, Ch, Si, Sk, O, fu. Archetypal <i>Cruziana</i> ichnofacies	BI 0-2; highly sporadically distributed traces. Suite: Te, P, Ma, Ta, An/Ph, Ro, lesser H, Cy, Pa, Sk, fu, uncommon Rh, Ar. Proximal expression of <i>Cruziana</i> ichnofacies.	BI 0-2, Ma in "toe of the beach" position reaches BI 3. Ichnogenera uncommon. Suite: P, roots, Ma (<i>M. segregatis</i>). Ichnofacies uncertain.
Ferron Sandstone (U. Cretaceous) Utah, USA Outcrop Data	BI 1-3; sporadic distribution and diminutive. Suite: An/Ph, H, Ch, P, T, As, Th, Te; tempestites contain Cy, Pa, bivalve e/a, fu. Archetypal <i>Cruziana</i> ichnofacies.	BI 0-3; sporadic distribution and diminutive. Suite: O, Cy, Th, Ar, As, P, Ro, Pa, An/Ph, Ch, H, Lo, bivalve e/a, Ter, fu. Proximal expression of <i>Cruziana</i> to mixed <i>Skolithos-Cruziana</i> ichnofacies.	BI 0-2, mainly BI 0-1; sporadically distributed and diminutive traces. Suite: Ar, O, Ro, Pa, Th, P, Sk, fu, D (<i>D. habichi</i>), bivalve e/a, Ter, ?Co. Mixed <i>Skolithos-Cruziana</i> ichnofacies

substrates. Heightened rates of deposition make it difficult for infauna to colonize the substrate. Furthermore, what bioturbation does occur is typically soft-sediment deformed during dewatering and/or liquefaction, making identification of trace-fossil elements problematic.

Marine Influence in Delta-Plain Distributary Channels.—

During times of little or no discharge, the salt wedge may extend many kilometers upstream, resulting in brackish-water to

marine fossils in the distributary channels of the lower delta plain (Plint, 1990, Corbeau et al., 2004). Muddy drapes associated with lower delta plain point bars in distributary channels of the Cretaceous Ferron sandstone Member show a low-diversity, low BI (0–2) ichnological assemblage, characterized by *Arenicolites*, small-diameter *Skolithos*, and *Planolites* (Corbeau et al., 2004) Channel floors commonly contain *Teredolites*-bored allochthonous wood fragments. Associated mouth-bar deposits display low bioturbation intensities (BI 0-1) with fugichnia, *Palaeophycus*, *Ophiomorpha*, and *Diplocraterion*. Comparable suites occur in chan-

TABLE 1.—(Continued).

Mouth Bar	Distributary Channel	Interpretation	References
Not reported	Not reported	Interpreted as river-dominated delta	Bhattacharya et al., 2003.
"sparsely burrowed"	unburrowed	Interpreted as river-dominated delta	Tye et al., 1999. Suites incomplete.
Not reported	Bi 0-2; mainly \leq BI1. Traces uncommon and associated with pauses in channel deposition. Suite: O, fu, bivalve <i>e/a</i> . Facies-crossing elements, ichnofacies uncertain.	Interpreted as river-dominated coarse-grained fan delta with weak tidal influence.	Rahman, 1997; Soegaard and MacEachern, 2002. Suites augmented with unpublished data.
BI 1-3; generally \leq BI 2. Sporadic distribution of elements. Suite: Pa, Ch, H, Ar, P, As, Ma, ?Sc. Archetypal <i>Cruziana</i> ichnofacies.	BI 1-3; generally \leq BI 1. Sporadic distribution. Suite: Ma, Ch, Ar. Suite too impoverished to determine ichnofacies.	Interpreted as tide-influenced river-dominated delta	Gani et al., 2004. Suites augmented by unpublished data.
Not reported	Not reported	Interpreted as hyperpycnal discharge-prone, tidally influenced, river-dominated delta lobe.	Howell et al., 2004. Suites augmented with unpublished data.
Not reported	BI 0-1; very low diversity and abundance; sporadic distribution. Suite: P, Te, Ro (reworked), Pa, O. Facies-crossing suite, mixed <i>Skolithos-Cruziana</i> ichnofacies.	Interpreted as a river-dominated delta.	Bhattacharya, 1989; Gingras et al., 1998; Coates and MacEachern, 1999; 2000; MacEachern and Coates, 2002.
BI 0-3; sporadic distribution. Suite: O, P, Pa, Cy, Ter (<i>T. longissimus</i> & <i>T. clavatus</i>), Te, Sk,. Proximal expression <i>Cruziana</i> ichnofacies.	BI 0-1; burrows at pause planes. Suites: O, Ter (allochthonous; <i>T. clavatus</i> & <i>T. longissimus</i>), fu. Likely stressed <i>Skolithos</i> ichnofacies	Interpreted as inertial-dominated (hyperpycnal) river-dominated delta.	Frey and Howard, 1985; Olariu and Bhattacharya, this volume. Suites include unpublished data.
Not reported	BI 0-1; sporadically distributed ichnogenera. Suite: P, Sk, Te, Cy, Ta, Ar. Facies-crossing suite of mixed <i>Skolithos-Cruziana</i> ichnofacies.	Mixed river-wave influenced delta; more river influenced.	Coates and MacEachern, 1999, 2000; Coates, 2001; MacEachern and Coates, 2002.
BI 0-1; Traces uncommon. Suite: O, Pa, D, fu. Facies-crossing forms, but probable <i>Skolithos</i> ichnofacies.	BI 0-1; ichnogenera uncommon. Suite: O, fu. Facies-crossing forms, but probable <i>Skolithos</i> ichnofacies.	Mixed river-wave influenced delta, but stronger storm and wave influences	Garrison et al., 1997. Suite augmented with unpublished data.

nels and mouth bars of the Panther Tongue (Table 1). Regional mapping of the Ferron delta lobes shows that the shorelines that were fed by the distributary channels lay about 15 kilometers seaward, demonstrating significant landward ingress of the salt wedge and accompanying marine faunal occupation of the lower delta plain (Garrison et al., 1997; Corbeau et al., 2004; Garrison and van den Berg, 2004). Bioturbation in these distributary channels, though sporadically distributed, contrasts with the much greater paucity of bioturbation associated with fully nonmarine rivers. In the subsurface of Alberta, Canada, distributary-channel deposits have been identified from the Dunvegan Formation and the Belly River Formation (Coates, 2001). The channels of the wave-dominated Allomember D lobes are largely unburrowed (BI 0-1) and display reworked, allochthonous *Rosselia* and *Asterosoma*. Mudstone beds display *Planolites* and *Teichichnus* with associated syneresis cracks. Dunvegan Allomember E chan-

nels of river-dominated lobes also have low bioturbation intensities (BI 0-2; mainly 0-1). The suite consists of small numbers of *Planolites*, *Teichichnus*, *Asterosoma* (allochthonous), *Palaeophycus* and *Ophiomorpha*. Mixed-influence Belly River distributary channels likewise show low bioturbation intensities (BI 0-2), with *Planolites*, *Skolithos* (though some are likely truncated *Rosselia* and *Cylindrichnus*), *Teichichnus*, *Cylindrichnus*, *Arenicolites*, and *Taenidium*.

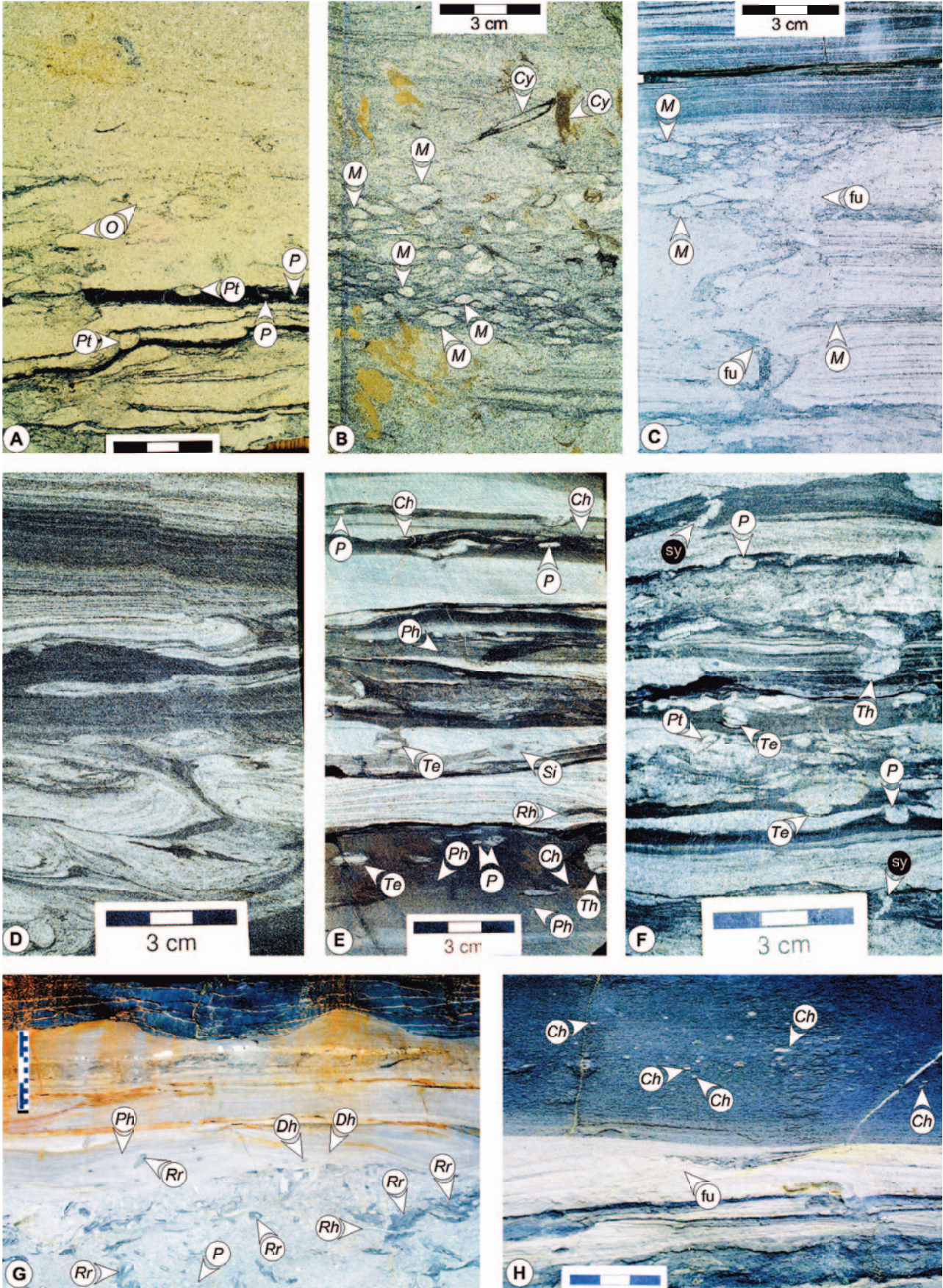
In contrast, channel sandstones of terrestrial settings generally show even less bioturbation, with biogenic structures typically confined toward channel-margin positions (Stagliano and Benke, 1996). Dominant tracemakers include vertebrates, terrestrial crustaceans, insects and their larvae, gastropods, bivalves, nematodes, and oligochaetes (e.g., Chamberlain, 1975). Such suites are markedly different from those of delta distributaries, and may include *Camborygma*, tetrapod dwellings, *Daimonelix*,

TABLE 2.—Case-study examples that address the ichnological characteristics of wave-, storm-, and tide-dominated delta deposits and their subenvironments. Abbreviations for trace fossils are given in Table 1.

Unit	Prodelta	Distal Delta Front	Proximal Delta Front
Denison Trough (Permian) Queensland, Au. Core & Outcrop	BI 0-5; typically \leq BI 3. Traces sporadically distributed. Suite: An/Ph, H, As, P, Ch, Ma, Te, Z, fu. <i>Cruziana</i> ichnofacies.	BI 0-5; generally < BI 4. Ichnogenera sporadically distributed. Suite: Ma, An/Ph, Te, Ro, Ch, Rh, As, Ps, P, Z, D (<i>D. habichi</i>), fu. <i>Cruziana</i> ichnofacies.	BI 0-4; generally BI 3 or less. Traces sporadically distributed. Suite: Ma, Gyr, An/Ph, P, Ro, Ch, D (<i>D. habichi</i>), fu. <i>Cruziana</i> ichnofacies.
Snapper Point Fm (Permian) NSW, Australia Outcrop Data	BI 0-5; typically \leq BI 2. Ichnogenera sporadically distributed. Suite: An/Ph, Te, Ch, D (<i>D. habichi</i>), P, Ro, Z, fu, Ta. <i>Cruziana</i> ichnofacies.	BI 0-6; mainly < BI 5; tempestites BI 0-2. Sporadic distributions in tempestites; more uniform in fair-weather beds. Suite: An/Ph, P, Te, He, Pa, D (<i>D. habichi</i> ; <i>D. parallelum</i>), Co, Ro, Ma, Ch, fu. Facies-crossing elements mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-4; tempestites < BI 2. Distributions sporadic in tempestites, uniform in fair-weather units. Suite: An/Ph, Pa, Ro, P, Rh, Te, D (<i>D. habichi</i> & <i>D. parallelum</i>), Ch, fu, Ta. Facies-crossing elements of mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.
Tarbert Fm (M. Jurassic) Norwegian shelf, Norway Core Data	BI 0-3; mainly BI 1-2. Sporadically distributed forms. Suite: P, D, fu. More marine intervals higher in the section contain Ma, Ch, D, H. Impoverished archetypal <i>Cruziana</i> ichnofacies.	BI 1-4; mainly BI 2-4. Sporadic distributions. Suite: O, Pa, Ro, Ma, bivalve e/a, fu. More marine intervals: cryptobioturbation, Ma, Sk, D, Sch, H. Facies-crossing elements of mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-2; BI 0-1. Traces sporadically distributed. Suite: Ro, Cy, O, D, Ma, Pa, fu, bivalve e/a, Sk, cryptobioturbation. Facies-crossing elements of the mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.
Tilje Fm (E. Jurassic) Norwegian shelf, Norway Core Data	BI 0-2; sporadically distributed traces, concentrated at pause planes. Suite: P, Te, fu, D. Rare Th, Si, Pa, Cy, Ch, An/Ph. Earlier work lists Sk, Be, Rh, Ta. Archetypal <i>Cruziana</i> ichnofacies.	BI 0-2; generally BI 0-1. Sporadically distributed forms, concentrated at pause planes. Suite: P, Pa, Te, An/Ph, Rh, Ch, Si, D, Sk. Rare Th, fu, Gy. Archetypal to proximal expression of <i>Cruziana</i> ichnofacies.	BI 0-1. Sporadic distributions; diminutive elements concentrated at pause planes. Suite: Te, Rh, Si, Pa, P, An/Ph, Sk, bivalve e/a, Gy, D, fu. Proximal expression of <i>Cruziana</i> ichnofacies.
Harlan, Posey, Willow (outcrops) Frontier Fm (U. Cretaceous) Wyoming, USA	BI 3-5. Uniformly distributed traces. Suite: diminutive Z, As, Pa, P, T, H, Te, Th, Ch, Sk. Distal expression of <i>Cruziana</i> ichnofacies	BI 3-5. Uniform distributions Suite: P, Pa, As, Sk, Ar, T, O, Pi, Ro, D (<i>D. habichi</i>), Lo, Th, Ch, Te, Rh, Z, H, bivalve e/a, fu. Archetypal <i>Cruziana</i> ichnofacies	BI 2-4; mainly BI 3. Somewhat sporadic distributions. Suite: Ma, Sk, O, D, habichi, Ar, Pi, bivalve e/a, P, Th, Te, Lo, Ch, fu. Proximal <i>Cruziana</i> to distal <i>Skolithos</i> ichnofacies.
Frewens–Frontier Fm (outcrop data) (U. Cretaceous) Wyoming, USA	BI 0-2; mainly \leq BI 1). Traces very sporadically distributed. Suite: P, Pi, bivalve e/a, Te, Th, Ch, Ter, fu. Highly impoverished <i>Cruziana</i> ichnofacies.	BI 0-1. Traces extremely sporadically distributed. Suite: Ar, O, Ter, Th, P, Cy, D, Lo, Z. Mainly facies-crossing elements defining <i>Cruziana</i> ichnofacies.	BI 0-1. Extremely sporadic distributions. Suite: O, Ma, Pa, Pi, Te, Sk, Ar, bivalve e/a, Lo, fu. Mainly facies-crossing elements of <i>Cruziana</i> ichnofacies.
Bow Island Fm (L. Cretaceous) Alberta, Canada Core Data	BI 4-5. Ichnogenera are uniformly distributed. Suite: H, Phy, Ro, Sk, Ar, Be, Ch, D, As, O, P, Rh, Te, T, Th, Z, An/Ph, Cy, Gyr, Ma, Pk, Pa, Si. Archetypal <i>Cruziana</i> ichnofacies.	BI 1-4; mainly BI 2-3. More sporadically distributed (storm-prone intervals). Suite: Be, Ch, Lo, P, Rh, T, An/Ph, As, H, Pa, Te, Th, Z, O (<i>O. irregulaire</i> & <i>O. nodosa</i>), fu. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 1-4; mainly BI 2-3. Traces show sporadic distributions in storm-prone intervals. Suite: An/Ph, As, H, Pa, O (<i>O. irregulaire</i> & <i>O. nodosa</i>), Te, Th, Z, fu. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.
Kenilworth Mbr Blackhawk Fm (U. Cretaceous) Utah, USA Outcrop Data	BI 2-3; though locally BI 4-5 bands. Sporadically distributed traces. Suite: H, P, Te, Pa, Ch, T, An, An/Ph, Lo. Archetypal <i>Cruziana</i> ichnofacies.	BI 2-5; mainly BI 2-3, tempestites BI 0-2. Sporadic distributions. Suite: O, Cy, Sch, Ro, P, Ch, Pa, T, Co, Rh, D, habichi, Th, Ar, Ma, An/Ph, H, As, Ter, Sk, fu. Suite records the mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-3; mainly \leq BI 2. Sporadic distributions. Suite: O, Cy, Sk, Ar, Ma, Co, bivalve e/a, Ro, Cy, fu, roots. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies to distal <i>Skolithos</i> ichnofacies.
Dunvegan Fm (Allomember D) (U. Cretaceous) Alberta, Canada Core Data	BI 1-3; rare bands BI 4. Traces sporadically distributed & diminutive. Suite: P, Te, An/Ph, H, Z, T, Ch, Cy, Si, As, Lo, Ro, fu. Tempestites with D, Sk. Archetypal <i>Cruziana</i> ichnofacies.	BI 0-4; mainly BI 0-3. Ichnogenera concentrated near tops of tempestites and diminutive. Suite: H, Z, An/Ph, Cy, P, Te, Pa, Th, T, Ro, Sk, D, fu. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-2; rare bands BI 5 with Ma in “toe of the beach” assemblage. Suite: Ma (<i>M. segregatis</i>), O, Ro, Cy, Sk, D, roots. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.
Wilcox Fm (U. Cretaceous) Texas, USA Outcrop Data	BI 1-5; variable intensity & distribution. Suite: An/Ph, H, Ch, T, P, Th, Pa, As, Z, Cy, Te, Pho, Ro, Sc, fu, Sk, O, Ta, D, Si. Archetypal <i>Cruziana</i> ichnofacies	BI 3-5; tempestites BI 0-3. Some sporadic distributions. Suite: An/Ph, H, Ch, As, Th, Pa, P, Cy, Z, Sc, fu, O, Te, T, Ro, Si, D, Sk, Ar. Proximal/archetypal <i>Cruziana</i> ichnofacies	BI 0-2; traces sporadically distributed. Suite: Sk, O, P, Ar, fu. <i>Skolithos</i> ichnofacies, but mainly facies-crossing elements.
Belly River Fm Allombr F,G,H (U. Cretaceous) Alberta, Canada Core Data	BI 0-3; sporadic distribution. Suite: H, An/Ph, P; less Ch, Te, T, Cy, fu; rare Z, Si, Ro, Th, Ar, Sk, fu (in tempestites). Archetypal <i>Cruziana</i> ichnofacies.	BI 0-2; rare bands of BI 2. Sporadically distributed. Suite: An/Ph, P, Te, As, Pa, truncated Ro, Ma. Lesser As, Cy, O, Sk. Rare Ar, fu, Te. Facies-crossing elements of mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-2; mainly BI 0-1. Very sporadic distribution. Suite: truncated Ro, O, Cy, Te, P, Ma, fu, roots. Uncommon Ar, Sk, Ta. Facies-crossing elements. Likely mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.
Ferron Sst. (U. Cretaceous) Utah, USA Outcrop Data	BI 1-3 Sporadic distribution; diminutive forms. Suite: An/Ph, H, Ch, P, T, As, Th, Te; storm bed: Cy, Pa, bivalve e/a, fu. Archetypal <i>Cruziana</i> ichnofacies.	BI 0-3 Sporadic distribution; diminutive. Suite: O, Cy, Th, Ar, As, Ro, Pa, An/Ph, Ch, P, H, Lo, bivalve e/a, Ter, fu. Proximal <i>Cruziana</i> to mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies.	BI 0-2, \leq BI 1; sporadic distributions; diminutive. Suite: Ar, Pa, D (<i>D. habichi</i>), O, Ro, Th, Sk, fu, bivalve e/a, Ter, ?Co, P. Mixed <i>Skolithos</i> – <i>Cruziana</i> ichnofacies

TABLE 2.—Continued).

Mouth Bar	Distributary Channel	Interpretation	References
BI 0-2. Traces sporadically distributed. Suite: Ma, Te, Pa, P. <i>Cruziana</i> ichnofacies.	Mainly unburrowed; rare BI 0-3. Distribution sporadic or concentrated at pause planes. Suite: Cy, D (<i>D. parallelum</i>). Facies-crossing elements; ichnofacies uncertain.	Interpreted as wave-dominated deltas with storm influence.	Bann & Fielding, in press
BI 0-1. Ichnogenera sporadically distributed. Suite: D (<i>D. habichi</i>), Ma, Ro. <i>Cruziana</i> ichnofacies	Not reported	Interpreted as storm-dominated deltas with strong wave influence.	Bann, 1998; Bann et al., in press
Not reported	BI 0-3; mainly BI 0-1. Traces uncommon; associated with pauses in deposition. Suite: Sk, Cy, D, fu. Rare Ma, Ro, Te, Pa, bivalve e/a. Facies-crossing elements of mixed <i>Skolithos-Cruziana</i> ichnofacies.	Interpreted as storm-dominated delta with wave influence, locally building into brackish-water embayments.	Løseth et al., 2001; MacEachern and Løseth, 2002. Suites augmented with unpublished data.
BI 0-1. Sporadically distributed traces. Suite: Pa, Sk, P, fu, Gyr, Ro. Facies-crossing elements; probable proximal expression of <i>Cruziana</i> ichnofacies.	BI 0-1. Ichnogenera uncommon. Suite: D, P, fu, Sk. Previous studies also identified Be. Facies-crossing elements of proximal <i>Cruziana</i> ichnofacies.	Interpreted as hyperpycnal-prone (fluid mud-rich) tide-dominated delta, with wave influences near distributary mouths.	Martinius et al., 2001. Suites augmented by unpublished data.
Not reported	Not reported	Interpreted as wave-dominated, weakly storm affected delta	Bhattacharya and Willis, 2001. Suite augmented by unpublished data.
Not reported	Not reported	Interpreted as strongly tide-dominated delta	Willis et al., 1999; Bhattacharya & Willis, 2001. Suites include unpublished data.
Not reported	Not reported	Interpreted as wave-dominated; storm-prone delta (upward increase in storm influence)	(Raychaudhuri and Pemberton, 1992; Raychaudhuri, 1993).
BI 0-1. Traces sporadically distributed. Suite: O, fu. Facies crossing forms but likely indicative of <i>Skolithos</i> ichnofacies.	Not reported	Interpreted as a storm-dominated delta with strong wave influences.	Pattison, 1995; Taylor & Lovell, 1995; Hampson & Howell, this volume. Suites with unpublished data.
Not reported	BI 0-1; burrows concentrated at pause planes. Sporadic distributions. Suite: P, Te, Ro. Facies-crossing suite; ichnofacies uncertain.	Interpreted as a storm-dominated delta with strong wave influence.	Bhattacharya, 1989; Gingras et al., 1998; Coates & MacEachern, 1999; MacEachern & Coates, 2002.
Not reported	Not reported	Wave-dominated delta with moderate to strong storm influences.	Weise, 1980; Tyler et al., 1986. Suites augmented with unpublished data.
Not reported	BI 0-1; sporadically distributed traces. Suite: P, Sk, Te, Cy, Ta, Ar. Facies-crossing forms, but possible <i>Skolithos</i> ichnofacies.	Mixed river-wave influenced delta; more wave and storm influenced.	Coates & MacEachern, 1999, 2000; Coates, 2001; MacEachern & Coates, 2002.
BI 0-1; Traces uncommon. Suite: O, Pa, D, fu. Facies-crossing forms, but probable <i>Skolithos</i> ichnofacies.	BI 0-1; traces uncommon. Suite: O, fu. Facies-crossing forms, but probable <i>Skolithos</i> ichnofacies.	Mixed river-wave influenced delta, but stronger storm and wave influences	Garrison et al. 1997. Suites augmented with unpublished data.



adhesive meniscate burrows, *Scopenia*, *Cochlichnus*, *Planolites*, *Coprinisphaera*, *Ancorichnus*, *Macanopsis*, various trackways and flying traces (Voorhies, 1975; Smith, 1987; Groenewald et al., 2001; Hasiotis, 2002), depending upon organism responses to different stresses in the continental setting (e.g., soil moisture, water-table position, water clarity and salinity, oxygen richness, wind, temperature, precipitation, etc.; Hasiotis and Bown, 1992; Hasiotis, 1997, 2002).

Water Turbidity.—

Hypopycnal conditions commonly result in development of buoyant mud plumes that extend from the delta front to the prodelta region. Where the suspended load is held high above the sediment–water interface, and where suspension fallout is low, there is probably little detrimental effect on infaunal feeding strategies. However, high suspended loads in the water column near the sea floor ultimately preclude suspension-feeding behaviors in infaunal communities (Perkins, 1974). Heightened water turbidity interferes with filter-feeding behaviors of suspension-feeding organisms. On one hand, turbid conditions serve to clog the filter-feeding apparatus of the organism. In addition, high suspended loads lower the overall concentration of food resources available to the fauna. Suspension feeders must therefore process a higher volume of inorganic clastic debris in order to acquire food resources. At some critical concentration, which varies for different species, suspension feeding is precluded. Consequently, despite the availability of sandy substrates, biogenic structures are overwhelmingly those reflecting deposit-feeding behaviors (e.g., Fig. 3A, B). Empirical observations of inferred delta complexes strongly support this relationship, though the modern basis for this model has yet to be rigorously tested.

Most studies of animal / sediment relationships in turbid settings have been from inshore tidal environments. In these settings, increased suspended-sediment concentrations are only one of a number of physicochemical stresses. Additional stresses

imposed on infauna include salinity reductions, salinity fluctuations, periodic subaerial exposure, temperature changes, substrate consistency variations, and energy fluctuations. Howard et al. (1975), for example, conducted detailed studies of infauna of several tidal point bars of the modern Ogeechee River–Ossabaw Sound Estuary of the Georgia coast. Their work demonstrated that Point Bar 3, which showed the highest water turbidities of the entire estuary reach (corresponding to the turbidity maximum), showed a marked reduction in infaunal diversity and abundance. Bar 3 showed a decrease from 11 species with abundances averaging 1460 individuals/m² in the more seaward-lying Bar 2 to a mere three species (one amphipod and two polychaetes) with abundances of 740 individuals/m². Most of this reduction was attributed to salinity reduction, increased range in salinity change, and temperature variations during the tidal cycle (Howard et al., 1975). However, Bar 4, which lies immediately landward of Bar 3 and shows further salinity reductions, contains seven species with abundances averaging 1240 individuals/m². Even Bar 5, lying in the most landward position studied and with the lowest-salinity conditions of all, shows the persistence of four species with abundances of 3973 individual/m². Given that water turbidity is the other principal factor that differs between Bar 3 and those bars lying proximal and distal of it, it is possible that the anomalously low diversity and abundance of infauna there may be attributed to the impact of the turbidity maximum on infaunal colonization.

Such turbid water conditions contrast with those persisting in strandplain, wave-dominated shoreface systems. Impoverishment of *Skolithos* ichnofacies elements and abundance of structures produced by deposit-feeding organisms, referable to the *Cruziana* ichnofacies, have been used as one of the diagnostic indicators of deltaic conditions (e.g., Moslow and Pemberton, 1988; Gingras et al., 1998; Coates and MacEachern, 1999, 2000). Buatois and Angriman (1992) also recognized the predominance of deposit-feeding structures associated with high-water-turbidity settings in the submarine-fan deposits of the Cretaceous

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FIG. 3 (opposite page).—River-induced stresses: suppression of *Skolithos* ichnofacies, rapid deposition, and hyperpycnal mud drapes. **A**) Sandy delta-front deposit with an absence of suspension-feeding structures and a predominance of facies-crossing elements. Note the dark, probable hyperpycnal mud drape in the lower third of the photo. Trace fossils include *Ophiomorpha* (O), *Planolites* (P), and *Palaeophycus tubularis* (Pt). Oseberg Formation, well 30/6-22, 2985.3 m, Oseberg South Field, Norwegian Shelf, Norway. **B**) Clean sandy tempestites of the delta front lacking suspension-feeding structures. The interval is dominated by *Macaronichnus simplicatus* (M), an intrastratal deposit-feeding structure, and *Cylindrichnus* (Cy), a dwelling structure of an inferred trophic generalist. Dunvegan Formation (Allomember D), well 07-10-63-01W6, 1974.5 m, Alberta, Canada. **C**) Tempestite emplaced in wave/storm-dominated lobe. Biogenic structures are restricted to fugichnia (fu) and the intrastratal deposit-feeding structure *Macaronichnus simplicatus* (M). Note the dark, fissile, unburrowed mud drape capping the event bed. Freitag Formation, Yandina Core 4, 628 m, Denison Trough, Queensland, Australia. **D**) Soft-sediment deformation in the distal delta front of a river-dominated lobe. Gravity faults and convolute bedding are apparent. The unit is unburrowed. Dunvegan Formation (Allomember E), well 13-25-60-22W5, 1958.4 m, Alberta, Canada. **E**) Tempestites from the prodelta of a wave/storm-dominated lobe, with dark, carbonaceous mudstone drapes. BI values range from 1 to 2. Traces include *Chondrites* (Ch), *Planolites* (P), *Anconichnus/Phycosiphon* (Ph), *Teichichnus* (Te), *Siphonichnus* (Si), *Rhizocorallium* (Rh), and *Thalassinoides* (Th). Dunvegan Formation, (Allomember D), well 10-33-60-05W6, 2835.9 m, Alberta, Canada. **F**) Tempestites draped by dark, carbonaceous, probable hyperpycnal muds in the distal delta front of a wave/storm-dominated lobe. BI 2–3. Presence of synaeresis cracks (sy) suggest freshet emplacement of some layers. Trace fossils include *Planolites* (P), *Thalassinoides* (Th), *Teichichnus* (Te), and *Palaeophycus tubularis* (Pt). Dunvegan Formation (Allomember E), well 11-05-63-26W5, 1961.9 m, Alberta, Canada. **G**) Laminated to burrowed bedding in the delta front of a wave/storm-dominated lobe. Note the bioturbated top of the underlying tempestite, erosionally truncated by the overlying tempestites. Note also the dark, fissile, unburrowed mudstone drape capping the tempestite. The underlying tempestite shows BI 5, whereas the overlying tempestite is virtually unburrowed. The underlying suite lacks suspension-feeding structures and is characterized by *Diplocraterion habichi* (Dh), *Rosselia rotatus* (Rr), *Rhizocorallium* (Rh), *Planolites* (P), and *Phycosiphon* (Ph). Permian Wasp Head Formation, South Pebbles, Southern Sydney Basin, Australia. **H**) Tempestites capped by black, fissile, carbonaceous and weakly burrowed mudstone in the distal delta front of a wave/storm-dominated lobe. The lower part of the photo displays BI 1, with fugichnia (fu) characteristic. The dark mudstone drape contains deep-tier *Chondrites* (Ch). Snapper Point Formation, South Snapper Point, Southern Sydney Basin, Australia.

Whisky Bay Formation of Antarctica. Gingras et al. (1998) speculated that *Skolithos* ichnofacies elements, particularly those reflecting suspension feeding, were even less common in distributary-mouth-bar deposits and proximal delta-front sandstones of river-dominated delta lobes, on the basis of their preliminary assessment of the Dunvegan Formation (Table 1). Deltaic successions of the Wall Creek Member (Gani et al., 2004; Howell et al., 2004), the Norwegian Tarbert Formation (MacEachern and Løseth, 2003) and Oseberg Formation (Soegaard and MacEachern, 2003), the Kenilworth Member, Utah (Hampson and Howell, this volume), Permian examples from the Denison Trough, Australia (Bann and Fielding, 2004), and others observed by the authors show comparable levels of *Skolithos* ichnofacies element impoverishment (Tables 1, 2).

Microfossil studies have shown that high water turbidity also limits primary productivity, particularly in more proximal delta positions (e.g., Nix-Morris, 1996; Leithold and Dean, 1998), which could impose a food impoverishment upon both suspension-feeding and deposit-feeding infauna. If mud plumes are allowed to disperse seaward, they tend to be dilute and probably do not exert a strong influence. Analysis of microfossils from prodelta mudstones of the Turonian Tununk and Tropic Shale Member, for example, show that primary productivity persisted in the bottomset prodelta areas, even though mud-plume sedimentation occurred (Leithold and Dean, 1998). In settings where the mud plumes are held as coherent masses and banked up along the delta front, or forced back on shore by waves, storm surge, or tidal flux, however, hypopycnal mud plumes could preclude biogenic activity in the area. This is characteristic of deposition in muddy chenier plains, such as those that exist along the Louisiana coast downdrift of the Mississippi delta (Penland and Suter, 1989).

In wave-swept substrates, clay may be winnowed from the bed, but it remains suspended in the overlying water column, inhibiting suspension-feeding behaviors. This leads to the apparent paradox of clean sandy substrates dominated by structures produced by deposit feeders—the persistent occurrence of such a scenario may be a strong indicator of deltaic conditions. This is particularly apparent as an empirical observation from delta-front sandstones of several wave- and storm-influenced delta front intervals (Table 2). In several intervals, however, strong storm overprinting of the facies succession masks the significance

of this impoverishment. Such storm-dominated intervals commonly show low bioturbation indices (BI0–2) and low trace-fossil diversities, making the absence of *Skolithos* ichnofacies elements less apparent. This is also the case in prodelta deposits, where thin tempestites are interstratified with mudstone drapes and bioturbated silty mudstone beds (Fig. 3E–H). In strandplain shoreface settings, offshore deposits in comparable depositional positions commonly display *Skolithos* ichnofacies elements as opportunistic colonizers of the tempestites, subsequently superseded by deposit-feeding and grazing structures of the resident community (e.g., Pemberton and Frey, 1984; Pemberton et al., 1992a; Pemberton et al., 1992b; Pemberton and MacEachern, 1997). In prodelta settings, tempestites are either generally unburrowed or display ichnogenera recording only deposit-feeding and grazing behaviors (Fig. 3E, F). This may be due to rapid mantling of the event beds by mud layers and/or turbid post-storm conditions that inhibit successful colonization of the sea bottom by suspension-feeding opportunists (Fig. 3G, H).

Spatially, variations in water turbidity along the delta front are controlled by waves and tidal flux on the hypopycnal plumes. Temporally, variations reflect changes in storm frequency, seasonal (or longer term; e.g., El Niño-type climatic oscillations) precipitation events, and fluvial discharge (also possibly seasonal). In addition, temporarily stored mud from such surface plumes along the delta front is also especially susceptible to resuspension and downslope transport as hyperpycnal mud turbidites (e.g., Wright et al., 1990; Cacchione et al., 1995).

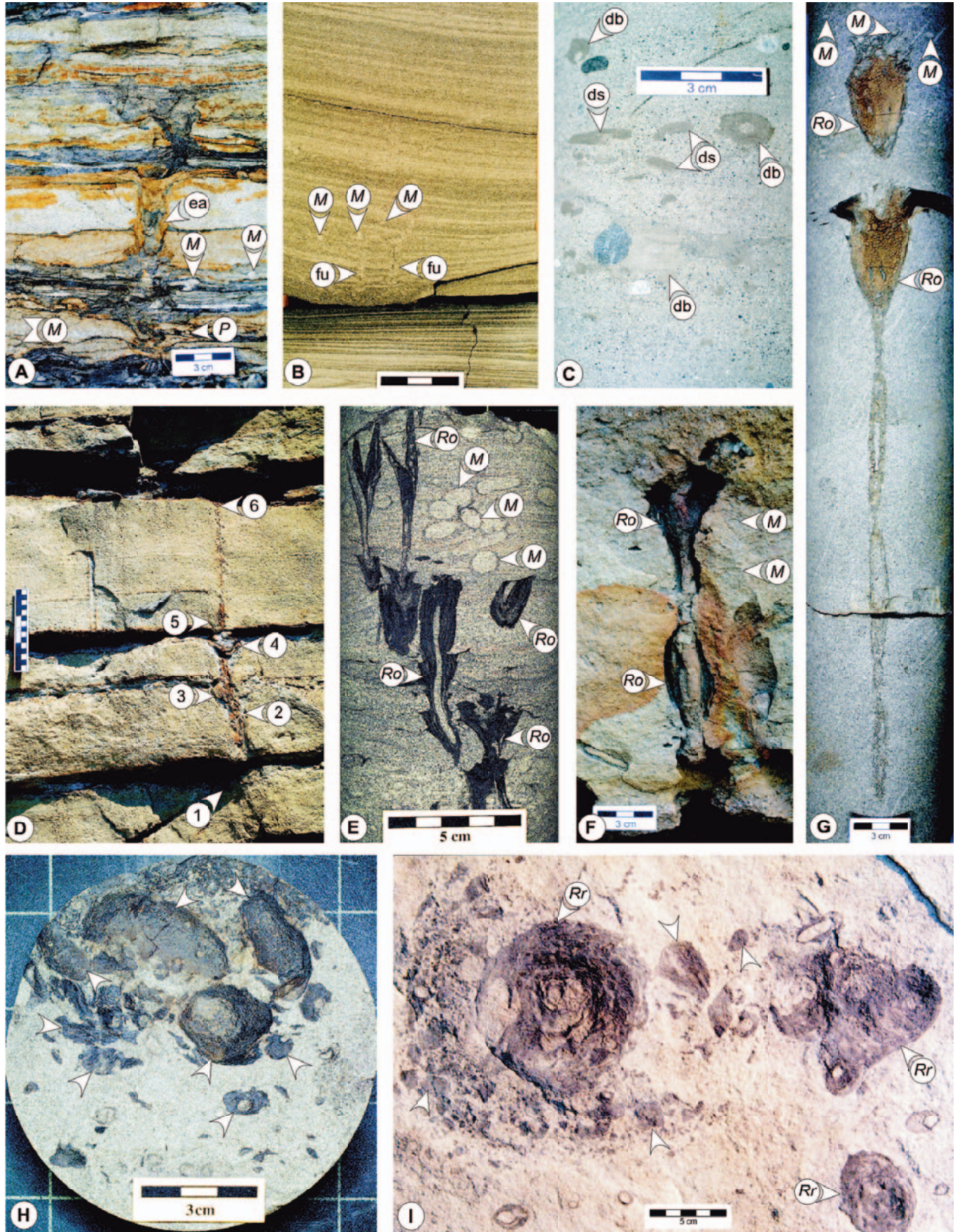
Although the turbidity model appears entirely reasonable, the spatial distributions of associated infaunal behaviors along discrete delta lobes have yet to be rigorously evaluated on either modern or ancient delta systems. In a rare exception, Hampson and Howell (this volume) used lateral variations in ichnology to identify fluvially stressed, deltaic regions along an otherwise wave-dominated, prograding strandplain in the Kenilworth Member of the extensively studied Book Cliffs of Utah (e.g., Van Wagoner, 1995; Pattison, 1995; Taylor and Lovell, 1995).

Rapid Sediment Influx.—

There is a long-recognized direct correlation between increasing sedimentation rate and declining bioturbation intensity (e.g.,

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FIG. 4 (opposite page).—River-induced stresses: responses to episodic deposition. **A**) Rapid, episodic emplacement of sediment in the distal delta front. Burrowing is confined to narrow horizons giving sporadic distribution of bioturbation, ranging from BI 0 to 3. Bivalve equilibrium-adjustment structure (e-a) indicates multiple shifts of the tracemaker. The suite also includes *Macaraoichnus simplicatus* (M) and *Planolites* (P). Willow Member, Frontier Formation, Wyoming. **B**) Rapid deposition of an event bed (tempesteite) in a wave/storm-dominated delta front. Parallel-laminated sandstone displays multiple fugichnia (fu), *Macaraoichnus segregatis* (Ma), and probable cryptobioturbation, creating subtle “fuzzy” lamination above. Tarbert Formation, well 30/9-10, 2858.9 m, Norwegian Shelf, Norway. **C**) Tempesteite in the proximal delta front, with allochthonous *Rosselia* fragments manifested by detrital shafts (ds) and detrital mud balls (db). Notikewin Member, well 08-15-67-11W6, 2464 m, Alberta, Canada. **D**) Rapid and high-frequency emplacement of turbidite beds in the delta front has required a single infaunal organism to readjust its structure (*Rosselia*) at least five times (from position 1 to position 6). Wall Creek Member, Murphy Reservoir, Wyoming, USA. **E**) High-frequency tempesteite emplacement that has resulted in readjustment of several *Rosselia socialis* (Ro). Note the associated *Macaraoichnus simplicatus* (M), a common constituent of wave- and storm-dominated delta-front deposits. Bluesky Formation, well 07-27-72-13W6, 2144.5 m, Alberta, Canada. **F**) Tempestites in a wave/storm-dominated delta front, showing stacked *Rosselia socialis* (Ro) and associated *Macaraoichnus simplicatus* (M) in the distal delta front. Snapper Point Formation, North Snapper Point, Southern Sydney Basin, Australia. **G**) Stacked *Rosselia socialis* (Ro) with associated *Macaraoichnus simplicatus* (M) in a mixed river and wave influenced delta front, Belly River Fm, well 10-19-43-27W4, 941.2 m, Alberta, Canada. **H**) Bedding-plane view of core showing reworked *Rosselia* mud balls (arrows) strewn as a lag in a tempesteite. Cadotte Member, well 10-01-68-09W6, 2050.5 m. **I**) Bedding-plane view of outcrop, showing *in situ* *Rosselia rotatus* (Rr) truncated at different levels within the burrow. The large *Rosselia rotatus* has scattered allochthonous mud-ball debris (arrows) surrounding it. Snapper Point Formation, South Snapper Point, Southern Sydney Basin, Australia.



Howard, 1975; Leithold, 1993, 1994; Leithold and Dean, 1998). Increased deposition rates make it difficult for permanent domiciles to be constructed and maintained, reduce the concentration of food resources per unit volume of sedimentary debris at the sea floor, and rapidly bury sedimentary material beyond the reach of even deep-probing deposit feeders (e.g., *Chondrites* and *Zoophycos* tracemakers). Although such stresses are not uncommon to many depositional environments, they tend to be pronounced in settings such as river-dominated deltas and submarine fans. In both settings, rapid deposition is also commonly associated with emplacement of event beds (turbidites, tempestites, phytodetrital pulses), and is accompanied by soft-sediment deformation, including loading, convolute bedding liquefaction, dish and pillar structure, and other dewatering phenomena (Fig. 3C, D). In deltaic settings, such increases in depositional rates are commonly associated with increasing proximity to the delta front, and are observed in most modern subaqueous deltas (e.g., Nittrouer et al., 1986; Kuehl et al., 1986a, 1986b; Alexander et al., 1991).

Heightened sedimentation affects bioturbation in several ways. Most event beds have a number of common characteristics: the onset, culmination, and waning of water turbulence; distinctive erosional and depositional structures; and redistribution of organic and inorganic material, both vertically through the bed and spatially along the depositional gradient (Seilacher, 1982a). More importantly, they change the ecological situation for benthic organisms by altering the consistency of the substrate and/or the food content of the local sea floor for a biologically significant period of time after the event. This profoundly influences the nature of infaunal behavior and, consequently, the ichnological record they leave behind.

Classical ichnological models of incremental event-bed deposition have been established for both tempestite and turbidite successions (e.g., Seilacher, 1962, 1982a, 1982b, 1991; Crimes, 1973, 1977; Howard and Frey, 1984; Pemberton and Frey, 1984; Frey, 1990; Seilacher and Aigner, 1991; Frey and Goldring, 1992; Pemberton and Maceachern, 1997). Many robust organisms are able to move through the event bed, either via escape structures (fugichnia) or readjustment (e.g., Fig. 4A, B). Some tracemakers are able to repeatedly shift their structure to the new sediment-water interface, keeping pace with episodic deposition. This is particularly true for the tracemaker(s) of *Roselia* (e.g., Fig. 4D–G). Such structures are also particularly prone to erosional truncation and the transport and deposition of their elements as

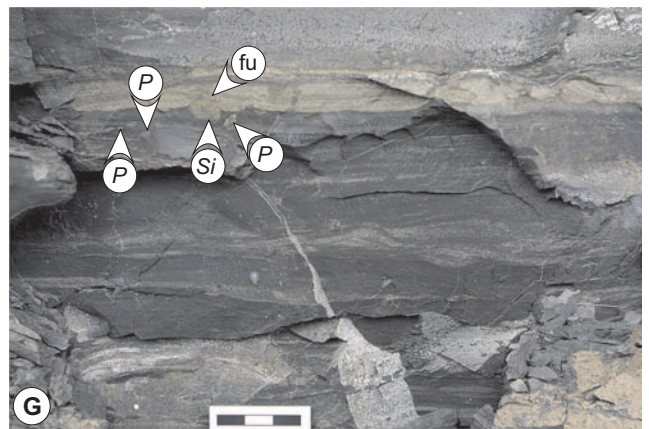
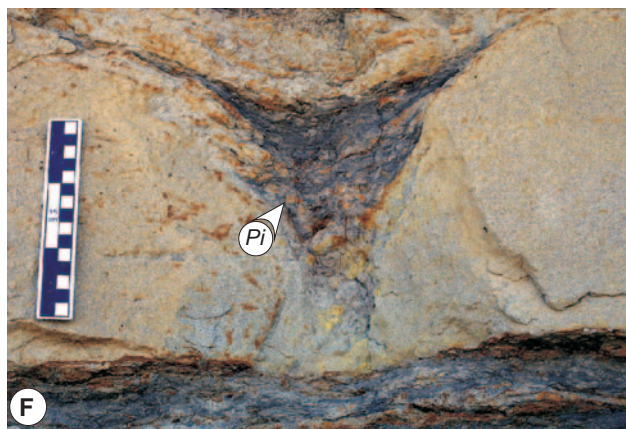
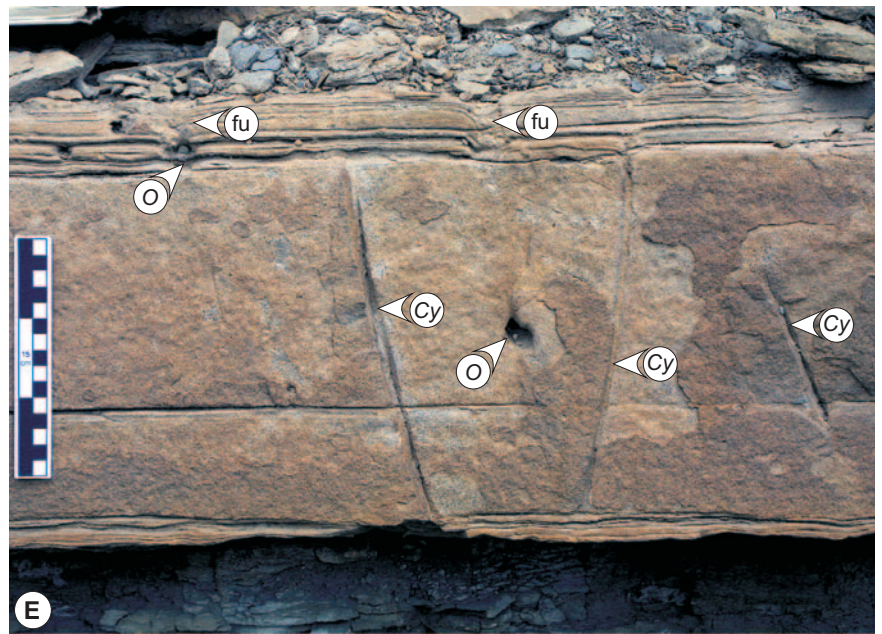
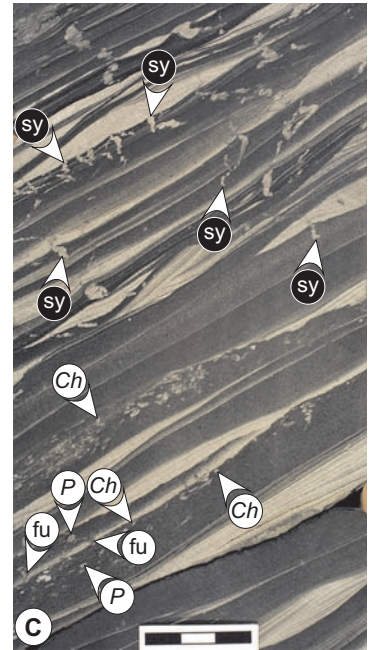
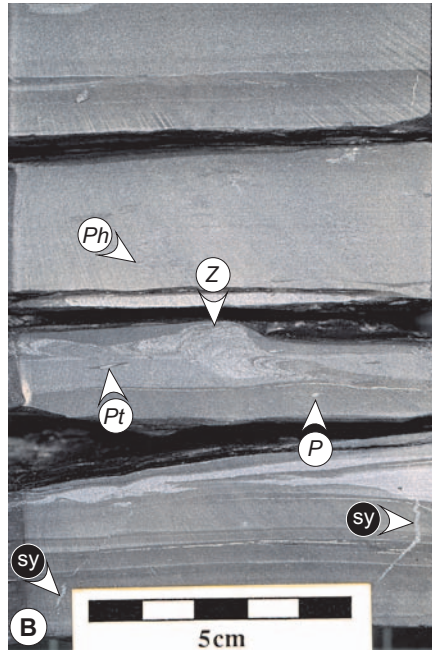
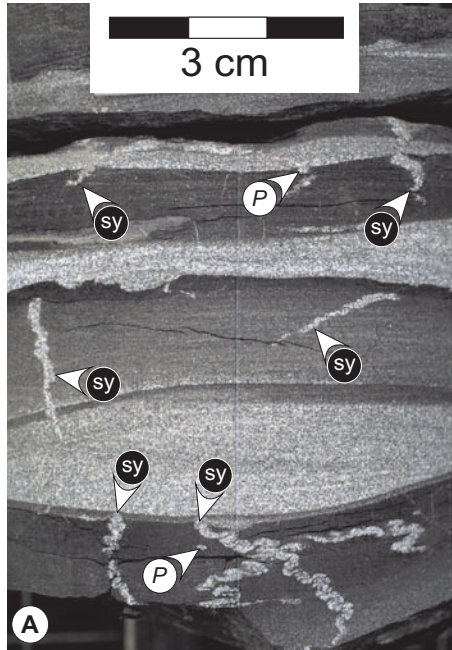
lags in sediment-gravity-flow deposits and tempestites (e.g., Fig. 4C, H, I).

Rapid sediment emplacement associated with thick beds typically denudes the substrate and limits the ability of buried infauna to reach the new sediment–water interface via fugichnia (escape structures). As such, recolonization occurs principally through new larval settling (Sousa, 1984; Whitlatch and Zajac, 1985). Where deposition rates are persistently high, or sediment emplacement is less predictable, recolonization by these means may be insufficient to yield biogenic structures. This is exacerbated in settings where the lithologic contrast between the event beds and the ambient fair-weather beds are greatest. Resident infauna may find it impossible to occupy an anomalously sandy or muddy substrate, and the seafloor may remain uncolonized or colonized only by facies-crossing opportunistic forms until the event bed is finally buried under ambient sediment. Finally, settings characterized by long periods of environmental stability are dominated by K-selected communities, which are in balance with the carrying capacity of the environment (cf. Jumars, 1993). K-selected communities tend to be more adversely affected by the physiological stresses associated with event deposition, and recover slowly (cf. Dauer and Simon, 1976; Jern lou and Rosenberg, 1976; Grassle, 1977). Such conditions presumably reach a maximum in deep-sea (neritic to abyssal) turbidite-bearing successions, but they also are likely significant in prodelta and distal delta-front settings prone to event-bed emplacement.

Stable, distal settings are also typically characterized by much lower infaunal recolonization rates than that of shallow marine and estuarine environments (e.g., Grassle and Grassle, 1974; Grassle, 1977; McCall, 1977; Sousa, 1984; Whitlatch and Zajac, 1985). In an experimental defaunation study of the deep sea at 1760 m, McCall (1977) demonstrated that in two months a first colonist, *Priapulid atlantsi*, arrived, but that the second colonist, *Capitella* sp., did not arrive until 28 months later. In offshore settings (between fair-weather and storm wave base), the recolonization rate appears to be closer to six months (e.g., Thistle, 1981; Bonvinci Paglial et al., 1985). Storm-induced defaunation, in contrast, appears to be associated with significantly more rapid recolonization rates (approximately two months) (Boesch et al., 1976; Rees et al., 1977; Berry, 1989), probably because in high-latitude settings where storm seasons are more predictable, many infauna schedule their larval dispersal to coincide with the storm period (Hannan, 1984; Jumars and Nowell, 1984; Butman, 1987).

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FIG. 5 (opposite page).—River-induced stresses: freshets, phytodetrital pulses, and delta-front turbidites. **A**) Hyperpycnal muds in the prodelta of a river-dominated lobe. The abundant synaeresis cracks (sy) suggest salinity contrast near the bed, probably associated with freshet-induced sediment-gravity emplacement. The unit shows BI 0-1 with isolated *Planolites* (P). Dunvegan Formation (Allomember E), well 05-27-61-01W6, 2432.4 m, Alberta, Canada. **B**) Freshet-emplaced hyperpycnal muds in the prodelta of a wave/storm-dominated lobe. Note the well developed syneresis crack (sy) intercalated with *Zoophycos* (Z), *Anconichmus* / *Phycosiphon* (Ph), *Planolites* (P), and *Palaeophycus tubularis* (Pt). Dunvegan Formation (Allomember D), well 07-10-63-01W6, 1980.4 m, Alberta, Canada. **C**) Prodelta deposits with abundant synaeresis cracks (sy) associated with probable freshet-related deposition. Unit shows a highly impoverished trace fossil suite consisting of *Chondrites* (Ch), *Planolites* (P) and fugichnia (fu). Tarbert Formation, well 30-9-B27, 3157.9 m, Norwegian Shelf, Norway. **D**) Clean sandy event bed of sediment-gravity origin on the delta front. Note that the sandstone is unburrowed and draped by a thick bed of organic detritus, interpreted to reflect a phytodetrital pulse. Basal Belly River Formation, well 04-22-47-03W5, 1045.5 m, Alberta, Canada. **E**) Delta-front turbidite with *Cylindrichnus* (Cy), *Ophiomorpha* (O), and fugichnia (fu), Panther Tongue, Utah. **F**) Robust *Piscichnus* (Pi), a fish feeding structure, at the top of a delta-front turbidite, Wall Creek Fm, Wyoming. **G**) Highly impoverished suite consisting of *Planolites* (P), fugichnia (fu), and *Siphonichnus* (Si) in prodelta mudstones. Note the dark, generally unburrowed (BI0–1) character of the mudstone. Ferron Sandstone, Utah.



Hyperpycnal Conditions: Episodic Sediment Gravity Deposition, Organic Mud Drapes, Oxygen Reduction, and Salinity Changes

Hyperpycnal discharge generally leads to event-style deposition. Dense sediment gravity flows, generally with high concentrations of entrained sediment, are commonly seasonal and linked to river flood stages (Mulder and Syvitsky; 1995, Leithold, 1989). Many of these events may be linked to freshets and increased phytodetrital influx into the setting (e.g., Fig. 5). Storm events may also be succeeded by sediment-gravity hyperpycnal discharge, because of concomitant heightened precipitation and increases in sediment concentration at times of peak flood discharge. Hyperpycnal conditions are inferred to be common in small rivers draining mountainous terrains in humid climates (e.g. the northern coast of California) and may have characterized many rivers draining into the Cretaceous Western Interior (Bhattacharya and Tye, 2004). Similar situations have been recognized from the larger-scale Huanghe and Yangtze deltas, where fine-grained sediment deposited from sediment plumes in front of the river mouth are resuspended by tidal currents and storm events and transported basinward via turbidity currents (Wright et al., 1990). Most of the sediment reaches the more distal parts of the delta front through hyperpycnal processes. A comparable scenario was described by Cacchione et al. (1995) from the subaqueous part of the Amazon Delta. Leithold and Dean (1998) proposed a similar mechanism to explain the presence of mud turbidites in prodelta deposits of the Turonian Tununk and Tropic Shales, in the Western Interior Seaway of Utah.

Delta-Front Sediment Gravity Flows.—

Bedload-dominated, hyperpycnal-discharge sediment gravity flows are common to many coarse-grained deltas (e.g., Prior and Bornhold, 1989, 1990; Nemeč, 1990; Postma, 1990; Burns et al., 1997; Ulicny, 2001; Soria et al., 2003), and range from grain flows to turbidity flows. Sandy sediment gravity flows may reflect hyperpycnal conditions, or gradual buildup and failure of sediment deposited in terminal distributary channels and mouth bars (Mulder and Syvitsky, 1995, Mulder et al., 1996). Failure may be triggered by the simple instability of an aggrading bar that reaches a threshold slope, or by earthquake-induced seismic shock. In hyperpycnal-flow-prone settings, hyperpycnal conditions may persist for days or weeks, reflecting the persistence of storm or seasonal floods (e.g., monsoonal rains). Sandy delta-front turbidites, associated with hyperpycnal conditions, tend to show stacked amalgamated bedsets of alternating Bouma AB, BC, or more complete ABCDE beds (Plink-Björklund and Steel, this volume, Kneller and Branney, 1995).

Bar-failure deposits are more likely to consist of single beds of poorly stratified grain-flow deposits, characterized by massive to planar parallel lamination (Bouma A–B cycles), with or without suspension-fallout drapes. Beds may range markedly in thickness, and are commonly erosionally amalgamated into thick bedsets. Coarse-grained deltaic intervals show considerable numbers of such grain-flow deposits (e.g., the Upper Jurassic Oseberg Formation; Soegaard and MacEachern, 2003). Suspended-sediment deposition (or at least its preservation) is minor or absent in these deposits. Rapid emplacement of sandstone beds generally makes infaunal colonization of the substrate difficult. Mobile substrates are challenging to colonize. In addition, high-frequency emplacement of beds tends to limit colonization, resulting in overall lowered BI values (e.g., Fig. 3E, F, G; Fig. 4B, D; Fig. 5A, D–G). Suites range from *Skolithos* ichnofacies elements to the high-energy expressions of the *Cruziana* ichnofacies. The delta-

front foresets of the Oseberg Formation, for example, show avalanche grain-flow beds burrowed by a low-diversity suite dominated by *Cylindrichnus*, *Palaeophycus*, *Rosselia*, *Diplocraterion*, and fugichnia, with lesser *Asterosoma*, *Ophiomorpha*, *Planolites*, and *Skolithos*, reflecting a proximal expression of the *Cruziana* ichnofacies (Table 1).

Where sediment gravity flows are triggered by earthquakes, we suppose that the timing between successive events is typically much longer (hundreds to tens of thousands of years) than those associated with seasonal floods. Clearly, in earthquake-driven deposits the greater time between events would allow total recolonization of the substrate. We also assume that storm-derived event beds would occur at a much higher frequency (months to decades) than earthquake-triggered sediment gravity flows, although these may coincide with so-called hundred-year floods.

Hyperpycnal conditions in mixed-load delta settings lead to the development of sand-prone delta-front turbidites. Such event beds are characterized by Bouma cycle development, dominated by Bouma BCE but also locally by ABCE and CDE beds. Sediment-gravity emplacement of event beds acts in a fashion broadly comparable to that of tempestite emplacement (Seilacher, 1982a). Depending upon the magnitude of contrast between the ambient conditions and the event-bed substrate, resulting ichnological suites can be expected to vary from *Zoophycos* or distal expressions of the *Cruziana* ichnofacies alternating with the archetypal *Skolithos* ichnofacies in distal positions, to the archetypal *Skolithos* ichnofacies alternating with opportunistic expressions of the *Skolithos* ichnofacies. The greater the contrast between the consistency of the fair-weather substrates and event-bed substrates, the weaker are the bioturbation intensities of the event beds, and trace-fossil distributions are more sporadic. In many instances, bioturbation may be confined largely to pauses in deposition between the event beds, with the event beds themselves being unburrowed (Fig. 5D), or displaying only fugichnia and facies-crossing elements such as *Ophiomorpha*, *Cylindrichnus*, *Rosselia*, *Diplocraterion*, and *Arenicolites* (e.g., Fig. 4D; Fig. 5E, F). Numerous outcrop examples show cone-like excavations in the turbidites, passively infilled with muddy sand and sandy mudstone, interpreted as *Piscichnus*, a fish feeding structure reflecting top-down modification of the substrate by mobile nektonic elements (Fig. 5F). Several others display bivalve equilibrium adjustment structures. Delta-front turbidite successions in the Wall Creek Member of Wyoming (Howell et al., 2004; Gani et al., 2004) and from the Panther Tongue of Utah (Olariu and Bhattacharya, this volume) display comparable suites (Table 1).

Careful analysis of trace-fossil suites associated with the delta-front turbidites in the Wall Creek Member of Wyoming shows that vertical accretion rates can be high in proximal positions. Most soft-bodied infauna probably have estimated life spans of 1–2 years, and therefore their structures can help to constrain sedimentation rates (e.g., Howell et al., 2004). Multiple reestablishment of the same causative burrow has been identified from several stacked turbidite beds, indicating that emplacement of up to 2 meters of sediment occurred during a single trace-maker's life span (Fig. 4D). In several ancient examples, persistent reestablishment of *Ophiomorpha*, *Diplocraterion*, *Rosselia*, and *Cylindrichnus* have been recorded in facies characterized by rapid sediment-gravity emplacement. Fossilized bivalves record life spans of 5–10 years, and help to constrain sedimentation rates in quiescent interdistributary facies. Howell et al. (2004) were able to estimate that basinward delta front progradation in a low-accommodation setting occurred at magnitudes of 10–24 m per year, with vertical accretion rates of up to 1 m per year. Further, they indicated that these time constraints are conservative, given

that most observable traces appear to have been produced during the adult stages of the tracemaker's existence.

Fine-grained turbidites (i.e., mud turbidites; cf. Piper, 1978; Stow and Shanmugam, 1980; Stow and Piper, 1984; Stow et al., 1984) consist of thin, commonly loaded sandstone and siltstone stringers at the base of the bed, passing into graded silty claystones with discontinuous siltstone laminae. In the ideal model, the upper margins may show burrowing, though the specifics of the trace-fossil suites were not indicated. Values of bioturbation index range from 0 to 3, though most units show BI of 2 or less. Deep-sea examples carry the *Zoophycos* and *Nereites* ichnofacies, consisting of *Zoophycos*, *Chondrites*, *Thalassinoides*, *Anconichnus*/*Phycosiphon*, *Cosmorhaphie*, *Nereites*, *Scolicia*, *Taphrhelminthopsis*, *Lorenzina*, and *Paleodictyon* (e.g., Seilacher, 1962; Ekdale, 1980; Pickerill, 1980; Crimes, 1973, 1977; Crimes et al., 1981; Leszczyński and Seilacher, 1991; Miller, 1991a, 1991b; Leszczyński, 1993; Crimes and Fedonkin, 1994).

Muddy prodelta sediment-gravity-flow-deposits (tautology?) show lithologies and physical sedimentary structures similar to those of deep-water turbidites, such as weakly burrowed (BI 0–2), laminated mudstones and sandstones with abundant soft-sediment deformation structures. Shallow prodelta shelf turbidites, however, contain trace-fossil assemblages atypical of deep-sea settings and characteristic of archetypal to distal expressions of the *Cruziana* ichnofacies. The shelf suites are characterized by very low numbers of *Anconichnus*/*Phycosiphon*, *Planolites*, *Helminthopsis*, *Asterosoma*, *Chondrites*, *Teichichnus*, and very rare *Zoophycos*.

Many of these muddy delta-front turbidites are also capped by thin layers of dark, silt-poor, carbonaceous mudstone, interpreted to reflect settling of terrestrial organic debris (e.g., Fig. 5D), comparable to the phytodetriral pulses of Rice et al. (1986). Unfortunately, the effects of such seasonally supplied concentrations of organic debris to the marine realm on infaunal communities have yet to be fully explored (cf. Pearson and Rosenberg, 1978).

Periodically Reduced Oxygenation.—

The association between bottom-water oxygenation and preservation of carbon has been debated for some time (see Leithold and Dean, 1998, for a detailed discussion). Phytodetriral pulses (anomalous concentrations of event-emplaced comminuted plant debris; cf. Rice et al., 1986) are probably more common in deltaic settings than previously identified and may be indicative of proximity to distributary channels. As such, an assessment of the interplay of infaunal impoverishment and preservation of these detrital organic concentrations may be relevant to the discussion of recognition of deltaic deposits in the ancient record.

One model suggests that it is the oxidation of anomalous concentrations of organic carbon in such phytodetriral pulses that depletes oxygen near the sea floor, particularly in distal settings below fair-weather wave base with poor circulation or turnover of the water column (e.g., Savrda and Bottjer, 1987, 1989; Wignall and Pickering, 1993). Such conditions would, at least temporarily, result in dysaerobic conditions and hamper bed colonization. Storms, which mix the water column, or eventual burial of the organic detritus, would permit the return to aerobic conditions. This mechanism has been used to explain the paucity of burrowing and the specific ichnological suites within such organic-rich layers (Raychaudhuri and Pemberton, 1992; Saunders et al., 1994; Gingras et al., 1998; Coates and MacEachern, 1999, 2000). An alternate model suggests that oxygen levels themselves have little or no direct effect on the degradation rates of organic matter (Heinrichs and Reeburgh, 1987; Kristensen and Blackburn,

1987; Pederson and Calvert, 1990, 1991; Betts and Holland, 1991; Cowie and Hedges, 1991, 1992; Lee, 1992; Calvert et al., 1992). Rather, reduced oxygen levels are seen to eliminate or reduce the numbers of burrowing organisms themselves (Pearson and Rosenberg, 1978; Savrda and Bottjer, 1987, 1991; Föllmi and Grimm, 1990; Grimm and Föllmi, 1990; Savrda, 1992, 1995), therefore preserving the organic carbon (Lee, 1992; Hedges and Kiel, 1995). In both models, infaunal impoverishment is therefore taken as the *effect* of oxygen depletion. This is consistent with ichnological observations of many prodelta mudstones and phytodetriral drapes on event beds, though the latter model does not explain *why* oxygen levels should have declined in the first place to reduce infaunal and epifaunal activity.

The depauperate suites that are generated both in fluid-mud settings and in the organic-rich muds of possible phytodetriral origin are consistent with the ichnological characteristics of deposits in lowered-oxygen bottom water. Impoverishment of trace diversity, coupled with ichnogenera size reductions, and shifts towards *Chondrites*-dominated suites have long been regarded to be indicative of conditions of reduced oxygen (e.g., Rhoads and Morse, 1971; Bromley and Ekdale, 1984a; Savrda and Bottjer, 1987, 1989, 1991; Wignall and Pickering, 1993). Where the sediment is burrowed, the suites tend to comprise deeper-tier ichnogenera that have exploited the layers at depth. Values of bioturbation index tend to be low overall (BI 0–2), with *Chondrites*, *Planolites*, and *Thalassinoides* constituting the most common elements. In their study of the Cardium Formation of Alberta, Vossler and Pemberton (1988) suggested that accumulations of organic debris, which become buried before complete oxidation, may provide an ideal food source for deep-tier deposit-feeding organisms, leading to superabundant concentrations of *Chondrites*, and possibly *Planolites*. This is consistent with observations of dark mudstone layers that commonly drape the turbidites and tempestites of prodelta and delta-front intervals, which are largely unburrowed by surface grazing structures or shallow-tier deposit-feeding structures, and contain only low numbers of deeper-tier elements (e.g., Fig. 3E–H).

Salinity Changes.—

Reduced salinity and the development of brackish-water conditions are always associated with deltas, at least locally, and reflect proximity to freshwater input from the rivers (e.g., Moslow and Pemberton, 1988; Gingras et al., 1998). This is particularly true of lower-delta-plain settings, interdistributary-bay complexes, and distributary-mouth bars, where ephemeral bodies of water experience persistent mixing of fresh and marine waters. In such settings, the brackish-water ichnological model likely has widespread application (cf. Wightman et al., 1987; Beynon et al., 1988; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Gingras et al., 1999; MacEachern et al., 1999a). The model suggests that:

1. Brackish-water settings typically show a reduction in the number and diversity of animal species. This is a direct reflection of the unpredictable and unstable nature of the environment (Howard et al., 1975).
2. Brackish-water suites consist of greater proportions of marine than freshwater organisms. In general, the reduction of marine forms in response to declining salinity is gradual. In contrast, freshwater forms tend to be highly intolerant of even minor increases in salinity. Thus, brackish-water assemblages represent impoverished marine communities, not simple mixtures of freshwater and marine biota (Barnes, 1989).

3. Settings characterized by reduced and / or fluctuating salinity show a pronounced size reduction of fauna compared to fully marine counterparts (Milne, 1940). This appears, in part, to be a response to the physiological difficulties in ionic regulation and osmo-regulation (Croghan, 1983). Further, the rigors of inhabiting brackish water imposes an increased oxygen requirement on the fauna, which is minimized by small body sizes (Remane and Schlieper, 1971). Also, because of high mortality rates, rapid reproduction capacity, short life cycles, and early sexual maturity (Rees et al., 1977), the bulk of the community consists of smaller-sized juvenile animals.
4. In response to the ability of the substrate to damp the magnitude of salinity variations, brackish-water benthic communities are dominated by infaunal rather than epifaunal benthic organisms (Sanders et al., 1965; Knox, 1986).
5. Most fauna inhabiting brackish-water settings correspond to omnivores or trophic generalists (Grassle and Grassle, 1974). Individual organisms may employ deposit feeding, suspension feeding, predation, or scavenging behaviors, and change these as conditions demand (Cadeé, 1984). Wolff (1973) found that 35% of the animal species in Dutch estuaries were omnivores, in contrast to the 6–16% that characterize the adjacent freshwater and fully marine settings.
6. Despite the reduced diversity of species inhabiting brackish-water settings, many marginal-marine environments support a large biomass (Rosenberg et al., 1977). This high abundance of organisms can be attributed partly to the sheltered character of most marginal marine settings, an abundant food supply from rivers, salt marshes, and mangroves, and *in situ* primary production (cf. Pemberton and Wightman, 1992).
7. The fauna of brackish-water environments predominantly employ an r-selected strategy in population dynamics (Levinton, 1970; Pianka, 1970; Jumars, 1993). Organisms employing an r-strategy are opportunistic and can respond rapidly to an open or unexploited niche. This leads to local dominance by single species displaying gregarious colonization patterns (Rhoads et al., 1978; Whitlach and Zajac, 1985).

The details of the brackish-water ichnological model have been considered and refined for at least the past forty years, and the model is therefore reasonably well understood. Neoichnological analyses of Holocene intertidal and shallow subtidal areas (e.g., German and Dutch North Sea; Schäfer, 1956, 1962; Reineck, 1958; Reineck et al., 1967; Reineck et al., 1968; Dörjes, 1970; Hertweck, 1970; the Normandy coast of France; Larsonneur, 1975; the Georgia coast of the United States; Frey and Howard, 1972; Hertweck, 1972; Dörjes and Howard, 1975; Howard and Frey, 1973, 1975; Howard et al., 1975; Majou and Howard, 1975; the tidal flats of Taiwan; Dörjes, 1978; Reineck and Cheng, 1978; and Willapa Bay, Washington; Gingras et al., 1999; Gingras et al., 2004) have been integrated with ancient studies to produce a robust model for recognizing reduced-salinity settings. Such settings are exceedingly important in the characterization of the lower delta plain, particularly of river- and tide-influenced deltas.

In contrast, persistent or even extended periods of salinity reduction are far more variable in the more distal delta front and prodelta areas, and they depend on the water depth, as well as location and nature of fresh-water river plumes. Warne et al. (2002) showed that seasonally, buoyant freshwater surface plumes may extend many tens of kilometers basinward of the

Orinoco delta front. They also showed that these plumes may be deflected for many tens of kilometers downdrift before finally mixing with marine water. Although the effects of such surface plumes upon the infaunal community are unknown, the potential of extending the reach of brackish-water conditions long distances basinward and down depositional strike should not be ignored. Shallow-water deltas, such as those associated with the Volga delta in the Caspian Sea (< 5 m), and the Atchafalya and Wax Lake deltas (< 10 m) that feed into Atchafalya Bay may be persistently brackish for much of the time, especially where discharge is persistently high (Kroonberg, et al. 1997; H.H. Roberts, personal communication, 2004). Even with significant persistent fluvial discharge, marked reductions of salinity throughout a water column 15–30 m deep are unlikely. Nevertheless, prodelta and distal delta-front complexes locally *do* display ichnological responses consistent with salinity reduction, and such are also commonly associated with occurrences of synaeresis cracks. This suggests that salinity reductions do occur in these more distal positions. The close association of the impoverished trace-fossil suites, development of synaeresis cracks, and dark, carbonaceous mudstone interbeds suggests that salinity reductions may have been concomitant with hyperpycnal-flow-emplaced mud turbidites, as indicated by abundant, normally graded but otherwise massive silt beds (e.g., Fig. 5A–C). Abundant, early-formed siderite nodules are also a common feature in many river-dominated prodelta mudstones and are thought to indicate dilution of seawater, with a concomitant reduction in sulfate activity, as well as formation of low-eH conditions, reflecting low oxygenation of the substrate (Mozely, 1989). Under conditions of heightened river discharge, freshets associated with seasonal floods or anomalous periods of precipitation could lead to hyperpycnal muddy sediment gravity flows, associated with dense, bottom-hugging freshwater plumes. Where flow coherence persisted to the prodelta, a short-lived freshwater lens would lie immediately above the sea bottom. Such salinity contrasts would likely kill off much of the infaunal community and perhaps facilitate synaeresis formation (e.g., Fig. 5A–C). Most organisms occupying offshore and other distal settings are intolerant to marked salinity variations (e.g., Dauer and Simon, 1976; Jernélou and Rosenberg, 1976; Grassle, 1977). The return to more normal marine conditions that would follow soon after would permit recolonization of the substrate by the resident community. Such juxtapositions of apparent salinity reduction with “open marine” ichnogenera are common in many of the prodelta and distal delta-front deposits of the Dunvegan Formation (Fig. 5B; Coates and MacEachern, 1999, 2000; Coates, 2001), which also contains abundant early diagenetic siderite (Bhattacharya, 1989). Freshet conditions in the fluvial system, as well as increased surface runoff from the delta plain following storm-induced precipitation events, are also probably common to most delta complexes. Nevertheless, studies of animal responses to such conditions in modern deltaic settings are essential to evaluate the validity of this model.

WAVE ENERGY

Energy Dissipation, Longshore Drift, and Delta Asymmetry

Prograding strandplains typically form major to dominant components of the updrift and downdrift wings of large wave-influenced deltas (e.g., Paraibo do Sul; Danube Delta; Bhattacharya and Giosan, 2003). Many large prograding strandplains, such as the modern coast of Nayarit (Curry et al., 1969) or the Cretaceous shorefaces of the Book Cliffs (Hampson and Howell, this vol-

ume), contain local deltaic promontories, reflecting the fact that most of the sediment supplied to the shoreline is ultimately fed from rivers. The influence of fluvial deposition decreases laterally away from the sites of fluvial input, such that the deltaic stresses may be very localized. Spatially removed from the fluvially induced physicochemically stressed areas, the "strandplains" will likely be indistinguishable from nondeltaic shorefaces, although we suggest that it is virtually impossible to create extensive, progradational strandplain deposits that are not ultimately linked to an active, river-supplied sediment source. Ichnology can thus be a critical tool in identifying localized fluvial input along otherwise wave-dominated coastlines.

Waves mediate the various stresses of the delta system, through their dissipation both down depositional dip and along depositional strike. In particular, water stratification, reduced oxygenation, and freshet-induced hyperpycnal salinity reductions are less likely to persist under conditions of aggressive and persistent wave agitation. Wave energy progressively moves suspended mud basinward and remobilizes sand, shifting it landward and along depositional strike. Suspended mud may move offshore or may be transported downdrift. In the extreme case, highly muddy coastlines form extensive chenier plains. Chenier plains are common features on the downdrift side of major, muddy deltas, such as the Amazon and Mississippi (Penland and Suter, 1989). High water turbidity, on the other hand, increases the overall water viscosity and serves to impede the effectiveness of waves. Consequently, following distributary flood discharge or storm events, overall wave energies may be subdued (Rodriguez and Mehta, 1998). Under these conditions, fluid muds may form extensive but poorly burrowed soupgrounds (Augustinus, 1989).

In proximal settings, wave energy may be entirely effective at winnowing clay from the seabed, imparting a clean sandy substrate. Nevertheless, the overlying water column would likely remain highly turbid, helping to preclude most suspension-feeding behaviors. This scenario would produce the apparent paradox of well-sorted sandstones, nevertheless impoverished with respect to *Skolithos* ichnofacies elements and hosting significant numbers of deposit-feeding and passive carnivore structures (Table 2). Fair-weather delta-front sandstones, like the interstratified tempestites, commonly contain *Macaronichnus*, *Rosselia* and *Cylindrichnus*, with lesser *Ophiomorpha* and *Palaeophycus* (e.g., Fig. 3B, C, G; Fig. 4E, F; cf. Coates and MacEachern, 1999; 2000; MacEachern and Coates, 2002; Bann and Fielding, 2004).

Ichnological analysis of wave-dominated delta complexes from the Upper Cretaceous Dunvegan Formation (Gingras et al., 1998; Coates and MacEachern, 1999, 2000; MacEachern and Coates, 2002), the Upper Jurassic Tarbert Formation (MacEachern and Løseth, 2003), several Permian units of the southern Sydney Basin of Australia (Bann and Fielding, 2004), and the Upper Cretaceous Parkman Member suggests that such settings yield the most diverse and abundant trace-fossil suites of all the delta types (Fig. 6; Table 2). Unfortunately, many of these wave-dominated delta systems are also strongly storm influenced (Fig. 7). Although the two processes are distinct, it is also common for systems with a strong wave climate to also be extensively reworked by storms. The Dunvegan, in particular, serves as a limited analogue for "wave-dominated" deltas because of its strong storm overprinting; divorcing storm-induced ichnological responses from those reflecting wave-dominated fair-weather conditions during progradation is challenging. Similar problems surround the use of the Tarbert Formation of the Norwegian Shelf (MacEachern and Løseth, 2003) and the Permian of the Denison Trough, Australia (Bann and Fielding, 2004), as case study examples. In contrast, detailed ichnological assessment of the Albian Bow Island For-

mation of southern Alberta demonstrates some of the most diverse ichnological suites of any shoreline setting, with bioturbation intensities ranging from moderate to abundant (BI 2–5, and commonly BI 4–5) (Table 2; Raychaudhuri and Pemberton, 1992; Raychaudhuri, 1994). The degree of storm influence on the more wave-dominated Bow Island Formation is considerably lower than in that of the more storm-influenced successions above, and tempestites are rarely erosional amalgamated into beds thicker than 1 m. The resulting successions show a progressive upward decrease in trace-fossil abundance and diversity within the unit, displaying increased sedimentation rates, higher depositional energies, and increased erosional amalgamation of beds. Raychaudhuri and Pemberton (1992) found that distal settings showed diverse trace-fossil suites that contain up to 21 ichnogenera, recording prodelta and distal delta-front environments. More proximal deposits display evidence of rapid deposition (e.g., abundant soft-sediment deformation), salinity changes (e.g., synaeresis cracks), and reduced oxygenation (e.g., black mudstone drapes of presumed phytodetrital pulses) in a wave-dominated and storm-influenced delta-front setting. Suites nevertheless remain dominated by deposit-feeding and grazing structures, with diversities of 12–14 ichnogenera. Broadly similar trace-fossil suites, ichnogenera diversities, and bioturbation intensities are encountered in the Frontier Formation, such as the Harlan, Willow, and Posey allomembers (Fig. 6E; Table 2; Bhattacharya and Willis, 2001), as well as several Permian units of the southern Sydney Basin of Australia (e.g., Wasp Head Formation; Fig. 6D).

These ichnological characteristics are hinted at in the prodelta and distal deltafront deposits of numerous more strongly storm-influenced deltaic successions (see Table 2), such as the Upper Cretaceous San Miguel Formation of the Big Wells Field, Texas (Tyler et al., 1986), the basal Belly River Formation of Alberta (Coates and MacEachern, 2000; MacEachern and Coates, 2002), Allomember D of the Dunvegan Formation of Alberta (e.g., Fig. 6A, B; Gingras et al., 1998; Coates and MacEachern, 1999), the Kenilworth Member of Utah (Pattison, 1995; Taylor and Lovell, 1995; Hampson and Howell, this volume); some cycles in the Tarbert Formation of offshore Norwegian Shelf (Løseth et al., 2001; MacEachern and Løseth, 2003), the Permian of the Denison Trough, Australia (e.g., Fig. 6E; Bann and Fielding, 2004), the Snapper Point Formation (e.g., Fig. 6C), and the Haystack Mountain Formation of Wyoming (Mellere and Steel, 1995; Mellere, 1996). Preliminary assessment of the Parkman Formation delta deposits of Wyoming shows considerable similarity with the strongly storm-influenced delta-front deposits of Allomember D of the Dunvegan Formation. These "deltaic" ichnological characteristics are identifiable in more distal facies, owing to the decreased degree of tempestite erosional amalgamation and concomitant preservation of fair-weather beds (e.g., Fig. 3E–H). The increased diversity and abundance of ichnogenera recorded in remnants of fair-weather deposits demonstrate the effect that vigorous wave climates on mitigating the accompanying physicochemical stresses prevalent along the delta front (Fig. 6). Proximal delta front settings, however, are characterized by strong erosional amalgamation of storm beds, masking the fair-weather ichnological record entirely (Fig. 6G).

Delta Asymmetry and Distributary Proximity.—

In settings with strong longshore drift, and a mixed river- and wave-influenced delta front, preferential movement of sediment downdrift of the distributary mouth favors the development of an asymmetric delta (Bhattacharya and Giosan, 2003). In this recent model, river-induced stresses may be extended long dis-

tances downdrift of the river mouth. In particular, turbid mud plumes might be expected to affect long stretches of the delta front following river flood and/or storm events. The construction of elongate spits and bars downdrift also permits the sheltering of low-energy embayments and extensive brackish-water conditions in the proximal delta front and lower delta plain. In such settings, which are characterized by strongly heterolithic successions, recognition of marine versus brackish-water ichnological suites may be essential in order to differentiate prodelta and distal delta-front deposits from elongate-bay successions. In contrast, updrift of the distributary mouth, little river influence would be expected, and that part of the delta front effectively operates as a strandplain shoreface. It is therefore critical to realize that these depositional environments are not mutually exclusive. Wave-influenced deltas may be linked to or contain extensive wave-formed strandplains (Bhattacharya and Giosan, 2003). Also, other depositional systems (e.g., estuaries) may contain bay-head deltas as a subenvironment of the complex (Bhattacharya, 2003).

The resulting ichnological suites in a wave-influenced asymmetric delta would likely display only those stresses that persist downdrift of distributary complexes lying farther up the coast. Ichnological suites, therefore, could be evaluated with respect to the presence and magnitude of river-induced stresses on the prodelta and delta-front successions. Spatial variations in these ichnological characteristics may be highly effective in predicting the proximity of distributary complexes, and in helping to identify an asymmetric delta type. This would have valuable application to hydrocarbon exploration and reservoir development in deltaic successions. Novel work by Hampson and Howell (this volume) serves as a preliminary test of this, by using lateral variations in ichnology integrated with sedimentological evidence in order to identify localized distributary-channel point sources within the overall prograding, wave-dominated shoreface strandplain and delta-front deposits of the Cretaceous Kenilworth Member, central Utah (see Table 2). Surprisingly, they found that the deposits of the wave-influenced delta front contained similar suites but more uniform bioturbation intensities than that of lower-shoreface counterparts. Lower-shoreface deposits were seen to display bioturbation intensities that vary from low to intense. The principal sedimentological differences were the presence of current ripples (locally aggradational) and planar-

parallel lamination in the delta fronts. Nevertheless, this initial case study is encouraging. To our knowledge, no such other ichnological assessment has yet been attempted from modern or ancient examples in order to test this asymmetric delta model. Previous studies on the Bow Island Formation, Dunvegan Formation (Allomember D), and basal Belly River Formation (Table 2) hint at spatial distributions of facies consistent with delta asymmetry. This will certainly constitute a fruitful line of future research.

STORM INFLUENCES

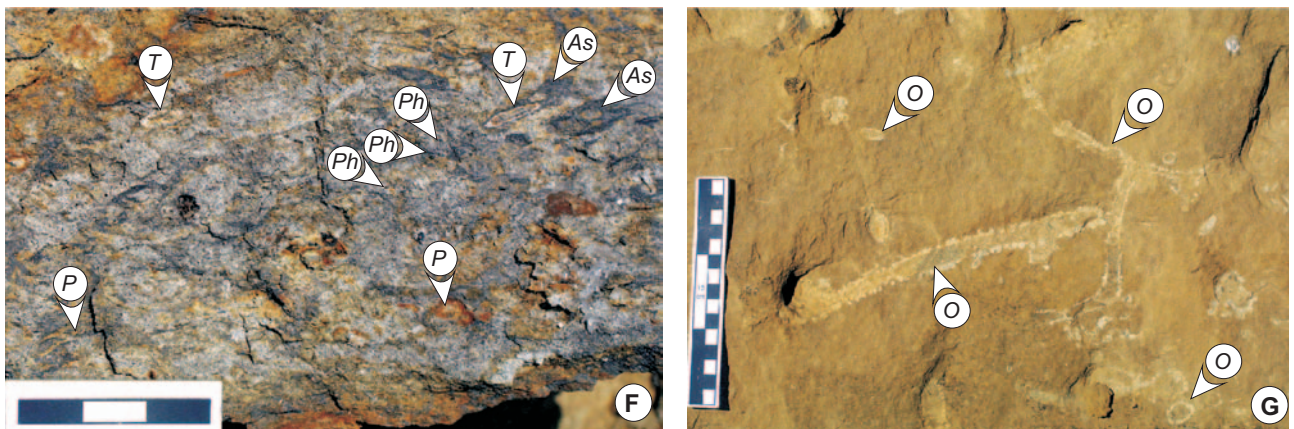
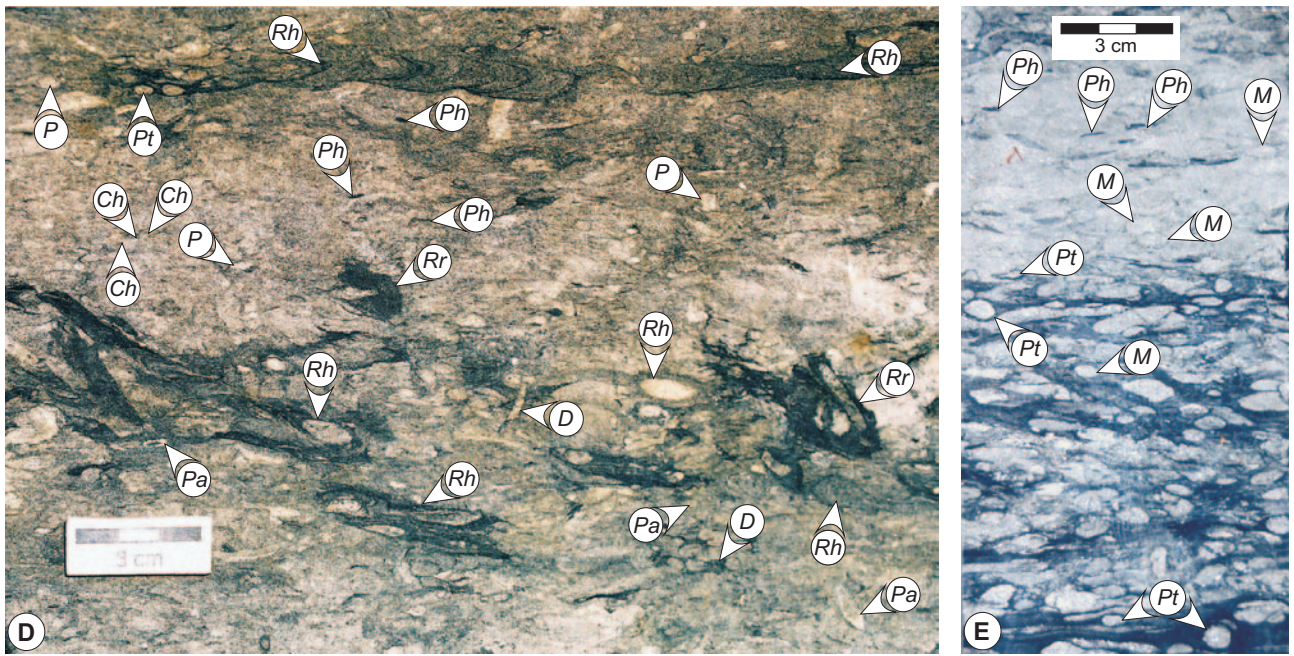
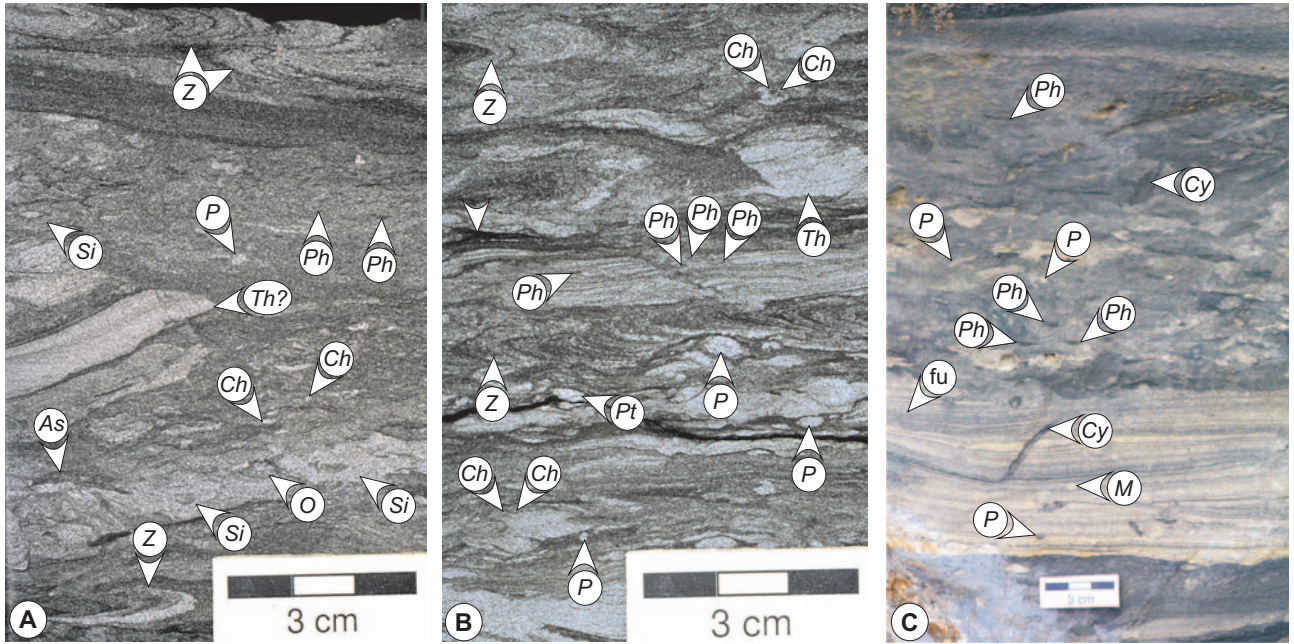
Defaunation, Episodic Deposition, and Opportunistic Colonization

Storms and fair-weather waves are discrete processes operating on the subaqueous delta, though wave dominance commonly is accompanied by a strong storm influence as well. Nevertheless, storm effects need not, and indeed *are not*, limited to wave-dominated portions of the shoreline. All delta types are susceptible to storm influence, though lacustrine deltas and bay-head deltas of protected embayments are accorded more shelter than deltas on open coasts. As such, the presence of tempestites and associated storm influence is widespread in virtually all delta types, regardless of the degree of river, wave, or tidal influence. Occurrences of hummocky cross-stratification (HCS) or indeed even of swaly cross-stratification (SCS) in the delta front are NOT compelling evidence of wave domination of the system. Such storm influences are particularly common in delta complexes of the Western Interior Seaway of North America (e.g., Leithold, 1993, 1994; Bhattacharya and Walker, 1991b; Moslow and Pemberton, 1988; Power and Walker, 1996; Gingras et al., 1998; Coates and MacEachern, 1999). High-latitude settings are particularly susceptible to strong seasonality of storm events, and this is well reflected in virtually all marine sandstones of the Cretaceous Western Interior (e.g., Barron and Washington, 1982; Duke, 1985; Swift et al., 1987; Erikson and Slingerland, 1990; Saunders et al., 1994).

A number of deltaic successions have been interpreted to record wave-dominated systems, though many are also wholly dominated by the emplacement and erosional amalgamation of tempestites (e.g., Allomember D of the Upper Cretaceous

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FIG. 6 (opposite page).—Wave-energy influences on delta deposition. **A**) Thoroughly bioturbated (BI 5) fair-weather deposits of the prodelta to distal delta front in a wave-dominated lobe. Suite contains well-developed *Phycosiphon* (Ph), *Zoophycos* (Z), *Planolites* (P), *Ophiomorpha* (O), *Asterosoma* (As), *Siphonichnus* (Si), *Chondrites* (Ch), and possible *Thalassinoides* (Th?). Dunvegan Formation (Allomember D), well 02-18-64-23W5; 1542.9 m, Alberta, Canada. **B**) Highly bioturbated (BI 4–5) prodelta of a wave-dominated lobe, showing *Zoophycos* (Z), *Thalassinoides* (Th), *Planolites* (P), *Palaeophycus tubularis* (Pt), *Anconichnus/Phycosiphon* (Ph), and *Chondrites* (Ch). Note the probable hyperpycnal mud drape preserved above a thin, remnant tempestite (arrow). Dunvegan Formation (Allomember D), well 02-18-64-23W5, 1542.7 m. **C**) Outcrop of prodelta mudstones from a wave/storm-dominated lobe, showing remnant tempestite near the base, with more thoroughly burrowed (BI 5) fair-weather beds above it. Suite includes *Phycosiphon* (Ph), *Planolites* (P), fugichnia (fu), *Cylindrichnus* (Cy), and *Macaronichnus simplicatus* (M). Note the dark, largely unburrowed mud layer underlying the tempestite and a remnant of one draping the tempestite. Permian Snapper Point Formation, South Snapper Point, Southern Sydney Basin, Australia. **D**) Thoroughly bioturbated (BI 5) fair-weather bed in the distal delta front of a wave/storm-dominated lobe. Facies comprises one of the burrowed intervening layers in Fig. 7D. Suite includes *Rhizocorallium* (Rh), *Phycosiphon* (Ph), *Planolites* (P), *Palaeophycus tubularis* (Pt), *Palaeophycus heberti* (Pa), *Chondrites* (Ch), *Rosselia rotatus* (Rr), and *Diplocraterion* (D). Permian Wasp Head Formation, South Pebbles, Southern Sydney Basin, Australia. **E**) Moderately burrowed (BI 4) fair-weather interval from the distal delta front of a wave/storm-dominated delta. Trace fossils include *Phycosiphon* (Ph), *Macaronichnus simplicatus* (M), and *Palaeophycus tubularis* (Pt). Permian Freitag Formation, GSQ Springsure Core No. 17, 135 m, Denison Trough, Queensland, Australia. **F**) Thoroughly bioturbated (BI 5), muddy sandstone of the distal delta front in a wave-dominated lobe. Suite includes *Phycosiphon* (Ph), *Terebellina* (T), *Asterosoma* (As), and *Planolites* (P). Posey Member, Frontier Formation, Wyoming, USA. **G**) Proximal delta front of a wave/storm-dominated lobe. The unit displays well-sorted sandstone showing robust *Ophiomorpha nodosa* (O). Parkman Formation, Wyoming, USA.



Dunvegan Fm; Bhattacharya and Walker, 1991a, 1991b; Gingras et al., 1998; Coates and MacEachern, 1999, 2000; MacEachern and Coates, 2002; the Upper Jurassic Tarbert Formation; Løseth et al., 2001; MacEachern and Løseth, 2003; the Parkman Member of Wyoming; Hubert et al., 1972, and the Permian of the Denison Trough, Australia; Bann and Fielding, 2004; see Table 2). In these intervals, ichnological characteristics primarily record the episodic nature of storm erosion and tempestite deposition in the prodelta and delta front, and differ only subtly from suites generated in the tempestites of storm-dominated strandplains (Fig. 7). Ambient conditions, presumably mainly wave-dominated, can be discerned through the careful analysis of fair-weather beds preserved as erosional remnants between the tempestites (e.g., Fig. 6D and Fig. 7D). These fair-weather beds possess the characteristics that permit differentiation between delta-front and strandplain settings (Fig. 3E, F; Fig. 5C, G; Fig. 7A–C). Unfortunately, strong storm influence overprints these suites, limits the preservability of fair-weather beds, and masks these differences, making identification of their deltaic origins challenging.

Storm-induced stresses, regardless of the depositional site, are associated mainly with (1) defaunation during high-energy erosional emplacement of tempestites, (2) contrasting substrate consistencies compared with the ambient or fair-weather substrate types, and (3) phytodetrital influx associated with concomitant heightened precipitation. In many high-latitude, shallow marine settings, storm events are seasonal and larval dispersal is timed to coincide with them, using a “passive deposition” strategy (Rees et al., 1977; Hagerman and Rieger, 1981; Dobbs and Vozarik, 1983; Butman, 1987). This affords infauna the opportunity to disperse their larvae greater distances. Organisms that prefer sandy substrates have larval fall velocities comparable to that of sand, so that they settle with the appropriate media (Hannan, 1984; Jumars and Newell, 1984). Adult recruitment from surrounding areas may also be appreciable (Santos and Simon, 1980). Consequently, storm events commonly facilitate rapid recolonization of newly available substrates (e.g., approximately two months; cf. Boesch et al., 1976; Rees et al., 1977; Berry, 1989). In addition, organisms preferring a sandy substrate tend to be suspension feeders. Consequently, in unstressed settings, initial colonization of tempestites is dominated by elements of the *Skolithos* ichnofacies (Howard and Frey, 1984; Pemberton and Frey, 1984).

The details of storm-induced defaunation of the substrate and subsequent tempestite colonization by infauna have been extensively reported (e.g., Howard and Reineck, 1981; Seilacher, 1982a,

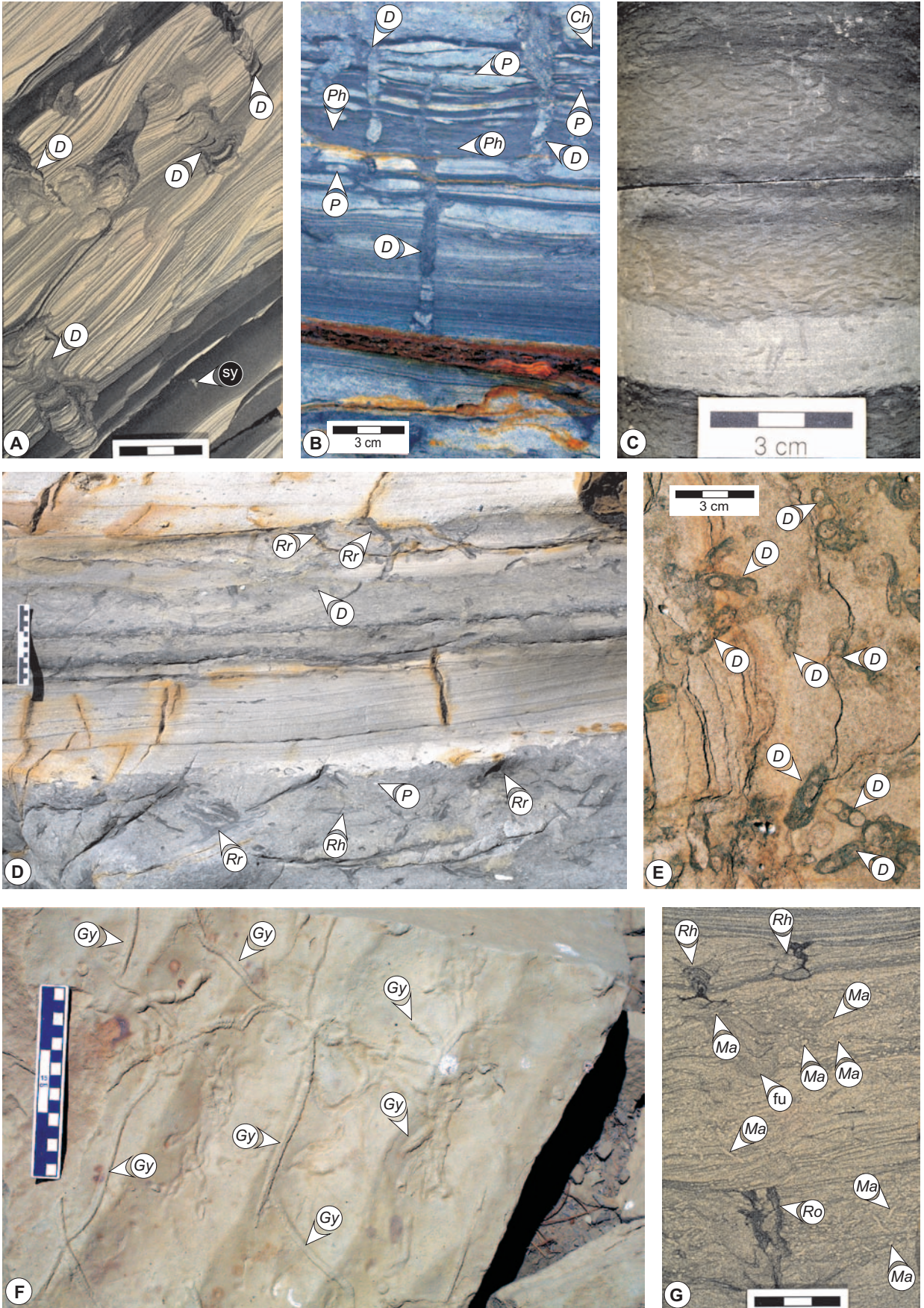
1982b; Howard and Frey, 1984; Pemberton and Frey, 1984; Vossler and Pemberton, 1988, 1989; Dam, 1990; Frey, 1990; Wheatcroft, 1990; Frey and Howard, 1990; Frey, 1990; Seilacher and Aigner, 1991; Frey and Goldring, 1992; MacEachern and Pemberton, 1992; Pemberton et al., 1992b; Pemberton and MacEachern, 1997). Tempestites tend to show erosional truncation of the underlying strata, and commonly of the biogenic structures as well. Lags made up of allocthonous *Rosselia* mud balls are common (Fig. 4C, H, I), with their truncated tubes preserved below the erosion surface. Such tubes are commonly misidentified as *Cylindrichnus* or *Skolithos*. Tempestites may display well-developed fugichnia, recording the passage of entrained or buried organisms as they made their way to the new sediment–water interface (Fig. 4B). In some instances, buried dwelling structures show breaching, and fugichnia extending upward to a new dwelling site, or multiple reestablishment of dwelling structures (Fig. 3A, E–G). Tempestites may also become colonized by abundant meiofauna, resulting in subtle disruptions of original grain fabrics and stratification, referred to as cryptobioturbation (e.g., Howard and Frey, 1975; Bromley, 1990; Saunders et al., 1994; Pemberton et al., 2001).

Initial colonization of storm beds is commonly by opportunistic, facies-crossing organisms that employ an r-selected strategy in population dynamics (Levinton, 1970; Pianka, 1970; Grassle and Grassle, 1974; Rees et al., 1977; Boesch and Rosenberg, 1981; Cadée, 1984; Jumars, 1993). In open marine strandplain settings (lower-shoreface to lower-offshore settings), these suites reflect archetypal to distal expressions of the *Skolithos* ichnofacies and generally contrast markedly with high-diversity *Cruziana* ichnofacies assemblages typical of the resident fair-weather community to produce the mixed *Skolithos*–*Cruziana* ichnofacies (e.g., Pemberton and Frey, 1984; MacEachern and Pemberton, 1992; Pemberton and MacEachern, 1997). In contrast, tempestites associated with delta-front and prodelta settings show anomalous impoverishment of *Skolithos* ichnofacies elements and a predominance of deposit-feeding structures. Resulting suites reflect facies-crossing elements of the *Cruziana* ichnofacies, typified by small numbers of *Rosselia*, *Cylindrichnus*, *Macaronichnus*, *Planolites*, and *Anconichnus*/*Phycosiphon*, with much less common *Ophiomorpha*, *Diplocraterion*, and *Skolithos* (e.g., Fig. 7; Gingras et al., 1998; Coates and MacEachern, 1999, 2000; MacEachern and Løseth, 2003; Soegaard and MacEachern, 2003; Bann and Fielding, 2004).

In deltas, where physicochemical stresses prevail, the “resident” (fair-weather) suite is commonly dominated by opportunists (Rhoads et al., 1978; Ekdale et al., 1984; Ekdale, 1985; Whitlatch

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FIG. 7.—Storm-energy influences on delta deposition. **A)** Tempestites in the distal delta front of a strongly storm-influenced delta lobe. Largely unburrowed post-storm muds containing high organic content alternate with laminated oscillation-rippled and hummocky cross-stratified (HCS) tempestites. Possible freshet emplacement may be indicated by the presence of synaeresis cracks (sy). The trace-fossil suite is impoverished and shows BI 1–2, with *Diplocraterion* (D). Tarbert Formation, well 30/9-B13, 3192.1 m. **B)** Distal tempestites in the prodelta to offshore transition of a storm-influenced lobe, with sporadic bioturbation (BI 0–2). The suite includes *Diplocraterion* (D), *Phycosiphon* (Ph), *Planolites* (P), and *Chondrites* (Ch). Permian Pebbly Beach Formation, Mill Point, Southern Sydney Basin, Australia. **C)** Tempestite in the distal delta front, displaying opportunistic colonization by tracemakers of *Anconichnus*/*Phycosiphon*. The unit is pervasively burrowed above the tempestite (BI 5). Basal Belly River Formation, well 06-16-46-01W5, 1010.3 m, Alberta, Canada. **D)** Laminated to burrowed bedding (Lam-Scram) in the delta front of a storm-dominated lobe. Virtually unburrowed tempestites alternating with pervasively bioturbated fair-weather beds. Bioturbated bed is the same as in Figure 6D. Facies displays abundant burrows, including *Rosselia rotatus* (Rr), *Diplocraterion* (D), *Rhizocorallium* (Rh), and *Planolites* (P). Wasp Head Formation, South Pebbles, Southern Sydney Basin, Australia. **E)** Bedding-plane view of distal delta-front tempestite in outcrop, showing well developed *Diplocraterion* (D). Snapper Point Formation, South Snapper Point, Southern Sydney Basin, Australia. **F)** Oscillation-rippled top of a tempestite in the distal delta front of a storm-dominated lobe. Rippled layer contains abundant *Gyrochorte* (Gy). Parkman Formation, Wyoming, USA. **G)** Laminated to burrowed bedding in the delta front of a storm-dominated lobe. Interval displays *Rhizocorallium* (Rh), *Macaronichnus segregatis* (Ma), fugichnia (fu), and *Rosselia socialis* (Ro). Tarbert Formation, well 30/9-14, 3174.9 m; Norwegian Shelf, Norway.



and Zajac, 1985), making discrimination between initial tempestite colonization and fair-weather colonization challenging. Cadée (1984) noted that opportunistic organisms have a great capacity to vary their feeding habits depending on food type and availability. Most opportunists are also omnivores and trophic generalists (Beynon et al., 1988; Moslow and Pemberton, 1988; Pemberton et al., 1992a). In deltaic settings characterized by heightened water turbidity, such opportunistic infauna would be expected to switch to mobile and sessile deposit-feeding strategies, resulting in ichnological suites dominated by elements of the *Cruziana* ichnofacies (Gingras et al., 1998; Coates and MacEachern, 1999, 2000; Bann and Fielding, 2004). Because most of the suite would consist of the more simple facies-crossing structures, the overall appearance of the *Cruziana* ichnofacies would be one of diversity impoverishment, departing markedly from the original description of the ichnofacies (cf. Seilacher, 1967). This impoverishment of the *Cruziana* ichnofacies, coupled with a lack of ichnologic juxtaposition between event beds and fair-weather beds is probably characteristic of delta-front tempestite emplacement, particularly in more river- and tide-influenced delta settings (Fig. 7; Coates and MacEachern, 1999, 2000; Coates, 2001). Where deposition of suspended sediment following storm abatement is high, as may be associated with thick, buoyant mud plumes, fluid-mud deposition due to heightened river discharge, or phytodetrital pulses, the tempestite may be entirely buried by fine-grained sediment before it can be colonized (Fig. 3E, G, H; Fig. 5A). In delta-front and prodelta successions, a large proportion of tempestites appear entirely unburrowed, with the exception of small numbers of escape structures (Saunders et al., 1994; Coates and MacEachern, 1999; 2000; MacEachern and Løseth, 2003).

TIDAL FLUX

Clay Flocculation and Fluid Mud

Tidal variations in flow intensity, direction, and duration operate on a number of temporal scales, and strongly affect the

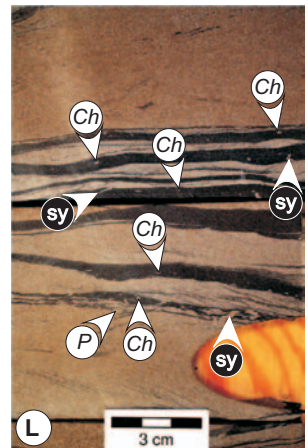
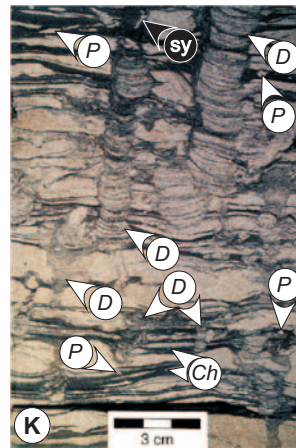
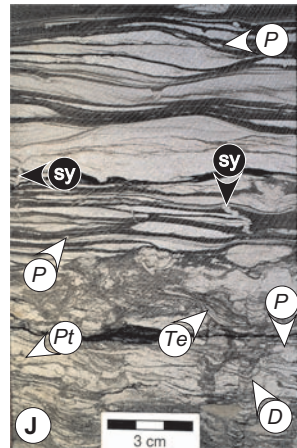
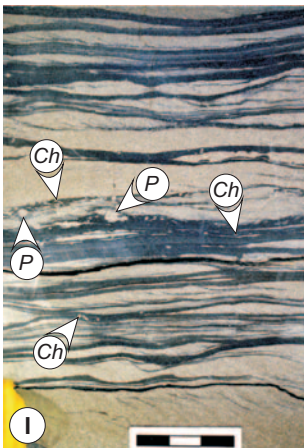
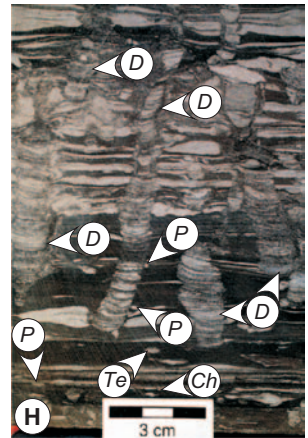
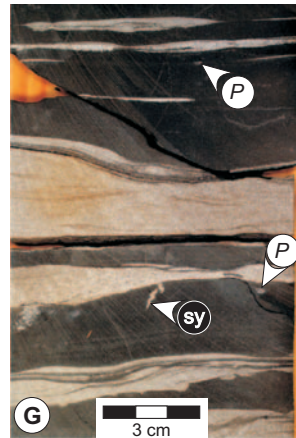
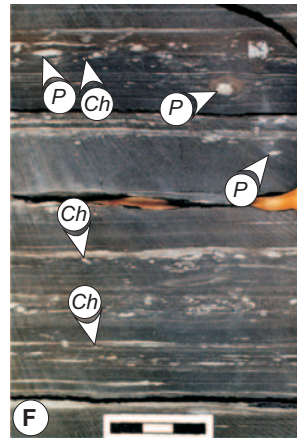
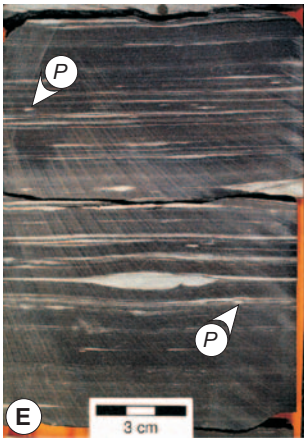
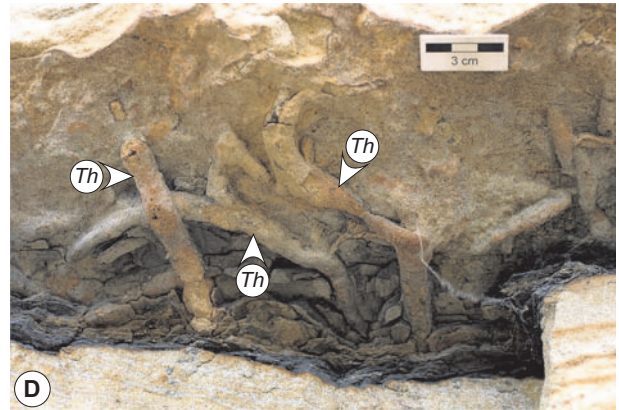
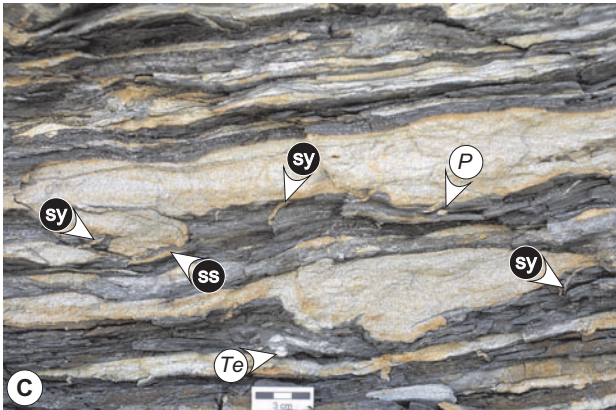
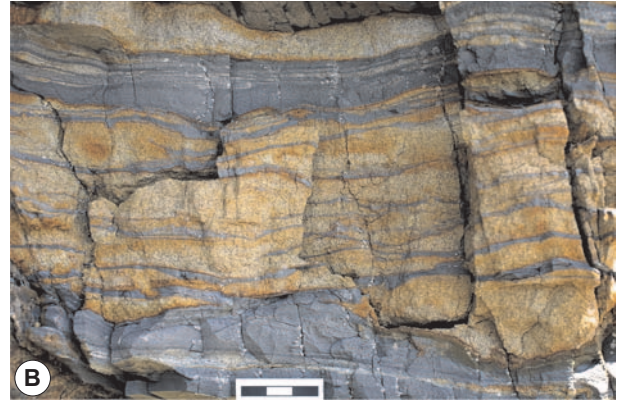
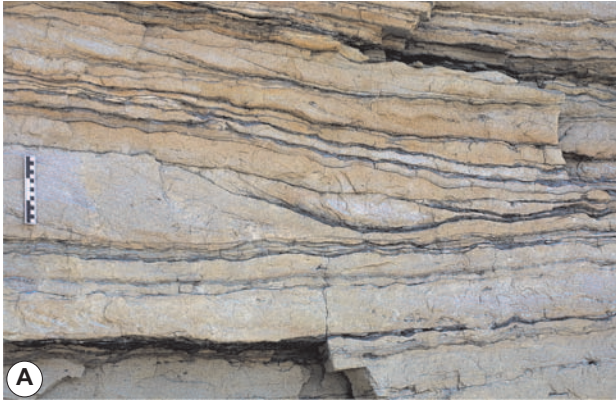
infaunal community of associated environments. Organisms occupying these settings must endure marked changes in energy, substrate consistency, water salinity, water turbidity, and deposition rates. Sandy environments are typically overlain by turbid water columns and contain bedforms that migrate incrementally (Fig. 8A, B). Foresets and topsets are commonly draped by mud during periods when the bedform is moribund. Sand-loving organisms are challenged by the heterolithic nature of the substrate, energy variations, and periodic suspension deposition. Although reasonably well understood in the intertidal and shallow subtidal settings of lagoons, bays and estuaries (e.g., Reineck et al., 1967; Reineck et al., 1968; Dörjes, 1970; Hertweck, 1970; Howard et al., 1973, 1975; Frey and Howard, 1972; Hertweck, 1972; Dörjes and Howard, 1975; Howard and Frey, 1973, 1975; Howard et al., 1975; Majou and Howard, 1975; Dörjes, 1978; Reineck and Cheng, 1978; Beynon et al., 1988; Pemberton and Wightman, 1992; MacEachern and Pemberton, 1994; Gingras et al., 1999; MacEachern et al., 1999a) much of the ichnological work has surrounded the effects of changing water salinity rather than of turbidity. Organism responses to tidal flux itself, and to its effects on the resulting substrate, are poorly understood. As such, the inferences of animal-sediment relationships in a tidally dominated delta front are largely conjectural. Comparison of the ichnology of tide-swept shelves, tide-dominated delta fronts, and inshore tidal settings of bays, lagoons, and estuaries may highlight unique "tidal" signals to the ichnological suites, and indicate how organisms of various ethologies adapt to these unique processes.

Fluid Mud.—

Mud-prone tidal settings are characterized by high deposition rates, and dense, accumulations of flocculated fluid mud. These soupground conditions are difficult for large endobenthic deposit-feeders to inhabit (e.g., Schäfer, 1956; Bromley, 1990). Soupground substrates generally favor only surface grazing, mobile deposit feeding, and some penetrative structures, pro-

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FIG. 8 (opposite page).—Tide-influenced delta deposition. A–D: Frewens Sandstone, Wyoming, USA. **A)** Proximal delta front deposits displaying tidal bundles, heterolithic rhythmic lamination, and reactivation structures. The interval is virtually unburrowed (BI 0–1). **B)** Delta front with thick, intervening mud drapes, interpreted to reflect fluid-mud deposits. Mudstones are unburrowed, consistent with soupground conditions and rapid deposition. **C)** Heterolithic bedding of the distal delta front, showing soft-sediment deformation (ss), synaeresis cracks (sy), and unburrowed dark mud drapes (= fluid muds?). The interval displays BI 1, with isolated and diminutive *Planolites* (P) and *Teichichnus* (Te). **D)** Pause plane in the delta front, with *Thalassinoides* (Th) occupying dark mudstones at the interface between tidal sandstone beds. E–L: Tilje Formation, Norwegian Shelf, Norway. **E)** Prodelta mudstones showing isolated current ripples in a lenticular-bedded composite bedset. Unit displays BI 0–1, with isolated, diminutive *Planolites* (P). Well 6407/7-3, 2975.4 m. **F)** Prodelta mudstones showing isolated current ripples in a lenticular-bedded composite bedset. The unit displays BI 1, with isolated, diminutive *Planolites* (P), and *Chondrites* (Ch). Well 6407/7-3, 2974.8 m. **G)** Distal delta front with current ripples, loading structures, and synaeresis cracks (sy) in wavy-bedded composite bedset. Unit shows BI 0–1 with isolated *Planolites* (P). Well 6407/7-3, 2976.5 m. **H)** Wavy to lenticular bedding in distal-delta-front to prodelta setting. Unit shows *Diplocraterion* (D), which subtend from an overlying pause plane. Remainder of the suite comprises diminutive *Planolites* (P), *Teichichnus* (Te), and *Chondrites* (Ch). Unit displays BI 1–2. Well 6407/7-3, 2947.6 m. **I)** Wavy-bedded interval of a probable distal-delta-front setting. Current ripples and cross-stratified sandstones are draped by largely unburrowed, thin, dark mudstones of either hyperpycnal or fluid-mud origin. The unit displays BI 1, with *Planolites* (P) and *Chondrites* (Ch). Well 6407/7-3, 2963.4 m. **J)** Distal delta-front deposits showing more pervasively burrowed muddy sandstone (BI 5) abruptly overlain by heterolithic wavy-bedded unit with low bioturbation intensity (BI). Underlying unit records slower and continuous deposition, and contains retrusive *Diplocraterion* (D), *Teichichnus* (Te), *Planolites* (P), and *Palaeophycus tubularis* (Pt). The overlying unit shows current ripples with dark mudstone drapes, containing synaeresis cracks (sy), and *Planolites* (P). Well 6407/7-5, 3369.2 m. **K)** Distal delta front characterized by slower, continuous rates of deposition, reflected by more intense bioturbation and elongate, retrusive *Diplocraterion* (D), with diminutive *Planolites* (P) and *Chondrites* (Ch). Note the synaeresis cracks (sy) toward the top. Well 6407/7-3, 2943.4 m. **L)** Probable delta-front deposit showing wavy bedding with synaeresis cracks (sy), and dark, largely unburrowed mudstone drapes (BI 0–1). Traces include *Chondrites* (Ch) and *Planolites* (P). Well 6407/7-3, 2964.5 m.



duced by diminutive organisms, and generally lead to mottled bioturbated fabrics (Bromley, 1990). The low turbulence that facilitates flocculated mud to become concentrated and deposited on the seabed precludes suspension-feeding organisms. The organisms that inhabit soupy substrates and watery softgrounds either use mucous to construct structures, which leave cavities that readily collapse, or are slime-covered to ease their passage through the sediment, and produce diffusive turbulence leading to structureless fabrics. Biogenic structures that lack lithologic contrast with the host media are unlikely to survive the extensive compaction experienced by these fluid muds, display marked shortening. As a consequence, following burial and compaction, most soupground biogenic features are easily destroyed. Soupground mudstones therefore carry a taphonomic bias against preservation of structures (e.g., Bromley, 1996; MacEachern et al., 1999a).

Comparable relationships are clear from many softground and soupground chalk intervals, which likewise may retain only ghosted expressions of biogenic activity, highly compacted forms (cf. Bromley, 1975; Ekdale and Bromley, 1983, 1991; Bromley and Ekdale, 1984b). In the case of some Danish chalks, applying oils of varying gravities to smooth dry surfaces are required in order to highlight ichnological details in strata that otherwise appears structureless (Bromley, 1981, 1990). Comparable studies of siliciclastic mudstones are unknown to the authors.

Some fluid muds contain high organic contents, as described from the Fly River delta (Dalrymple, 1999; Dalrymple et al., 2003). Like the rapid emplacement of phytodetrital layers in the deep sea (e.g., Rice et al., 1986), such organic-rich fluid muds may also lead to periods of dysoxic to anoxic conditions near the seabed, limiting or even precluding a benthic community. As such, fluid muds generally lead to unburrowed mudstones, unless colonized after burial from a higher tier. Separating the effects of soupground conditions from reduced oxygenation may be highly problematic. Wignall and Pickering (1993) demonstrated that substrate softening from softground to soupground conditions could produce similar reductions in tier depth, endobenthic biodiversity, and animal size, broadly comparable to reduced-oxygen conditions.

Outcrop examples of heterolithic, strongly tide-influenced delta systems such as the Frewens Sandstone (Frontier Formation) in Wyoming show exactly these ichnological characteristics (Fig. 8A–D; cf. Willis et al., 1999; Bhattacharya and Willis, 2001). Sandstone intervals are largely unburrowed (BI 0–1), with only very rare fugichnia, bivalve equilibrium-adjustment structures, *Palaeophycus*, *Macaronichnus*, *Ophiomorpha*, *Piscichnus*, *Arenicolites*, *Skolithos*, and *Cylindrichnus* present (see Table 2). Mudstone interbeds that drape foresets and/or bedform topsets show unburrowed to weakly bioturbated (BI 0–2; typically BI 0–1) fabrics, with *Thalassinoides*, *Planolites*, *Teichichnus*, and *Chondrites* most typical (Fig. 8C, D). Such structures do not penetrate deeply into the sediment, and are generally diminutive, though some *Thalassinoides* may be robust (tubes 0.5–1 cm in diameter) (Fig. 8D). Most of these burrowed zones occur where entire bedforms are mantled, suggesting marked pauses in deposition. Mudstone colonization appears to be dominated by either deeper-tier deposit-feeding penetrations, or following some compaction of the mud to more typical softground consistencies. Comparable expressions are visible in the tide-dominated facies of the Wall Creek Member of Wyoming (e.g., “Raptor Ridge”; Gani et al., 2004).

The Lower Jurassic Tilje Formation of the Norwegian Shelf (Martinius et al., 2001) (Table 2), as core, well expresses the impoverished nature of fluid-mud infaunal colonization (Fig. 8E–L), with low diversities and low abundances of trace fossils

persisting across the facies of the prodelta and delta front. Burrow concentrations occur at pauses in sedimentation (Fig. 8J), and the rapid though incremental deposition of sediment is expressed by strongly retrusive *Diplocraterion parallelum*. Salinity fluctuations, possibly associated with variations in river discharge or to freshet-emplaced hyperpynal muds, are indicated by sporadic distributions of synaeresis cracks (Fig. 8G, J–L). These characteristics mirror the features observed from the Frewens Sandstone (Table 2).

In contrast, an ichnofabric assessment of the Middle Jurassic (Aalenian) Ile Formation of offshore Norway (McIlroy, 2004) indicates markedly higher BI values and greater trace fossil diversities in each of the facies of the tide-dominated delta succession (Table 2), compared to their Frewens Sandstone and Tilje Fm counterparts. McIlroy (2004) identified 24 discrete ichnofabrics characterizing 15 subenvironments, with facies of the delta front containing suites with the highest ichnodiversities and bioturbation intensities. The general paucity of case studies of tide-dominated deltas precludes determining whether the Ile Formation records an anomalous expression or a specific recurring type.

The infaunal responses to the tidal signal, particularly with respect to fluid-mud concentrations near the delta front and in the distributary channels, the effects of energy flux and changing substrate consistency, in possible oxygen reductions associated with dense fluid mud accumulations have not been explored in deltaic environments. Despite what little we know about infaunal responses in river-, wave-, and storm-influenced deltas, this is far more refined than that postulated for tide-dominated deltas. These systems are understudied in the ancient record and in the modern, even from sedimentological perspectives. From the ichnological perspective, they constitute a major gap in our understanding, which cannot be rectified without numerous case studies. This promises to be one of the most fruitful lines of deltaic ichnological research for the next several years.

SUMMARY

Understanding organism responses to the complex interplay of processes operating in deltaic settings is still in its infancy. In contrast, a relatively wide range of both modern and ancient case studies have been published for strandplain shoreface and in-shore tidal settings. Paleoichnologists have sought to adapt animal-sediment responses derived from these pivotal works in order to design models that explain empirical observations derived from ancient deltaic deposits. Consequently, most of the proposed “deltaic” models presented in this paper are rather more conjectural. Compelling models must await rigorous neoichnological treatment of modern deltaic complexes. Such work requires case studies from several deltaic systems, analyzing the physical, chemical, hydrologic, and biologic characteristics of prodelta, delta-front, and lower-delta-plain environments. These observations must then be integrated with a number of ancient case studies of discrete delta-lobe complexes, paying particular attention to along strike variations and proximity of fluvial influx.

Wave-influenced deltas, which receive their clastic material initially from river discharge, typically have prograding strandplain “wings” on the updrift and downdrift margins. The influences of fluvial influx and deposition decrease laterally away from the sites of fluvial input, such that the deltaic stresses may be very localized. The more removed from the fluvially induced stresses, the more the coastal deposits are indistinguishable from nondeltaic shorefaces. As such, a continuum from river-stressed delta fronts to strandplains, well removed

from river-induced physicochemical stresses, can be expected along depositional strike. Ultimately, quantified estimates of how far updrift or downdrift these fluvial stresses might be identified would be desirable in order to predict distributary proximity and criteria for delta "identification" in the ancient record. One can anticipate that they will likely reflect ratios of wave energy to fluvial discharge, and can be expected to vary temporally in response to variations in climate and weather (variations in seasonal river discharge, monsoonal rains, El Niño climatic cycles, etc.), as well as spatially down depositional strike. Ichnological analyses are critical in identifying localized fluvial input along otherwise wave-dominated coastlines, and therefore useful in estimating the positions and magnitudes of river discharge.

Empirical observations of trace fossil suites from a number of deltaic deposits in the ancient record *do* appear to indicate marked departures from comparable settings of nondeltaic (or spatially removed) strandplain systems (e.g., Coates and MacEachern, 1999, 2000; MacEachern and Coates, 2002; MacEachern and Løseth, 2003; Gani et al., 2004; Howell et al., 2004; Bann and Fielding, 2004). The most pronounced differences occur within the prodelta and the delta front, namely, the subaqueous delta (Figs. 10, 11). Most of what we believe we understand about animal-sediment responses in deltas comes from the recognition of the unique stresses imparted by pronounced fluvial influx into the coastal regime. Ichnological characteristics of facies produced in the prodelta (Fig. 10) and the distal delta front (Fig. 11) suggest that environmental stresses appear to be at a maximum in river-dominated and tide-dominated systems, decreasing through storm-dominated and into relatively unstressed wave-dominated complexes. Consequently, strongly river-dominated delta deposits were some of the earliest to be differentiated ichnologically from nondeltaic shallow marine sandstones. The trace-fossil suites from subaqueous delta successions depart markedly from those of the better-studied strandplain offshore-to-shoreface environments (Fig. 9), owing to the paucity of river-induced stresses in these nondeltaic settings. With decreasing river influence, the deltaic signal becomes less clearly differentiated from that of strandplains, particularly where wave and storm influences are predominant (compare Fig. 7 and Fig. 9). In the past, depositional models developed for strandplain shorefaces and offshore/shelf settings (both sedimentological and ichnological; e.g., Fig. 2) have been applied routinely to deltafront and prodelta complexes. Many researchers working in the ancient record use the term "shoreface" interchangeably with "delta front" (though not vice versa), as a consequence of this broad similarity. Nevertheless, empirical observations demonstrate that there are subtle differences between the two that can be discerned through careful analysis of the facies and the associated ichnological suites. The persistent depositional interplay with nearby fluvial influx leads to hypopycnal-flow-induced heightened water turbidity, deposition of flocculated mud, freshet discharges, hyperpycnal-flow-induced sediment gravity flows, salinity fluctuations, increased deposition rates, and periods of reduced oxygenation. Each of these has greater or lesser influence on prodelta (Fig. 10) and delta-front (Fig. 11) settings, and leads to specific infaunal responses, which depart from the benign conditions that persist in strandplain shoreface settings (Fig. 9). Ichnological responses to river-induced stresses, in general, appear to be marked by (1) suspension-feeding impoverishment, even in predominantly sandy facies, (2) predominance of opportunistic (facies-crossing) deposit-feeding and grazing structures, (3) reduced bioturbation intensities, (4) strongly sporadic distributions of bioturbation, (5) reduced trace-fossil diversities, and (6) general size reductions of ichnogenera. Most of these features, unfortunately, are typical

responses to physicochemical stresses that may occur in a variety of depositional settings. With the current interest in deltaic successions, refinements in the various "shoreface models" have been proposed to better apply to deltaic successions, and certainly some of the sedimentological responses are far better understood, as numerous papers in this volume demonstrate. The addition of these ichnological responses to some of the sedimentological features common to deltas (e.g., delta-front turbidites, mud turbidites, abundant soft-sediment deformation features, massive sandstone and siltstone beds, synaeresis cracks, carbonaceous-rich mudstone drapes, etc.) can greatly assist in the recognition and interpretation of ancient deltaic successions.

The role of storms is problematic, because they are common in a wide variety of shallow water marine and nonmarine environments, and are *not* unique to wave-dominated shorelines. Storm effects serve to mask many of the unique characteristics of deltas, particularly where successions (i.e., the *preserved* deposits) are storm dominated. Likewise, storms are more effective at reworking proximal parts of the shoreline, and preserved "deltaic signals" may be encountered only in more distal facies. Given that many wave-dominated delta successions also display a strong storm signal, differentiating them from storm-dominated shorefaces is challenging. The focus should be on differentiation of offshore transition deposits from those of the prodelta (e.g., Fig. 10). General impoverishment of bioturbation intensities, lowered ichnological diversities and abundances, and general absence of opportunistic colonization of tempestites by *Skolithos* ichnofacies elements, coupled with hyperpycnal organics-rich mud drapes, common soft-sediment-deformed beds, synaeresis cracks, sediment-gravity-flow deposits, tool marks, and current ripples all may indicate proximity to fluvial discharge. More proximal facies may be manifested by preferential erosional amalgamation of tempestites, resulting in thick successions of hummocky and swaly cross-stratified sandstones, such that distinctions may be well reflected only in the distal delta front (Fig. 11; cf. Tables 1 and 2). Numerous successions of the Western Interior Seaway of North America are characterized by strong storm domination, yet most are widely regarded to reflect wave-dominated shoreface deposits (e.g., Bluesky Fm, Falher Member, Notikewin Member, and Cadotte Member, subsurface of Alberta, Virgelle Member of southern Alberta, the Eagle Sandstone of Montana and Wyoming, etc.). Certainly, alongstrike variations in these systems can be expected, and ichnological variations may prove useful in highlighting the position(s) of fluvial influx and the development of deltaic conditions.

Shoreline settings with stronger tidal signals are less well understood, but they appear to have numerous similarities with inshore tidally influenced settings such as estuarine valley fills, tidal flats, and lagoon/embayments. Although inshore tidal settings do experience similar energy variations on a variety of temporal scales, changing substrate consistencies, and heightened mud flocculation and deposition leading to fluid muds and high water turbidity, they also display marked changes in salinity, periodic subaerial exposure, changes in temperature, and other stresses unique to inshore positions. As such, inshore models are only broadly applicable to the facies characteristics of the subaqueous delta. More ichnological case studies of tide-influenced deltas are necessary in order to refine the "tidal signal", particularly with respect to organism responses to deposition of fluid muds.

To date, most trace-fossil case studies have concentrated on the characterization of end-member delta types. Suites have been proposed that demonstrate "river domination", "wave domination", and "tide domination" (Tables 1 and 2). In the future, less emphasis should be placed on the extreme cases (with the excep-

tion of strongly tide-influenced deltas), and greater effort put into characterizing the mixed-influence delta deposits. Discerning the effects of hypopycnal, homopycnal, and hyperpycnal fluvial discharge, freshet conditions, wave energy, storm influence, tidal flux, and their dynamic interplay are far more useful in interpreting the ancient record. Ichnological suites associated with deltas of varying sediment grade are also lacking. Most of the ancient examples have concentrated on mixed-load successions. To date, the ichnology of coarse-grained fan-delta deposits is largely unstudied, with the study of the Eocene Sant Llorenç del Munt fan delta, SE Ebro Basin, Spain (Siggerud and Steel, 1999), and the Upper Jurassic Oseberg Formation of the Norwegian Shelf, Norway (Soegaard and MacEachern, 2003), being notable exceptions. In addition, the nature of organism colonization and burrow reestablishment locally yields insights into depositional rates in the delta front (e.g., Howell et al., 2004), which may be useful in characterizing such things as seasonal episodic deposition and fluvial discharge volumes. Most delta deposits probably record conditions of mixed influence, and the relative significance of these variables likely changed during the history of lobe progradation and eventual abandonment. Provided that the ichnological and sedimentological responses of these processes can be discerned and differentiated, a more powerful tool would become available to the facies analyst.

The asymmetric-delta model (Bhattacharya and Giosan, 2003) reflects exactly such a mixed-influence delta type that has yet to be clearly identified in the ancient record. The interplay of wave influence and strong longshore drift with strong river influence results in marked facies variation both updrift and downdrift of the distributary system. Ichnology is ideally suited to assist in the recognition of the spatial distribution of these river-induced

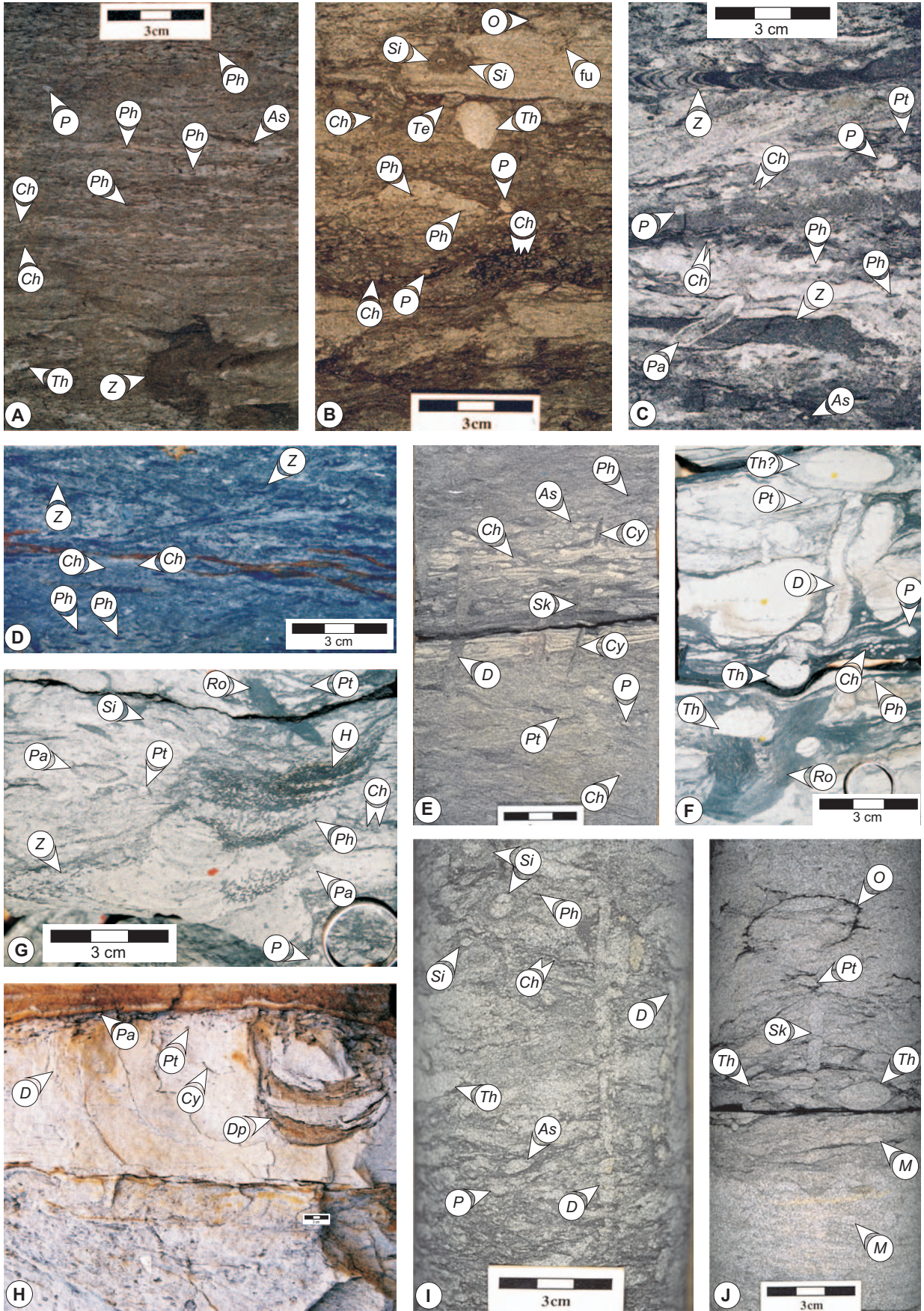
stresses. Recognition of such stresses concentrated preferentially along one margin of the subaqueous delta, coupled with observations of heterolithic brackish interdistributary-bay and bay-head delta deposition, would constitute a strong argument for delta asymmetry. More wave-influenced, less markedly stressed sandstones would record depositional positions updrift of the distributary system, where the shoreface model would apply. Given that distributary-channel complexes constitute one of the principal hydrocarbon reservoirs in deltaic systems, a technique that not only highlights proximity to fluvial discharge but also assists in delineating its relative position along the delta front would be invaluable to subsurface analysts. As such, ichnological analyses of deltas are exceedingly timely.

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FIG. 9.—Non-deltaic successions. The suites of nondeltaic shorelines tend to be more diverse and abundant than those of deltaic counterparts. **A**) Thoroughly bioturbated (BI 5) silty mudstone of the lower offshore to shelf, characterized by *Phycosiphon* (Ph), *Chondrites* (Ch), *Planolites* (P), *Thalassinoides* (Th), and *Zoophycos* (Z). Viking Formation, well 11-17-43-05W5, 2014.9 m, Alberta, Canada. **B**) Moderately to thoroughly bioturbated (BI 4–5) sandy mudstone of the upper offshore. Remnant tempestite near the top of the interval reflects some storm influence on deposition. Suite includes *Ophiomorpha* (O), *Siphonichnus* (Si), *Chondrites* (Ch), *Teichichnus* (Te), *Thalassinoides* (Th), *Phycosiphon* (Ph), *Planolites* (P), and fugichnia (fu). Viking Formation, well 10-34-54-20W5, 2577 m, Alberta, Canada. **C**) Thoroughly bioturbated (BI 5) sandy mudstone to muddy sandstone, reflecting proximal upper offshore to distal lower shoreface conditions. Suite includes *Zoophycos* (Z), *Chondrites* (Ch), *Planolites* (P), *Anconichnus* / *Phycosiphon* (Ph), *Palaeophycus heberti* (Pa), *Palaeophycus tubularis* (Pt), and *Asterosoma* (As). Cardium Formation, well 07-14-28-05W5, 2435.7 m. **D**) Thoroughly bioturbated (BI 5) lower offshore silty mudstone containing *Zoophycos* (Z), *Chondrites* (Ch) and *Phycosiphon* (Ph). Snapper Point Formation, Bannister's Point, Southern Sydney Basin, Australia. **E**) Bioturbated (BI 4–5) muddy sandstone of the lower shoreface. Remnant tempestite occurs halfway up the interval. The suite includes *Anconichnus* / *Phycosiphon* (Ph), *Asterosoma* (As), *Chondrites* (Ch), *Skolithos* (Sk), *Cylindrichnus* (Cy), *Diplocraterion* (D), *Planolites* (P), and *Palaeophycus tubularis* (Pt). Note the comparatively higher proportion of *Skolithos* ichnofacies elements. Heather Formation, well 30/9-08, 2801.1 m, Norwegian Shelf, Norway. **F**) Proximal lower-shoreface moderately to thoroughly bioturbated (BI 4–5) muddy sandstone. Suite includes *Palaeophycus tubularis* (Pt), *Diplocraterion* (D), *Planolites* (P), *Chondrites* (Ch), *Phycosiphon* (Ph), *Rosselia socialis* (Ro), and *Thalassinoides* (Th). Tern Formation, Tern Core-5, 2571 m, Permian Bonaparte Basin, Timor Sea. **G**) Distal lower-shoreface muddy sandstone showing thorough bioturbation (BI 5) with *Rosselia socialis* (Ro), *Helminthopsis* (H), *Siphonichnus* (Si), *Palaeophycus tubularis* (Pt), *Palaeophycus heberti* (Pa), *Chondrites* (Ch), *Phycosiphon* (Ph), *Zoophycos* (Z), and *Planolites* (P). Tern Formation, Tern Core-5, 2576 m, Permian Bonaparte Basin, Timor Sea. **H**) Proximal lower-shoreface sandstone with sporadic bioturbation (BI 2–5), showing a tempestite colonized top down. Suite includes *Palaeophycus heberti* (Pa), *Palaeophycus tubularis* (Pt), *Diplocraterion habichi* (D), *Diplocraterion parallelum* (Dp), and *Cylindrichnus* (Cy). Snapper Point Formation, South Snapper Point, Southern Sydney Basin, Australia. **I**) Bioturbated (BI 5) muddy sandstone of the lower shoreface, showing *Asterosoma* (As), *Chondrites* (Ch), *Diplocraterion* (D), *Thalassinoides* (Th), *Siphonichnus* (Si), *Planolites* (P), and *Anconichnus* / *Phycosiphon* (Ph). Viking Formation, well 06-29-47-21W4, 1035.7 m, Alberta, Canada. **J**) Laminated to burrowed bedding (BI 1–4) in sandstones of the proximal lower shoreface, showing *Ophiomorpha irregulaire* (O), *Palaeophycus tubularis* (Pt), *Skolithos* (Sk), *Thalassinoides* (Th), and *Macaronichnus simplicatus* (M). Viking Formation, well 11-29-62-20W5, 1701.8 m, Alberta, Canada.



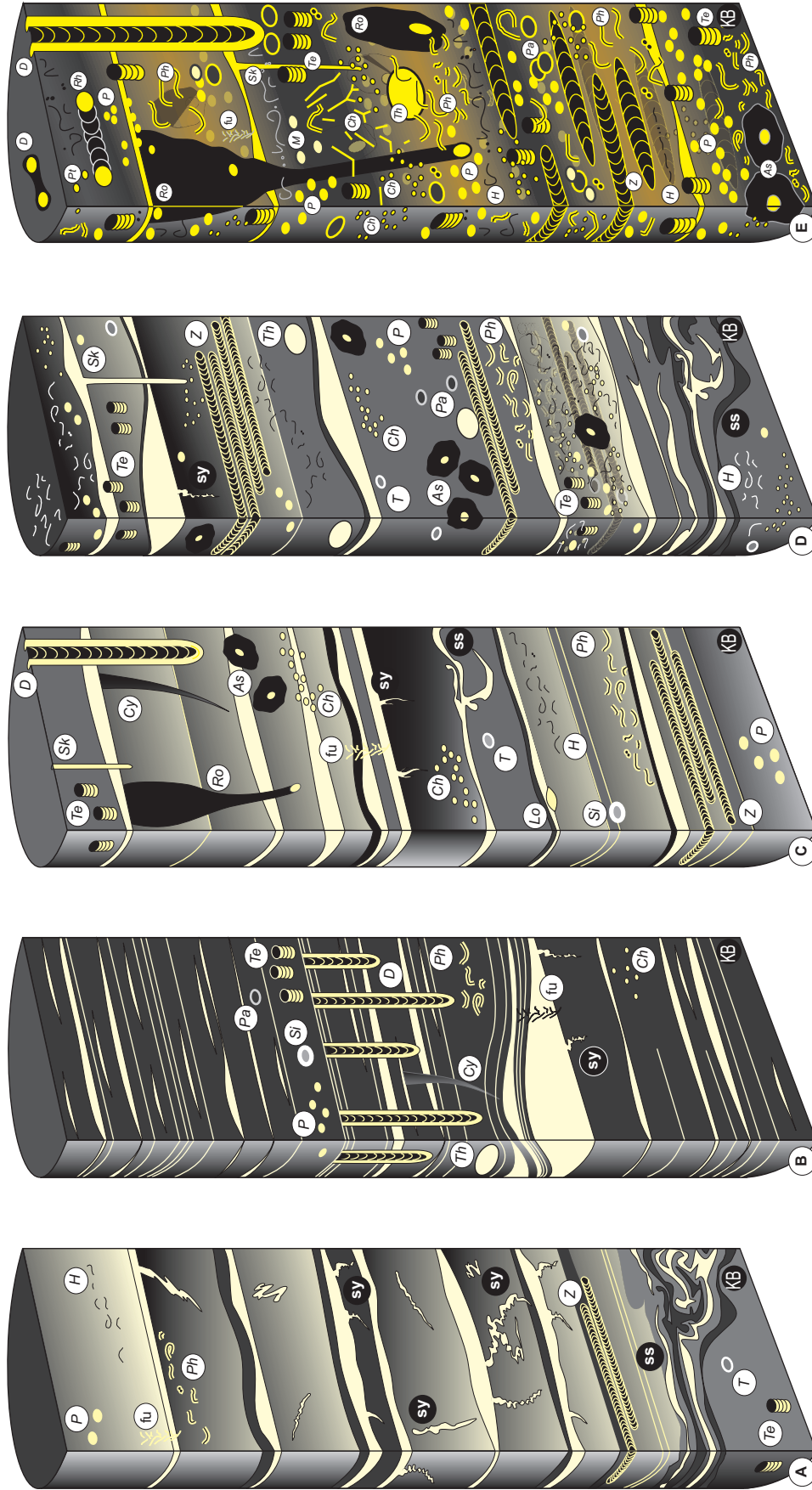


FIG. 10.—Schematic split-core expression of different prodelta types (A–E). **A**) River-dominated offshore example for comparison (E). **B**) tide-dominated expression, based on the Tije Formation, Norway (see Table 2); **C**) storm-dominated expression, based on the Dunvegan Fm (Allomember E) of Alberta, Canada (see Table 2); **D**) wave-dominated expression, based on Harlan, Willow, and Posey allomembers of the Frontier Fm, Wyoming, USA (see Table 2); **E**) characteristic offshore (nondeltaic) expression, based on a number of units from North America, Australia, and Norway. *Chondrites* (Ch), *Helminthopsis* (H), *Ancorichmus* / *Phycosiphon* (Ph), *Planolites* (P), *Zoophycos* (Z), *Thalassinoides* (Th), *Asterosoma* (As), *Rossetia* (R. socialis = Ro; R. rotatus = Rr), *Palaeophycus* (P. heberti = Ph), *Rhizocorallium* (Rh), *Tetrichmus* (Te), *Terebellina* (T), *Siphonichmus* (Si), *Cylindrichmus* (Cy), *Diplocraterion* (D), *Skolithos* (Sk), *Lockeia* (Lo), fugichnia (fu), synaeresis cracks (sy), and soft-sediment deformation (ss).

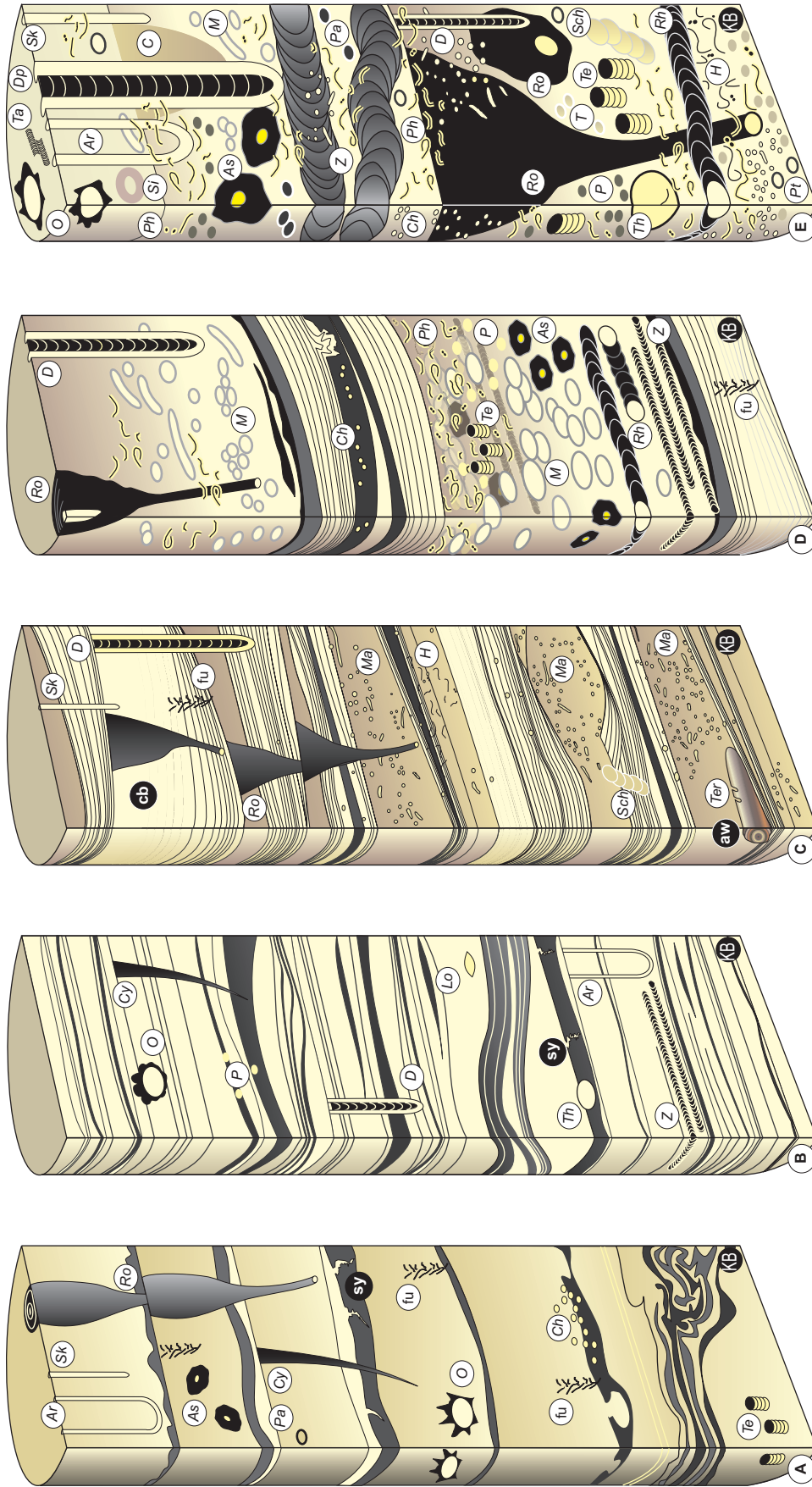


FIG. 11.—Schematic split-core expression of different distal delta front types (A–D) with a nondeltaic lower shoreface example for comparison (E). A) River-dominated expression, based on the Oseberg Fm of Norway (see Table 1); B) tide-dominated expression, based on the Frewens Formation, Wyoming, USA (see Table 2); C) storm-dominated expression, based on the Tarbert Fm, Norway (see Table 2); D) wave-dominated expression, based on intervals of the Denison Trough, Australia (see Table 2); E) characteristic offshore (nondeltaic) expression, based on a number of units from North America, Australia, and Norway. *Chondrites* (Ch), *Helminthopsis* (H), *Anconichnus* / *Phycosiphon* (Ph), *Planolites* (P), *Zoophycos* (Z), *Thalassinoides* (Th), *Asterosoma* (As), *Rosselia* (R. socialis = Ro, R. rotatus = Rr), *Palaeophycus* (P. heberti = Pa; P. tubularis = Pt), *Rhizocorallium* (Rh), *Teichichnus* (Te), *Terebellina* (T), *Siphonichnus* (Si), *Cylindrichnus* (Cy), *Diplocraterion* (D. habichi = D, D. parallelum = Dp, *Skolithos* (Sk), *Ophiomorpha* (O), *Arenicolites* (Ar), *Teredolites* (Ter), *Taenidium* (Ta), *Conichnus* (C), *Lockeia* (Lo), *Macaronichnus* (M. segregatis = Ma; M. simplicatus = M), *Schaubcylindrichnus* (Sch), fugichnia (fu), cryptobioturbation (cb), allocthonous wood (aw), synaeresis cracks (sy), and soft-sediment deformation (ss).

GLOSSARY OF SELECTED ICHNOLOGICAL TERMS

- bioturbation index:** a semiquantitative estimate of bioturbation intensities based on the abundance of biogenic structures and the proportion of burrow overlap. The usage of BI follows that of Bann et al. (2004). The concept derives from Reineck (1963), adapted by Taylor and Goldring (1993) and Taylor et al. (2003). Original codes concentrated on percentages of burrow overlap, but they are deemed unwieldy for field and core analysis and are, at best, semiquantitative (Bann et al., 2004). Original Bioturbation Index (BI) codes are as follows but can be tied to more qualitative descriptions as: BI 0 (0% bioturbated) = unburrowed; BI 1 (1–5% bioturbated) = very rare bioturbation; BI 2 (6–30% bioturbated) = rare to moderate bioturbation; BI 3 (31–60% bioturbated) = moderate bioturbation; BI 4 (61–90% bioturbated) = moderate to common bioturbation; BI 5 (91–99% bioturbated) = common to abundant bioturbation; BI 6 (100% bioturbated) = complete bioturbation.
- cryptobioturbation:** subtle disruptions of original grain fabrics and stratification, in sedimentary bodies, inferred to result from the activity of small infauna and meiofauna (faunal intermediate in size between macrofauna and microfauna). Cryptobioturbation is particularly common in tempestites.
- deposit feeding:** said of an organism that consumes organic material that has been deposited on or in the sediment.
- ethology:** the study and interpretation of organism behavior, based on the specific details of the biogenic structure.
- fugichnia:** a term used to describe an escape behavior made by an organism entrained within and/or buried by an event bed. Because organisms need to maintain a connection to the water column, rapid burial under a sediment body results in an upward motion of the animal to the new sediment–water interface.
- grazing:** said of an organism that consumes deposited organic material that lies on the sediment–water interface. This feeding strategy is broadly akin to “strip mining”. Most such structures are cored with fecal material.
- ichnofacies:** the concept that the character of the depositional environment leads to recurring groupings of organism behaviors and hence, biogenic structures. Faunal communities, therefore, yield recurring, strongly facies-controlled ethological groupings of trace fossils that have been designated “ichnofacies”.
- infaunal organism:** said of an organism that inhabits the substrate, whether occupying a burrow or a mobile intrastratal position. Most deposit feeders, passive carnivores, and suspension feeders are infaunal.
- k-selected population dynamics:** communities consisting mainly of specialized organisms exploiting a wide variety of niches. Such organisms are said to reflect equilibrium communities, characterized by population sizes in balance with the carrying capacity of the environment. K-selected populations are characterized by density-dependent mortality. Such organisms are good competitors but do not tolerate physiologically stressful settings. Ichnological expressions of such populations are high diversity and locally high abundance of most ethologies that are appropriate to the depositional conditions.
- opportunistic organisms:** said of organisms that occupy new environmental niches rapidly. Such organisms employ r-selected population dynamics (see below), emphasizing rapid growth, and rapid reproduction
- phytodetrital pulses:** rapid emplacement of macerated or otherwise allochthonous plant debris into the marine realm. Such pulses typically consist of terrestrial plant material carried seaward during river floods or surface runoff of the coastal margin. In some instances, this material may be carried into deep-water settings by sediment gravity flows.
- r-selected population dynamics:** communities consisting mainly of opportunistic organisms that emphasize rapid growth rates, largely independent of the carrying capacity of the environment. Such organisms rapidly exploit newly available niches and increase in abundance until food resources dwindle. These r-selected communities show density-independent mortality. They are characterized by short life cycles and rapid reproduction rates. Such organisms are tolerant of physiologically stressful environments. Ichnological expressions of such populations are low diversity and locally high abundance of simple, facies-crossing forms.
- suspension feeding:** said of an organism that occupies a more or less permanent dwelling and uses a filter-feeding apparatus to strain suspended organic particles and planktonic organisms from the water column. Current or wave energy is typically needed to deliver the food material to the organism.
- Synaeresis Cracks:** silt- or sand-filled, commonly pygmetrically folded, fractures with high length-to-width ratios, typically formed in heterolithic successions. They are believed to form subaqueously, attributed by most workers to reflect clay shrinkage associated with salinity changes near the bed. They are particularly abundant in inshore brackish settings, where salinity variations are common, though they also appear to form in a variety of other settings.
- taphonomy:** the study and interpretation of the preservation of fossil elements. From an ichnological perspective, soft or soupy substrates, lack of burrow lining, or lack of lithologic contrast between the burrow fill and the host media may result in a lack of preservation of those structures.
- trophic generalist:** said of an organism that is able to eat a wide variety of food types. Most such organisms are omnivores. Trophic generalists also tend to employ simple feeding strategies, or to vary their feeding strategies in accordance with the nature of the available food. Biogenic structures of such organisms tend to be simple facies-crossing elements.

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