“Geology is a capital science to begin, as it requires nothing
but a little reading, thinking, and hammering.”
– Charles Darwin (1835)

University of Alberta

BUILDING UPON ICHNOLOGICAL PRINCIPLES: MODERN BIOGENIC STRUCTURES, ICHNOTAXONOMIC CLASSIFICATION, AND PALEOECOLOGICAL AND STRATIGRAPHIC SIGNIFICANCE OF ICHNOFOSSIL ASSEMBLAGES

by

LYNN THERESA DAFOE

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Examining Committee

S. George Pemberton, Earth and Atmospheric Sciences

Murray Gingras, Earth and Atmospheric Sciences

Charles Stelck, Earth and Atmospheric Sciences

James MacEachern, Earth Sciences, Simon Fraser University

Maya Evenden, Biological Sciences

Charles Savrda, Geology and Geography, Auburn University

This work is dedicated to my loving and supportive husband, Chris, and to our wonderful daughter, Chloe, who was an endless (but enjoyable) distraction during completion of this thesis. Also to my parents for their love, encouragement and assistance in lugging prized rocks down steep trails.

ABSTRACT

Biogenic structures can impart important information regarding animal behaviors and depositional conditions at the time of colonization including: sedimentation rate, current velocities, distribution of food resources, oxygenation, salinity, and temperature. This thesis utilizes various ichnological subdisciplines to build upon these underlying ichnological principles.

Neoichnology is a newly emerging field that can provide invaluable information about modern and ancient organisms. Burrowing activities of a population of deposit-feeding, freshwater *Limnodrilus* and *Tubifex* is found to produce biogenic graded bedding. Similarly, the burrowing activities of *Euzonus mucronata* are studied in relation to the trace fossil *Macaronichnus segregatis*, which displays mineralogical segregation between the burrow infill and mantle. The process of grain partitioning was assessed using videographic analyses of ingested and excreted grains by these deposit-feeding polychaetes, which selectively ingest felsic grains through en-masse feeding in felsic-rich locales.

Macaronichnus is an important trace in ancient deposits of nearshore settings; however, since its inception, the genus had not been formally diagnosed. Accordingly, a unique approach to classification of these traces was undertaken, using grain sorting and collective morphology as ichnotaxobases, in addition to the diagnosis of a new, related genus—*Harenaparietis*. In the Permian Snapper Point Formation of SE Australia, a new ichnospecies of *Piscichnus* was diagnosed and interpreted to reflect fish or cephalopod feeding via hydraulic jetting into the substrate in search of infaunal food sources.

The delineation of trace fossils through ichnotaxonomy provides a basis for identifying trace fossil suites, which can be interpreted through ichnofacies analysis. Subtle ichnological and sedimentological attributes of deltaic strata in

the Viking Formation permits the identification of wave-influenced and mixed river- and wave-influenced deposits in the Hamilton Lake and Wayne-Rosedale-Chain areas of Alberta, Canada, respectively. Facies analysis combined with the identification of palimpsest stratigraphic surfaces led to the identification of transgressively incised shoreface deposits at Hamilton Lake. Examples of palimpsest ichnofossils from the Hamilton Lake area and from other strata are used in an assessment of soft-, stiff- and firmground suites. This study revealed the importance of substrate properties, environment, stratigraphy and processes leading to the formation and expression of allocyclic and autocyclic surfaces.

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TABLE OF CONTENTS

CHAPTER 1 - INTRODUCTION **1**

REFERENCES 4

CHAPTER 2 – A NEW TECHNIQUE FOR ASSESSING TUBIFICID BURROWING ACTIVITIES, AND RECOGNITION OF BIOGENIC GRADING FORMED BY THESE OLIGOCHAETES **6**

INTRODUCTION 6

Tubificid Burrowing Activities 7

Measuring Burrowing Rates 7

METHODS 9

RESULTS 12

Burrow Descriptions 12

Mound Characteristics 16

Layer Thickness 18

Volumetric Burrowing Rate 19

Tubificid Population Assessment 19

INTERPRETATIONS 21

Burrow Structures 21

Fecal Mounds 22

Layer Thickness 23

Volumetric Burrowing Rate 23

Tubificid Population Assessment 24

DISCUSSION 26

Variation in Egestion Rate 26

Volumetric Tracing Assessment 28

Sedimentological Importance 29

Ichnological Importance 31

SUMMARY 33

REFERENCES 34

CHAPTER 3 – DETERMINING *EUZONUS MUCRONATA* BURROWING RATES WITH APPLICATION TO ANCIENT *MACARONICHNUS SEGREGATIS* TRACE-MAKERS 38

INTRODUCTION 38

Euzonus mucronata 39

METHODS 41

BEHAVIORAL ANALYSES 44

Field Observations 44

Thin-Walled Aquarium Observations 46

Interpretations 46

VOLUMETRIC BURROWING RATES 49

Results 49

Interpretations 50

DISCUSSION 54

Distinctive Characteristics at Pachena Bay 56

CONCLUSIONS 57

REFERENCES 59

CHAPTER 4 – ANALYSIS OF MINERAL SEGREGATION IN *EUZONUS MUCRONATA* BURROW STRUCTURES: ONE POSSIBLE METHOD USED IN THE CONSTRUCTION OF ANCIENT *MACA-*

RONICHNUS SEGREGATIS ***63***

INTRODUCTION 63

Analogous Modern Trace-Makers 64

STUDY AREA 66

METHODS 66

RESULTS 70

Field-Based Observations 70

Ingestion and Excretion 72

Mineralogical Segregation 74

DISCUSSION 76

Mechanisms of Mineral Segregation 77

CONCLUSIONS 81

REFERENCES 82

CHAPTER 5 – AN UNORTHODOX TAXONOMIC APPROACH USING GRAIN SORTING AND COLLECTIVE ICHNOFOSSIL MORPHOLOGY IN DEFINING *MACARONICHNUS* AND *HARENAPARIETIS* NEW ICHNOGENUS **86**

INTRODUCTION 86

SYSTEMATIC ICHNOLOGY 92

Macaronichnus Clifton and Thompson, 1978 92

Macaronichnus segregatis Clifton and Thompson, 1978 102

Macaronichnus simplicatus new ichnospecies 114

Macaronichnus spiralis new ichnospecies 119

Harenaparietis n. ichnogen. 122

DISCUSSION 134

Reservoir Properties 134

The Future of Ichnotaxonomy 135

REFERENCES 136

CHAPTER 6 – ICHNOLOGICAL ASPECTS OF A NEW FORM OF *PISCICHNUS* IN THE SNAPPER POINT FORMATION, NEW SOUTH WALES, AUSTRALIA 151

INTRODUCTION 151

Mechanisms of *Piscichnus* Generation 151

Geological Setting 155

Study Area and Methods 158

OBSERVATIONS 160

Snapper Point 160

Clear Point 160

SYSTEMATIC ICHNOLOGY 161

Piscichnus Feibel 1987 161

Piscichnus brownii Feibel 1987 162

Piscichnus waitemata Gregory 1991 162

Piscichnus gregorii n. ichnosp. 164

DISCUSSION 165

Stratigraphic Interpretations 165

Substrate Properties and *Piscichnus* Preservation 166

Nature of the Trace-maker 168

Gutter and Pot Casts 171

SUMMARY 173

REFERENCES 173

CHAPTER 7 – ICHNOLOGICAL ASSEMBLAGES OF WAVE-INFLUENCED AND MIXED RIVER- AND WAVE-INFLUENCED DELTAIC DEPOSITS IN THE LOWER CRETACEOUS VIKING FORMATION, ALBERTA, CANADA 181

INTRODUCTION 181

Study area 182

Previous work 182

FACIES DESCRIPTIONS 185

FACIES ASSOCIATION 1: HAMILTON LAKE AREA 185

Facies A: Burrowed Muddy Sandstone to Sandy Mudstone 185

Sedimentology 185

Ichnology 187

Interpretation 187

Facies B: Burrowed Muddy Sandstone 189

Sedimentology 189

Ichnology 189

Interpretation 189

Facies C: Moderately Burrowed Sandstone 190

Sedimentology 190

Ichnology 190

Interpretation 192

Facies D: Sparsely Burrowed Sandstone 192

Sedimentology 192
Ichnology 193
Interpretation 193
Facies Association 1: Summary 194
FACIES ASSOCIATION 2: WAYNE-ROSEDALE TO CHAIN AREA 195
Facies E: Burrowed Sandy Mudstone 195
Sedimentology 195
Ichnology 197
Interpretation 198
Facies F: Burrowed Interbedded Sandstone and Mudstone 198
Sedimentology 198
Ichnology 199
Interpretation 199
Facies G: Burrowed Sandstone with Muddy Laminae 200
Sedimentology 200
Ichnology 200
Interpretation 202
Facies H: Weakly Burrowed Sandstone 202
Sedimentology 202
Ichnology 203
Interpretation 203
Facies Association 2: Summary 204
DISCUSSION 207

CONCLUSIONS 209

REFERENCES 210

CHAPTER 8 – WAVE-INFLUENCED DELTAIC SANDSTONE BODIES AND OFFSHORE DEPOSITS WITHIN A STRATIGRAPHIC FRAMEWORK IN THE VIKING FORMATION, HAMILTON LAKE AREA, SOUTH-CENTRAL ALBERTA, CANADA 217

INTRODUCTION 217

Study Area and Methods 219

FACIES DESCRIPTIONS 220

FACIES ASSOCIATIONS 220

Facies Association 1: Delta Front and Prodelta 220

Interpretation of Facies A: Sparsely Burrowed Sandstone – Proximal Delta Front 224

Interpretation of Facies B: Moderately Burrowed Sandstone – Distal Delta Front 227

Interpretation of Facies C: Burrowed Muddy Sandstone – Proximal Prodelta 228

Interpretation of Facies D: Burrowed Muddy Sandstone to Sandy Mudstone – Distal Prodelta 228

Facies Association 2: The Distal Lower Shoreface and Upper Offshore 230

Interpretation of Facies E: Homogenized Muddy Sandstone – Distal Lower Shoreface 231

Interpretation of Facies F: Homogenized Silty to Muddy Sandstone – Proximal Upper Offshore 231

Interpretation of Facies G: Homogenized Sandy Siltstone to Sandy Mudstone – Distal Upper Offshore 233

Facies Association 3: Lower Offshore and Transgressive Deposits 233

Interpretation of Facies H: Burrowed Sandy Mudstone to Silty Mudstone – Proximal Lower Offshore 233

Interpretation of Facies I: Sparsely Burrowed Sandy Mudstone – Distal Lower Offshore 235

Interpretation of Facies J: Massive Mudstone/Shale – Shelf 235

Interpretation of Facies K: Chaotic Sandy Mudstone to Muddy Sandstone – Transgressive Lag 236

Interpretation of Facies J: Convolute Bedded Sandy Siltstone to Sandy Mudstone – Slump Deposit 236

STRATIGRAPHY 237

Lower Viking Formation 238

Middle Viking Formation 243

Upper Viking Formation 246

FAS1: WAVE-INFLUENCED DELTAIC DEPOSITS 249

CONCLUSIONS 251

REFERENCES 252

CHAPTER 9 – DEFINING THE NATURE OF PALIMPSEST SOFTGROUND, STIFFGROUND, AND FIRMGROUND TRACE FOSSIL SUITES USING MODERN AND ANCIENT EXAMPLES 259

INTRODUCTION 259

Overprinting, Tiering and Palimpsest Suites 261

Discriminating Between Soft-, Stiff- and Firmgrounds 263

Challenges in Defining Palimpsest Suites 264

METHODS 266

SUBSTRATE INFLUENCE ON PALIMPSEST SUITES 275

Substrate Properties 275

Palimpsest Softground Suites 276
Principal Attributes 276
Primary Attributes 277
Secondary Attributes 284
Palimpsest Stiffground Suites 286
Principal Attribute 286
Primary Attributes 286
Secondary Attributes 291
Firmground *Glossifungites* Ichnofacies 295
Principal Attribute 295
Primary Attributes 295
Secondary Attributes 297
Localized Variability at the Ichnofossil Scale 298
Adjacent Ichnofossils Displaying Varied Characteristics 298
Vertical Variation in Homogeneous Sediment 299
Vertical Variation in Heterolithic Sediment 300
Variation as a Function of Incipient Cementation 300
Overall Character Reflects Different Interpretations 302
ENVIRONMENTAL INFLUENCE 303
Depositional Environment 305
Energy Regime 306
Sedimentation Rate 307
Progressive Palimpsesting 308

Trace-maker Colonization 310

STRATIGRAPHIC INFLUENCE ON PALIMPSESTING 311

Degree of Burial, Erosion, and Hiatus 311

Rates of Transgression or Erosion 313

Lag Deposition 314

Spatial and Temporal Surface Variability 314

Viking Formation – Spatial-Temporal Transition 315

Pebbley Beach Formation – Lateral Lithological Variation 316

Stratigraphic Surfaces 317

DEVELOPMENT AND PRESERVATION OF PALIMPSEST SUITES 318

Palimpsest Softground 318

Palimpsest Stiffground 319

Stiffgrounds Constructed During Continuous Deposition 321

Palimpsest Stiffgrounds Formed Due to a Compactional Gradient 323

Palimpsest Stiffground Formed Through Erosion 325

Development of the *Glossifungites* Ichnofacies 325

Taphonomy of Palimpsest Suites 326

APPLICATION OF PALIMPSEST SUITES 327

SUMMARY 329

REFERENCES 332

CHAPTER 10 - CONCLUSIONS 339

APPENDIX 342

LIST OF TABLES

TABLE 2.1—Highlights and limitations of methods utilized in determining tubificid bioadvection rates 8

TABLE 2.2—Recorded thickness for the total sediment package, the sand, silt, clay and fecal layers 11

TABLE 2.3—Table of measurements used in the burrowing rate calculations 13

TABLE 2.4—Number of active mounds recorded on all measurement days between days 8 and 34 13

TABLE 2.5—Table of particle redistribution rates from various publications 25

TABLE 3.1—*Euzonus mucronata* population densities extrapolated from box core sampling on Pachena Beach 42

TABLE 3.2—Percentage and volume of burrowed sediment observed on each side of the aquarium 44

TABLE 3.3—Calculated burrowing rates and burrowing times for various populations 52

TABLE 4.1—Approximate developmental stages of *Euzonus mucronata* 67

TABLE 4.2—Average grain compositions ingested and excreted by *Euzonus mucronata* 68

TABLE 4.3—Normalized proportions of mineral grains ingested or excreted versus the host sediment composition 69

TABLE 6.1—Measurements corresponding to *Piscichnus* documented in the Snapper Point Formation 153

TABLE 6.2—A comparison of width-to-depth ratios of traces from various publications 153

TABLE 6.3—Complied descriptions and interpretations of excavations constructed by modern organisms and processes 154

TABLE 7.1—Comparison of ichnological assemblages from the Hamilton Lake and Wayne-Rosedale-Chain study areas 206

TABLE 8.1—Facies descriptions for deposits in the Hamilton Lake area 221

TABLE 8.2—Comparison of ichnological assemblages interpreted from deltaic deposits 250

TABLE 9.1—Comparison of characteristics of palimpsest soft- and stiffground trace fossil suites, as well as the *Glossifungites*, *Trypanites* and *Teredolites* Ichnofacies 267

TABLE 9.2—Modern examples of palimpsest suites 268

TABLE 9.3—Ancient examples of palimpsest softground suites 269

TABLE 9.4—Ancient examples of palimpsest stiffground suites 271

TABLE 9.5—Ancient examples of palimpsest firmground suites 272

TABLE 9.6—Ancient examples of transitional palimpsest suites 273

LIST OF FIGURES

FIGURE 2.1—The collection site in Edmonton, Alberta, Canada 9

FIGURE 2.2—Cross-sectional images of the aquarium 14

FIGURE 2.3—Change in burrow structure and definition over the course of the experiment 15

FIGURE 2.4—Features on the sediment surface taken from the top of the aquarium 16

FIGURE 2.5—Surface (aerial) view of the tubificid aquarium on days 9 and 34 19

FIGURE 2.6—Plots against time for the area, volume, number of mounds and number of active mounds 20

FIGURE 2.7—Diagrammatic development of biogenic graded bedding by the tubificid population 22

FIGURE 2.8—Burrowing rates in cm/d/100,000 individuals/m^2 for species of *Limnodrilus* and/or *Tubifex* 26

FIGURE 2.9—Bed forms formed by varying degrees of physical and biogenic influence 30

FIGURE 3.1—*Macaronichnus segregatis* 39

FIGURE 3.2—The study area located on Vancouver Island 40

FIGURE 3.3—*Euzonus mucronata* 40

FIGURE 3.4—A grid overlay on the aquarium 43

FIGURE 3.5—*Euzonus mucronata* and burrows constructed by *E. mucronata* in the field 45

FIGURE 3.6—The large aquarium that contained 18 adult *Euzonus mucronata* 47

FIGURE 3.7—Onshore-offshore migrations of *Euzonus mucronata* 48

FIGURE 3.8—The small aquarium (side 1) that contained 5 *Euzonus mucronata* 49

FIGURE 3.9—The percentage of visible burrowed sediment and average volume of burrowed sediment plotted against time 51

FIGURE 4.1—*Macaronichnus segregatis* from the Horseshoe Canyon Formation of Alberta 64

FIGURE 4.2—*Euzonus mucronata* 65

FIGURE 4.3—The west coast of Vancouver Island showing the location of Pachena Bay 67

FIGURE 4.4—*Euzonus mucronata* and *E. mucronata* burrows in the field 71

FIGURE 4.5—Epoxy sediment peels from horizons within Pachena Beach 71

FIGURE 4.6—Video stills of ingestion and excretion of grains by *Euzonus mucronata* *73*

FIGURE 4.7—The average percentage of ingested and excreted grains 75

FIGURE 4.8—The proportions of ingested versus host sediment abundances and excreted versus host sediment abundances of felsic, mafic and shell grains 76

FIGURE 4.9—The everted proboscis of *Euzonus mucronata* 78

FIGURE 4.10—Sediment peels from Copalis Beach, Washington, USA 79

FIGURE 5.1—The main ichnotaxobases used to differentiate *Macaronichnus* and *Harenaparietis* 87

FIGURE 5.2—Paratype specimens of *Macaronichnus segregatis* 87

FIGURE 5.3—Holotype specimen of *Macaronichnus simplicatus* 88

FIGURE 5.4—*Macaronichnus spiralis* 88

FIGURE 5.5—Low population densities of *Macaronichnus* 97

FIGURE 5.6—*Macaronichnus segregatis* exhibiting cryptobioturbation 98

FIGURE 5.7—Onshore-offshore migrations of *Euzonus mucronata* 108

FIGURE 5.8—Plan view representation of *Macaronichnus simplicatus*,

M. segregatis and *M. spiralis* 111

FIGURE 5.9—Three dimensional surface rendering of a Magnetic Resonance Image of a specimen containing *Macaronichnus segregatis* 111

FIGURE 5.10—The relationships between the various ichnospecies of *Macaronichnus* and important environmental conditions 113

FIGURE 5.11—Various forms of branching 116

FIGURE 5.12—*Macaronichnus simplicatus-segregatis* 118

FIGURE 5.13—Holotype specimens of *Harenaparietis* 124

FIGURE 5.14—*Harenaparietis* examples from various units 125

FIGURE 5.15—*Macaronichnus* occurring in conjunction with *Harenaparietis* 126

FIGURE 5.16—Formation of *Harenaparietis* 129

FIGURE 5.17—A typical *Lumbrineris* cf. *latreilli* burrow 131

FIGURE 6.1—*Piscichnus* in the Snapper Point Formation 152

FIGURE 6.2—Modern animals capable of forming *Piscichnus*-like structures 156

FIGURE 6.3—Stratigraphic chart of the Early Permian from New South Wales, Australia 157

FIGURE 6.4—The study area along the SE coast of Australia 157

FIGURE 6.5—Evidence of cold-climate conditions during deposition of the Shoalhaven Group 159

FIGURE 6.6—Various forms of *Piscichnus* 161

FIGURE 6.7—The generation of softground palimpsest trace fossil suites 167

FIGURE 7.1—Stratigraphic correlation chart for the Viking Formation and equivalents 182

FIGURE 7.2—The Hamilton Lake and Wayne-Rosedale-Chain study

areas 183

FIGURE 7.3—Logged core from the Hamilton Lake and Wayne-Rosedale-Chain study areas 183

FIGURE 7.4—Hamilton Lake Deposits (Facies A and B) 186

FIGURE 7.5—Shoreface model for ichnological assemblages in the Western Canada Sedimentary Basin 188

FIGURE 7.6—Hamilton Lake Deposits (Facies C and D) 191

FIGURE 7.7—Wayne-Rosedale-Chain Deposits (Facies E and F) 196

FIGURE 7.8—Wayne-Rosedale-Chain deposits (Facies G and H) 201

FIGURE 7.9—Tripartite classification of deltaic systems 205

FIGURE 7.10—Wave-influenced and mixed river- and wave-influenced deposits 205

FIGURE 8.1—Stratigraphic correlation chart for the Viking Formation 218

FIGURE 8.2—The Hamilton Lake study area 218

FIGURE 8.3—The study area with locations of logged core 219

FIGURE 8.4—Facies A-B 225

FIGURE 8.5—Ichnological assemblages characteristic of shoreface strata in the Western Canada Sedimentary Basin 226

FIGURE 8.6—Facies C-D 229

FIGURE 8.7—Facies E-G 232

FIGURE 8.8—Facies H-L 234

FIGURE 8.9—Cross section A–A′ along dip through the Hamilton Lake area 239

FIGURE 8.10—Cross section B–B′ along strike near the northeastern edge of Hamilton Lake 241

FIGURE 8.11—Aspects of Bounding Discontinuity 1 242

FIGURE 8.12—Bounding Discontinuity 2 and Flooding Surface 2 244

FIGURE 8.13—Type core log from the Castor area 245

FIGURE 8.14—Bounding Discontinuities 3 and 4 248

FIGURE 8.15—Delta morphologies produced as a result of increasing wave influence 249

FIGURE 9.1—The firmground *Glossifungites* Ichnofacies 260

FIGURE 9.2—The *Trypanites* and *Teredolites* Ichnofacies 261

FIGURE 9.3—Various forms of overprinting 262

FIGURE 9.4—The diameter of the indentation in the substrate as a function of the pressure exerted by the substrate 265

FIGURE 9.5—Softground trace fossil suite versus palimpsest softground trace fossil suite 277

FIGURE 9.6—Examples of palimpsest softground trace fossil suites 278

FIGURE 9.7—X-ray images of modern sediment 281

FIGURE 9.8—Progressive palimpsesting 282

FIGURE 9.9—Palimpsest surfaces displaying spatial and/or temporal variation 283

FIGURE 9.10—Representative examples of the models depicted in Figure 9.18 287

FIGURE 9.11—Transitional palimpsest softground to stiffground suites 289

FIGURE 9.12—A transitional stiffground to firmground 290

FIGURE 9.13—Palimpsest stiffground suites 292

FIGURE 9.14—Modern examples of different substrate consistencies 295

FIGURE 9.15—The environmental influence on palimpsest suites 304

FIGURE 9.16—The formation of incised shorefaces 313

FIGURE 9.17—Models depicting the formation of softground trace fossil suites formed during continuous and discontinuous deposition 319

FIGURE 9.18—Models depicting the development of trace fossil suites in stiffground and firmground 320

FIGURE 9.19—Repeating sand and mud couplets in the McMurray Formation 323

FIGURE 9.20—Example of a coarse, thick lag deposit 327

LIST OF SYMBOLS AND ABBREVIATIONS

LOCALITIES AND UNITS

HL	Hamilton Lake
NSR	North Saskatchewan River
NSW	New South Wales
SPF	Snapper Point Formation
WRC	Wayne-Rosedale-Chain

MISCELLANEOUS

BI	Bioturbation Index
HCS	Hummocky Cross Stratification
IHS	Inclined Heterolithic Stratification
RSL	Relative Sea Level
VBR	Volumetric Burrowing Rate

ICHNOFOSSILS

Ar	*Arenicolites*
As	*Asterosoma*
Ch	*Chondrites*
Co	*Conichnus*
Cy	*Cylindrichnus*
Di	*Diplocraterion*
fu	fugichnia
He	*Helminthopsis*
Op	*Ophiomorpha*
Pa	*Palaeophycus*
Ph	*Phycosiphon*
Pl	*Planolites*
Rh	*Rhizocorallium*
Ro	*Rosselia*
Sc	*Schaubcylindrichnus*
Si	*Siphonichnus*
Sk	*Skolithos*
So	*Scolicia*
Te	*Teichichnus*
Th	*Thalassinoides*
Zo	*Zoophycos*

DEPOSITIONAL ENVIRONMENTS

PDF	Proximal delta front
DDF	Distal delta front
PPD	Proximal prodelta
DPD	Distal prodelta
DLS	Distal lower shoreface
PUO	Proximal upper offshore
DUO	Distal upper offshore
Lag	Lag deposit
SLU	Slump deposit
Shelf	Shelf/distal ramp

CHAPTER 7 ABBREVIATIONS

FAS1	Facies Association 1
FAS2	Facies Association 2
FA	Facies A
FB	Facies B
FC	Facies C
FD	Facies D
FE	Facies E
FF	Facies F
FG	Facies G
FH	Facies H

CHAPTER 8 ABBREVIATIONS

FAS1	Facies Association 1
FAS2	Facies Association 2
FAS3	Facies Association 3
FA	Facies A
FB	Facies B
FC	Facies C
FD	Facies D
FE	Facies E
FF	Facies F
FG	Facies G
FH	Facies H
FI	Facies I
FJ	Facies J
FS1	Flooding Surface 1
FS2	Flooding Surface 2
BD1	Bounding Discontinuity 1
BD2	Bounding Discontinuity 2
BD3	Bounding Discontinuity 3
BD4	Bounding Discontinuity 4

CHAPTER 9 ABBREVIATIONS

FS Flooding Surface

SB Sequence Boundary

TRS Tidal Ravinement Surface

TSE Transgressive Surface of Erosion

WRS Wave Ravinement Surface

CHAPTER 1 - INTRODUCTION

The field of ichnology comprises a diverse subset of disciplines that promote the overall understanding of ancient trace-makers, their behaviors and the environmental conditions that persisted during sediment colonization (cf. Gingras et al., 2007). This thesis combines various aspects of ichnology including: neoichnology (the study of modern burrowing activities), ichnotaxonomy (the classification of trace fossils), ichnofacies analysis (the use of ichnofossil suites), and the study of palimpsest suites to assess stratigraphic discontinuities in order to build upon ichnological principles and the understanding of ancient organisms and environments.

Determining the temporal significance of invertebrate ichnofossils is essential in the interpretation of ancient organism behaviors, depositional settings, and bioturbation versus sedimentation rates. Two studies addressed temporal significance by assessing the burrowing rates of selected modern animals. Tubificids are important head-down, "conveyor-belt" feeders in freshwater settings as dense populations can rapidly rework bottom deposits to transport segregated silt and clay particles to the sediment surface (Fisher et al., 1980). This thesis presents a new method in determining tubificid bioadvection rates, which addresses some of the limitations associated with previous studies. The new approach consists of an aquarium inoculated with sediment and worms in which tubificids produce fecal mounds over time as the sediment surface is photographed and analyzed using computer software. The worms were found to rework the sediment into a unique form of stratification that has the potential for preservation in the rock record.

The second chapter that deals with bioturbation rates incorporates laboratory studies of the polychaete *Euzonus mucronata*, which produces structures similar to the ichnofossil *Macaronichnus segregatis*. This trace fossil is known to represent the activity of deposit-feeding polychaetes, and commonly occurs as a pervasive structure in shallow-marine sandstones (e.g., Saunders, 1989). Field measurements from Pachena Beach, Vancouver Island, Canada included assessment of population densities and worm behaviors. Volumetric burrowing rates were obtained from a thin-walled aquarium constructed in the laboratory using a new technique that involves grid overlay analysis. These burrowing rates can be applied to ancient successions in order to approximate the activities of similar, ancient organisms. *Macaronichnus segregatis* is a

distinctive ichnofossil characterized by the mineralogical segregation of sand grains forming a felsic burrow infill and a mafic- and mica-rich burrow mantle (Clifton and Thompson, 1978). The second aspect of the *Euzonus* study focused on determining the mechanism by which *M. segregatis* trace-makers segregate mineral grains during deposit feeding. *Euzonus mucronata* were microscopically videotaped to collect data on ingestion and excretion through visual grain counts of felsic, mafic and shell components. The method by which the polychaetes form the felsic-rich burrow infills is determined. However, in regards to application to *M. segregatis*, the method is thought to reflect the unique sediment properties and species of polychaete selected and may be one possible process used in mineral segregation.

Although *Macaronichnus* is an important trace fossil in nearshore deposits, the original description of the trace did not include a proper ichnotaxonomic diagnosis (cf. Clifton and Thompson, 1978). Another aspect of this thesis includes a unique taxonomic assessment of the *Macaronichnus* ichnogenus and its ichnospecies, in addition to the introduction of a new ichnogenus—*Harenaparietis*. The traditional taxonomic approach in ichnology involves differentiation of ichnogenera and ichnospecies based upon standard morphological attributes of individual specimens (Bertling et al., 2006). Particular ichnofossils, however, may be characterized on other, more apparent, criteria. *Macaronichnus segregatis*, for instance, consists of unlined, non-branching, cylindrical ichnofossils produced through deposit-feeding strategies that result in compositional differences between individual burrow fills, burrow mantles, and the matrix. The chapter herein proposes a new approach to a revised *Macaronichnus* taxonomy that involves the introduction of new ichnotaxobases or criteria for defining trace fossils.

In addition to the *Macaronichnus* taxonomy, a new form of *Piscichnus* was identified from the Permian Snapper Point Formation of SE Australia. These traces occur as anomalously large depressions with morphological variations that include: 1) steep-walled, cylindrical to conical forms; and 2) shallow- to steep-walled, hook-shaped depressions. The width-to-depth ratios of these features are comparable to documented biogenic structures from ancient and modern settings referred to as *Piscichnus* or *Piscichnus*-like, respectively (e.g.,, Gregory et al., 1979; Gregory, 1991). Cylindrical and conical structures in the Snapper Point Formation are interpreted as *P. waitemata*, whereas the hooked-shaped depressions reflect a new ichnospecies termed *Piscichnus gregorii*. A taxonomic

assessment of *Piscichnus* is undertaken and the potential trace-makers and associated behaviors are discussed.

Once trace fossils have been identified within a suite, the collective occurrence of the traces can be assessed using ichnofacies analysis (cf. Pemberton et al., 2001). This paradigm is a powerful tool that can be used to interpret the environment in which deposition took place. In the Viking Formation at Hamilton Lake (Alberta, Canada), sandy units were interpreted as shoreface in origin by Burton (1997). This study uses detailed sedimentological and ichnological data to refine this interpretation through the identification of the deltaic nature of strata of Viking Formation deposits from the Hamilton Lake and Wayne-Rosedale-Chain areas (Alberta, Canada). Deltaic deposition is implied based on evidence of high sedimentation rates, variable salinity, and stressed ichnological assemblages (e.g.,, MacEachern et al., 2005). The sedimentological and ichnological attributes of these deposits reflect different degrees of riverine, wave, and storm influence. In the Hamilton Lake area, a second study focused on distinguishing between these deltaic deposits and strata reflecting normal-marine (non-deltaic) depositional conditions, and relating these facies within the stratigraphic framework. Facies are grouped into three facies associations interpreted as: 1) deltaic, 2) upper offshore, and 3) lower offshore in conjunction with transgressive deposits. These facies associations, in conjunction with interpreting stratigraphic discontinuities, reveal a depositional history that includes periods of progradation alternating with transgressive flooding, subaerial exposure, progradation during stillstand and wave ravinement.

The importance of a distal expression of the *Glossifungites* Ichnofacies at Hamilton Lake was first recognized by MacEachern and Burton (2000). This distal *Glossifungites* Ichnofacies reflects an atypical firmground colonization in which deposit-feeding, foraging and probing traces demarcate the stratigraphic horizon. Examples from this area, other ancient successions, and modern deposits are used to discriminate between these newly recognized palimpsest softground and stiffground suites and those from the well-established firmground *Glossifungites* Ichnofacies (cf. Pemberton et al., 2001). Palimpsest trace fossil suites involve a post-depositional overprinting produced by substrate recolonization that follows a depositional hiatus and/or erosion. Difficulty in defining these suites is related to the gradational nature of substrate firmness, which is observed in modern sediments (e.g.,, Gingras et al., 2000). The depositional break associated with the overprinted assemblage can demarcate

stratigraphically significant and autocyclically generated surfaces. The influence of substrate, environment and stratigraphy, in addition to the processes by which palimpsest suites form is discussed, and a revised application of these suites is proposed.

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CHAPTER 2 – A NEW TECHNIQUE FOR ASSESSING TUBIFICID BURROWING ACTIVITIES, AND RECOGNITION OF BIOGENIC GRADING FORMED BY THESE OLIGOCHAETES

INTRODUCTION

Tubificids are oligochaetes common to muddy and sandy stream and lake bottoms, as well as marine sediments (see appendix; Appleby and Brinkhurst, 1970; Rogaar, 1980). In freshwater environments, tubificids are the primary infaunal burrowers (Fisher et al., 1980) that mix sediment through conveyor-belt feeding activities, resulting in egestion of underlying deposits at the sediment-water interface (Rhoads, 1974). This sediment reworking alters the physical, chemical and stratigraphic properties of the deposits (Fisher et al., 1980). Physically, tubificid oligochaetes selectively ingest silt and clay particles, and produce a pelletized layer that possesses: a higher water content; enhanced organic matter content; a larger median grain size; increased settling velocity; enhanced transportability; and increased porosity (McCall and Fisher, 1980; Tevesz et al., 1980). Chemical alteration includes: an increase in oxygen demand; inhibition of phosphorus release into the water column; enhanced flux of ammonium bicarbonate and silica from sediments; decreased iron and phosphate flux in anoxic conditions; inhibition of nitrification; decreased sediment pH; and alteration of microbial processes and concordant water chemistry (Davis, 1974b; Kikuchi and Kurihara, 1977; McCall and Fisher, 1980; Matisoff et al., 1985; Mermillod-Blondin et al., 2001). Rogaar (1980) reported that stratification also can be destroyed by tubificids depending on the duration and intensity of feeding activities, as well as the population density, burrowing depth, and rate of sedimentation. For example, Davis (1974a) reported that the activities of tubificids can displace pollen and other microfossils.

Along the North Saskatchewan River in the Edmonton area of Alberta, Canada, common genera of the family Naididae, *Limnodrilus* and *Tubifex,* persist within fine-grained marginal river sediments. This chapter aims to further evaluate the impact of activities of these tubificids on sediment characteristics by: 1) presenting a new method for analyzing tubificid burrowing rates; 2) determining

the rate of biogenic modification by a population of *Limnodrilus* and *Tubifex*; and 3) assessing the sedimentological and ichnological implications of the bioturbation.

Tubificid Burrowing Activities

Tubificid conveyor-belt burrowing activities involve sediment ingestion at depth and egestion at the sediment-water interface. Respiration occurs through the posterior, which undulates in the water column during this process (Appleby and Brinkhurst, 1970; Rogaar, 1980). Deposit feeding includes selective ingestion of silt and clay grains (particles less than 63 μm), but fine sand up to 260 μm in diameter may also be ingested (Brinkhurst et al., 1972; Davis, 1974a; Kikuchi and Kurihara, 1977; Tevesz et al., 1980; Rodriguez et al., 2001; Ciutat et al., 2006). The ingestion of grains takes place at a shallow depth that is generally within 2-9 cm of the sediment surface (Appleby and Brinkhurst, 1970; Davis, 1974b; Fisher et al., 1980), but can extend down to 10-20 cm depth (Appleby and Brinkhurst, 1970; McCall and Fisher, 1980; Matisoff et al., 1999; Ciutat et al., 2006). Selection of fine particles is thought to be associated with foraging for organic-rich sediment (Brinkhurst et al., 1972; Rodriguez et al., 2001) or specific bacteria populations (Brinkhurst and Chua, 1969; Wavre and Brinkhurst, 1971; Tevesz et al., 1980). The sediment ingested at depth is processed in the gut of the worms and egested as mucous-bound fecal matter, which is deposited as long, thin strings or short pieces (sand-sized) that collect at the burrow exit on the sediment surface (McCall, 1979; Rogaar, 1980; Tevesz et al., 1980; Matisoff et al., 1985).

Measuring Burrowing Rates

Substantial tubificid deposits in freshwater settings have prompted the development of various methods used to measure bioadvection rates of these oligochaetes. These methods include: 1) direct collection of fecal pellets for volumetric, mass or energetic determination; 2) measuring accumulation depth of the fecal layer over time; 3) estimating burrowing from contaminant flux; and 4) determining the rate of redistribution of marked particles (fluorescent or radiolabeled; Table 2.1). Robbins et al. (1979) suggested that the best method for determining the effects of tubificid bioturbation would be one that allows for frequent measurements, is non-destructive, incorporates high resolution, and is designed such that organisms are unable to discern any differences in sediment

Method	Highlights	Limitations	References
Direct Collection Inverted and upright defecation chambers covered by a membrane through which worms protrude and egest fecal pellets.	• Fecal material is directly collected • Simplistic	• Fluctuation in egestion rates due to intermittent collection • Small population • Unnatural setting (inverted in vials) • Does not account for organism movements, compaction and diagenesis • Upright experiments suggest inverted collection results in reduced fecal output	Ivlev (1939) Appleby and Brinkhurst (1970) Brinkhurst et al. (1972) Kaster et al. (1984) Fukuhara et al. (1987) Reible et al. (1996)
Accumulation Depth Records the depth of fecal accumulation in a small experimental cell with or without the use of a marker horizon.	• Simulates a natural setting • Measurements are simple • Sediment and worms are undisturbed	• Irregular worm and fecal pellet distribution leads to measurement error • Sediment surface may require estimation away from the walls of the experimental unit • Differentiation between the fecal layer and underlying layer may be difficult • Feeding depth may be limited • Compaction is not accounted for	Davis (1974) McCall and Fisher (1980) Ciutat et al. (2006)
Contaminant Flux Model Flux due to burrowing and contaminant concentrations.	• Can be applied to different organisms with similar behaviors	• Does not account for temperature variations • Flux varies depending on contaminant, population density and sediment properties • Contaminant release changes water chemistry and concordant burrowing rates	Reible et al. (1996) Reible and Mohanty (2002)
Marked particles			
Fluorescent Tracers Coloured particles are initially placed on the sediment surface, then sampled at depth and counted.	• Simulates a natural setting • Sediment and worms are undisturbed	• Unnatural particles • Ineffective distribution of large particles and small microspheres • Preferred grain sizes (<63 μm) were not marked • Limited depth range • Only works when tracers are within the feeding zone (i.e. requires a prolonged establishment period)	Mermillod-Blondin et al. (2000, 2001) Ciutat et al. (2005)
Radiolabeled Particles Illite clay is marked with ^{137}Cs and deposited in a layer producing an activity peak. Burial of the peak is used to determine the downward velocity of the layer or effective burrowing rate.	• Marked particles are of the typical size ingested • Multiple tracer layers can be used • Sediment and worms are undisturbed • Redistribution of marked particles accounts for all reworking activities not just fecal pellet production • Addresses compaction and diagenesis	• Tracer peak accuracy diminishes over time due to dispersion of marked particles • Lateral heterogeneities cannot be detected • Irregular piles of fecal material lead to greater uncertainties in peak position • Assumptions in the model lead to some discrepancies between simulated and measured tracer profiles • The model does not account for material moved below the zone of feeding • The depth of maximum feeding is assumed to be constant over time • Limited depth range • Uncertainties over the degree of selective preference or avoidance of marked particles • Worms tend to selectively feed on marked particles when populations are dense • Limited time frame (due to homogenization of marked particles)	Robbins et al. (1979) Fisher et al. (1980) Matisoff et al. (1999)
Volumetric Tracing The sediment surface is photographed, fecal mounds on the photos are traced, the area is calculated and converted to volume of upturned sediment or burrowing rate.	• Sediment and worms are undisturbed • Large available surface area • Simulates a natural setting • Simple measurements and calculations • Accounts for irregular distribution of worms and mounds • Mound compaction is not a major factor and mound heights are averaged to compensate • No limitations to feeding depth • No specific particles to ingest and redistribute • Fluctuations in fecal production are minimized through continual monitoring	• Small populations • Short time frame • Assumptions in the mound height and shape of the mounds as cones • Overestimation for ring-shaped mounds and underestimation where overprinting occurred and for deflated mounds • Burrowing activities that do not lead to fecal pellet production are not assessed	This study

TABLE 2.1—Highlights and limitations of methods utilized in determining tubificid bioadvection rates.

that may be marked. The volumetric tracing method used in this study allows for numerous measurements within a short time frame, assessment without disturbance to the sediment or worm population, high resolution data collection (individual fecal mounds are measured), and requires no marked particles.

METHODS

The collection site was located along the North Saskatchewan River (NSR) near the University of Alberta campus in Edmonton, Alberta, Canada (Fig. 2.1). The small sampling of sediment and worms collected from the NSR in the spring of 2007 was derived from an area of slack current near the river bank. The sediment comprised fine sand, silt and clay. In the Edmonton area, *Tubifex*

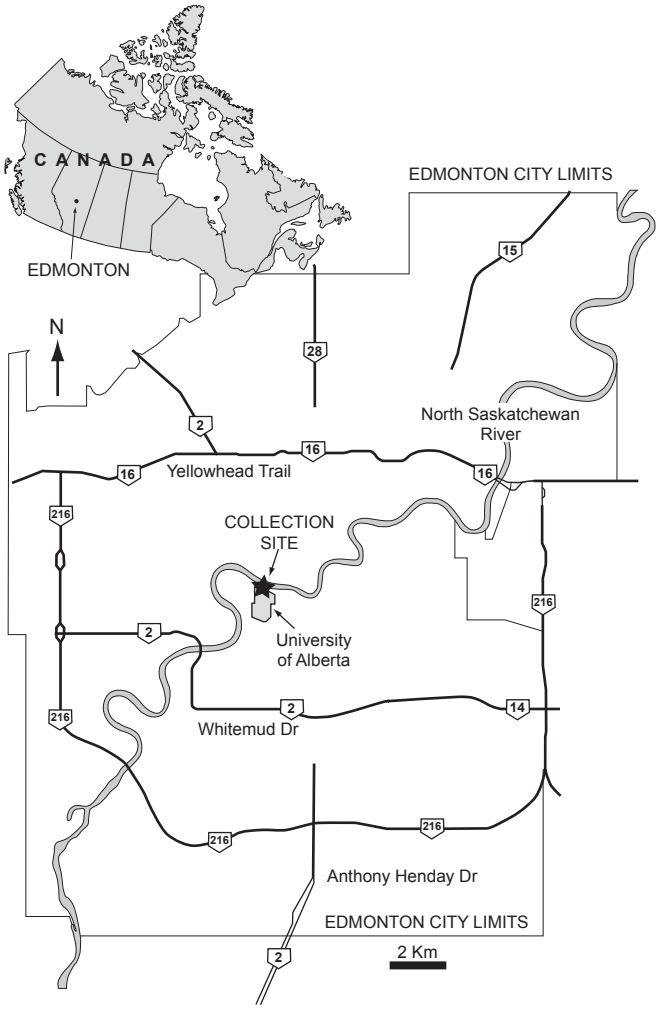


FIGURE 2.1—Edmonton, Alberta, Canada showing the collection site (star) on the North Saskatchewan River near the University of Alberta campus.

and *Limnodrilus* predominate the oligochaete population, while *Nais elinguis* are less common (Paterson, 1966). The particular species observed by Paterson (1966) include: *Limnodrilus hoffmeisteri*, *Limnodrilus udekemianus*, *Limnodrilus claparedeanus*, *Limnodrilus profundicola*, *Tubifex tubifex*, and *Nais elinguis*. The worms collected from a single collection site belong to the family Naididae (see appendix), and based on the species identified by Paterson (1966), they are likely of the genus *Limnodrilus* and/or *Tubifex*. As a result of the small size of the worms and difficulty in discriminating between genera, the population was not fully assessed in terms of density and particular species. These tubificids were acclimated to laboratory conditions for 2 months in a standard aquarium measuring 61 by 31.5 cm at 21°C. To simulate stagnate, low energy conditions, the aquarium was periodically refilled with local city water as required.

At the start of the experiment, the aquarium was filled with city (tap) water, and the sediment and water was thoroughly mixed to ensure suspension of fine particles. To facilitate measurements, an approximately level sediment surface was formed by hand. Within a day, most of the sediment had settled out of suspension forming a normally graded bed. However, the water column remained cloudy for approximately 7 days, after which primary bioturbation measurements began on day 8. The ability of the tubificids to rework this stratification was the focus of the analyses performed over the course of 34 days.

The total sediment thickness and thickness of the sand, silt, clay and fecal layers were recorded at consistent 10-cm intervals along the two short sides and accessible front (long) side of the aquarium. The back (long) side was inaccessible and some sediment sampling occurred along this boundary; accordingly sediment thickness was not recorded along the back side. These measurements began on day 2 to allow for sufficient settling of sediment and were subsequently performed on selected days for a total of 22 thickness measurements. Additional settling of sediment following day 2 was insignificant in adding to the thickness of the clay layer. Layer-thickness measurements were averaged each day for the sand, silt, clay, and fecal layers, as well as the total sediment package (Table 2.2). Visible burrow structures were described and the general characteristics of the fecal piles were also recorded.

Burrowing-rate measurements consisted of photographing the progressive accumulation of fecal material on the sediment surface. During photographing, direct fluorescent lighting along the sides of the aquarium was used to illuminate surface features. Following photographing, direct lighting was removed and

Day	Time (hours)	Total (mm)	Sand (mm)	Silt (mm)	Clay (mm)	Fecal (mm)
1	0.0	—	—	—	—	—
2	23.2	35.8	29.3	3.5	3.0	0.0
5	95.1	34.1	28.3	3.2	2.6	0.0
6	118.8	33.8	27.9	3.3	2.6	0.0
7	142.5	33.8	27.9	3.2	2.7	0.0
8	167.6	33.6	27.8	3.0	2.8	0.0
9	191.3	33.6	27.7	3.3	2.6	0.0
12	262.5	33.4	27.4	3.3	2.6	0.1
13	286.4	33.2	27.4	3.2	2.5	0.1
14	310.5	33.2	27.7	3.1	2.3	0.1
15	334.4	33.3	27.7	3.1	2.3	0.1
16	358.3	33.1	27.5	3.1	2.3	0.2
19	430.3	32.8	27.3	3.1	2.2	0.2
20	454.3	32.8	27.4	3.0	2.2	0.2
21	478.3	32.8	27.6	2.9	2.2	0.2
22	502.3	32.8	27.8	2.8	2.0	0.2
23	526.3	32.6	27.4	2.8	2.2	0.2
26	598.4	32.5	27.4	2.9	2.0	0.2
27	623.0	32.5	27.4	3.0	1.9	0.2
28	646.3	32.6	27.6	2.9	1.9	0.2
29	670.2	32.5	27.7	2.7	1.9	0.2
30	694.3	32.5	27.5	2.9	1.9	0.2
34	790.0	32.4	27.5	2.9	1.8	0.2
Total decrease (mm)		3.4	1.8	0.6	1.2	
Decrease as % of initial		9.5	6.1	17.1	40.0	

TABLE 2.2—Recorded thickness for the total sediment package, and the sand, silt, clay and fecal layers. The fecal layer reflects an overall increase in mounds present over time.

indirect fluorescent lighting was present predominantly on the front and sides of the aquarium during week day operational hours of the laboratory. Photographs of the sediment surface were analyzed using Adobe Photoshop CS3 Extended software, which calculates area based on a known length in a photo. For each photo, the inside length of the aquarium was used as the known length, from which a scale factor was determined by dividing the number of pixels of the known length by the actual length of the aquarium in centimeters. For example, on day 14, the length of the aquarium was set to 7059 pixels which was divided by 59.8 cm to acquire a scale factor of 118.04 pixels/cm. Each mound (or cluster of overlapping mounds) was numbered and traced. The program subsequently determined the number of pixels in each traced section of the photo and determined the concordant area in cm^2. The number of mounds measured per day was also recorded. For each measurement day, the sum of the area of fecal mounds was determined along with the average area per mound. Due to the time-consuming nature of tracing mounds, the area was calculated on specific days between days 8 and 20, and then less frequently until day 34 (for a total of 14

measurements). The area of the fecal mounds was tabulated and plotted against time (Table 2.3). By approximating the fecal mounds as conical shapes 1 mm in height, the volumetric increase in reworked sediment was also calculated and plotted against time (Table 2.3). A linear regression was applied to the data in the area, volume and number of mounds versus time plots to determine the rate of aerial increase in mounds, rate of volumetric burrowing, and increase in mounds over time, respectively.

A small tubificid population was introduced to ensure feasibility of mound tracing and to reduce overlapping of mounds. The population was acclimated to laboratory conditions to reduce mortality and promote stable burrowing rates during the experiment, such that the number of tubificids was not counted prior to start of the experiment. In order to assess the in place population density, the number of tubificids was approximated by determining the number of active mounds on all measurement days between days 8 and 34: i.e., an active mound suggests recent worm activity and the presence of a tubificid. These mounds are identified based on the degree of oxidation, whereby darker mounds (reduced) reflect fresh upturning of the sediment. The number of active mounds was tabulated (Table 2.4), averaged over the entire run of the experiment and plotted against time. A quadratic function was applied to the data to show the relationship between active mound construction and time.

RESULTS

Burrow Descriptions

In cross section, tubificid burrows primarily occur in the silt and clay layers (Fig. 2.2). Burrows in the sand layer are rare, but sometimes extend the full depth of the aquarium. Predominant burrow orientations are horizontal with fewer vertical structures (Fig. 2.2C). Horizontal burrows are generally found along the sand-silt interface and within the silt layer (Fig. 2.2A-E). These burrows tend to arc and curve, and branching is common in horizontal and vertical burrows especially in the upper 3-4 mm of sediment (Fig. 2.2B, C). Some vertical burrows appear to branch off of horizontal segments at depth (near the sand-silt interface). This branching and furcation of burrows is consistent with burrow structures

Day	Time (hours)	# Mounds	Average Mound area (cm^2)	Total Area (cm^2)	Average Mound Volume (cm^3)	Total Volume (cm^3)
1	0.0	0	0.000	0.00	0.00000	0.00
8	167.0	161	0.248	40.24	0.00828	1.33
9	190.7	164	0.288	47.17	0.00959	1.57
12	262.1	317	0.202	64.02	0.00673	2.13
13	286.1	363	0.194	70.57	0.00648	2.35
14	310.2	417	0.182	76.08	0.00608	2.54
15	335.3	520	0.163	84.79	0.00544	2.83
16	358.0	555	0.164	91.12	0.00547	3.04
19	430.0	825	0.152	125.24	0.00506	4.17
20	454.1	855	0.162	138.30	0.00539	4.61
22	502.0	921	0.163	150.04	0.00543	5.00
26	598.1	934	0.172	160.80	0.00574	5.36
28	646.0	941	0.185	173.78	0.00616	5.79
30	694.0	1002	0.168	168.56	0.00561	5.62
34	790.5	1158	0.168	194.17	0.00559	6.47

TABLE 2.3—Table of measurements used in the burrowing rate calculations. The average mound area was used to calculate the average volume of the mounds (assumed to be 1 mm in height) and then multiplied by the total number of mounds to calculate the total volume per measurement period.

Day	Time (hours)	# Active Mounds
1	0.0	0
8	167.0	16
9	190.7	18
12	262.1	39
13	286.1	42
14	310.2	51
15	335.3	42
16	358.0	56
19	430.0	26
20	454.1	38
21	478.0	34
22	502.0	44
23	526.0	46
26	598.1	70
27	622.3	77
28	646.0	45
29	670.6	43
30	694.0	32
34	790.5	42
	Average	42.3

TABLE 2.4—Number of active mounds recorded on all measurement days between days 8 and 34.

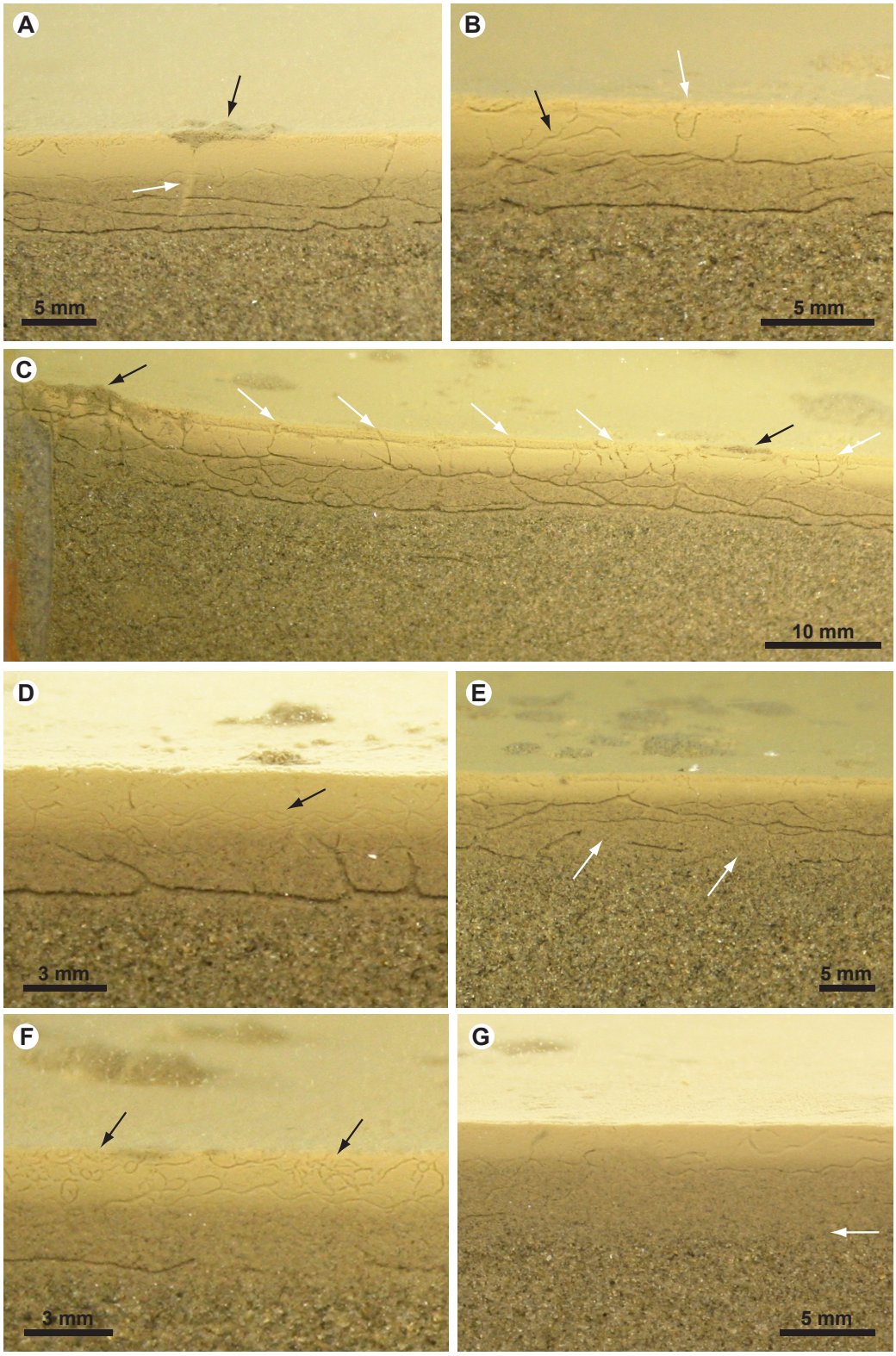


FIGURE 2.2—Cross-sectional images of the aquarium. **A:** A clay-infilled burrow (white arrow) with an associated mound (black arrow) at the sediment surface. Note the dark colouration of the mound, which is a function of the reduced nature of the sediment (day 8, front side of the aquarium). **B:** U-shaped burrow (white arrow) and branching burrow structures (black arrow) within the upper clay layer on day 9 along the aquarium front. **C:** A branching burrow network on

FIGURE 2.2 (Continued)—the right side of the aquarium on day 12. The black arrows point towards mounds at the sediment surface and the white arrows indicate vertical burrows without associated fecal mounds. **D:** Fine undulatory, horizontal burrows (black arrow) in the upper clay layer found on day 20 from the aquarium front. **E:** On day 22, discontinuous burrow segments are observed on the aquarium front, which suggests compaction of burrows (white arrows). **F:** Fine chaotic, looping burrows in the upper clay layer along the aquarium front on day 27. At this time, few burrows were present in the silt layer. **G:** On day 28, few burrow structures remain due to prevalent compaction and layer boundaries are diffuse, especially the sand-silt boundary (white arrow).

observed by Rogaar (1980). Some biogenic structures display U- or Y-shapes (Fig. 2.2B), and small, erratically oriented, looping burrows are observed in the clay layer (Fig. 2.2F). Vertical segments often do not connect with associated fecal mounds at the surface (Fig. 2.2C), and abandoned burrows are typically infilled with clay material (Fig. 2.2A).

During the early stages of the experiment, burrow abundance progressively increased over time, but evidence of reworking declined as burrows became compacted (Fig. 2.3). Initially, there were burrows predominantly near the silt-clay interface and an overall abundance of vertical structures. On day 6, evidence of compaction of early burrow segments is seen in disjointed burrow networks (Fig. 2.3B). Subsequently, on day 16, the number of burrow structures visible in cross section declined as a result of this compaction. On day 23, there are even fewer burrows in the silt and clay layers, and remnant burrows are common (Fig. 2.3C, D). Despite the overall decrease in burrow structures, fine erratic burrows continue to be formed on day 27.

The boundaries between sediment layers were altered during the 34 days of the experiment. Early in the experiment, a sharp boundary is observed between the silt and sand layers (partly due to burrowing along this boundary) and between the silt and clay layers (Fig. 2.3A). On day 14, the sand-silt boundary is more diffuse as a result of tubificid bioturbation. Also at this time, the silt and clay layers are becoming mixed in certain locales. On day 21, more burrows are present near the silt-clay interface than at the start of the experiment. Silt was reworked upwards into the clay via mound formation while clay particles collapsed into older burrow openings. Finally, boundaries are moderately reworked and slightly more undulatory on day 34 as compared to the start of the experiment (Fig. 2.3D).

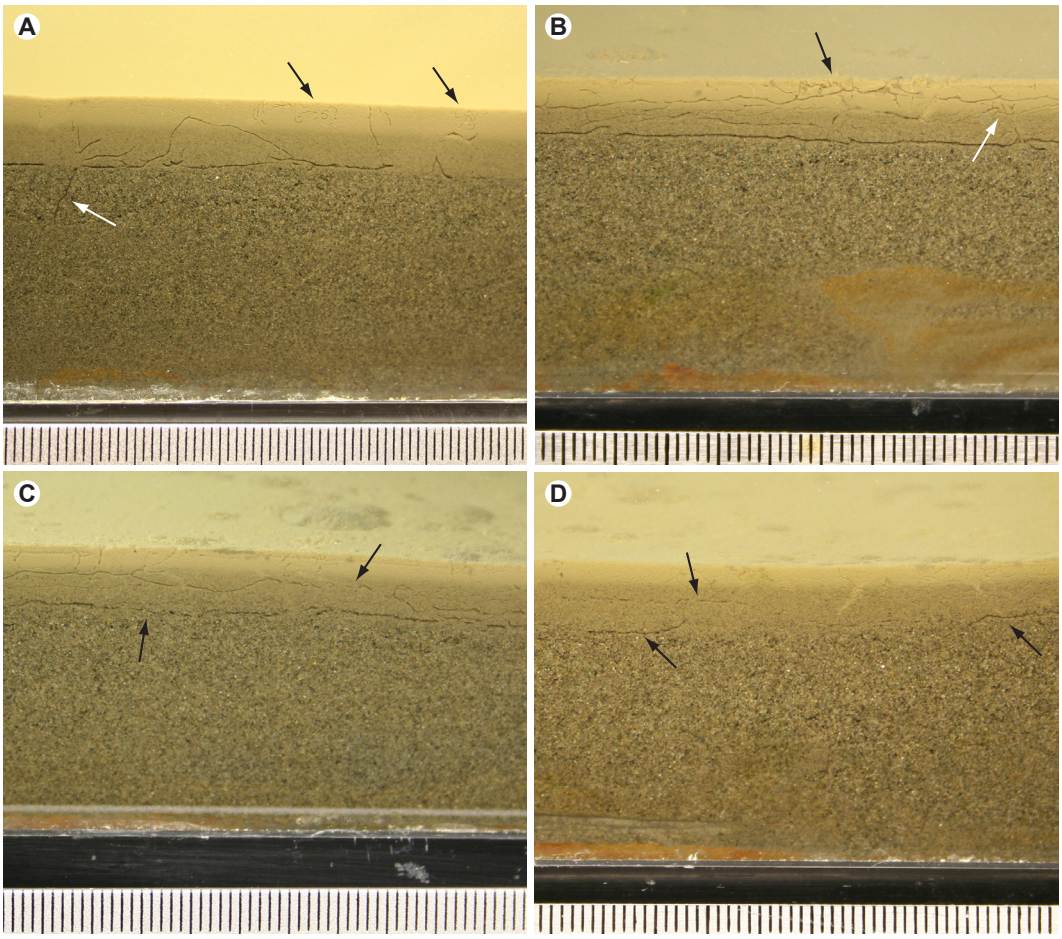


FIGURE 2.3—Change in burrow structure and definition over the course of the experiment (scale bars show millimeter increments). **A:** Photo of the aquarium front on day 2. Rare burrows are observed in the sand layer (white arrow), most structures are observed within the silt layer, and small, looping, erratic burrows are found in the clay layer (black arrows). The sand-silt and silt-clay interfaces are well defined. **B:** Day 9 photo from the front side of the aquarium. Overall, burrowing is more common in the silt and clay layers as compared to day 2. Branching of burrows is especially apparent in the clay layer (white arrow), and burrows are commonly horizontal with fewer vertical segments observed in the clay layer (black arrow). **C:** On day 21 (right side of aquarium), there is evidence of compaction of burrow structures due to the discontinuous or isolated nature of structures (black arrows). There is mixing at the sand-silt and silt-clay boundaries. **D:** Final day of the experiment (day 34 front side), burrows are highly compacted and show remnant segments (black arrows). Layer interfaces are significantly more diffuse as compared to day 2.

Mound Characteristics

Fecal mounds produced by tubificids in this study consist of: (1) abundant conical mounds (Fig. 2.4B-D), and (2) fewer ring- or crescent-shaped mounds (Fig. 2.4A, E). Conical mounds are observed as isolated, as clusters, or overlapping each other. The configuration of ring-shaped mounds includes a central burrow opening with an inner ring of disturbed clay sediment surrounded

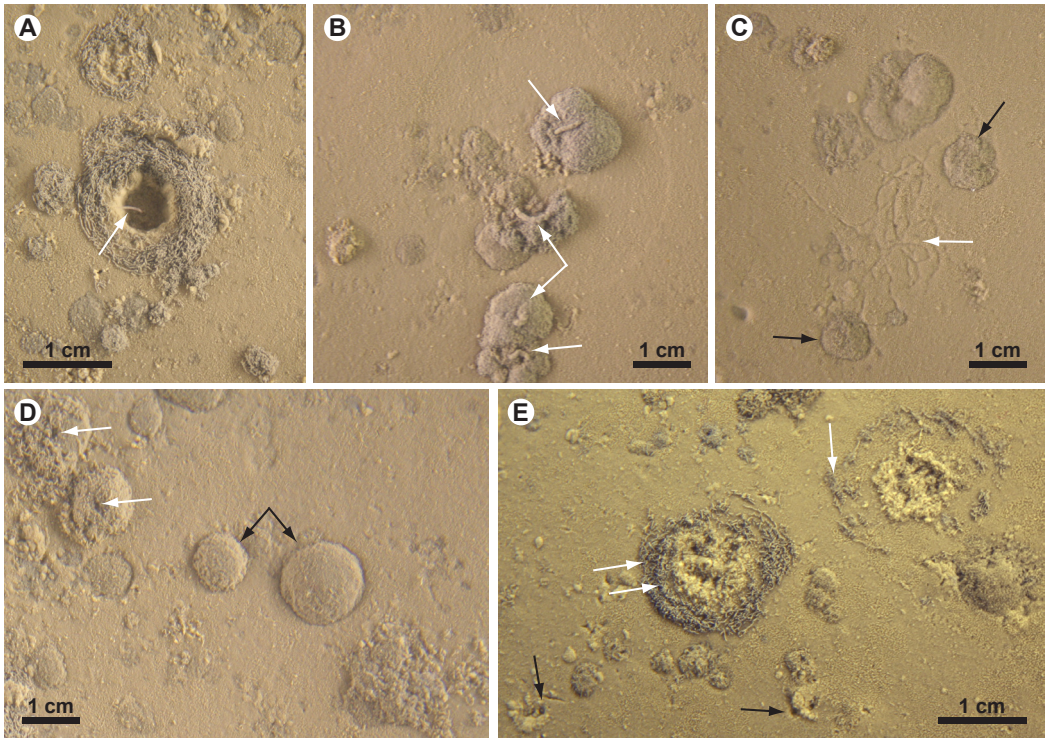


FIGURE 2.4—Features on the sediment surface taken from the top of the aquarium. **A:** A worm (white arrow) egesting fecal pellets in a ring-shaped mound. Note the cylindrical shape of the pellets. **B:** Recently active conical mounds with remnant tubes (white arrows). **C:** A looping surface trail (white arrow) with older deflated conical mounds (black arrows). **D:** Different stages of mound preservation. The white arrows indicate more recent mound formation with burrow holes and fecal pellets still present. The black arrows point to older mounds in which fecal pellets have been broken down into constituent grains. **E:** Ring-shaped mounds are circled by rings of fecal pellets. In the more developed example, two distinct rings were formed (white arrows). The colouration of this ring is consistent with an active mound that has dark grey fecal pellets (reduced). The black arrows indicate sediment holes that are surrounded by disturbed clay masses. These sediment holes resemble the inner portion of the ring-shaped mound.

by an outer ring (or crescent) of fecal material (Fig. 2.4E). Formation of a ring-shaped mound begins with the worm arching its posterior end away from the burrow opening and egesting fecal pellets as it rotates in the burrow opening to deposit the outer ring. The size of conical mounds varies; however, ring-shaped mounds possess a noticeably larger diameter as compared to conical mounds. Newly constructed mounds and rings are typically 1-2 mm in height. However, over time, the mounds and rings deflate to less than 1 mm in height. Overall, there is no clear pattern in mound distribution other than localized clustering of similar mound forms.

Fecal pellets are cylindrical and incorporate silt and clay ingested at depth. On day 8, tubificid mounds display variation in colour. Active mounds encompass

piles of dark grey, well-developed pellets in which the mounds are often more conical with steeper slopes. Older fecal piles are light brown-grey in colour and blend into the surrounding clay layer. Pellets on these older mounds are also in a state of disintegration (despite the lack of current) into smaller particles and even further into constituent grains. In addition, these mounds have no evident burrow openings, and some display evidence of central collapse where the burrowing opening was once located.

Additional surface features include tubes, surface trails, and holes in the sediment surface. Some of the fecal mounds possess distinctive tubes protruding from the burrowing openings (Fig. 2.4B). These tubes are composed of fine grained sediment covered with a mucous membrane similar to the structures observed by McCall and Fisher (1980) and Rogaar (1980). These tubes are found within the conical mounds and ring/crescent-shaped mounds, and are also subject to disintegration over time. Observed surface trails are rare and comprise looping, smooth to irregular, continuous or discontinuous trails, which are near or isolated from adjacent fecal piles (Fig. 2.4C). Holes in the sediment surface have no or very little association to fecal material and are characterized by irregular lumps of clay surrounding the opening (Fig. 2.4E). These holes are occasionally adjacent to mounds or, most often, isolated or clustered away from fecal piles.

Layer Thickness

Sedimentary layer thickness was monitored throughout the experiment to assess the effect of bioturbation (Table 2.2). Initially, the total sediment package thickness decreased by 1.7 mm between days 2 and 3. Subsequently, during the course of the experiment, the average total thickness typically decreased at a rate of 0.0-0.2 mm per day. In the sand layer, there was an initial decrease of 1.6 mm in thickness over the course of 9 days. Following the initial decrease, the thickness stabilized between 27.8 and 27.3 mm. The total decrease in the sand layer was 1.8 mm, which equates to a 6.1% decrease in the initial thickness. The silt layer displayed fluctuations in thickness over the course of the experiment with an overall 0.6 mm decrease representing a 17.1% reduction from the initial thickness. The clay layer decreased by 1.2 mm or 40.0% of the initial thickness with only minor fluctuations in the measurements. Finally, the fecal pellet layer increased from 0.0 to 0.2 mm by the end of the study.

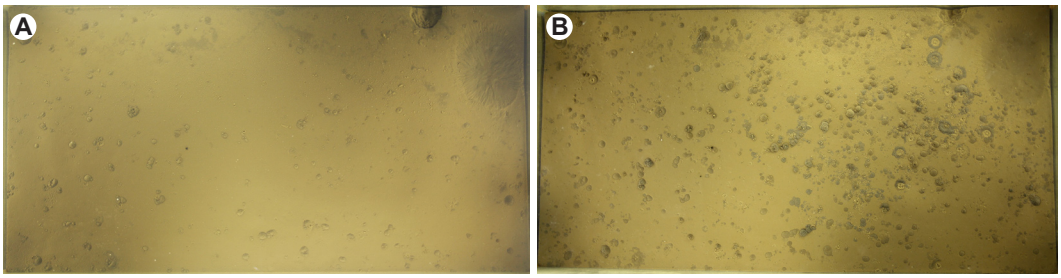


FIGURE 2.5—Surface (aerial) view of the tubificid aquarium on (A) day 9 and (B) day 34. **A:** The photo is slightly cloudy due to remnant suspended sediment. Depressions in the upper right corners are due to sampling processes prior to measurements. **B:** Note the increase in density of burrow structures. For scale, the aquarium is 61 by 31.5 cm.

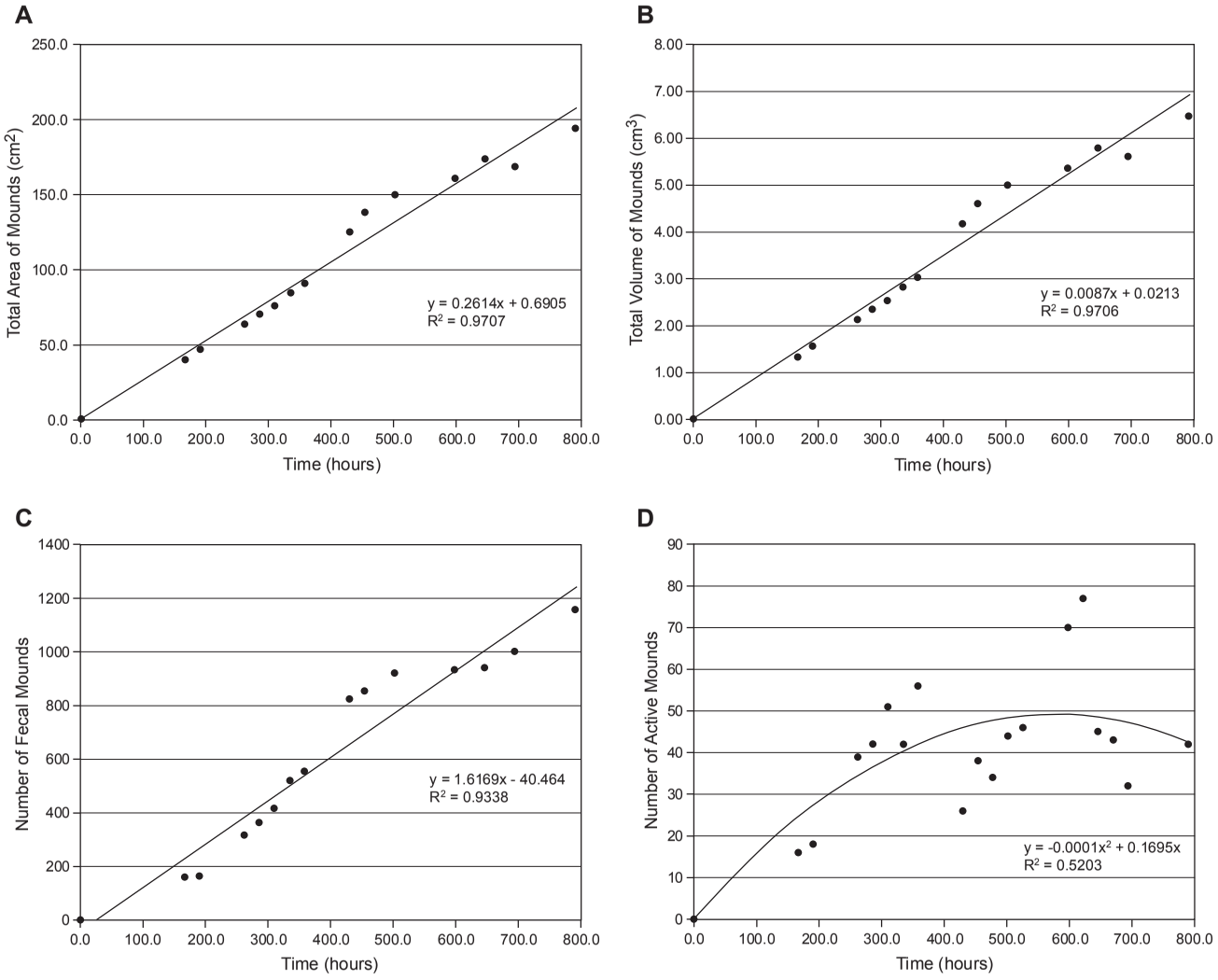
Volumetric Burrowing Rate

The number of mounds linearly increased over time to reach 1158 at 34 days (Table 2.3; Fig. 2.5). Based on the plot against time, this increase in mounds equates to 1.62 mounds/hour or 38.8 mounds/day (Fig. 2.6C). The pattern of fecal-mound increase resembles plots of the area and volume versus time. The area covered by egested pellets increased from 0 to 194.17 cm^2. On day 30, there was a slight decrease in total area, which can be attributed to various sources of error discussed below. In general, the aerial coverage increased by 0.261 cm^2/hr or 6.27 cm^2/day (Fig. 2.6A). The average area of individual fecal piles generally decreased during the study with some fluctuation. Assuming that the mounds reflect conical shapes with an approximate height of 1 mm, the volume of upturned sediment increased from 0 to 6.47 cm^3 over 34 days. From the plot of volume versus time, the rate of burrowing is 0.0087 cm^3/hour or 0.21 cm^3/day for the oligochaete population (Fig. 2.6B). At this rate, it would take 290 days for the tank of worms to completely bioturbate the sediment surface (1820 cm^2).

Tubificid Population Assessment

Tubificids ingest sediment at depth from within the anoxic zone and egest fecal pellets at the sediment surface into an oxic environment (McCall and Fisher,

FIGURE 2.6 (Next page)—Plots against time. **A:** Total area of mounds plotted against time. The data follows a roughly linear relationship that equates to a 0.261 cm^2/hour increase or a rate of 6.27 cm^2/day. **B:** The increase in volume of upturned sediment (assuming all mounds are conical in shape with a height of approximately 1 mm). The rate of burrowing is 0.0087 cm^3/hour or 0.21 cm^3/day for this worm population. **C:** The total number of fecal mounds follows a similar trend as compared to the area and volume plots versus time. The slope of the line equates to 38.8 mounds/day increase. **D:** The number of active mounds generally corresponds to a quadratic function.


A
Total Area of Mounds (cm2)
250.0
200.0
150.0
100.0
50.0
0.0
y = 0.2614x + 0.6905
R2 = 0.9707
0.0 100.0 200.0 300.0 400.0 500.0 600.0 700.0 800.0
Time (hours)
B
Total Volume of Mounds (cm3)
8.00
7.00
6.00
5.00
4.00
3.00
2.00
1.00
0.00
y = 0.0087x + 0.0213
R2 = 0.9706
0.0 100.0 200.0 300.0 400.0 500.0 600.0 700.0 800.0
Time (hours)
C
Number of Fecal Mounds
1400
1200
1000
800
600
400
200
0
y = 1.6169x - 40.464
R2 = 0.9338
0.0 100.0 200.0 300.0 400.0 500.0 600.0 700.0 800.0
Time (hours)
D
Number of Active Mounds
90
80
70
60
50
40
30
20
10
0
y = -0.0001x2 + 0.1695x
R2 = 0.5203
0.0 100.0 200.0 300.0 400.0 500.0 600.0 700.0 800.0
Time (hours)

1980; Matisoff et al., 1985; Ciutat et al., 2006). Sediment transported upwards by tubificids is reduced and dark grey in colour, compared to the surrounding surface sediment (Doeksen and Minderman 1962; Matisoff et al., 1985). The reduced state of fresh pellets is utilized to estimate the number of active (recently constructed) fecal mounds per day (Fig. 2.6D; Table 2.3). For the most part, the number of active mounds falls between 30 and 50, and averages 42 per day (Fig. 2.6D). This reflects an approximation of the population, which is equivalent to 230 individuals/m^2. A population of 42 worms generally corresponds to the average increase in fecal mounds per day (38.8; Fig. 2.6C). Accordingly, the tubificid population in the aquarium is estimated to be 42 individuals. The quadratic function in Figure 2.6D suggests an initial establishment of the population followed by a plateau in the number of new active mounds with a successive decline possibly related to mortality.

INTERPRETATIONS

Burrow Structures

The prevalence of burrows in the silt and clay layers is a function of tubificid grain-size selective feeding on these particles (cf. Brinkhurst et al., 1972). Burrows occurring in the sand layer were likely formed during initial onset of the experiment at which time oligochaetes locomoted towards the sediment surface. Erratic, looping burrows in the clay layer may have been related to juvenile worm activities, although the presence of juveniles is unknown. The shallow depth of burrowing (within the upper 1 cm) is inconsistent with the usual depth of feeding between 2 and 9 cm (Appleby and Brinkhurst, 1970; Davis, 1974b; Fisher et al., 1980). However, McCall and Fisher (1980) reported that 70% of the tubificid population is typically found within the upper 3 cm of sediment, and the maximum feeding depth depends on the worm density and associated food supply. In this study, the primary food supply (attached to silt and clay particles) was located in the upper 1 cm of sediment, and a low population density allowed for exploitation of these uppermost deposits. Rogaar (1980) also reported more abundant burrows in clayey sediment as compared to sandy sediment, as a result of sediment stability and increased organic matter.

Over the course of the study, burrow structures visible in cross section

decreased due to compaction. This suggests that tubificid burrows tend to evade preservation in the rock record. Sedimentologically, the bedding changed from a well-sorted, normally graded bed to a diffuse, moderately-sorted, graded bed due to the mixing of particles at layer boundaries (Fig. 2.7). Previous studies have used initially homogeneous sediment that became segregated with tubificid bioadvection (McCall and Fisher, 1980; Tevesz et al., 1980; Ciutat et al., 2006). In this study, well-sorted, layered sediment became more homogenous over time.

Fecal Mounds

There were three main surface features constructed by tubificids: conical mounds, ring-/crescent-shaped mounds, and open holes. Variation in mound form may be related to size or species (*Limnodrilus* or *Tubifex*) of worms or possibly even burrowing technique. Mounds containing a tube at the burrow opening are attributed to construction by *Tubifex*, which is known to construct tubes (cf. Rogaar, 1980). More commonly, fecal mounds did not possess a tube, and these mounds are attributed to the genus *Limnodrilus*. It is unknown whether the ring-shaped mounds reflect activities by a certain species or reflect a different behavior altogether. Although, crescent-shaped mounds simply exhibit deposition of fecal material preferentially along one side of the burrow rather than completely

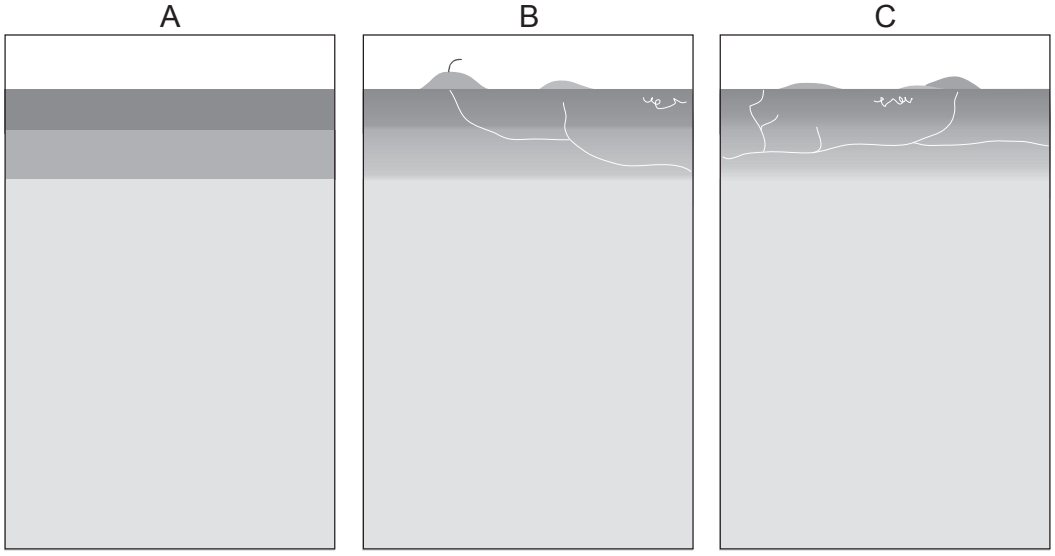


FIGURE 2.7—Diagrammatic development of biogenic graded bedding by the tubificid population. **A:** Initial sediment characteristics in which there are distinct boundaries between the sand, silt and clay layers. **B:** Day 17 in which there is mixing along the layer boundaries. **C:** Day 34 of the experiment in which there is a distinctive biogenic graded bed forming due to tubificid reworking.

surrounding the inner ring. The surface holes resemble the inner portion of ring-shaped mounds, and may be related to respiration or abandoned feeding sites. These features appear to reflect a disturbance in the clay layer with no clear boundaries. It is also unclear whether the surface trails are associated with fecal piles or even tubificid activity.

Fecal pellet alteration was twofold—pellets became oxidized and disintegrated over time. These observations are consistent with those of Tevesz et al. (1980) in which early conical mounds were overprinted by newer ones and older fecal pellets began breaking down. This suggests that pellet preservation is very rare even in the presence of stagnant waters in natural settings.

Layer Thickness

Over the course of the experiment, the thickness of the sediment package decreased due to compaction and dewatering. After the first 9 days, the sand layer had been compacted, and slight variation in thickness (0.5 mm) is mainly a function of measurement errors or changes in burrow structures at the measuring points over time (especially at the sand-silt interface). The overlying silt layer displayed fluctuations in sediment thickness likely as a result of the pervasive burrowing in this layer. The greatest decrease in thickness was observed within the clay layer, which is consistent with enhanced dewatering and compaction of clay particles in addition to mixing of clay into the underlying silt layer.

The short period of time and small tubificid population was insufficient to allow a distinctive fecal layer to collect at the sediment surface. The fecal layer in Table 2.2 reflects recorded heights of fecal mounds that occurred only at measurement points. Due to the sparse nature of mounds at measurement points, the averages are not indicative of actual mound heights or the distribution of fecal pellets along the surface. These values merely illustrate the increased presence of fecal mounds at the sediment surface over time. Overall, the layer measurements suggest that dewatering and compaction played a major role in the physical alteration of the sediment, especially in the fine-grained layers.

Volumetric Burrowing Rate

There was a relatively steady increase in the number of fecal mounds produced over the course of the study. Variation in mound increase depended on

the measurement day. For example, 270 additional mounds were counted between days 16 and 19 (Fig. 2.6). This pronounced increase was likely a function of favorable lab conditions between measurement days in which there was no direct light and minimal indirect light influence. Minor fluctuations in the total area and volume of fecal pellets are attributed to sources of error including: tracing error; measurement error (i.e., pixel resolution); assumption of mounds as perfect conical shapes; estimation of mound height at 1 mm; overestimation of pellets produced in the low-profile, ring-shaped mounds; underestimation of pellets where mounds were overprinted; deflation of mounds over time; and advanced disintegration of early mounds precluding measurement in the late stages of the experiment. Over time, it is expected that the rate of volumetric increase in mounds would fall as old mounds begin to degrade and are no longer measured.

The calculated volumetric burrowing rate of 0.21 cm^3/day represents the activity of 42 individuals, which corresponds to 0.0050 cm^3/day/individual. For a population of 100,000 tubificids, the burrowing rate would be 497.1 cm^3/day, which is equivalent to 0.050 cm/d/100,000 individuals/m^2. In comparison to previous studies conducted at a similar temperature (21°C), the rate recorded from this study is comparable to the direct collection and contaminant flux methods of Reible et al. (1996) and the accumulation depth rate calculated by Ciutat et al. (2006; Table 2.5, Fig. 2.8).

Tubificid Population Assessment

The method used in assessing the population density reflects an estimation of the population without considering possible mortality or natality during the experiment. Initially, there were fewer active mounds, which is interpreted to reflect establishment of the population (Fig. 2.6). There are also a few outliers on days 26 and 27, which may be related to increased activity during prior days (24 and 25). On average, it was assumed that each worm creates approximately 1 new mound per day. However, based on the burrow activity seen in cross-section and the additional holes on the sediment surface, tubificids most likely undergo other burrowing activities (e.g., locomotion, selection of feeding sites, abandonment of feeding localities) during a 24 hour period.

Organism(s)	Burrowing Rate	Temperature (°C)	Method	Reference
Tubifex tubifex	0.061	16-18	Direct collection	Ivlev, 1939
Peloscolex ferox	0.003	6.5	Direct collection	Ravera, 1955
Peloscolex ferox	0.004	10	Direct collection	Ravera, 1955
Bythonomus lemani	0.004	6.5	Direct collection	Ravera, 1955
Bythonomus lemani	0.005	10	Direct collection	Ravera, 1955
Psammoryctes barbatus	0.011	6.5	Direct collection	Ravera, 1955
Psammoryctes barbatus	0.008	10	Direct collection	Ravera, 1955
Tubifex tubifex	0.120	14-21	Direct collection	Appleby and Brinkhurst, 1970
Tubifex tubifex	0.054	7-14	Direct collection	Appleby and Brinkhurst, 1970
Tubifex tubifex	0.015	0-7	Direct collection	Appleby and Brinkhurst, 1970
Limnodrilus hoffmeisteri	0.032	14-21	Direct collection	Appleby and Brinkhurst, 1970
Limnodrilus hoffmeisteri	0.024	7-14	Direct collection	Appleby and Brinkhurst, 1970
Limnodrilus hoffmeisteri	0.005	0-7	Direct collection	Appleby and Brinkhurst, 1970
Peloscolex multisetosus	0.015	14-21	Direct collection	Appleby and Brinkhurst, 1970
Peloscolex multisetosus	0.094	7-14	Direct collection	Appleby and Brinkhurst, 1970
Peloscolex multisetosus	0.005	0-7	Direct collection	Appleby and Brinkhurst, 1970
Limnodrilus	0.466	10	Accumulation depth	Davis, 1974
Tubifex tubifex	0.104	20	Marked particles	Robbins et al., 1979
Tubifex tubifex	0.120	20	Marked particles	Fisher et al., 1980
Tubifex tubifex	0.200	22	Accumulation depth	McCall and Fisher, 1980
Tubifex tubifex	0.100	15	Accumulation depth	McCall and Fisher, 1980
Tubifex tubifex	0.030	7	Accumulation depth	McCall and Fisher, 1980
Limnodrilus hoffmeisteri	0.358	23	Direct collection (upright)	Kaster et al., 1984
Limnodrilus hoffmeisteri	0.248	23	Direct collection	Kaster et al., 1984
Limnodrilus spp.	0.006	4	Direct collection	Fukuhara et al., 1987
Limnodrilus spp.	0.058	18	Direct collection	Fukuhara et al., 1987
Tubifex tubifex and *Limnodrilus hoffmeisteri*	0.079	21	Direct collection (upright)	Reible et al., 1996
Tubifex tubifex and *Limnodrilus hoffmeisteri*	0.002	21	Contaminant flux model (min - O_2 saturated)	Reible et al., 1996
Tubifex tubifex and *Limnodrilus hoffmeisteri*	0.077	21	Contaminant flux model (max - hypoxic)	Reible et al., 1996
Limnodrilus hoffmeisteri and *Tubifex tubifex*	0.330	12	Marked particles (min)	Matisoff et al., 1999
Limnodrilus hoffmeisteri and *Tubifex tubifex*	0.490	12	Marked particles (max)	Matisoff et al., 1999
Branchiura sowerbyi	2.870	12	Marked particles (min)	Matisoff et al., 1999
Branchiura sowerbyi	3.660	12	Marked particles (max)	Matisoff et al., 1999
Limnodrilus hoffmeisteri	0.012	21	Contaminant flux model	Reible and Mohanty, 2002
Tubifex tubifex, Limnodrilus hoffmeisteri and *L. claparedeianus*	0.230	20	Marked particles (min)	Ciutat et al., 2005
Tubifex tubifex, Limnodrilus hoffmeisteri and *L. claparedeianus*	0.400	20	Marked particles (max)	Ciutat et al., 2005
Tubifex tubifex, Limnodrilus hoffmeisteri and *L. claparedeianus*	0.160	20	Accumulation depth	Ciutat et al., 2006
Tubifex tubifex, Limnodrilus hoffmeisteri and *L. claparedeianus*	0.075	20	Accumulation depth	Ciutat et al., 2006
Limnodrilus and *Tubifex*	0.050	21	Volumetric tracing	This study

TABLE 2.5—Table of particle redistribution rates from various publications that were either reported in or converted to cm/d/100,000 individuals/m^2.

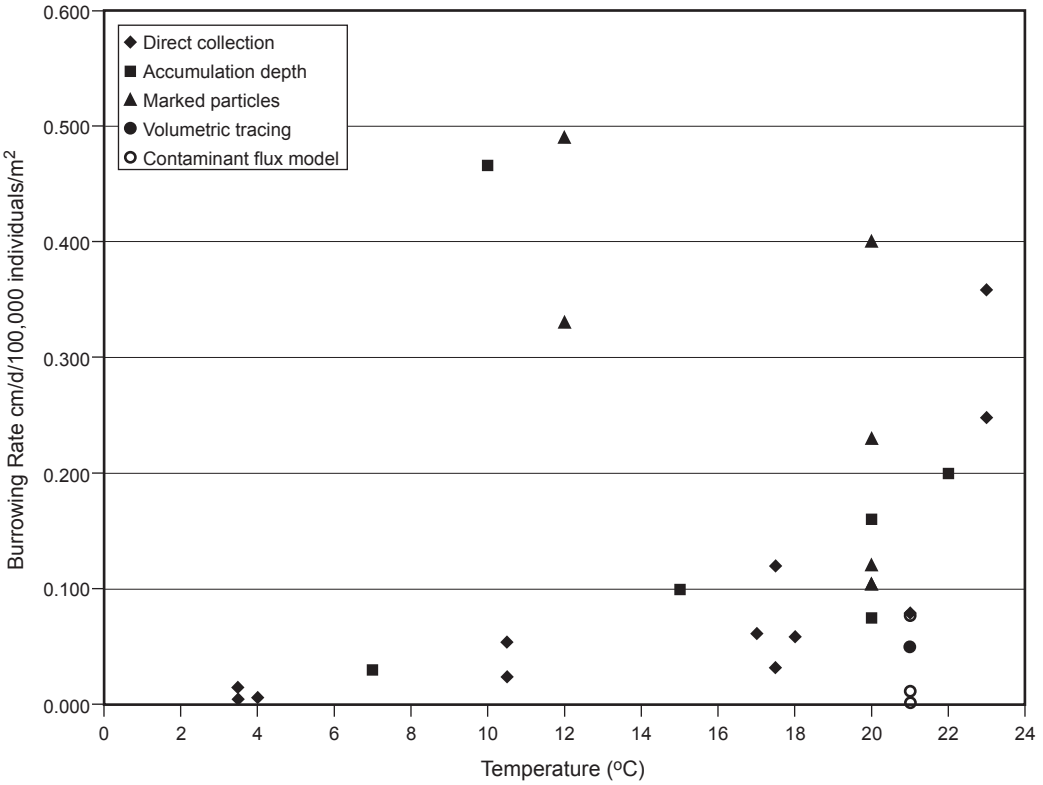


FIGURE 2.8—Burrowing rates in cm/d/100,000 individuals/m^2 for species of *Limnodrilus* and/or *Tubifex* (see Table 4). In instances where minimum and maximum rates were reported, both values are plotted. For studies in which a temperature range was reported, the temperature was averaged.

DISCUSSION

Variation in Egestion Rate

Tubificid biogenic activities are difficult to assess as reworking takes place within a narrow zone in the sediment and burrows are small and easily destroyed by compaction. In such cases, methods for measuring burrowing rates used by Gingras et al. (2008) in which x-rays are used to assess sediment reworking in a thin-walled aquarium and the grid overlay method of Dafoe et al. (2008) would be ineffective. In addition, primary tubificid activities involve upturning of deposits at the sediment-water interface. Accordingly, measuring the rate of upturning or fecal pellet production provides an accurate assessment of tubificid burrowing.

In this study, a new method in determining tubificid reworking rates was presented, which calculated a rate within range of previously reported values (Table 2.5, Fig. 2.8). In general, the reworking rates of *Limnodrilus* and *Tubifex* increase exponentially above 20°C, and the rate recorded from this study

is generally comparable with the direct collection method. Based on Figure 2.8, the various experimental methods exhibit generalized trends. The direct collection method produces comparable rates except for the upright experiments conducted by Kaster et al. (1984), which resulted in much higher burrowing rates. Measuring accumulation depth also produces comparable reworking rates, except for the study by Davis (1974a) in which the depth was estimated due to surface irregularities. Early studies that utilized marked particles are within range of other methods; however later experiments with marked particles (e.g., Matisoff et al., 1999 and Ciutat et al., 2005) produced much higher rates. The contaminant flux model seems to underestimate burrowing rates, which may be a function of the sensitivity of worms to changes in water chemistry or the presence of contaminants.

There are a number of factors that influence the egestion rate of tubificids, and they are grouped into physical and biological factors:

Biological factors:

1. Size and species of tubificids produce variation in burrowing rates due to behavioral and anatomical differences.
2. Population density influences egestion rate as a result of increased interference competition, longer search time for food, enhanced particle selectivity, or an increase in gut-processing time to extract nutrients (McCall and Fisher, 1980; Rogaar, 1980; Matisoff et al., 1999).
3. Mortality and reproduction also will affect the egestion rate by influencing population health (Appleby and Brinkhurst, 1970).
4. Duration and intensity of feeding also alters tubificid egestion (Rogaar, 1980). Egestion rates typically increase after a population has become established, and rates also can vary between individuals.
5. Depth of tubificid penetration (Rogaar, 1980) can influence how far sediment must travel to reach the sediment surface.

Physical factors:

1. Temperature plays a major role in determination of the egestion rate of tubificids (Table 2.5; Fig. 2.8; Appleby and Brinkhurst, 1970; McCall and Fisher, 1980). Lower temperatures depress egestion rates, which affect reworking rates throughout the seasons. In laboratory studies, Fukuhara et al. (1987) determined the effect of temperature on the production of fecal pellets by *Limnodrilus* spp., which significantly increased above 15°C.

2. Substrate properties (McCall and Fisher, 1980), including grain size, sorting and consistency (e.g., firm versus soupy) also can affect bioadvection.
3. Organic content of the sediment influences egestion. Increased organic matter is associated with a reduction in burrowing activities as nutrient requirements are more rapidly met (Appleby and Brinkhurst, 1970).
4. Change in food supply (Appleby and Brinkhurst, 1970) encompasses deposition of new food particles or a reduction in nutrients (bacteria or organics) due to intense activity.
5. Sedimentation rate (Rogaar, 1980) can reduce burrowing activities if a population needs to continually readjust to a new sediment-water interface.
6. Dissolved oxygen (McCall and Fisher, 1980; Reible and Mohanty, 2002) will affect the burrowing activities of tubificids. As oxygen concentrations began to decrease to hypoxic conditions, Reible and Mohanty (2002) reported increased burrowing activity.

In addition to physical and biological factors, the method used to measure reworking rates is another primary determinant. The highlights and limitations of methods used in previous studies are listed in Table 2.1, and the volumetric tracing used in this study is assessed in the following section.

Volumetric Tracing Assessment

In this study, photographic analysis was completed of the sediment surface in order to determine the rate of fecal material accumulation over time. The positive aspects of this method account for some of the major drawbacks incurred through the use of other techniques (Table 2.1). Volumetric tracing allows for direct assessment of upturned sediment over an aquarium-sized surface area with no disturbance to the sediment or population. Laboratory conditions can be designed to simulate natural conditions—a graded bed deposited out of suspension under stagnate conditions. Each mound is directly measured and irregular mound and worm distribution is not a factor in this method. Furthermore, mound compaction is not a major influence over a short time frame, and mound heights were averaged to compensate for any deflation. Volumetric

tracing also records continuous fecal pellet production, which reduces fluctuations in measured egestion rates as compared to intermittent sampling used in the direct collection method.

Some drawbacks of volumetric tracing are also apparent in other methods (Table 2.1). Similar to the direct collection method, a small population was used in this study to reduce the overprinting of fecal mounds and to maintain realistic measurements as tracing was time consuming. Most other studies utilize 60 or fewer individuals that simulate denser populations. In addition, a short time frame was required to keep measurements manageable, which is similar to the marked particle method in which activity peaks diminish rapidly. Another limitation to the volumetric tracing method is that burrowing activities unassociated to fecal pellet production are not taken into account in the bioturbation rate. As described previously, not all burrow structures were associated with fecal mounds, indicating that tubificids locomote as well as form feeding tubes. The degree to which these other activities contribute to particle reworking is uncertain; however, they likely play a minor role.

Sedimentological Importance

Ciutat et al. (2006) proposed that bioturbation by tubificids could produce bedding-like structures that mimic physical stratification. These biostratification structures are biogenically formed sedimentary structures that encompass stratification features constructed by the activity of organisms (Frey, 1978). Two forms of biostratification have been previously described—biogenic graded beds and biogenic stratification (Fig. 2.9).

Rhoads and Stanley (1965) proposed that graded beds could be produced by selective deposit-feeding activities in intertidal and shallow subtidal deposits. In their study of the polychaete *Clymenella torquata*, Rhoads and Stanley (1965) found the animal to ingest sediment at depth (10-30 cm) and egest fecal pellets at the sediment surface. Particles greater than 1 mm in diameter were concentrated at the base of the tubes, which formed a graded bed less than 30 cm thick. Overall, the maximum and average grain sizes decreased from the base to the top of the poorly sort bed (Fig. 2.9C; Rhoads and Stanley, 1965). In the intertidal of Mugu Lagoon, California, Warme (1967) observed graded bedding formed by *Callianassa californiensis* and *C. longimana*, in which an underlying sand unit was mixed with overlying marsh mud. Again, the grading was unique in the

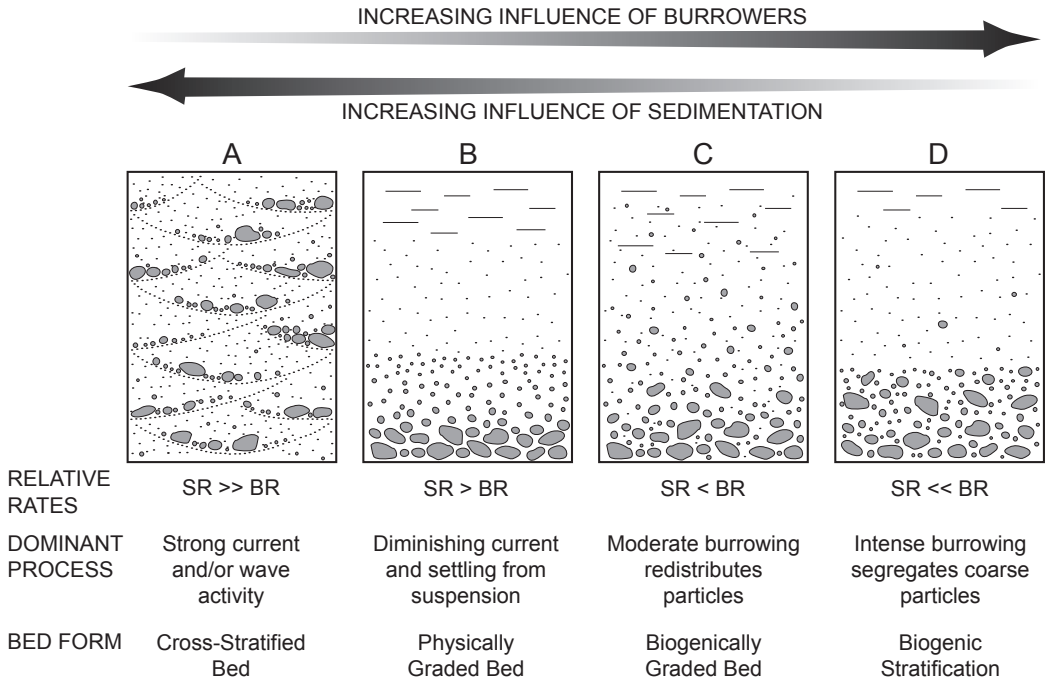


FIGURE 2.9—Bedding formed by varying degrees of physical and biogenic influence. SR = sedimentation rate and BR = burrowing rate. Adapted from Meldahl (1987).

presence of coarse particles throughout the unit; however, there were fewer coarse particles towards the top of the bed (Warme, 1967). Warme (1967) proposed that the shrimp upturned underlying sand deposits, which were reworked by currents, waves and other organisms before settling into the mud.

Biogenic stratification is distinguished from biogenic graded bedding in the presence of a sharp contact between the lower coarse-grained interval and upper fine-grained unit (Fig. 2.9D; Meldahl, 1987). Meldahl (1987) observed the formation of biogenic stratification on the intertidal flats of Cholla Bay through feeding and burrow excavation by callianassid shrimp and polychaetes. Biogenic stratification at Cholla Bay comprised a 20-50 cm lower, coarse, poorly-sorted, oxidized, shell-rich layer and an upper 10-40 cm unit of moderately-sorted, medium and fine sand that contained little shell material. Formation of biogenic stratification requires low sedimentation rates that permit organisms to remain at the same level within the sediment (Meldahl, 1987). This allows for continuous recycling of the upper fine layer and concentration of coarse material in the lower unit.

Meldahl (1987) further suggested that biogenic graded bedding forms in deposits where the reworking rates are only a few times greater than the

sedimentation rate (Fig. 2.9). In this case, sediment is only partially sorted before the organisms are forced to shift upwards with sedimentation. Accordingly, biogenic graded bedding reflects a form of incomplete biogenic stratification (Meldahl, 1987). The presence or degree of grading or stratification depends largely on: the activities and population density of burrowers (Warme, 1967); burrowing rate; sedimentation rate; degree of size-selective sorting; current and/or wave reworking; and initial sediment properties.

In this study, the sedimentary package began as a well-sorted, normally graded bed with distinctive contacts between the sand, silt and clay layers. Over time, the layer boundaries became increasingly diffuse and undulatory, and sediment was mixed by burrowing activities and burrow collapse (Fig. 2.7). Assuming continuation of the experiment beyond 34 days, the boundaries would likely have become more diffuse, forming a poorly sorted, biogenically graded bed. Biogenic graded bedding formed by oligochaetes was also reported by Tevesz et al. (1980). This graded bed consisted of three distinctive layers: an upper sand-sized fecal pellet layer, a middle silt-clay layer (representing compacted pellets), and a lower sandy concentrate (the zone of feeding). The laboratory conditions utilized by Tevesz et al. (1980; a small experimental unit and dense population) reflect ideal conditions in which biogenic stratification could be formed over a long period of time and in the absence of sedimentation. However, upon compaction and preservation in the rock record, layers described by Tevesz et al. (1980) would typically reflect a biogenically graded bed. This study used an initially heterogeneous deposit while Tevesz et al. (1980) used initially homogeneous sediment, which suggests that the reworking activities of tubificids tend towards a biogenically graded bed (and potentially biogenic stratification) regardless of the nature of the initial sediment.

Ichnological Importance

Over time, the fine burrow structures of tubificids become compacted and have very low preservation potential. In the rock record, sediments that appear otherwise unbioturbated may actually reflect intense reworking by dense populations of oligochaetes. The presence of tubificid reworking can be identified through grain-size distributions that typify biogenic graded beds (Ciutat et al. 2005, 2006). More specifically: 1) the median, modal and mean grain sizes decrease upward systematically; 2) the beds are poorly sorted; and 3) there is

a general increase in organic carbon upwards as a result of increased fines and abundance of fecal material (Rhoads and Stanley, 1965; McCall and Fisher, 1980; Tevesz et al., 1980; Rodriguez et al., 2001). Particular attributes of tubificid biostratification would also encompass: 4) a thin bed likely less than 20 cm thick due to the limited feeding depth; and 5) redistribution of particles less than 260 μm in diameter.

In addition to grain-size distributions, textural properties, associated sedimentary structures, geometry of the beds, and lithology of interfingering deposits also may help to discriminate biogenic grading (Rhoads and Stanley, 1965). These may include some of the following: 1) local areal extent of a single graded bed; 2) lack of laterally extensive beds and other sedimentary structures; 3) burrows, mottling, and disrupted laminae are the most abundant structures within the bed; 4) bed thickness is determined by feeding depth; 5) the lower contact of the bed is irregular due to variation in feeding depth; and 6) graded beds may alternate with non-graded stratum (Rhoads and Stanley, 1965). Enhanced porosity and permeability of tubificid fecal material in comparison to the bulk sediment (McCall and Fisher, 1980; Ciutat et al., 2006) may also be sustained upon preservation in the rock record.

Identification of biogenic graded beds formed by tubificids or other conveyor belt feeders would aid in overall interpretation of the biological impact, initial sediment properties, sedimentation rates, current velocities, and environmental conditions. Biogenic graded bedding requires a dense population of conveyor-belt feeders to rework an initially poorly sorted sediment (homogeneous or heterogeneous). Sedimentation rates must be low in order to allow sufficient time for intense burrowing activities (Fig. 9; Rhoads and Stanley, 1965). Pervasive reworking also requires low current energy such that fecal material, which possesses a high water content and low density (Tevesz et al., 1980), is not transported. Identification of a biogenically graded bed can also indicate general environmental conditions such as: favorable temperature, adequate organic content within the sediment, and sufficient oxygenation to support an oligochaete population. These characteristics may be in contrast to those of physically graded beds, which may have no associated animal reworking, suggest relatively rapid sedimentation rates, indicate waning current velocities, and suggest very little about the overall environmental conditions.

SUMMARY

1. A new method in tubificid reworking—volumetric tracing—was presented for determining the burrowing rate of a population of *Limnodrilus* and *Tubifex,* which was calculated at 0.050 cm/d/100,000 individuals/m^2.

2. Cross-sectional area of burrow networks initially increased and subsequently decreased due to compaction. Physical alteration of the sediment was primarily a function of dewatering and compaction.

3. Boundaries between the sand, silt and clay layers became diffuse over time due to sediment mixing. In addition, the low population density and time frame prevented accumulation of a distinctive fecal pellet layer.

4. Surface features constructed by the tubificids included: conical mounds, ring-shaped mounds, surface holes and tubes. Mounds containing tubes are attributed to the genus *Tubifex* and remaining structures are interpreted to reflect activity of the genus *Limnodrilus*.

5. The reworking rate from this study falls within the range of previously reported rates and provides a reasonable estimation of natural burrowing rates by tubificids. Volumetric tracing was found to be an adequate and straightforward method that allows for continuous and frequent measurements, is non-destructive, simulates a natural setting, allows for individual mound measurements reducing estimations due to irregular distribution, and does not require ingestion of specific particles. This new method has the potential to be used for other conveyor-belt deposit feeders.

6. Prolonged reworking by tubificids produces biogenic graded beds regardless of the nature of the initial sediment (i.e., homogeneous or heterogeneous). These beds are primarily identified based on grain-size distributions and poor sorting. There is a limited preservation potential of this form of grading due to the ease with which fecal material is eroded and the requirement that reworking rates must exceed sedimentation.

7. Identification of similarly reworked beds would aid in overall interpretation

of biological impact, initial sediment properties, sedimentation rate, current velocities and environmental conditions in ancient settings.

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CHAPTER 3 – DETERMINING *EUZONUS MUCRONATA* BURROWING RATES WITH APPLICATION TO ANCIENT *MACARONICHNUS SEGREGATIS* TRACE-MAKERS

INTRODUCTION

Evaluating the rates at which modern burrows are constructed can provide valuable information regarding ancient trace-maker behaviors and corresponding depositional conditions. One approach that has been developed to ascertain burrowing rates applies mathematical models to the preservation potential of sedimentary and/or biogenic fabric under generalized biogenic diffusion (e.g., Guinasso and Schink, 1975; Matisoff, 1982; Matisoff and Robbins, 1987; Wheatcroft, 1990; Wheatcroft et al., 1990; Bentley and Sheremet, 2003; Bentley et al., 2006). Using mathematical models, the preservation potential of sedimentary event layers has been described as a function of transit time and dissipation time by Wheatcroft (1990). The transit time reflects the time necessary to bury an event bed beyond the influence of infaunal burrowers, and the dissipation time is the time required to burrow an event bed (i.e., the burrowing rate). If the transit time is less than the dissipation time, a portion of the sedimentary fabric will be preserved. In response to Wheatcroft's (1990) work, Gingras et al. (2008) suggested a number of factors that influence the dissipation time: (1) size of the infaunal organisms, (2) their burrowing behavior, (3) food resource distribution, (4) appeal of the event bed as a colonization site, (5) absolute time available for burrowing, and (6) destruction of the benthic community by erosion or excessive burial. These factors are difficult to quantify and limit the effectiveness of using mathematical models in determining bed preservation and concordant burrowing rates (Jumars et al., 2007; Gingras et al., 2008).

In some modern studies, burrowing rates of individual organisms (e.g., Fox et al., 1948; McConnaughey and Fox, 1949; Rhoads, 1963; Kemp, 1985, 1986, 1987) and assemblages of organisms (e.g., Rice, 1986; Gerino, 1990; Hily

A version of this chapter has been published. Dafoe et al. 2008. Ichnos, 15: 78-90.

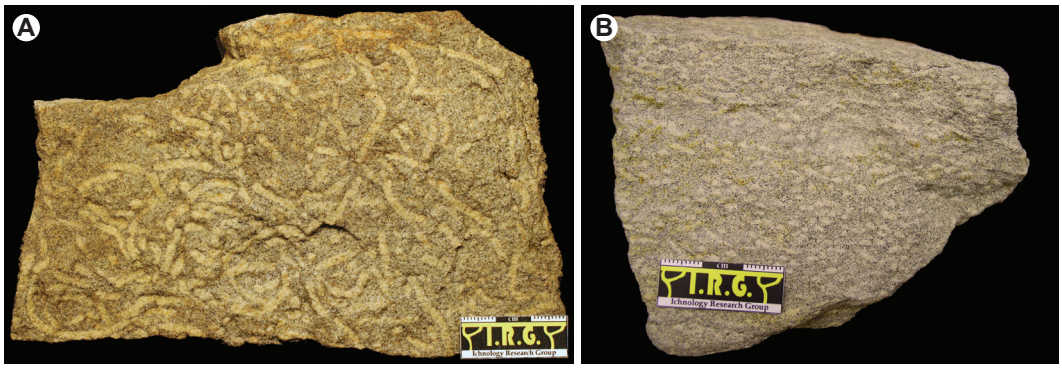

FIGURE 3.1—*Macaronichnus segregatis* from the Upper Cretaceous Appaloosa Sandstone, Horseshoe Canyon Formation of Alberta, Canada. **A:** Plan view of the traces exhibiting random avoidance of meandering pathways. **B:** Cross-sectional view of the traces, which illustrate the predominantly horizontal orientation of the structures (scales are 3 cm long).

and Frouin, 1998) have been directly assessed. However, only a few studies have related quantified modern animal-sediment interactions to trace fossil occurrences (e.g., Risk et al., 1978; Alexander et al., 1993; Dashtgard and Gingras, 2005; Needham et al., 2005; Gingras et al., 2008). In accordance with these works, this chapter attempts to evaluate the burrowing behaviors and, particularly, the burrowing rates of ancient organisms that constructed *Macaronichnus segregatis*. These ichnofossils are recognized as cylindrical, sinuous, intrastratal trails 2-5 mm in diameter with mineralogical segregation between the burrow fill and mantle (Fig. 3.1; Clifton and Thompson, 1978; Saunders, 1989). This trace is ichnologically significant as a component of some high-energy, foreshore to shoreface transitions preserved in the rock record (Pemberton et al., 2001). The modern analogue used in this study is an opheliid polychaete, *Euzonus mucronata*, which constructs *M. segregatis*-like structures on the mid-latitude (marine) coastal foreshore of Pachena Bay, Vancouver Island, Canada (Fig. 3.2).

Euzonus mucronata

At certain (foreshore) locales, upper intertidal, fine-to-medium sands are pervasively reworked by *Euzonus mucronata* (Fig. 3.3) during deposit-feeding activities (Dales, 1952; Eikenberry, 1966; Ruby and Fox, 1976; Kemp, 1985). These polychaetes, occupy a zone parallel to the shoreline near the mean high-water mark (McConnaughey and Fox, 1949). The width of this zone ranges from 3-20 m and varies with the beach slope, width, and grain size. Population densities of *Euzonus* have been reported to range from 3,500-43,000 individuals/

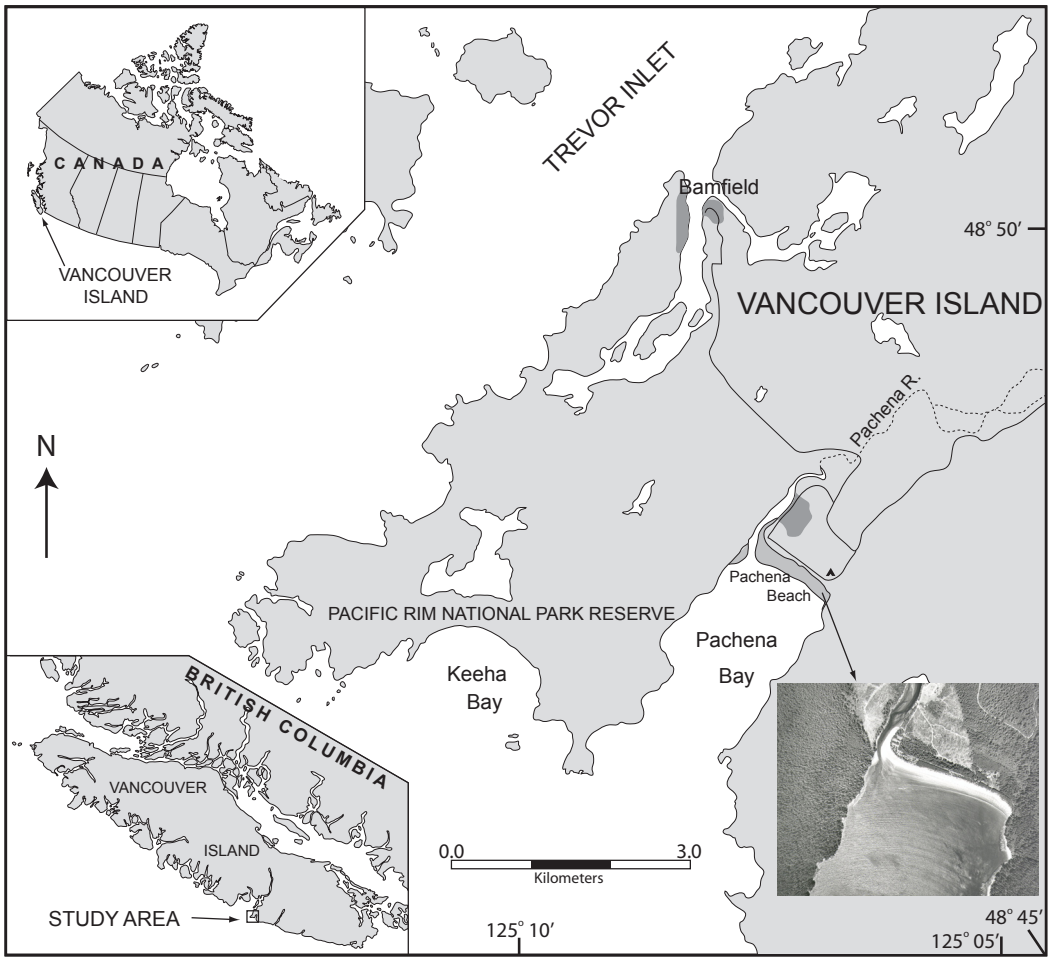

FIGURE 3.2—A portion of the west coast of Vancouver Island with Pachena Bay located near the town of Bamfield. The aerial photograph depicts the accretion of sediment on Pachena Beach. The lower inset map shows the location of the study area on Vancouver Island. The upper inset map of Canada shows the location of Vancouver Island on the west coast of Canada.



FIGURE 3.3—*Euzonus mucronata.* Note the pointed head region of the worm on the right, and the extruded proboscis on the worm on the left.

m^2 on Vancouver Island beaches; Long Beach and La Jolla, California; and the Oregon coast (McConnaughey and Fox, 1949; Dales, 1952; Eikenberry, 1966; Kemp, 1985; Saunders, 1989).

The polychaete, *Euzonus mucronata*, exhibits two primary behaviors – deposit feeding and locomotion. Deposit feeding involves the collection of sand grains by the proboscis, ingestion of grains through the mouth, nutrient processing by the gut, and grain excretion through the pygidium. This deposit feeding occurs in conjunction with vertical and horizontal locomotion which are primarily driven by fluctuations in diurnal tides, as well as changes in oxygenation, salinity and temperature. Vertical migration is associated with rising tides in which *Euzonus* burrow deeper to escape dislodgement due to surf action (McConnaughey and Fox, 1949; Eikenberry, 1966; Dangott and Terwilliger, 1986). Subsequently, a lack of interstitial oxygen stimulates the upward migration of the worms at low tide (Eikenberry, 1966). At the sediment-air interface, *Euzonus* respires through its posterior (pygidium) until resumption of deposit-feeding activities (Eikenberry, 1966).

By studying the burrowing activities of *Euzonus mucronata*, the objective is to establish a baseline for the burrowing rates of opheliid polychaetes. Utilizing this modern assessment, the results can be applied to ancient occurrences of *Macaronichnus segregatis*.

METHODS

The study area comprises the sandy, partially enclosed foreshore of Pachena Bay, Vancouver Island, Canada (Fig. 3.2). The bay is mesotidal with a tidal range up to 3.8 m. Sediments of Pachena Beach consist of lower fine to upper medium sand that is predominantly composed of quartz, feldspar, lithic fragments and shell fragments. *Euzonus mucronata* were generally observed at the base of the swash line that recorded the position of the last high tide. Neap-spring variations in the tidal range resulted in seaward and subsequent landward shifting of the burrowed zone throughout the study period (similar worm migrations were noted by Eikenberry (1966)).

Field studies included daytime observations of opheliid burrow structures over approximately 2 weeks during late August 2004, and completion of a basic

population-density survey using box cores. Box cores measuring 15 cm by 12 cm in cross section and 30 cm in length were extracted from the foreshore. Core sampling was limited to undisturbed and accessible localities on the public beach. The depth of sampling was also restricted beyond the beach berm as a result of a pebbly winter storm lag found within centimeters of the sediment surface. Four samples were collected from the narrow 5-m-wide zone occupied by *Euzonus mucronata*. This zone was established by overturning sediment in an area adjacent to the sampling sites. Two samples (cores 2 and 3) were obtained from the base of the beach berm formed by the last high tide. Another sample was taken from the crest of the beach berm (core 4), and the other from the maximum landward extent of the worm population (core 1). This sampling, although limited, allowed for approximate maximum and minimum population densities to be documented (Table 3.1).

Sediments in box cores were wet sieved through a fine (1 mm) mesh screen to separate organisms from sand grains. Adult and juvenile *Euzonus mucronata* collected on the mesh were counted for each box core. In this study, juveniles are defined as 1 mm or less in diameter and/or less than 1.5 cm in length (to a minimum of only 3-4 mm in length). Using the cross-sectional area penetrated by the box core (15 cm by 12 cm), the number of worms per meter square area of foreshore was determined (Table 3.1).

Laboratory analyses involved construction of two thin-walled aquaria to study burrow characteristics and burrowing rates (cf. Dashtgard and Gingras, 2005). The aquaria were constructed using thin glass plates with semi-rigid plastic tubing as a spacer between the glass. These materials were secured with clamps, and the aquaria were filled with water. Alternating layers of sand from the worms' environment and mafic- and shell-rich foreshore sands were disseminated into the aquaria to attain mm to cm thick laminations. The aquaria were designed to slowly drain their water each day (and were reflooded daily) to simulate tidal

Station	# Adult	# Juvenile	Adult/m^2	Juvenile/m^2	Worms/m^2
1	2	24	110	1325	1435
2	0	20	0	1104	1104
3	29	63	1600	3477	5077
4	9	51	497	2815	3311
Average	10	40	552	2180	2732

TABLE 3.1—*Euzonus mucronata* population densities extrapolated from box core sampling on Pachena Beach.

cycles. Temperature was consistent at 20ºC and light exposure was minimized by covering aquaria with black plastic between observations. The first aquarium was constructed to study burrow characteristics and measured 22.5 cm by 35.5 cm with 7 mm of sand between the glass plates.

A smaller aquarium was constructed specifically to study burrowing rates. The volume of sand in this aquarium measured 15 cm high by 15.7 cm long and 6 mm wide (about 140 cm^3). Layering in this aquarium comprised 1-1.3 cm thick quartz-rich sand beds with interlaminated shell- and mafic-rich layers 3-4 mm thick. Following the addition of 5 polychaetes, each side of the aquarium was photographed approximately every 24 hours to document progressive burrowing. Photographs of the aquarium (from both sides) were overlain by a grid with spacing that approximated the average burrow width (about 2 mm). The grid squares were then assigned to one of four categories: burrowed, unburrowed, no data (behind clamps), and outside of the aquarium (rounded corners) based on the dominant observation therein (Fig. 3.4). The proportion of burrowing behind

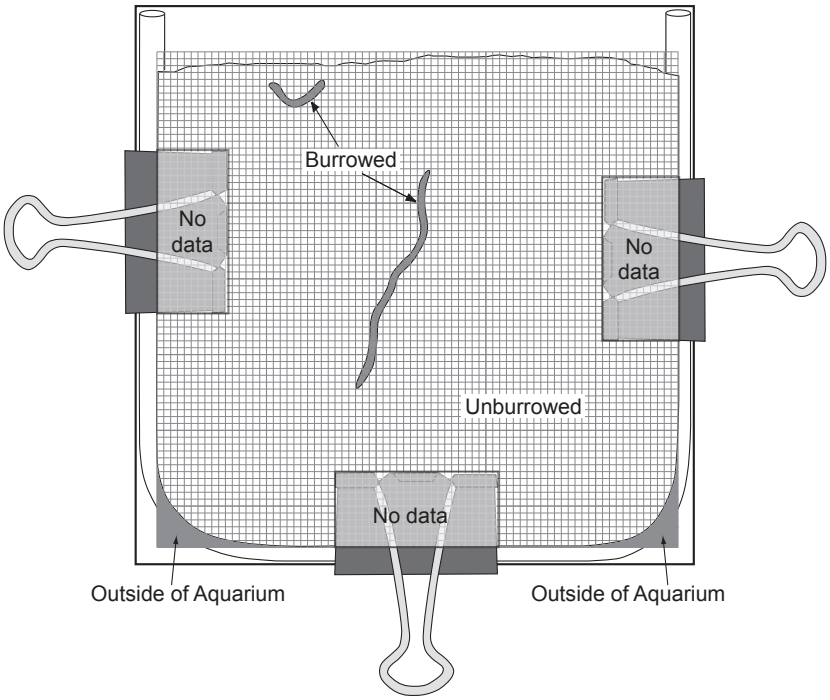

FIGURE 3.4—A grid overlay on the aquarium. Grid squares are assigned to one of four categories: burrowed, unburrowed, no data and outside of the aquarium. Burrowed grid squares overlay portions of *Euzonus* burrows, while unburrowed grid squares overlay undisturbed sediment. The no data category represents the sediment behind the clamps which cannot be viewed. These areas are assumed to have the same proportion of burrowing as the remainder of the aquarium. Outside of the aquarium reflects the grid squares that lay outside the sediment wedge, which encompasses the rounded corners at the base of the aquarium.

the clamps (no data category) was assumed to be equivalent to the proportion of observable burrowing.

Volumetric burrowing rates were calculated from the grid counts by first determining the percentage of burrowed sediment, which was calculated by dividing the number of burrowed grid squares by the total number of grid squares (Table 3.2). The percentage of burrowed substrate was used to assess the volume of burrowed sediment by extrapolating through the 6 mm of sand by multiplying by the total volume. The total volume of sediment is 135.7 cm^3, which takes into account the rounded corners at the base of the aquarium. Finally, the volume of burrowed sediment was averaged for sides 1 and 2 and plotted against time. The burrowing rate subsequently was obtained through linear regression of these data.

BEHAVIORAL ANALYSES

Field Observations

The activity of *Euzonus mucronata* at Pachena imparted a resultant, shallowly tiered, mottled fabric on the sediment. During low tide, juveniles were restricted to the uppermost 5 cm of sediment, and adults were generally observed within 10 cm of the sediment surface (Fig. 3.5). Pervasive burrow-mottling (equivalent to a Bioturbation Index (BI) of 4) produced by *E. mucronata* occurred in the uppermost 6 cm, and faint laminations were evident below the uppermost 10 cm of sediment (Fig. 3.5A, B). Where the overlying sediment was comparatively dry, the mottled fabric extended to as much as 30 cm below the

Time (hours)	% Burrowed Sediment		Volume Burrowed Sediment (cm^3)		
	Side 1	Side 2	Side 1	Side 2	Average
0.00	0.00	0.00	0.00	0.00	0.00
20.75	4.29	4.43	5.82	6.02	5.92
41.00	6.82	5.64	9.26	7.65	8.45
65.50	8.33	7.42	11.31	10.06	10.69
89.50	9.37	ND	12.72	ND	12.72
114.00	10.68	9.49	14.49	12.88	13.69
137.25	12.71	11.19	17.25	15.18	16.21

TABLE 3.2—Percentage and volume of burrowed sediment observed on each side of the aquarium. Percentages of burrowed sediment are used to calculate the volume of burrowed sediment by multiplying by the total volume of the aquarium (135.72 cm^3). The average volume of burrowed sediment from both sides of the aquarium provides an overall burrowing rate. ND indicates that no data was collected.

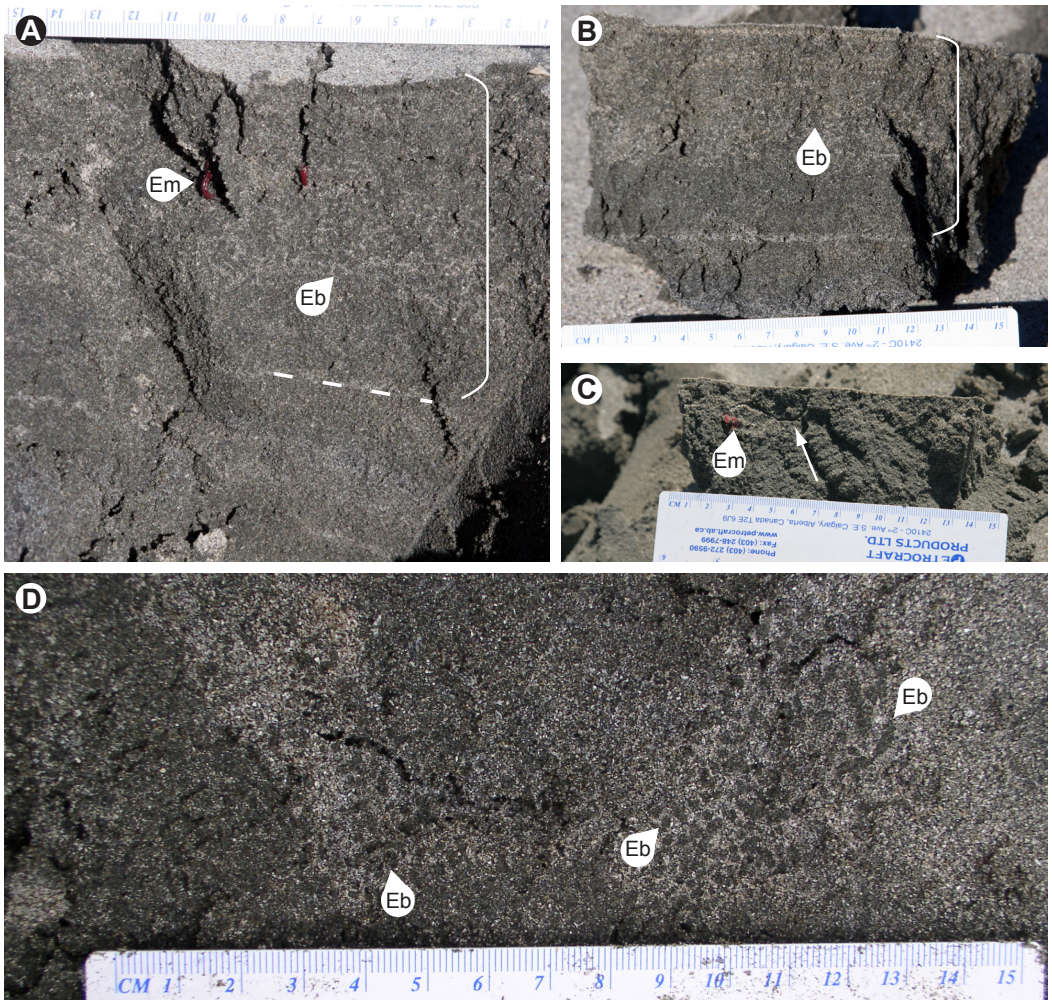

FIGURE 3.5—*Euzonus mucronata* (Em) and burrows constructed by *E. mucronata* (Eb) in the field. **A:** Vertical cross-section through the upper foreshore sediment displaying thorough reworking by the polychaetes and underlying remnant laminations (dashed line). The prevailing burrow cross-sections are circular to ovate, which is indicative of horizontal burrowing. **B:** Another vertical section exemplifying the highly burrowed nature of the upper 5 cm of foreshore. **C:** An open, inclined burrow (indicated by the white arrow) leading to the sediment surface on a vertical section of foreshore. **D:** Plan view of the burrows highlighted by a shell-rich lamination that has been reworked.

sediment surface. Individual burrows included predominantly horizontal paths (Fig. 3.5A, D), as well as oblique trails (Fig. 3.5C) and vertical burrows (Fig. 3.5D), all of which were cylindrical and 1-2 mm in diameter. Vertical to inclined, open burrow holes were also observed adjacent to the sediment surface (Fig. 3.5C).

Box cores were collected to estimate variation in *Euzonus mucronata* population densities within the zone occupied by the polychaetes (Table 3.1). The landward core (station 1) was dominated by juvenile opheliids with 1325/m^2 and adult worms comprised 110/m^2. Only juvenile opheliids, corresponding

to a population density of 1100/m^2, were recovered from station 2 at the base of the beach berm. The adjacent core from station 3 contained profuse worms with densities of 1600 adults/m^2 and 3477 juveniles/m^2. The top of the beach berm also contained abundant juvenile worms (2811/m^2) and fewer adult polychaetes (497/m^2). Based on the timing of the study, Pachena Beach contains approximately 1100 to 5000 worms/m^2 (predominantly juveniles); however, there is likely to be considerable seasonal variation in population densities.

Thin-Walled Aquarium Observations

To assess *Euzonus mucronata* burrowing behaviors and burrow characteristics, a large thin-walled aquarium was constructed (Fig. 3.6) and 18 adult opheliids were added to the aquarium. Simulated tidal cycles resulted in worms migrating to the sediment surface as seawater drained from the aquarium, and concordantly *Euzonus* burrowed at depth during "high tide." This relatively low population density was chosen to ensure an abundance of burrows could be observed without excessive cross-cutting of structures. Burrows constructed by the worms were typically 1 to 2 mm wide, extended to the base of the aquarium (22.5 cm; Fig. 3.6C), and were predominantly subvertical to vertical (Fig. 3.6C) with rarer U- (Fig. 3.6A) and J-shaped (Fig. 3.6B) segments.

Five days after inoculation of the aquarium, pervasive mottling (BI 4) was apparent in the upper 2-3 cm of sediment, and burrows were generally restricted to the upper 17 cm. A few burrows and burrow segments remained open especially near the sediment surface. These open burrows were typically vertical to subvertical, J-shaped, and irregular (Fig. 3.6A), and connected to open holes at the sediment surface (2 to 5 holes/cm^2). After 8 days, the upper 6 cm of sediment was pervasively burrowed (BI 4) while the upper 11 cm displayed a high degree of reworking consistent with a BI 3 (Fig. 3.6A). By the 17th day of the experiment the upper 17 cm displayed an overall highly burrowed fabric (BI 3-4; Fig. 3.6C).

Interpretations

Biogenic reworking by *Euzonus mucronata* is directly related to the worms' deposit-feeding activities and response to the tidal cycles. Based on the predominantly horizontal orientation of burrows, the opheliids principally deposit-feed as they locomote laterally. These activities occur (1) parallel to the

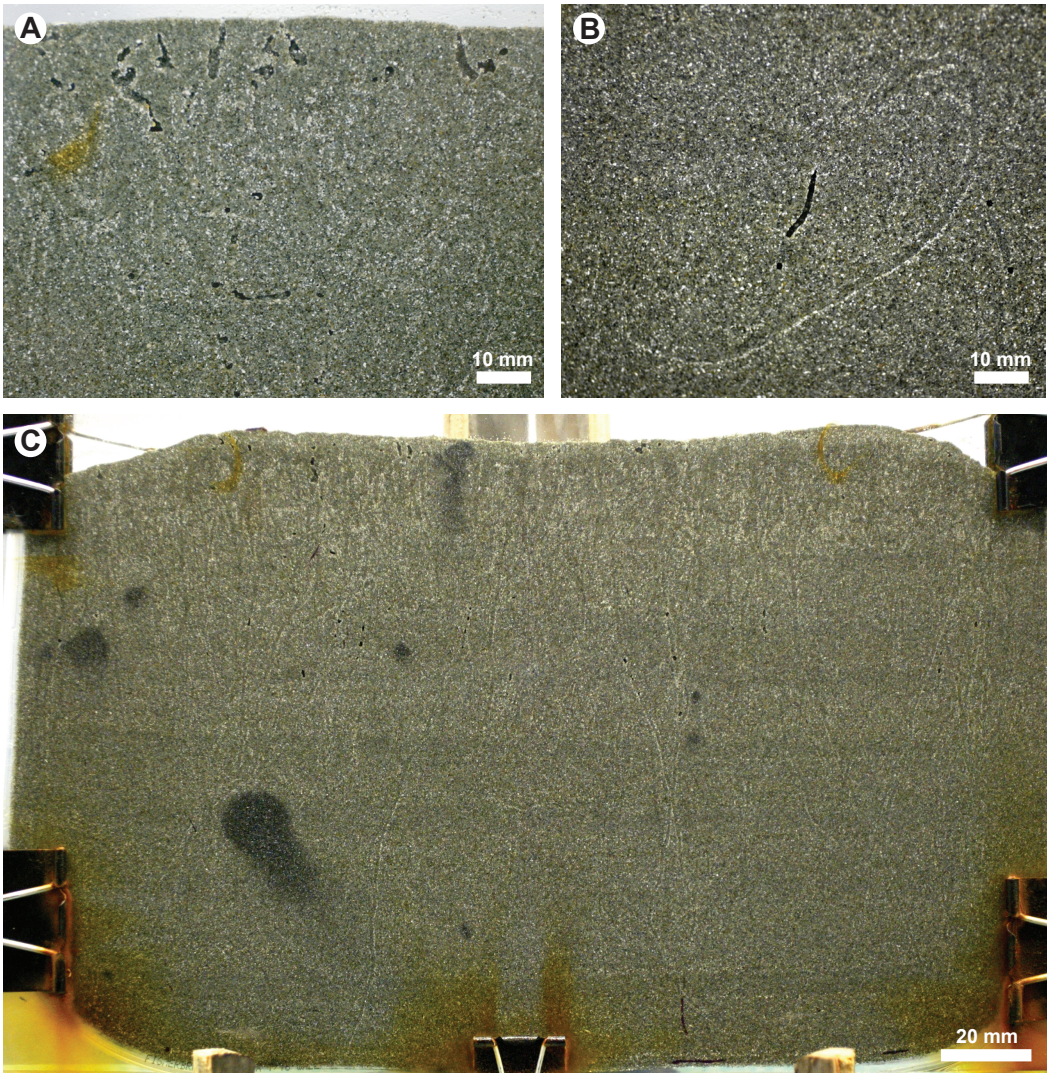

FIGURE 3.6—The large aquarium that contained 18 adult *Euzonus mucronata* (burrows are generally 1-2 mm wide). **A:** Top of the aquarium on day 8, in which there is thorough reworking of the sediment, and burrows are highlighted by shell fragments. Open burrows are common at the top of the sediment and connect to open holes at the sediment-air interface. **B:** A prominent J-shaped burrow observed on day 4. This structure has a shell-fragment lining on the underside of the burrow, which is hypothesized to be a result of gravitational settling. **C:** The aquarium on day 17 of the experiment. Subtle laminations are poorly defined, the upper 6 cm is thoroughly reworked, and traces penetrate the full depth of the aquarium.

shoreline where the polychaetes remain in an optimal zone, and (2) perpendicular to the shoreline in response to daily tidal variations that influence pore waters and oxygenation. Clear onshore-offshore migrations have been observed on wave- and wind-eroded surfaces (Fig. 3.7). These lateral migrations generally occur within the upper 10 cm of sediment, as this zone is thought to be aerated during low tide (Dangott and Terwilliger, 1986). In the aerated zone, worms also migrate

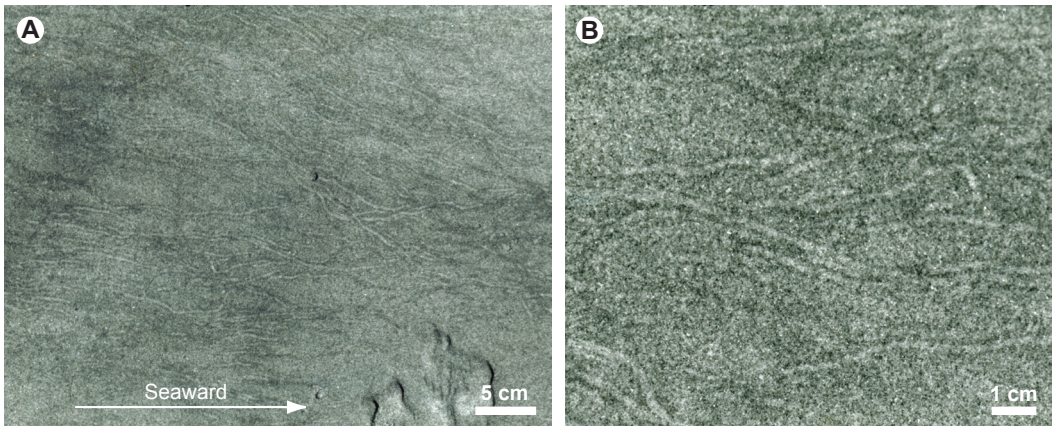

FIGURE 3.7—Onshore-offshore migrations of *Euzonus mucronata* on a wind- and wave-eroded beach surface (Courtesy of T.D.A. Saunders). The footprints at the bottom of photo (A) are for scale, and the arrow indicates the seaward direction. Photo (B) depicts a close-up view of structures seen in photo (A).

vertically to respire at or near the sediment surface, which can produce burrows that remain open (Fig. 3.5C). These open burrows suggest that the polychaetes can pass through sediment without ingesting sand grains during their upwards migration towards the sediment surface. However, infilled vertical trails are also observed.

The limited population density dataset suggests that there is notable patchiness in the *Euzonus* population, similar to that observed by Eikenberry (1966) and Kemp (1985). Another anomaly in the population assessment is the widespread dominance of juvenile opheliids, especially in the landward direction (Table 3.1). The abundance of juveniles could be due to the sampling times (August) and the timing of *Euzonus* larval release, which is reported to occur between April and September (cf. McConnaughey and Fox, 1949). The landward dominance of juveniles may reflect reduced lateral mobility of these worms perpendicular to the shoreline in comparison to adult worms that more readily keep pace with falling tides.

The opheliid behaviors and burrow characteristics observed in the field and aquarium are similar. However, the confining nature of the thin-walled aquarium can only approximate the behaviors observed in the field. In general, the upper 10 cm of sediment undergoes extensive reworking by *Euzonus mucronata*, while underlying sediment retains much of the original lamination (Figs. 3.5, 3.6).

VOLUMETRIC BURROWING RATES

Results

A thin-walled aquarium 15 cm by 15.7 cm by 6 mm wide was constructed and inoculated with 5 adult *Euzonus mucronata* (Fig. 3.8) to determine the volume of sediment processed in a predetermined time frame. The progressive burrowing (on side 1 of the aquarium) on days 2 and 7 of experiment is depicted in Figure 3.8A and B. Prominent 'smearing' of mafic- and shell-rich laminations to displacements of up to 1.5 cm is associated with *E. mucronata* burrows (Fig. 3.8C, D). Displaced mafic grains and shell fragments occur within and adjacent to burrows.

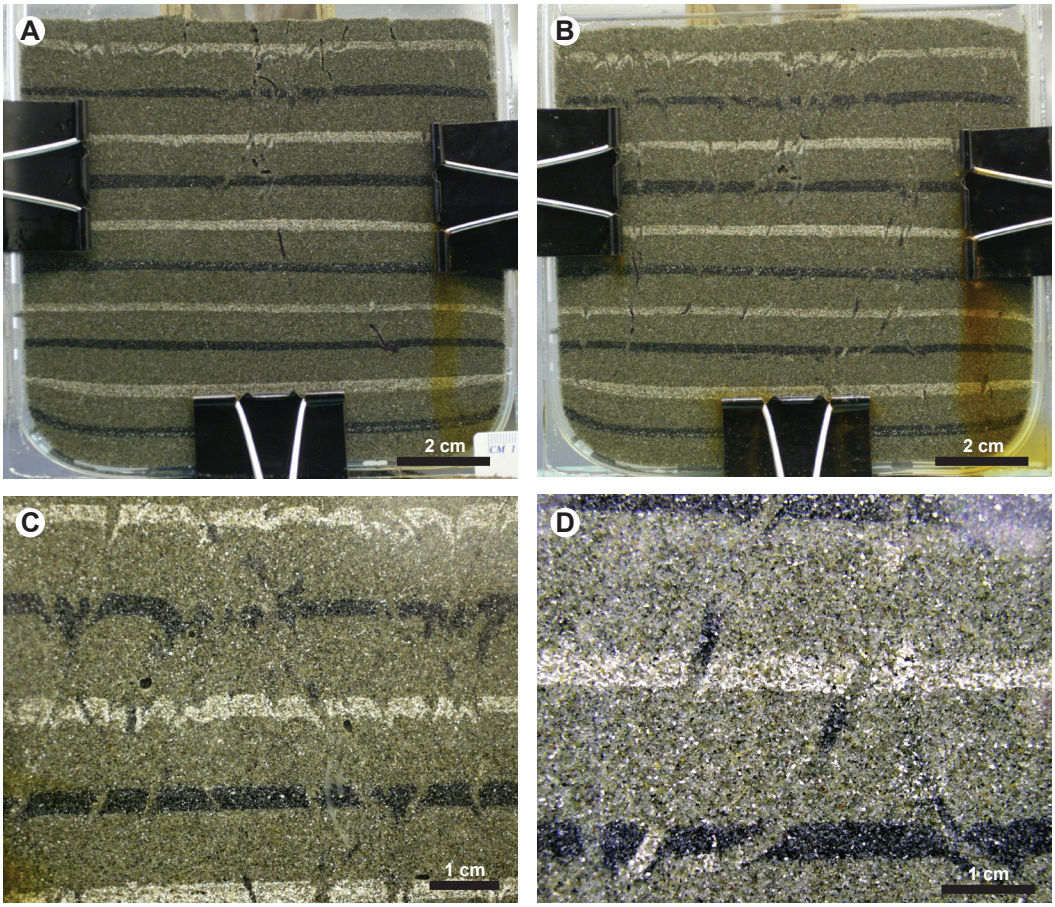

FIGURE 3.8—A-B: The small aquarium (side 1) that contained 5 *Euzonus mucronata*. **A:** On day 2, U- and J-shaped burrows, as well as vertical burrows are observed especially near the top of the aquarium. **B:** On day 7, more vertical burrows are present. **C:** Inclined burrows photographed on day 6 of the experiment. The marker laminations are smeared and displaced by the activity of the worms. **D:** Detailed photo of displaced grains in 3 J-shaped burrows observed on day 7 of the experiment.

The displacement of grains was used to estimate the percentage of burrowed sediment, which is plotted against time in Figure 3.9A. Bioturbation rates were initially rapid and subsequently declined following day 1. In comparison to side 1, side 2 of the aquarium displayed consistently reduced bioturbation intensities (except for day 1 of the experiment). The volume of burrowed sediment plotted against time in Figure 3.9B reflects the average volume of burrowed sediment recorded from both sides of the aquarium (Table 3.2). The volume of burrowed sediment increased rapidly from 0 to 20 hours, and subsequent data points follow a linear trend. A linear regression was plotted to approximate the subsequent linear trend in order to calculate the volumetric burrowing rate (VBR) of 0.089 cm^3/hr from the slope of the line.

The VBR of 0.089 cm^3/hr approximates the volume of sediment that is ingested per hour by 5 adult *Euzonus mucronata*. At this rate, the time required to bioturbate the entire aquarium would be 63.8 days (Table 3.3). This time assumes that burrowing is uniform vertically throughout the aquarium; however, the polychaetes preferentially bioturbate upper sediment layers during respiration at the simulated 'low tide.'

Interpretations

The offset of laminations associated with burrowing exemplifies the temporal aspect of *Euzonus mucronata* deposit-feeding activities. The time between the ingestion and excretion of sand grains is greater than the time required for the worm to locomote past the ingestion locality (see Chapter 4). This time lag reflects the time required to process nutrients from the surface of sand grains prior to excretion. Accordingly, the burrowing rates calculated in this study incorporate deposit-feeding activities with subordinate vertical migrations through the sediment.

Calculation of the volumetric burrowing rate involved averaging the volume of burrowed sediment observed on both sides of the aquarium. The reduced degree of bioturbation on side 2 of the aquarium could be explained by the slight tilt of the aquarium during storage in the laboratory tank. This aquarium was consistently stored such that side 1 was tilted upwards and side 2 tilted downwards. Accordingly, during upwards migration, the worms would most likely intersect the upper side (1) more often than the underside (2), which would result in increased reworking on side 1.

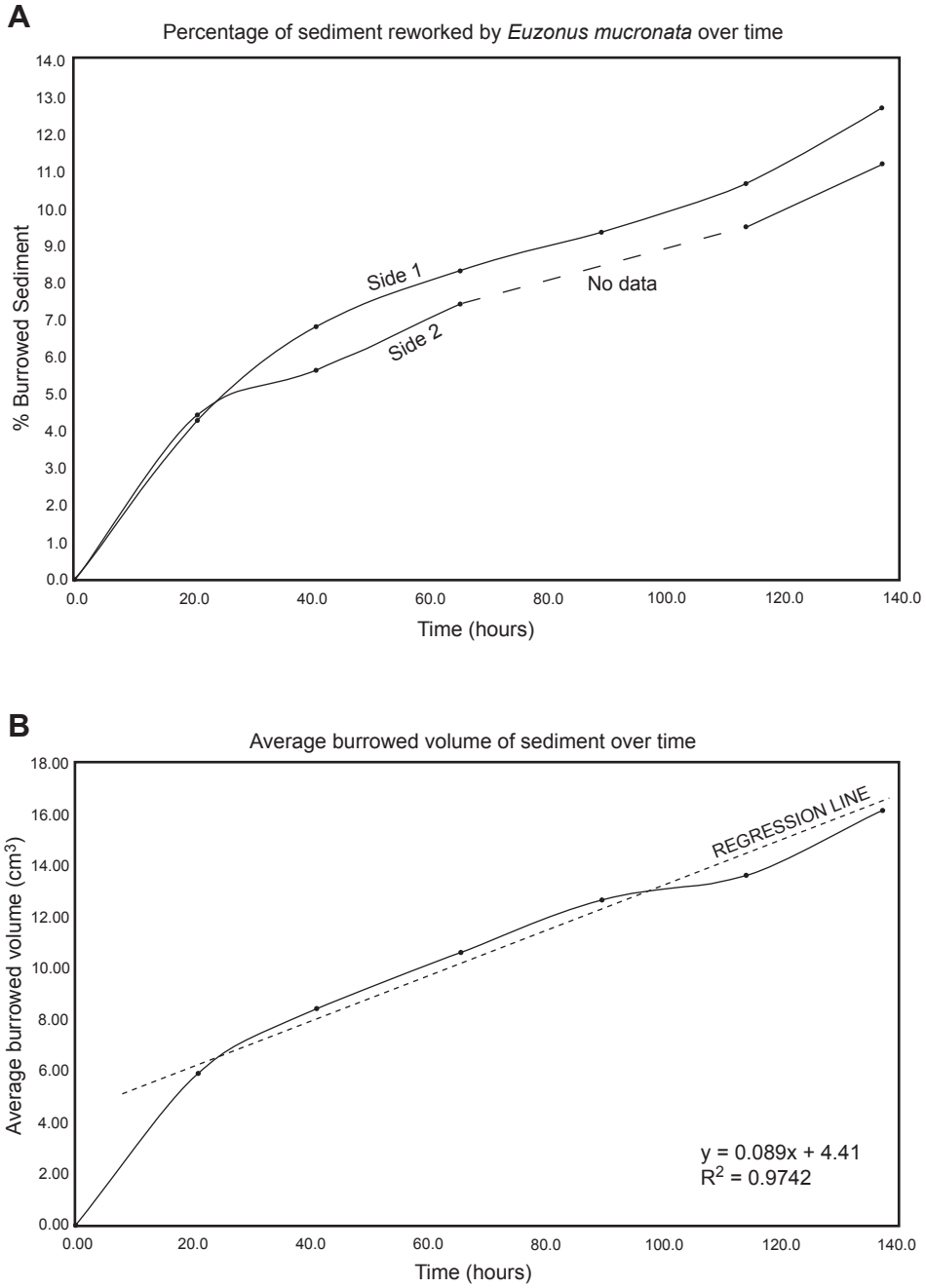

FIGURE 3.9—A: The percentage of visible burrowed sediment based on grid counts from each side of the small *Euzonus mucronata* aquarium plotted against time (Table 2). There was no photograph taken for side 2 on day 5 of the experiment. **B:** Graph of the average volume of burrowed sediment plotted against time (Table 2). There is a sudden increase in the volume of burrowed sediment from day 1 to day 2 as a result of the lack of burrowing prior to inoculation with worms. However, there is a shallower linear trend in the data between days 2 and 7 of the experiment, which is approximated with a linear regression (not including the 0 hour, 0 volume point). The two plotted values were used to calculate the slope Tic burrowing rate of 5 adult worms.

Population Density of *E. mucronata* in 1 m^2	Volumetric Burrowing Rate (cm^3/hr)	Burrowing Time (days)
5 adult (in aquarium)	0.089	63.8
100 adult	1.77	2348.5
1600 adult	28.39	146.8
100 adult + 1325 juvenile	13.71	304.0
1600 adult + 3477 juvenile	59.23	70.3

TABLE 3.3—Calculated burrowing rates and burrowing times for various populations. Values reflect volumetric burrowing rates and burrowing times required to bioturbate the upper 10 cm of sediment in a 1 m^2 area by the indicated population. The burrowing time for 5 adults reflects the reworking of the sediment within the aquarium (135.72 cm^3). Populations are obtained from the box core data collected at Pachena Beach (see Table 1). The burrowing rate of juveniles has been assumed to be one half the rate of adults.

Euzonus mucronata ingestion rates also have been calculated by Fox et al. (1948) and McConnaughey and Fox (1949) at 0.009 g/hr. Ingestion rates calculated by Kemp (1985, 1986, 1987) were significantly higher than this study at 0.104 g/hr to 0.35 g/hr. Conversion of the volumetric burrowing rate (for one worm) calculated in this study to grams per hour (density of Pachena sand is 1.48 g/cm^3) is 0.026 g/hr. The rate calculated for this experiment falls between the values calculated by previous authors (*ibid.*).

Extrapolating the VBR from this experiment to the observed populations on Pachena Beach provides estimates of natural *Euzonus mucronata* burrowing rates (Table 3.3). These extrapolations are based on an assumed linear relationship based on the data collected from vertical burrowing in the aquarium. With increasing population densities, however, the burrowing rate may change in response to increased avoidance of interpenetration of burrows due to scarcity of food resources. The estimated VBR for the lowest population density of adult *E. mucronata* recorded from Pachena (approximately 100 worms/m^2) is 1.77 cm^3/hr (Table 3.3). Observations from the field and larger aquarium indicate that the opheliids typically homogenize the upper 10 cm of sediment. Using this depth of burrowing, the VBR for 100 adult worms can be applied to a realistic volume of sediment—a 1 m^2 area to a depth of 10 cm. This small worm population would require over 6 years to completely bioturbate 0.1 m^3 of foreshore. Considering the maximum population density of adult worms observed at Pachena (1600 worms/m^2), the VBR for this population would be 28.39 cm^3/hr. The time required to bioturbate 0.1 m^3 of sediment by this population would be 146.8 days (Table 3.3).

Actual *Euzonus* populations at Pachena consist of adult and juvenile worms; therefore, the VBR should account for juveniles as well (Table 3.3). The burrowing rate of juveniles is approximated at one half the adult rate (see Chapter 4), and the total VBR is proportional to the number of juvenile and adult polychaetes. The minimum population density recorded in the field (110 adults/m^2 and 1325 juveniles/m^2) corresponds to a total VBR of 13.71 cm^3/hr and a burrowing time of 304 days for 0.1 m^3 of sediment. The maximum number of opheliids (1600 adults/m^2 and 3477 juveniles/m^2) equates to a VBR of 59.23 cm^3/hr, and a burrowing time frame of 70.3 days for 0.1 m^3 of foreshore.

Based on the observations, a dense population of *Euzonus mucronata* can mottle the upper 10 cm of foreshore sediment in a 1 m^2 area within 2.5 months. However, the VBR and time required for complete reworking of 0.1 m^3 of sediment are estimates under ideal conditions. These ideal conditions include: (1) no wave erosion during rising or falling tides; (2) burrowing is restricted to the upper 10 cm of sediment; (3) burrowing by all individuals is approximately equal and consistent over the time period; (4) natural burrowing rates are the same as in the aquaria; (5) no sediment is deposited; (6) oxygen concentrations are ample for survival; (7) maturation of juveniles does not occur over this time frame; (8) there is no lateral migration of the worm population; and (9) there are no other organisms burrowing in the sediment.

Based on the above assumptions, the burrowing rates and burrowing times are only approximations as erosion occurs due to rising and falling tides; new sediment can be deposited; the worms can burrow deeper than 10 cm; individual worms burrow at varying rates; the VBR for juveniles has been assumed; maturation of juveniles occurs and results in increased VBRs over time; other organisms are observed in the sediment with *Euzonus mucronata*; and increasing population densities likely result in increased avoidance behaviors. In addition, burrowing by *E. mucronata* in the thin-walled aquarium only approximates behaviors in the natural world. The calculated rates only take into account deposit feeding and vertical migration through the sediment as horizontal migration could not be measured in the aquarium. Calculated rates are also based on the observable burrowing adjacent to the aquarium glass. Burrowing further away from the glass plates was likely higher; as the worms are photophobic. In addition, as population densities increase, or as the sediment becomes highly reworked, the VBR may no longer correspond to a linear relationship over time due to changes in feeding activities in response to limited food resources. Due to the

constraints of the thin-walled aquaria, especially the inability for worms to feed horizontally, burrowing rates are likely more rapid in natural systems, which may be counterbalanced by physical processes.

DISCUSSION

Modern organism-sediment interactions approximate biogenic activities preserved in the rock record as ichnofossils. Accordingly, burrowing rates acquired from neoichnological studies can be applied to traces observed in outcrop and core. This study focused on using an analogous modern organism to obtain approximate volumetric burrowing rates for the *Macaronichnus segregatis* trace-maker. The calculated rates are, however, only approximations as the collected population density dataset is limited; burrowing in the aquarium only simulates the natural setting; and the opheliids and foreshore at Pachena Bay possess specific characteristics. Variation in burrowing rates between this modern study, other modern studies and rock record examples is likely dependent upon the beach character; size and species of the worms; mineralogical composition and grain size of foreshore sediment; hydraulic energy of the system (waves and tides); availability of food; temperature; oxygenation; and methods of calculation. Nonetheless, volumetric burrowing rates from this study provide initial estimates that can be applied to ancient examples of *M. segregatis*.

Utilizing data from this study, *Macaronichnus segregatis* from the Cretaceous Appaloosa Sandstone of the Horseshoe Canyon Formation of Alberta, Canada can be interpreted in terms of ancient organism populations and behaviors; prevailing depositional conditions; and bioturbation and sedimentation rates. High population densities would have been required to pervasively rework foreshore deposits to the extent observed in this rock record example (Fig. 3.1). Based on observations at Pachena, the depth at which *M. segregatis* trace-makers persisted may have been relatively shallow (10 cm). Although, the worms are capable of burrowing to greater depths, as observed in the aquaria and in the field where overlying foreshore sediment was comparatively dry. In the Appaloosa Sandstone, *M. segregatis* occur as predominantly horizontal traces with few vertical components (Fig. 3.1B). The paucity of vertical structures contrasts with the *Euzonus* burrowing observed in the field (Fig. 3.5) and aquaria (Figs. 3.6, 3.8). The lack of vertical components in the Appaloosa could be explained

by the aggradation of sediment over time and overprinting of traces. During aggradation, the upper layer comprising vertical burrows (related to respiration at low tide) would be overprinted by horizontal deposit-feeding activities at depth. Alternatively, extensive onshore-offshore migrations (Fig. 3.7) of polychaetes living at greater depths could have produced a predominantly horizontal burrow fabric. In general, the Appaloosa Sandstone reflects the work of dense populations of *M. segregatis* trace-makers that deposit fed on foreshore sediment during horizontal locomotion and subordinate vertical migrations in response to tidal cyclicity.

Modern *Euzonus mucronata* populations are influenced by a number of environmental factors including: beach configuration, foreshore slope, hydraulic energy, tidal regime, grain size, and sediment character. The formation of *Macaronichnus segregatis* requires some of these depositional parameters to fall within a narrow range, while other factors may be highly variable. Sediment character is limited by the nutrient requirements of the opheliids, which are primarily met by felsic-rich sands (see Chapter 4). Grain size is restricted to fine to medium sand due to a limited ingestible grain size and preferred sediment properties (e.g., pore volume, nutrient coatings, and oxygenation). Hydraulic energy can be assumed to be moderate to high to ensure ample oxygen and nutrient supply to polychaete populations. Some ancient trace-makers may have required more pronounced wave activity, as some *M. segregatis* have been interpreted to occur at the foreshore-shoreface transition (e.g., Clifton and Thompson, 1978; MacEachern and Pemberton, 1992; Saunders et al., 1994) rather than the mid to upper foreshore. On the other hand, trace-maker populations are likely sustained with a wide range of beach configurations and slopes, as well as tidal regimes.

The principles of Wheatcroft's (1990) transit time (time required to bury an event bed beyond the reach of burrowers) and dissipation time (time required to burrow an event bed) can be applied to the Appaloosa Sandstone. The effectiveness of bioturbation depends upon the sedimentation rate, bioturbation rate and physical reworking processes (Bentley and Sheremet, 2003). Preservation of any thickness of *Macaronichnus segregatis* burrowed strata requires that transit time exceeds dissipation time. The transit time is primarily an inverse function of the sedimentation rate (Wheatcroft, 1990). Therefore, the occurrence of a nearly 2 m thick package of sandstone containing pervasive *M. segregatis* in the Appaloosa (Pemberton and Saunders, 2003) suggests that transit time

exceeded dissipation time during deposition of this sedimentary unit. In other words, the sedimentation rate was surpassed by the rate of bioturbation. The degree of physical reworking was likely minimal or outpaced by biogenic mixing. Accordingly, rapid bioturbation rates or low sedimentation rates were required to preserve *M. segregatis* in the Appaloosa Sandstone. The thin interval of *Euzonus mucronata* burrowed foreshore at Pachena suggests that the calculated VBRs from this study represent a lower benchmark for *M. segregatis* trace-makers. Additionally, trace-makers likely burrowed at relatively shallow depths (less than 2 m), so beachface aggradation would have been required to accumulate the thick unit in the Appaloosa. This interpretation corresponds to the progradational nature of the Appaloosa as reported by Saunders (1989) and Ainsworth (1994).

Distinctive Characteristics at Pachena Bay

The burrowing rates determined from this study can only be used to estimate the rates of other modern *Euzonus* populations and analogous ancient organisms. The *Euzonus* population and foreshore characteristics at Pachena Bay reflect a specific balance between population dynamics and depositional conditions. The population density of *E. mucronata* at Pachena is relatively low in comparison to other reported populations (e.g., McConnaughey and Fox, 1949; Dales, 1952; Eikenberry, 1966; Kemp, 1985; Saunders, 1989). For 43,000 adult worms (the highest population density reported), the VBR would be 762.9 cm^3/hr, and the time required to rework 0.1 m^3 of sediment would be only 5.46 days. With such a dense population, there would likely be some variation in worm behavior such as increased avoidance of interpenetration of burrows, increased average burrow depths, and potentially a more pronounced horizontal burrow fabric due to overprinting. In addition, the *Euzonus* population at Pachena was overwhelmingly predominated by juvenile opheliids. This is likely associated with the time of year sampling took place, and potentially some reestablishment of the population due to harsh winter storms. Other modern opheliid polychaetes that form *Macaronichnus segregatis*-like structures have been identified (cf. Clifton and Thompson, 1978). In comparison to *Euzonus*, these polychaetes possess different morphological attributes and corresponding methods of burrowing that would result in differing rates of bioturbation (see Chapter 4).

Environmental factors that are characteristic to Pachena include the embayed nature of the foreshore, which is sheltered in comparison to many

other modern beaches. This embayment would influence wave and tidal energy and potentially erosional and depositional rates as well, and in fact, results in a relatively dissipative foreshore morphology. Despite the embayed nature of Pachena Beach, the pebble lag observed near the sediment surface implies that harsh winter storms can remove much of the sediment deposited during the summer months. The sediment at Pachena is also characteristically a specific grain size and composition. The average grain size is upper fine sand, which is finer than most beaches characterized by *Euzonus mucronata*. More importantly, Pachena sediment contains a high proportion of shell fragments, which tend to be larger and more angular as compared to other grains. As a result, *E. mucronata* are inclined to avoid deposit feeding on these grains, which correspondingly mantle burrow walls unlike the typical mafic mantle of *Macaronichnus segregatis* and *M. segregatis*-like structures (see Chapter 4). This process of mineral segregation is likely specific to this opheliid and sediment composition, which suggests that burrowing in other sediments by *E. mucronata* or other polychaetes could result in different bioturbation rates.

CONCLUSIONS

A relatively new facet of neoichnology is the use of modern analogous organisms to interpret the temporal significance of ancient traces (e.g., Gingras et al., 2008). This chapter utilized modern analogous *Euzonus mucronata* to assess the burrowing behaviors and burrowing rates of ancient *Macaronichnus segregatis* trace-makers as structures formed by *Euzonus* closely resemble *Macaronichnus*-like structures. Field analyses involved determination of population densities and burrowing behaviors of the worms. *Euzonus* were observed to deposit feed during vertical and onshore-offshore locomotion in response to tidal cyclicity. Based on field observations, the overall distribution of *E. mucronata* is generally dependent upon the position of the last high tide, the tidal cycle, substrate moisture content, population dynamics, food resources, and position of beach berms and runnels. Laboratory analyses further studied burrowing behaviors and burrowing rates using thin-walled glass aquaria. Thin-walled aquaria confirmed the concentration of *E. mucronata* in the upper 10 cm of sediment as observed in the field. A volumetric burrowing rate was calculated

from grid overlays of an aquarium containing 5 adult polychaetes. Under ideal conditions, this VBR was extrapolated to the largest population density at Pachena (59.2 cm^3/hr), which would require 70.3 days to rework 0.1 m^3 of foreshore. The burrowing rates calculated in this study can only estimate natural rates due to the limited population dataset, assumptions inherent in the calculations, simulation of a natural setting in an aquarium, and specific characteristics of the Pachena opheliids and depositional conditions.

This study suggests that the pervasively bioturbated *Macaronichnus segregatis* unit in the Appaloosa Sandstone represents reworking by dense populations during aggradation and progradation of beach facies. In order for the thick succession of burrowed strata to be preserved, bioturbation rates exceeded sedimentation rates and physical reworking was likely negligible.

The occurrence of foreshore sediment pervasively reworked by *Euzonus* or sandstone characterized by *Macaronichnus* reflects a departure from typical foreshore deposits. Frey et al. (1989) described archetypal beach sediments in which foreshore and upper shoreface strata are unbioturbated and dominated by physical sedimentary structures. In this model, the transition from physical to biogenic structures generally occurs between 1-4 m water depth. Accordingly, biogenic reworking of foreshore sediment reflects an atypical situation in which bioturbation rates are exceedingly high in order to outpace sedimentation rates and processes of physical reworking associated with tidal cyclicity. In contrast, the offshore is generally characterized by low sedimentation rates coupled with high bioturbation rates due to the abundance and diversity of organisms (cf. Pemberton et al., 2001). In this setting, bioturbation rates are difficult to assess as a result of continual reworking of the sediment by successive tiers which produces an overprinting of structures. Accordingly, a thick unit that is pervasively reworked by *M. segregatis* trace-makers may have an equivalent dissipation time to a much thinner unit of offshore strata. The transit time for these two cases would, however, be invariably dissimilar and would be greater (i.e. lower sedimentation rate) in the offshore. In shallow marine to nearshore settings such as the foreshore, dissipation time (time required for burrowing) will be dependent upon the burrowing efficiency and abundance of trace-makers. This study illustrates one example in which preservation of biogenically reworked strata is associated with exceedingly high burrowing rates that likely transcend the calculated rates in modern natural settings and ancient examples.

Based on this study and work by Gingras et al. (2008), the degree of

trace-maker activity required to pervasively rework strata generally involves very little time. The geological time reflected in an individual unit is a function of the delicate balance between bioturbation rates, sedimentation rates and physical reworking processes. By studying burrowing rates associated with individual traces and assemblages of ichnofossils, we can begin to understand the temporal interaction between biogenic and physical processes.

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CHAPTER 4 – ANALYSIS OF MINERAL SEGREGATION IN *EUZONUS MUCRONATA* BURROW STRUCTURES: ONE POSSIBLE METHOD USED IN THE CONSTRUCTION OF ANCIENT *MACARONICHNUS SEGREGATIS*

INTRODUCTION

Ancient sandy beach deposits characterized by a monospecific burrow fabric were first identified and described in Jurassic and younger strata by Clifton and Thompson (1978). The trace fossil characterizing this fabric is now recognized as *Macaronichnus segregatis* Clifton and Thompson, 1978, a cylindrical, unlined, sinuous intrastratal trail, commonly 2-5 mm in diameter (Fig. 4.1). This trace displays mineralogical segregation between the quartz-rich infill and the mica and heavy mineral mantle (Clifton and Thompson, 1978). The mechanism by which *M. segregatis* trace-makers segregate mineral grains is poorly understood and is the focus of this study.

Macaronichnus segregatis is an important trace fossil characterizing ancient high-energy nearshore settings (Pemberton et al., 2001). Since Clifton and Thompson's (1978) original description of *M. segregatis*, the trace fossil has been recognized in a number of other Cambrian to Pleistocene successions: SW-Norwegian Caledonides (Knaust, 2004); Upper Jurassic of Milne Land, Greenland (Heinberg, 1974; Fürsich, 1984); Bluesky Formation, Alberta (MacEachern and Pemberton, 1992); Cadotte Member, Alberta (MacEachern and Pemberton, 1992; Saunders et al., 1994); Dunvegan Formation, Alberta (Gingras et al., 1998); Bearpaw-Horseshoe Canyon Formation transition, Alberta (Fig. 4.1; Saunders, 1989; Saunders, et al., 1990; Pemberton and Saunders, 2003); Shimosa Group, Japan (Tokuhashi and Kondo, 1989); Narita Formation, Japan (Kikuchi, 1972); Shimosa and Kazusa Groups, Japan (Nara, 1994); and the Kujukurihama Coast, Japan (Nara and Seike, 2004). More recently, Savrda and Uddin (2005) described large *Macaronichnus* in the Eutaw Formation, which exhibit distinctive mineralogical segregation.

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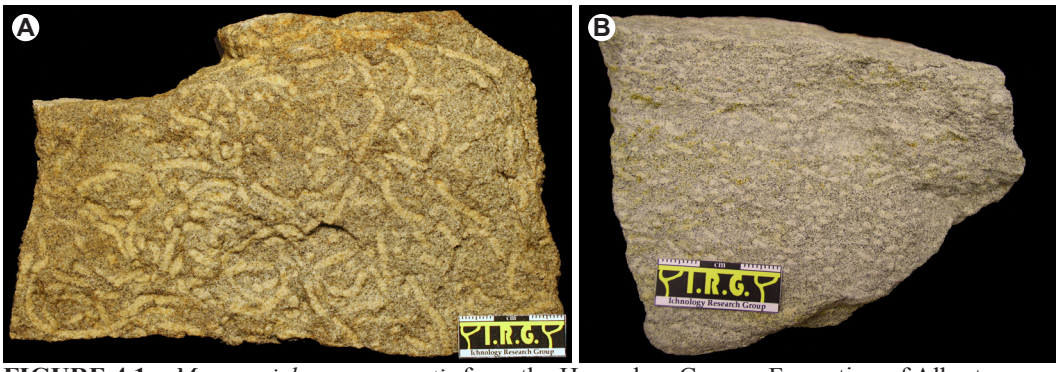

FIGURE 4.1—*Macaronichnus segregatis* from the Horseshoe Canyon Formation of Alberta (Upper Cretaceous). **A:** Plan view of the traces exhibiting random avoidance of meandering pathways. **B:** Cross-sectional view of the traces, which illustrates the predominantly horizontal orientation of the structures (scales are 3 cm long).

The grain sorting in *Macaronichnus segregatis* plays a role in the distribution and quality of sandstone porosity and permeability. Mineral segregation can influence post-depositional cement distribution as the network of traces can enhance isotropic bulk permeability in comparison to equivalent laminated foreshore strata. This was shown to occur in the Lower Cretaceous Toro Sandstone (Iagifu field, Papua New Guinea) by Pemberton and Gingras (2005), in which segregation of glauconite from quartz-rich burrow infills clearly enhanced the permeability of burrow networks. Improved understanding of such mineral partitioning may lead to further recognition of this trace fossil in the enhancement of reservoir properties.

Analogous Modern Trace-Makers

Previous studies have used modern analogous organisms to understand the behavior of *Macaronichnus segregatis* trace-makers. Clifton and Thompson (1978) examined the activities of *Ophelia limacina*, which is interpreted to reject heavy mineral grains, micas and aggregates of clays through the concentration of these grains within the organism's ventral groove. The isopod *Excirolana chiltoni japonica* also has been employed to explain the formation of *Macaronichnus segregatis* (Kikuchi, 1972; Tokuhashi and Kondo, 1989; Yokokawa and Masuda, 1991). However, experimental observations by Nara (1994) illustrated that a felsic grain-selective worm, rather than *E. chiltoni*, likely constructed *M. segregatis*. In other studies, the opheliid *Euzonus sp.* was recognized as constructing *Macaronichnus*-like traces (Saunders, 1989; Saunders et al., 1990; Nara and Seike, 2004). This study utilizes a specific polychaete, *Euzonus mucronata*



FIGURE 4.2—*Euzonus mucronata.* Note the pointed head region of the worm on the right, and the extruded proboscis of the worm on the left.

(Fig. 4.2), from Pachena Bay, Vancouver Island (Canada), to further assess the mechanism of grain sorting that occurs during deposit-feeding activities.

The opheliid polychaete, *Euzonus mucronata*, is found in sandy beaches along the North American Pacific Coast from Vancouver Island to the Punta Banda region of Mexico (Dales, 1952; Eikenberry, 1966; Ricketts and Calvin, 1968; Kemp, 1985). *Euzonus mucronata* generally inhabits fine- to medium-grained upper intertidal sands exposed to moderate surf action (Dales, 1952; Eikenberry, 1966; Ruby and Fox, 1976; Kemp, 1985). These polychaetes migrate vertically through beach sand in response to diurnal tides and associated changes in oxygen tension, salinity, and temperature (Dangott and Terwilliger, 1986).

Euzonus mucronata are red to purplish in color, approximately 2-5 cm long, 0.5-2.0 mm in diameter as adults, and have weak segmentation (Fig. 4.2; Fox et al., 1948; McConnaughey and Fox, 1949). The digestive system of this polychaete is adapted to processing nutrients from the surface of sand grains. Key components of the digestive system include the mouth, proboscis, and gut. The mouth is a transverse slit on the ventral side of the head from which the proboscis is everted. Three soft, ciliated lobes characterize the proboscis, which gathers sand and funnels it towards the gut. Nutrients extracted within the gut are thought to include detrital organic matter, protozoa, bacteria, and other microorganisms (Fox et al., 1948; McConnaughey and Fox, 1949; Eikenberry, 1966; Kemp, 1985, 1986). The lumen of the gut consists of multiple deep longitudinal folds with cilia on the inner surfaces that have been proposed to sweep grains towards the pygidium (posterior) for excretion (Fox et al., 1948). During ingestion and excretion, sand grains are commonly mineralogically segregated by the

polychaetes (Saunders, 1989). The objective of this study is to determine the process in which mineral grains are partitioned by *E. mucronata* and associated ancient *Macaronichnus segregatis* trace-makers.

STUDY AREA

Pachena Bay is located on the west side of Vancouver Island, Canada, and contains an exposed sandy beach subject to moderate wave energy in a partially enclosed setting (Fig. 4.3). The bay possesses a tidal range of up to 3.8 m (mesotidal). Pachena beach comprises lower fine- to upper medium-grained sand (modal size is upper fine). The mineralogical composition of the sand was studied and using thin-section petrography and was found to include: quartz, rock fragments, shell fragments, plagioclase, orthoclase, hornblende, opaque minerals, biotite, and muscovite. According to grain counting, typical components of the foreshore sand include 44% feldspar, 27% quartz, 22% lithic fragments, 5% hornblende and 2% shell fragments. This corresponds to 71% felsic material, 27% mafic material (nearly all lithic fragments are mafic), and 2% shell fragments.

METHODS

Field observations involved determination of sediment size and character, as well as *Euzonus* burrow characteristics. Burrow structures were preserved using box cores that were sliced or broken and set using epoxy resin to form sediment peels. *Euzonus mucronata* were collected from the foreshore of Pachena Beach for laboratory experiments at the Bamfield Marine Sciences Centre (Table 4.1). These experiments focused on *E. mucronata* ingestion and excretion behaviors, which are inferred to produce mineralogical segregation. Various worm populations were microscopically videotaped (at the individual scale) in petri dishes filled with water-saturated sand to approximately 2-3 mm depth. Videotaping was performed from the base of the dishes at 10x magnification, and experiments conducted on these worms focused on ingestion and excretion with: 1) variable substrates (proportions of felsic, mafic and shell material); 2) variation in worm maturity; and 3) a sterilized sediment (Table 4.2). The temperature was

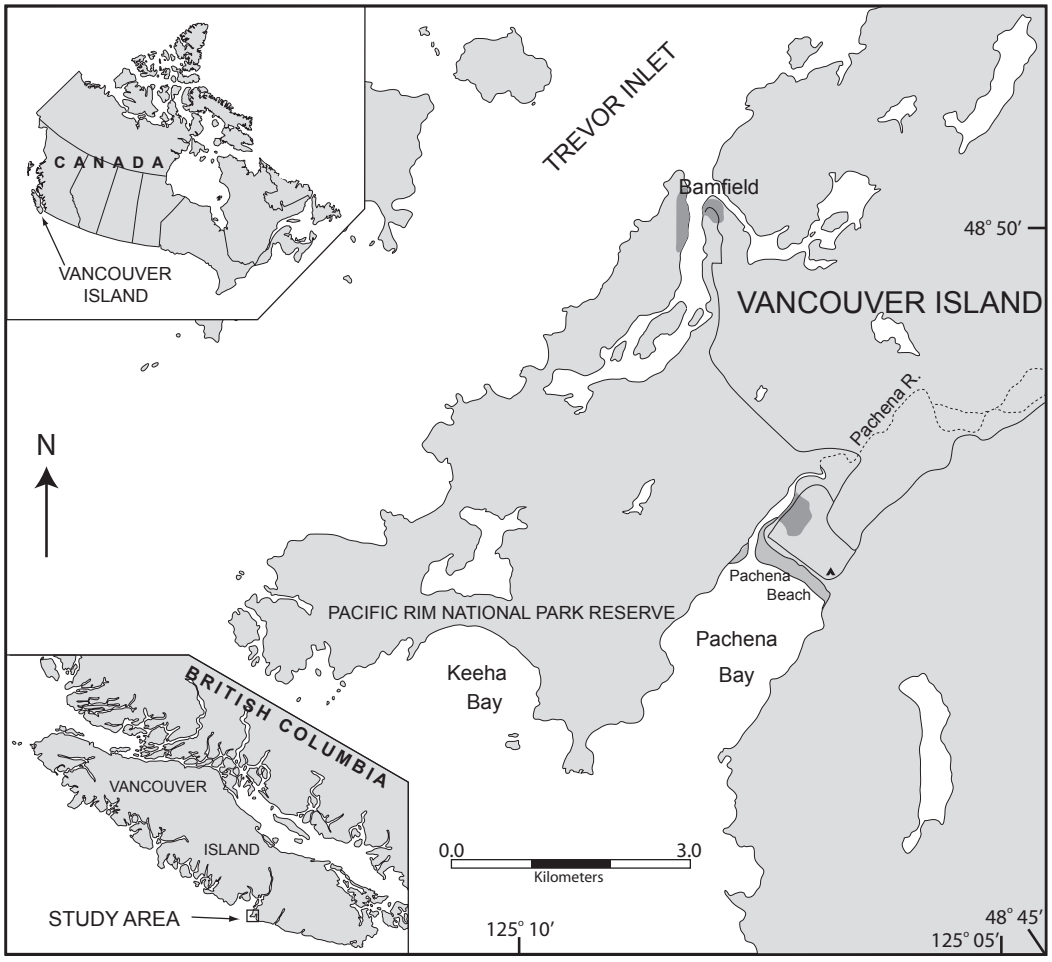

FIGURE 4.3—Part of the west coast of Vancouver Island showing the location of Pachena Bay near the town of Bamfield. The lower inset map shows the location of the study area on Vancouver Island. The upper inset map of Canada shows the location of Vancouver Island on the west coast of Canada.

Stage	Length	Width
Small juveniles	1 cm or less	About 1 mm
Juveniles	2 cm or less	About 1 mm
Small adults	1.5 - 2.5 cm	2 - 3 mm
Adults	> 2.5 cm	2 - 3 mm

TABLE 4.1—Approximate developmental stages of *Euzonus mucronata.*

(A) Average grain compositions ingested by *Euzonus mucronata*

Experiment	Average Time	# Felsic grains	# Mafic grains	# Shell grains	Total # of grains	% Felsic grains	% Mafic grains	% Shell grains
Quartz-rich sand	00:00:07	26.1	5.0	2.2	33.3	78.2	14.6	7.2
25% Mafic-rich sand	00:00:09	15.0	3.5	1.0	19.5	77.0	17.9	5.2
50% Mafic-rich sand	00:00:06	7.4	1.8	1.0	10.2	68.2	22.3	9.5
75% Mafic-rich sand	00:00:06	22.3	5.2	2.5	30.0	74.9	17.2	7.9
Mafic-rich sand	00:00:08	19.9	5.7	1.7	27.3	74.8	20.0	5.2
Shell-rich sand	00:00:06	21.3	3.5	6.0	30.8	65.7	11.5	22.8
Small juveniles	00:00:04	6.0	2.5	0.0	8.5	70.1	29.9	0.0
Juveniles	00:00:04	24.7	3.9	1.7	30.2	82.2	11.9	5.9
Small adults	00:00:07	17.7	3.7	0.7	22.0	79.9	16.4	3.7
Adults	00:00:07	22.0	4.1	2.4	28.6	77.8	14.0	8.2
Sterilized sand	00:00:06	12.0	1.9	0.8	14.7	82.1	12.7	5.2

(B) Average grain compositions excreted by *Euzonus mucronata*

Experiment	Average Time	# Felsic grains	# Mafic grains	# Shell grains	Total # of grains	% Felsic grains	% Mafic grains	% Shell grains
Quartz-rich sand	00:01:36	129.5	10.5	5.3	145.3	90.2	7.2	2.6
25% Mafic-rich sand	00:00:41	24.0	1.0	1.5	26.5	87.4	2.1	10.5
50% Mafic-rich sand	00:00:58	80.0	12.5	10.3	102.8	79.6	9.9	10.5
75% Mafic-rich sand	00:00:32	72.0	5.5	5.5	83.0	86.8	6.7	6.5
Mafic-rich sand	00:00:40	106.0	10.5	4.0	120.5	87.6	9.1	3.3
Shell-rich sand	00:02:31	143.3	10.3	22.3	175.8	76.1	5.3	18.6
Small juveniles	00:00:37	20.7	0.7	1.3	22.7	91.3	2.9	5.8
Juveniles	00:00:47	84.0	8.0	2.0	94.0	88.8	8.3	2.9
Small adults	00:00:56	51.8	3.2	2.8	57.8	89.8	5.5	4.7
Adults	00:03:21	265.2	20.0	13.0	298.2	90.2	5.2	4.6
Sterilized sand	00:02:21	143.0	9.5	8.5	161.0	90.0	5.4	4.7

TABLE 4.2 (Previous page)—A: Average grain compositions ingested by *Euzonus mucronata*. **B:** Average grain compositions excreted by *Euzonus mucronata*. The number of observed ingestion and excretion episodes varies for each sample and ranges from 2 to 37 observations.

constant at 21°C and direct light from the microscope was used to obtain clear images of deposit-feeding activities.

Substrate variations were prepared by combining selective proportions (by mass of water-saturated sand) of quartz-rich (72% felsic material) and mafic-rich (27% mafic material) sands to provide a spectrum of substrates, along with shell fragment-rich (42% shell material) sand. The composition of the sediments is given in Table 4.3 (see proportion of sands combined for various substrates). Six adult *Euzonus mucronata* were placed in each substrate and burrowed in the sediment for a few hours prior to videotaping. Grain counts were performed on the 3 original sand types using a grid with 204 equally spaced points. Two grain counts were performed for each sand type and the mineral percentages reflect an average of these two counts. These values were then proportionally extrapolated to the prepared substrates (Table 4.3–host sediment composition).

Worms of various maturities were videotaped to observe changes in deposit-feeding behaviors at different life stages. The sediment used in petri

Measurement	Mineral Type	Quartz-rich sand	25% Mafic-rich sand	50% Mafic-rich sand	75% Mafic-rich sand	Mafic-rich sand	Shell-rich sand
Proportion of sands combined for substrate variations	Quartz-rich (%)	100.00	75.00	50.03	25.02	0.00	0.00
	Mafic-rich (%)	0.00	25.00	49.97	74.98	100.00	0.00
	Shell-rich (%)	0.00	0.00	0.00	0.00	0.00	100.00
Resultant host sediment composition	Felsic (%)	71.63	67.46	63.28	59.11	54.93	45.93
	Mafic (%)	26.55	26.69	26.82	26.96	27.09	12.18
	Shell (%)	1.81	5.85	9.89	13.94	17.98	41.89
Proportion of ingested grains from video counts	Felsic (%)	78.20	76.98	68.18	74.86	74.81	65.67
	Mafic (%)	14.63	17.86	22.33	17.21	19.98	11.48
	Shell (%)	7.16	5.16	9.48	7.94	5.20	22.84
Proportion of excreted grains from video counts	Felsic (%)	90.20	87.41	79.56	86.75	87.58	76.08
	Mafic (%)	7.16	2.13	9.94	6.73	9.07	5.30
	Shell (%)	2.64	10.46	10.50	6.52	3.35	18.62
Proportion ingested versus host sediment abundance	Felsic IN:HS	1.09	1.14	1.08	1.27	1.36	1.43
	Mafic IN:HS	0.55	0.67	0.83	0.64	0.74	0.94
	Shell IN:HS	3.95	0.88	0.96	0.57	0.29	0.55
Proportion excreted versus host sediment abundance	Felsic EX:HS	1.26	1.30	1.26	1.47	1.59	1.66
	Mafic EX:HS	0.27	0.08	0.37	0.25	0.33	0.44
	Shell EX:HS	1.46	1.79	1.06	0.47	0.19	0.44

TABLE 4.3—Normalized proportions of mineral grains ingested or excreted versus the host sediment composition. A ratio greater than 1 indicates that the grains are more prevalent in the ingestion or excretion event than in the host sediment. A ratio of less than 1 indicates that there are fewer grains in the ingestion or excretion than in the host sediment.

dishes for this series of experiments was obtained from the worm collection site (the quartz-rich sand). Four sizes of worms were used based on the width and length of the worms (Table 4.1). A number of small juvenile and small adult worms were placed in separate dishes, and approximately 5-6 adult worms and three juvenile worms were placed in two other dishes. The final experiment involving sterilized sediment was prepared by boiling a portion of quartz-rich sand and seawater for an extended period of time prior to rinsing with fresh seawater. The sterilized sample was used as a control to test grain selectivity due to sensory perception of attached food particles with 6 *Euzonus mucronata*.

Video of the worms was analyzed (frame-by-frame) by counting and identifying mineral grains ingested and excreted by the polychaetes. Grains were identified as felsic (quartz and feldspar), mafic (rock fragments and amphibole) or shell. Ingestion by *Euzonus mucronata* consisted of proboscis eversion, collection of grains funneled toward the gut, proboscis retraction, and then a short period of locomotion. The time from initial proboscis eversion to the end of the retraction was recorded as the amount of time required for each ingestion episode. The length of time over which each excretion event occurred was also recorded.

From the video grain counts, the total number of grains and percentages of felsic, mafic and shell grains were averaged for ingestion and excretion events in each experiment (substrate type and worm size; Table 4.2). The substrate experiments were then normalized to the composition of the respective host sediment (Table 4.3). Normalization was calculated by dividing the percentage of each ingested grain type by the percentage of that grain type found in the host sediment. Likewise, normalization of the excreted grain counts were calculated by dividing the percentage of each excreted grain type by the percentage of that grain occurring in the host sediment (Table 4.3).

RESULTS

Field-Based Observations

Field photos illustrate the pervasive mottling by *Euzonus mucronata* within the upper 10 cm of foreshore sediment (Fig. 4.4). The burrow structures are overwhelmingly mantled by shell fragments especially when observed in plan view (Fig. 4.4B). Sediment peels collected from horizons rich in shell fragments

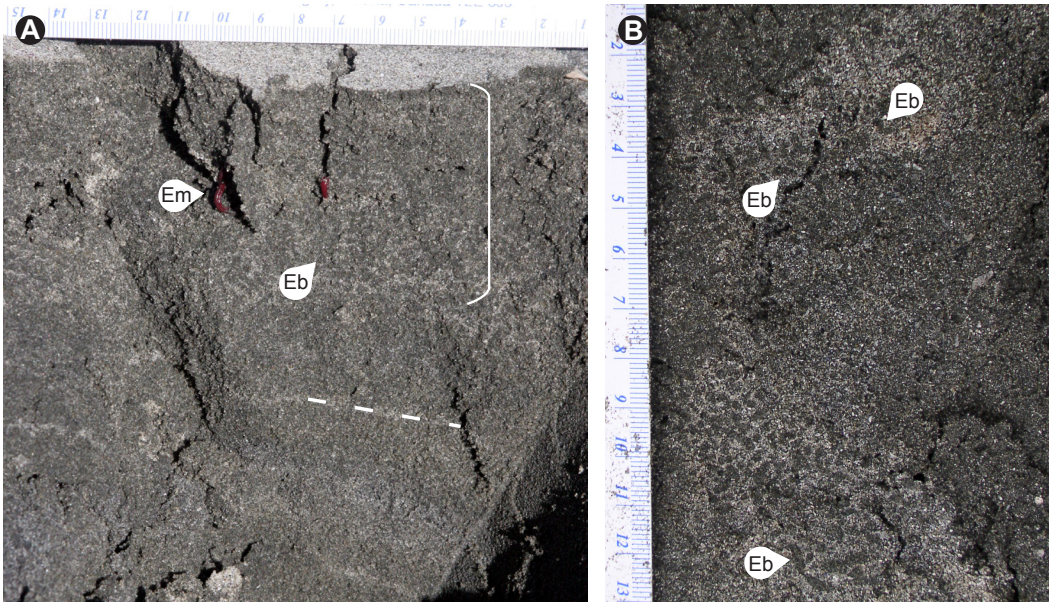

FIGURE 4.4—*Euzonus mucronata* (Em) and *E. mucronata* burrows (Eb) in the field. **A:** Vertical section of the upper portion of beach sediment. The upper 10 cm of sediment is thoroughly reworked by the polychaetes and remnant laminations can be seen below this zone (dashed line). **B:** Plan view of the burrows highlighted by a shell-rich horizon that has been thoroughly reworked. Note the inverse coloration of the *Macaronichnus*-like structures, which are mantled by light colored grains and infilled with darker grains.

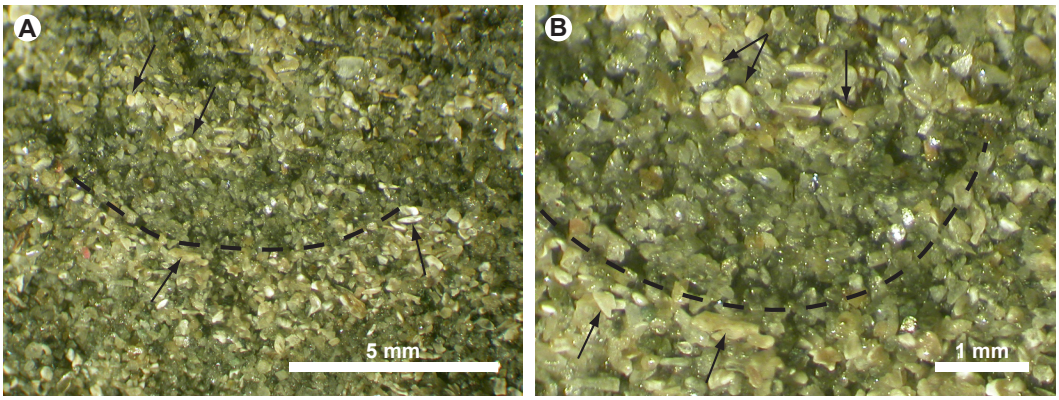

FIGURE 4.5—Epoxy sediment peels from horizons within Pachena Beach. Tangential alignment and segregation of shell fragments occurs along the sides of the burrow infills (dashed lines), and burrow fills are dominantly composed of felsic grains. Shell fragments are indicated by black arrows. Photo (B) is a close-up of the burrow from photo (A).

exhibit distinct *E. mucronata* burrow fills with enrichment in felsic grains in comparison to the host sediment (Fig. 4.5). The felsic burrow infills are consistent with typical *Macaronichnus segregatis*. However, the burrows are predominantly highlighted by shell fragments rather than mafic grains (Fig. 4.5). The horizontal peels also illustrate intermittent tangential alignment of shell fragments in burrow mantles (Fig. 4.5B). Scattered mafic grains are apparent within burrow fills; however, segregation of these heavier minerals is difficult to visually ascertain due to the abundance of shell fragments along burrow margins.

Ingestion and Excretion

Ingestion is a complex process that is initiated by *Euzonus mucronata* probing the sediment with the sensory-rich prostomium (head region) to locate a suitable feeding locale. Probing occurs during locomotion whereby coelomic fluid is forced into the head region, which consists of the first and second somites (McConnaughey and Fox, 1949). Inflation of the head begins at the segments posterior to the mouth. If locomotion continues without feeding, coelomic fluid drains back into the body, and through peristalsis, the body segments are pulled forward. Expansion of the head region drives the worm into the sediment and serves to push grains aside. Internally, with the flow of coelomic fluid, the proboscis also moves forward into the head region. If deposit feeding is chosen for a particular locality, the coelomic fluid may be partially drained as the proboscis is everted. However, significant swelling of the head region is not required for proboscis eversion. Feeding with the proboscis generally occurs straight forward or downwards as the opening (mouth) is located on the underside of the worm. The proboscis is extruded to gather grains that are funneled towards the gut (Fig. 4.6A, C, E), and is then retracted before the worm continues feeding or locomoting. Commonly, the opheliids will feed intermittently as they locomote short distances between extrusions of their proboscis. In other cases, worms may pause extensively to probe the sediment with their prostomium. Deposit feeding by *E. mucronata* results in ingestion of felsic, mafic, and shell grains even despite the large grain size of some shell fragments (Fig. 4.6F). The proportion of these ingested mineral grains primarily depends on the local concentrations at the site of feeding.

During excretion, the pygidium tends to move grains back and forth in a pendular motion to facilitate grain dispersion and efficient packing (Fig. 4.6H,

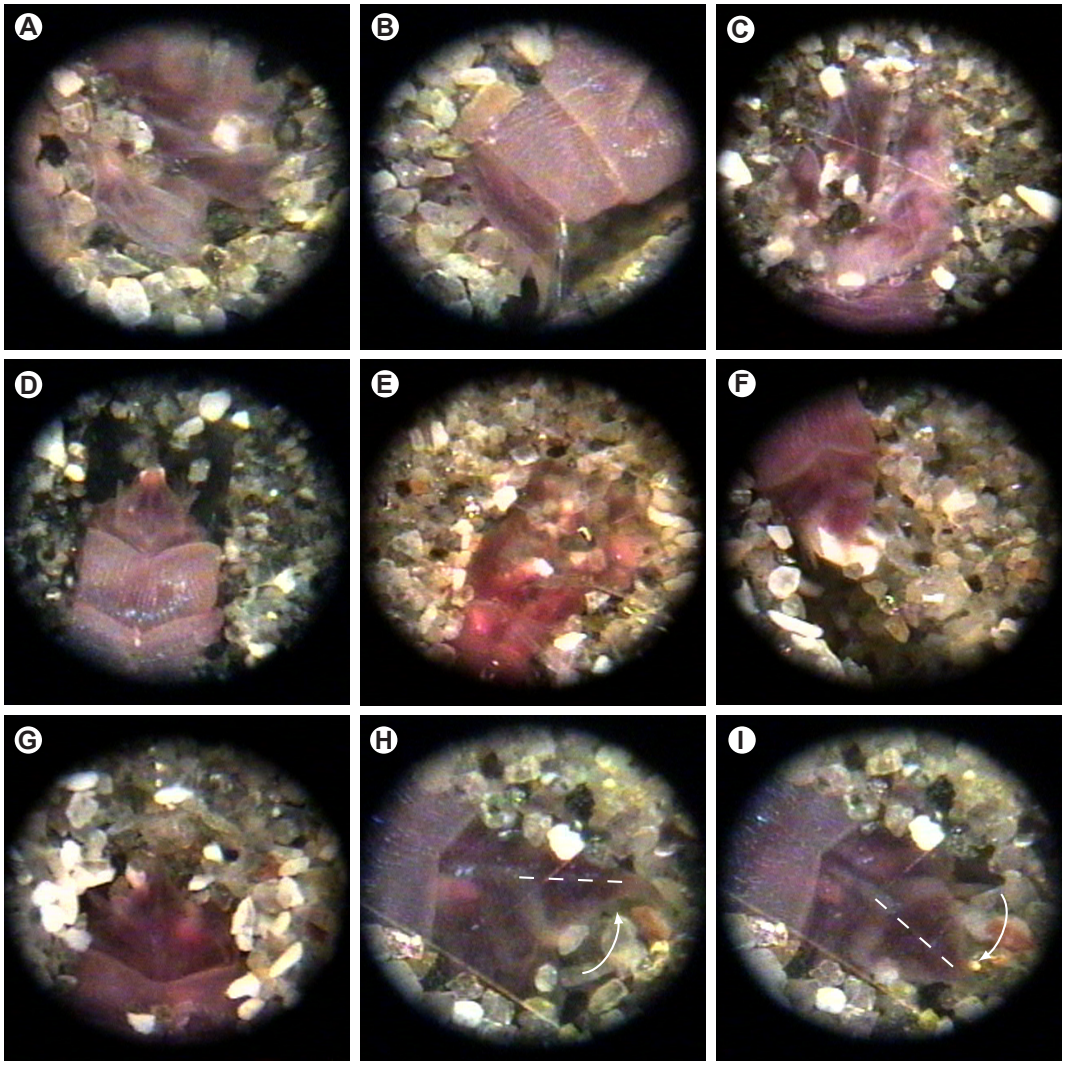

FIGURE 4.6—Video stills of ingestion and excretion of grains by *Euzonus mucronata*. For scale, the circular view is approximately 3 mm in diameter, and magnification is 10x. **A:** Ingestion in quartz-rich sediment. **B:** Side view of excretion in the quartz-rich sand. **C:** Ingestion of sand grains in 75% mafic-rich substrate. **D:** Excretion of a loosely packed burrow fill in the mafic-rich sand. **E:** Ingestion by a juvenile worm. Due to the transparent nature of the worm's body, grains are easily observed as they are funneled towards the gut during ingestion. **F:** Excretion of a large shell fragment by a small adult *E. mucronata*. **G:** Excretion of sediment in the shell-rich sand. Shell fragments are aligned alongside the worm as it passes through the sediment. **H, I:** An example of the pendular (back and forth) motion of the posterior of *E. mucronata* observed during excretion (in quartz-rich substrate).

I). This action, in combination with the work of the cirri, results in a mechanical shuffling that can work to force shell fragments (light, platy grains) to burrow boundaries. Angles at which pendular motion occurs ranges from only a few degrees to a maximum of 70 degrees. Pendular motion is pronounced when a densely packed burrow fill is produced. In contrast, in a loosely packed burrow fill there tends to be little or no pendular pygidium motion. Under artificial conditions of the experiment, burrow fills include discontinuous excreted masses, continuous loose ribbons (Fig. 4.6D, F), and tightly packed fills (Fig. 4.6B, G). Occasionally, *E. mucronata* shifted backwards to compact the burrow fill with the pygidium. Sediment is also observed to collapse into the burrow where the fill is not tightly packed.

Mineralogical Segregation

Video analysis of grain ingestion and excretion illustrates a general reduction in the percentage of felsic grains ingested and excreted in samples containing a proportion of mafic-rich sand as compared to the quartz-rich sand (Table 4.2, Fig. 4.7). In the shell-rich substrate, increased shell grains are ingested and excreted likely due to the overall abundance of shell material. The experiments involving variable worm maturity generally correspond to the results of the quartz-rich substrate. Similarly, worms in the sterilized sand displayed no deviation in behavior as compared to the unsterilized quartz-rich sand.

The most notable trend in the data presented in Figure 4.7 is the systematic variance between the ingested and excreted percentages of both felsic and mafic grains in every experiment. This variance averages about 11% for all experiments. The grain counts imply that more mafic grains are ingested than excreted, which results in a more felsic-rich burrow fill. On the other hand, the percentage of shell fragments is fairly consistent between ingestion and excretion observations (varies by 1.4% on average). The anomalous nature of the variation in ingested and excreted percentages of both felsic and mafic components is addressed in the discussion section.

The grain counts for the substrate experiments presented in Table 4.2 are normalized to the actual sediment composition in Table 4.3 and Figure 4.8. In all experiments, the proportion of ingested felsic grains is always greater than the proportion of felsic grains found in the host sediment, as the ratio between these values is >1. This ratio generally increases with increasing mafic content

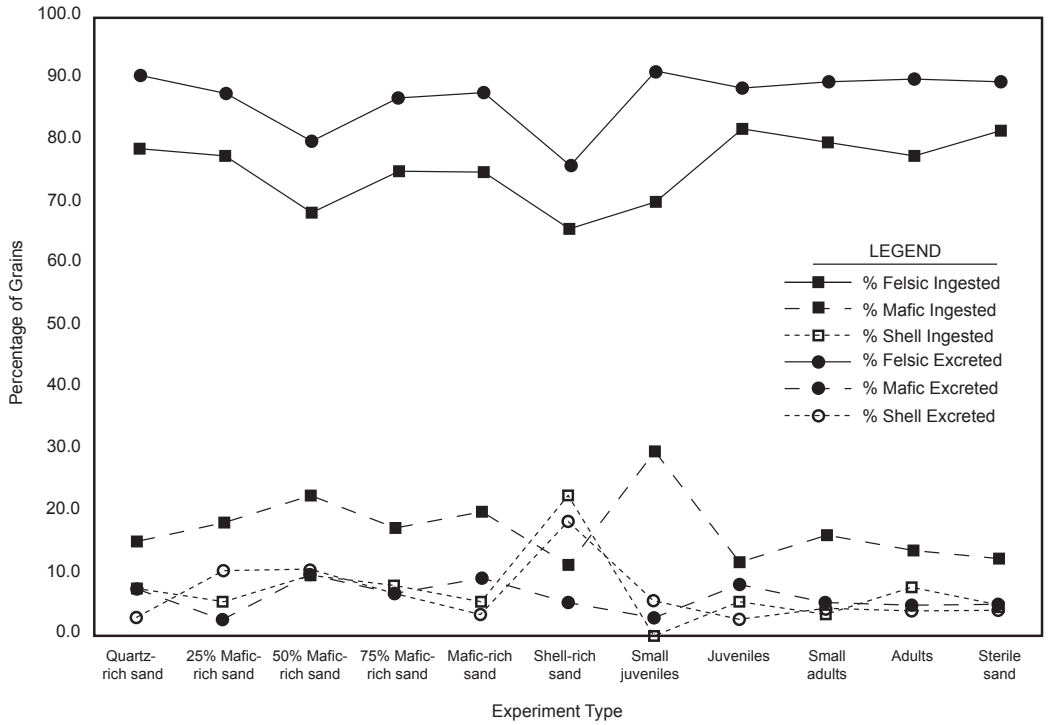

FIGURE 4.7—The average percentage of ingested and excreted grains determined from video grain counts of *Euzonus mucronata* in all of the experiments (see Table 4.2). Squares represent the percentage of ingested grains and circles represent the percentage of excreted grains. Across all experiments, there is a consistent variation in the percentage of ingested and excreted felsic grains and in the ingested and excreted mafic grains. This variation is observed in the separation between the circles and squares for these mineral types. Conversely, the variation in shell fragments is negligible in the experiments.

in the sediment, as well as in the shell-rich sand. Correspondingly, the ratio of ingested versus host sediment abundance of mafic grains is less than one in all experiments, which indicates that mafic grains are preferentially avoided (Table 4.3, Fig. 4.8). Avoidance of mafic grains generally decreases with increasing availability of mafic material in the sediment. The proportion of ingested versus host sediment abundance of shell fragments indicates that these particles are increasingly avoided with additional mafic content and shell fragments. Principally, these normalizations emphasize the preferential ingestion of felsic grains and avoidance of mafic grains in relation to the host substrate composition.

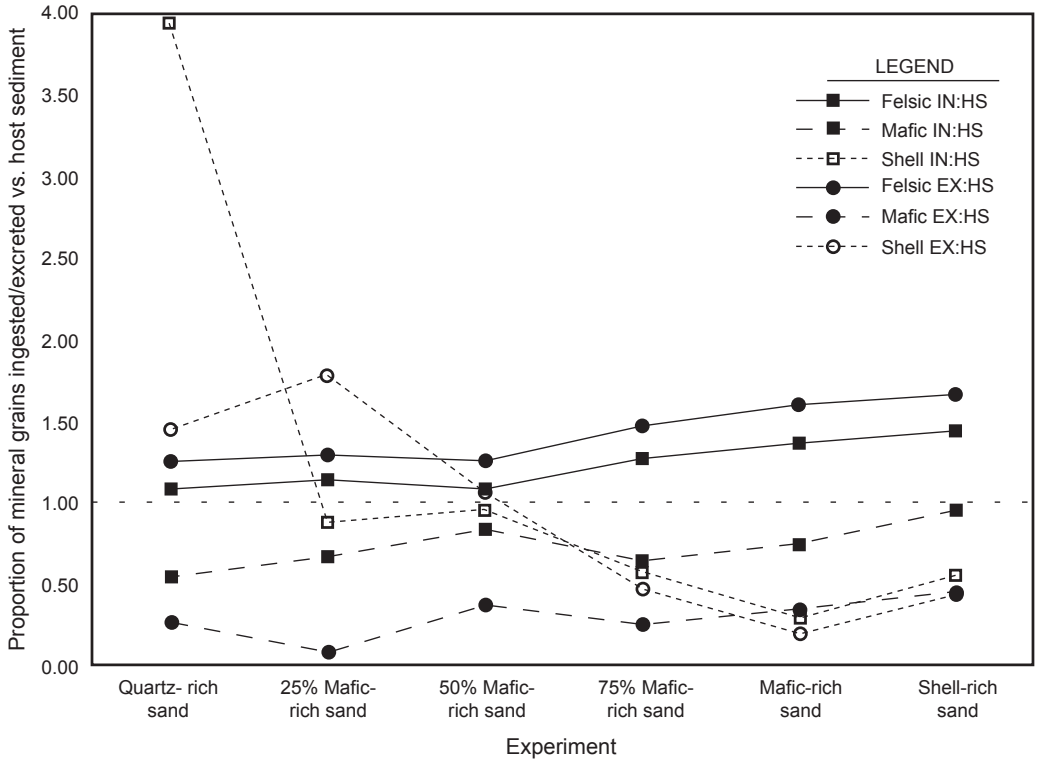

FIGURE 4.8—The proportions of ingested versus host sediment abundances and excreted versus host sediment abundances of felsic, mafic and shell grains in the substrate experiments (see Table 3). These ratios represent normalization of the video grain counts to the original mineralogical compositions of the sediment. Ratios greater than one indicate that the particular grain type is more concentrated in the ingestion or excretion episodes than in the host sediment. Based on the ratios, felsic grains are preferentially ingested while mafic grains are preferentially avoided.

DISCUSSION

Before the process of mineral segregation can be interpreted, variation in the abundance of mafic grains ingested as compared to excreted must be addressed. This observation is at odds with the expected trend – equal proportions of ingested and excreted mafic grains. This anomaly in the data cannot be refuted simply through observational bias or the explanation that different worms were observed for ingestion and excretion events, as the deviation is overwhelmingly systematic. Other possible explanations include a longer gut residence time for mafic grains. However, a string of mafic grains was never observed following excretion of the predominantly felsic burrow infill. The deviation may be explained by hydraulic winnowing or some form of sorting that is accomplished by the pygidium. Perhaps mafic grains are sorted within the gut such that they

are found near the top of the worm body and are excreted above the observable stream of felsic grains. This anomaly in the data cannot be easily explained; however, the data remains useful for interpreting general trends in mineral segregation.

Mechanisms of Mineral Segregation

A range of processes have been postulated to explain the process of mineral-grain segregation by *Macaronichnus segregatis* trace-makers. Clifton and Thompson (1978) proposed that chemoreceptors and nuchal organs in the head of *Ophelia limacina* aid in food detection, and in response to this detection, unwanted grains are shunted along the ventral groove of the worm. The rejection of angular grains (such as feldspar) by feel was proposed by Gingras et al. (2002) for *Euzonus mucronata*. However, Nara (1994) found greater proportions of angular and subangular grains in the burrow fills of *M. segregatis* as compared to the surrounding material. The avoidance of mafic grains may also be a function of the specific gravity or shape of the grains (Nara, 1994). Localized liquefaction of the sediment through proboscis eversion may serve to sort mineral grains by their specific gravity (cf. Jumars et al., 2007). This may explain thicker basal mantles observed with some examples of *Macaronichnus* (e.g., Clifton and Thompson, 1978; Savrda and Uddin, 2005).

Regardless of the surface texture, specific gravity, angularity, or nutritive value, individual particle selection or localized sediment liquefaction by the proboscis was not observed in the video of *Euzonus mucronata*. The lobate morphology of the proboscis does not allow for individual grain selection (Fig. 4.9). Conversely, the worms gather and ingest mineral grains en masse. If grains are ingested en masse, then ingested proportions of felsic, mafic and shell grains must primarily depend upon the local concentrations at the feeding site. Ingested proportions must depend upon local concentrations as the normalizations illustrate unequal proportions of ingested versus host sediment abundances. The ingestion locations are selectively chosen by the polychaetes through sediment probing by the head. The location the worms select is interpreted to reflect the identification of more felsic-rich locales. Gingras et al. (2002) also observed this non-random direction of feeding chosen by individual *E. mucronata*. What sort of sensory organs, if any, are associated with this probing are unknown. Speculation on sensory organ functionality has included the ability to identify geochemical or



FIGURE 4.9—The everted proboscis of *Euzonus mucronata*. Note that the large lobate structures do not have the capacity to select individual grains.

biological traces on minerals (Gingras et al., 2002). The underlying process by which *E. mucronata* segregate mineral grains in this study is a result of en masse site-selective feeding in more felsic-rich locales.

In addition to site selection of felsic-rich locales, partitioning of minerals is augmented by the pendular (back-and-forth) pygidium motion and rotation of platy grains. In this study, these mechanisms are effective in the segregation of shell fragments. The back-and-forth motion of the pygidium and compaction of the backfill were suggested by Gingras et al. (2002) to contribute to grain alignment perpendicular to the burrow axis. This grain alignment occurs with platy shell fragments that are easily moved to burrow boundaries by the mechanical shuffling produced by pendular motion. Large, platy shell fragments are also tangentially aligned to the burrow mantle as the worms move through sediment. Analogous tangential arrangement of mica flakes around *Ophelia limacina* burrows was reported by Clifton and Thompson (1978), and tangentially oriented micas around "*Planolites*" (now identified as *Macaronichnus*) were also described by Heinberg (1974). The pendular pygidium motion and rotation of grains contributes to the mantling of *Euzonus mucronata* burrows by shell fragments, but does not appear to affect the segregation of felsic or mafic grains.

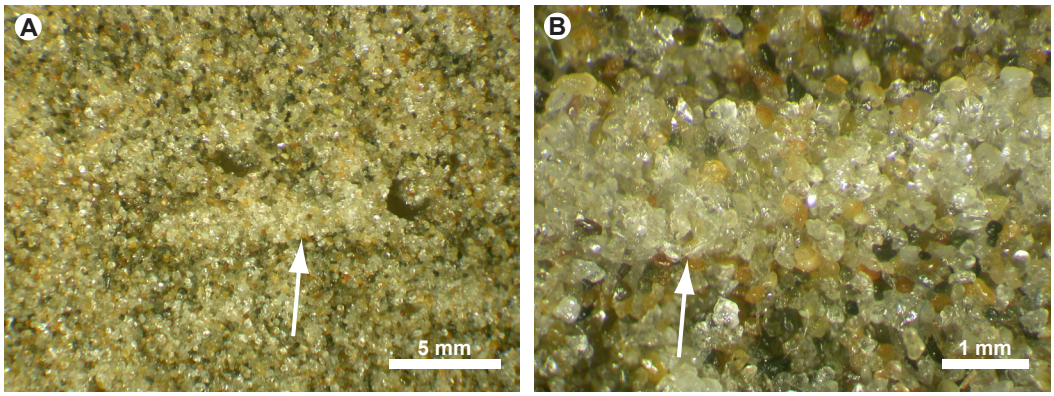

FIGURE 4.10—Sediment peels from Copalis Beach, Washington, USA (Courtesy of T.D.A. Saunders). The sediment from Copalis Beach contains no shell fragments and is composed of quartz, feldspar, lithic, and mafic grains. Segregation of quartz from lithic and mafic grains is more pronounced in this example. Arrows indicate the burrow fills from the surrounding mafic-rich sediment.

Well-segregated mantles and infills in typical *Macaronichnus segregatis* are unlikely explained by the site selection of more felsic-rich locales and en masse ingestion of grains. Limitations and distinctive features of the experiment could have resulted in the specific mineral segregation mechanism observed. The worms were only observed from the underside (base of the petri dish) and could not be easily observed from the top or side. Stress may also have played a factor, as the polychaetes were placed in shallow sediment layers under direct light. More importantly, the worm population and sediment characteristics at Pachena exhibit distinctive attributes. *Euzonus mucronata* is a particular species of opheliid, which can only be used as an analogue to other *Euzonus* species, opheliid polychaetes in general, and similar ancient organisms. Other worm species and genera possess varied specialized organs or adaptations that may produce mineralogical segregation through different processes. The sediment at Pachena is also slightly finer than most beaches characterized by *M. segregatis*-like trace-makers. Compositionally, there is an abundance of shell fragments that are generally absent from sediment in which *M. segregatis*-like structures are formed. For example, Copalis Beach on the Washington Coast (USA) is composed of quartz, feldspar, lithic fragments and mafic grains. *Euzonus* burrow fills are notably quartz-rich while the host sediment has abundant lithic and mafic grains (Fig. 4.10). The sediment at Copalis Beach is also very well sorted, and tangential alignment of grains is not observed. In this case, *Euzonus* burrows display pronounced segregation between mafic and felsic material.

The presence of shell fragments in Pachena Beach sediment increases the complexity of mineral segregation such that avoidance of mafic grains is masked by the mantling of burrows by shell fragments. Accordingly, in contrast to typical *Macaronichnus segregatis*, the *Euzonus* burrows exhibit an inverted coloration contrast; the mantle is lighter in color than the felsic burrow infill. Shell fragments are distinctive from other mineral grains as they possess a low specific gravity and are platy, more angular, and occasionally larger than the average grain size. As indicated in the normalizations (Table 4.3), shell fragments are increasingly avoided with increasing abundance. Perhaps shell fragments are more likely to become lodged in the gut, or are smooth and therefore coated with sparse nutrients in comparison to other mineral grains. It is theorized here that partitioning of shell fragments at Pachena may be a result of grain shape and size or surface texture and associated nutritive value, however, further study is required to assess the purpose of shell material segregation.

Site selectivity of more felsic-rich locales is one possible mechanism used in the formation of *Macaronichnus segregatis*; however, the function of this mineral segregation is still uncertain. The preferential ingestion of felsic grains may be associated with favorable nutrient coatings on these grains. The removal of grains prior to ingestion due to a lower nutritive value (and associated smooth surface texture) was proposed by Saunders (1989) for *E. mucronata* and by Clifton and Thompson (1978) for *Ophelia limacina*. Increased bacterial coatings typically occur in areas of high relief such as fissures, crevices, cleavage ledges and concave abrasions (DeFlaun and Mayer, 1983). In laboratory experiments, ampharetid polychaetes and spionid polychaetes have been shown to ingest particles based on surface texture; etched beads are preferentially chosen over smooth beads (Self and Jumars, 1978). However, studies by Kemp (1985, 1986, 1987) suggest that organic matter, both dissolved and particulate, rather than bacteria, is the major food source for *E. mucronata*. The adherence of organic material to sand as a function of grain surface textures has yet to be determined. Analysis of food particle adherence and opheliid sensory functions are potential future studies required to further describe behaviors of *Macaronichnus segregatis* trace-makers.

CONCLUSIONS

The product of *Euzonus* deposit feeding is a burrow that reflects mineralogical segregation between the infill and mantle similar to that of ancient *Macaronichnus segregatis*. This modern analogue was studied using microscopic videotaping in which felsic, mafic and shells grains were counted during ingestion and excretion events in various substrates and with various worm sizes. Normalization of the video grain counts (for the various substrate types) to the host sediment composition emphasizes a preferential ingestion of felsic grains and avoidance of mafics. This preferential ingestion is accomplished by probing with the head to identify more felsic-rich locales, which become the site of ingestion.

The preferential ingestion of felsic grains over mafic is, however, masked by the presence of distinctive shell fragment mantles. Shell fragments appear to be more readily avoided with increasing abundance in the host sediment. Two mechanisms that directly influence the mantling of *Euzonus mucronata* structures by shell fragments include pendular pygidium motion and tangential rotation of grains. These shell fragment mantles contrast with that of typical *Macaronichnus segregatis* traces, which are characterized by distinctive mafic- and mica-rich mantles. The preservational potential of Pachena Beach *Euzonus* burrows is relatively low due to the nature of the mantle. Shell fragments would likely be dissolved during diagenesis, and the subordinate segregation of mafic minerals would likely be insufficient to define the burrow structures. However, a rock containing this seemingly homogenized fabric could possess enhanced porosity and permeability as a result of dissolution and the indiscernible burrow network.

The characteristic nature of the structures observed in this study are a result of the examined polychaetes (species) and sediment (size and mineralogical composition) used in the experiments. Mineralogical segregation of shell fragments at Pachena is theorized to be a function of grain size and shape or surface texture and associated nutritive value. The site selection of felsic-rich locales and en masse ingestion of grains is only one possible mechanism used in the construction of *Macaronichnus segregatis*. This mechanism cannot likely explain the distinctive mineral segregation observed in typical *M. segregatis*. Individual particle selection by the proboscis was not observed and is thought to be nearly impossible based on the morphology of the organ. However, other mechanisms such as localized sediment liquefaction by proboscis eversion (cf. Jumars et al., 2007) or enhanced felsic particle adherence to the proboscis due to

bacterial or other coatings (e.g., Jumars et al., 1982; Taghon, 1982) may play a role in the formation of *M. segregatis* and *M. segregatis*-like structures. Analysis of the nutritive value of grains and sensory perception of opheliid polychaetes in more typical sediment would allow for improved understanding of *M. segregatis* construction and the purpose for mineralogical segregation.

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CHAPTER 5 – AN UNORTHODOX TAXONOMIC APPROACH USING GRAIN SORTING AND COLLECTIVE ICHNOFOSSIL MORPHOLOGY IN DEFINING *MACARONICHNUS* AND *HARENAPARIETIS* NEW ICHNOGENUS

INTRODUCTION

Ichnotaxonomy is an important aspect of ichnology that aims to enhance communication between ichnologists by defining reoccurring structures that record the activity of organisms. Traditional ichnotaxonomy is based upon defining traces that are morphologically distinctive (cf. Ekdale et al., 1984). However, the lack of a consistent scheme for determining the significance of particular morphological criteria has resulted in different prioritizing for naming ichnogenera and ichnospecies (cf. Bertling et al., 2006). Bromley (1990) suggested the use of ichnotaxobases or typical morphological features used as a basis for ichnotaxonomy. Subsequently, Bertling et al. (2006) asserted that trace fossil taxonomy requires a "uniform approach" that is independent of ethology. Bertling et al. (2006) further suggested that morphology was the most important criterion for defining ichnotaxobases; however, the same authors suggested possible exceptions such as substrate (e.g., bioerosional structures) and composition (e.g., coprolites). In general, size, producer, age, facies and preservation are not viable ichnotaxobases for defining trace fossils (cf. Bertling et al., 2006). The following chapter illustrates that a "uniform approach" may not be ideal for all forms of trace fossils. In addition, ethology may not always be neatly separated from trace fossil taxonomy. This chapter outlines a taxonomic methodology used to define two ichnogenera—*Macaronichnus* and *Harenaparietis* n. ichnogen.—that fail to fit into a "uniform approach" and necessitates the inclusion of some ethological aspects of the structures (Fig. 5.1).

The ichnogenus *Macaronichnus* Clifton and Thompson, 1978 is defined as unlined, non-branching, cylindrical burrows that are characterized by light-colored sand infills mantled by dark grains in which burrow components reflect segregation of grains comprising the host sediment (Figs. 5.2-5.4). This ichnogenus was first recognized and established by Clifton and Thompson

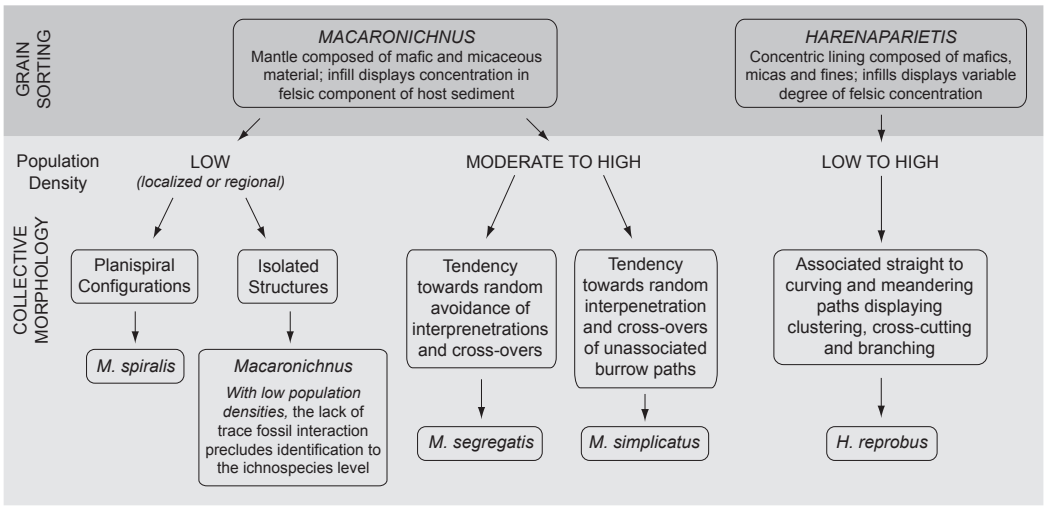

FIGURE 5.1—The main ichnotaxobases used to differentiate *Macaronichnus* ichnospecies and *Harenaparietis* n. ichnogen.

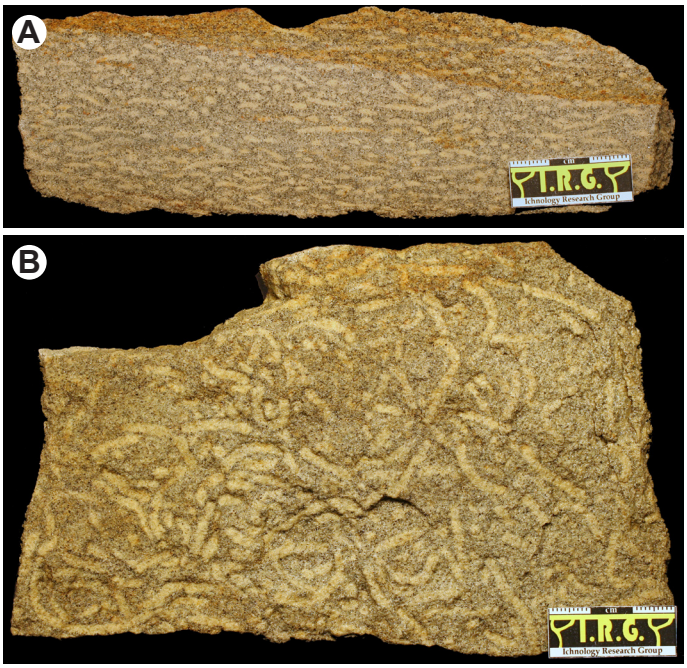

FIGURE 5.2—Paratype specimens of *Macaronichnus segregatis* Clifton and Thompson (1978) from the Horseshoe Canyon Formation of Alberta, Canada. **A:** Cross-sectional view of the traces exhibiting an overall tendency towards avoidance of interpenetration. **B:** Plan view of the structures, which display a general avoidance of interpenetration identified as mantles separating adjacent traces. Specimens TF020 and TF021 on storage at the University of Alberta, Edmonton, Alberta, Canada.

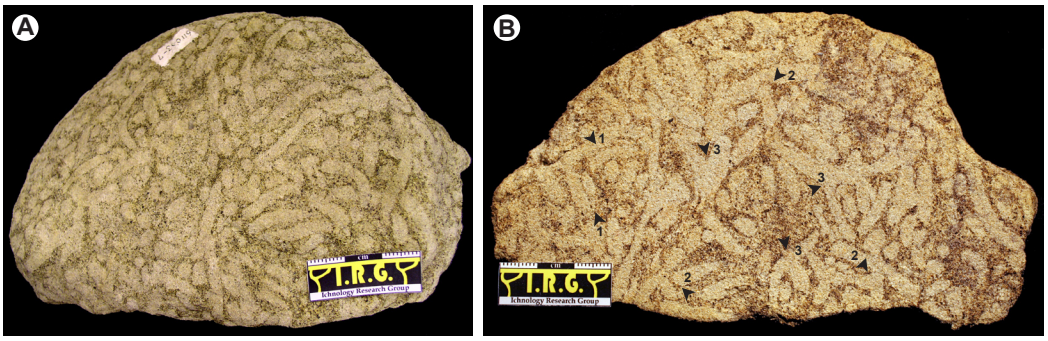

FIGURE 5.3—Holotype specimen of *Macaronichnus simplicatus* n. ichnosp. from the Painted Rock Sandstone Member of the Vaqueros Formation (Miocene). **A:** Oblique view of the traces. **B:** Plan view of the biogenic structures that exhibit common interpenetration where mantle material has been removed between intersecting structures. Arrows point to locations of intersection of structures (1=overlapping, 2=cross-cutting, 3=false branching). This specimen is on storage at the University of Alberta, Edmonton, Alberta, Canada (TF023).

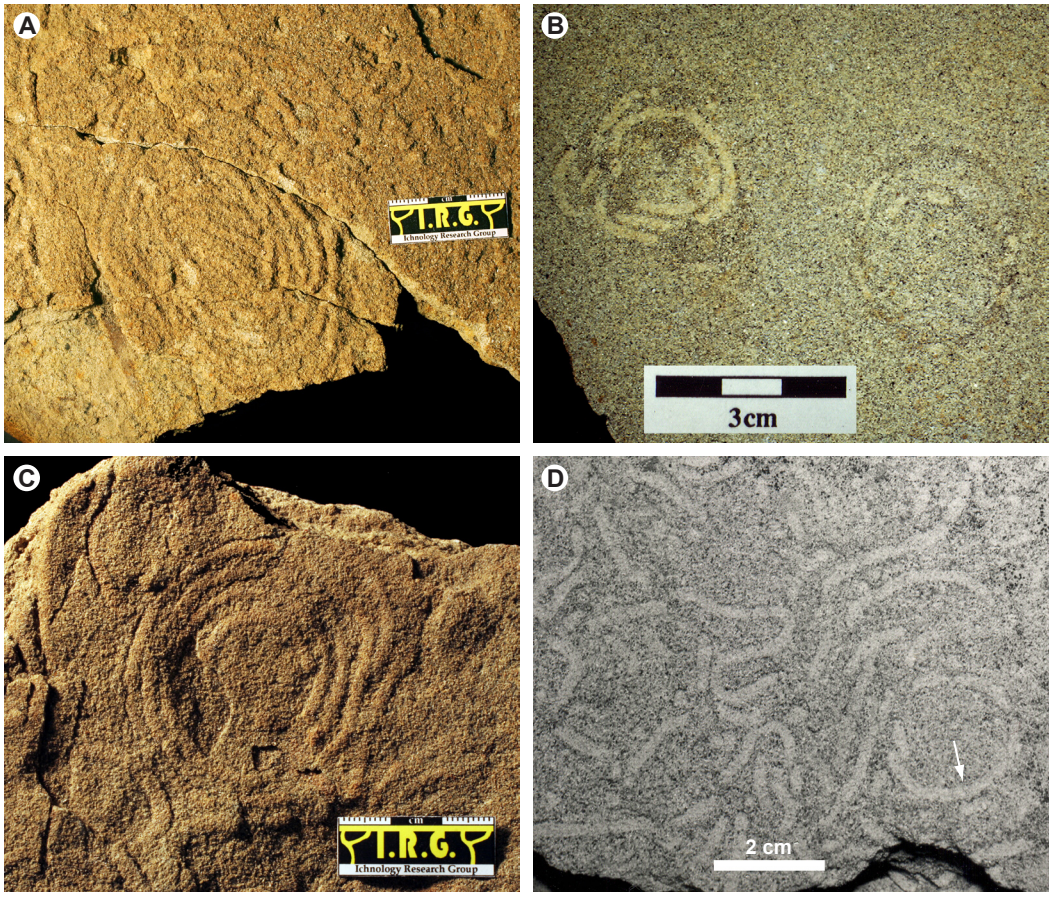

FIGURE 5.4—*Macaronichnus spiralis* n. ichnosp. from the Horseshoe Canyon Formation of Alberta, Canada. **A, C:** Holotypes of *M. spiralis* which display endmember perfect spiral forms with multiple coils. Specimens TF024 and TF025 on storage at the University of Alberta, Edmonton, Alberta, Canada. **B:** Irregular forms of *M. spiralis* in which spirals are incomplete and nested. **D:** *M. spiralis* characterized by a single coil (indicated by the white arrow), which occurs in conjunction with *M. segregatis* on a bedding plane surface.

(1978) from Jurassic and more recent examples. The defining characteristic of this ichnofossil is the segregation of mineral grains between the mantle and infill through modification of the host sediment. This diagnostic attribute is not a typical morphological criterion used for defining a trace fossil, which generally includes: overall shape, orientation, ornamentation and internal structure (cf. Bertling et al., 2006). Accordingly, it is proposed here that grain sorting be included as a viable ichnotaxobase as this is the primary feature differentiating these cylindrical, non-branching burrows from traces such as *Planolites*. Ethologically, the segregation of mineral grains is inherently linked to specialized deposit-feeding strategies that take place during active backfilling of burrow structures. This specialized deposit feeding reflects the primary form of foraging optimization exhibited by *Macaronichnus* trace-makers.

Clifton and Thompson (1978) defined the ichnospecies *M. segregatis* (Fig. 5.2), which was reassessed by Saunders and Pemberton (1988) and Saunders (1989) in addition to their proposal of two additional ichnospecies of *Macaronichnus—M. simplicatus* (Fig. 5.3) and *M. spiralis* (Fig. 5.4)—based on analysis of strata in the Drumheller area of Alberta, Canada. The use of these ichnofossil names has been strictly informal as diagnosis of the ichnogenus and ichnospecies has not been formally documented until recently. Bromley et al. (2009) introduced three new ichnosubspecies of *M. segregatis* as well as presented a formal diagnosis of the ichnogenus. However, the ichnosubspecies approach does not recognize characteristic and recurring burrow interrelationships that are useful in classifying occurrences of *Macaronichnus*. These characteristic burrow interrelationships occur within densely populated strata in which the relationship between traces is the most striking and the most viable means of differentiating ichnospecies.

In addition to the unique basis for defining the *Macaronichnus* ichnogenus, the taxonomic approach for defining ichnospecies follows that of Saunders and Pemberton (1988) and Saunders (1989) whereby ichnospecies are defined upon interactions between traces reflecting particular behavioral adaptations. As suggested by Bertling et al. (2006), the shape component of morphology may not always be the most relevant ichnotaxobase. In the case of *Macaronichnus* ichnospecies, the shape of individual burrows is not as important as the interaction between a group of burrows which produces an overall fabric. Due to the complex burrow geometries in such examples, the morphology of individual burrow structures are not readily apparent (e.g., Clifton and Thompson, 1978; Koyama,

1983; Ainsworth, 1994; Pemberton et al., 2001; Gingras et al., 2002; Fielding et al., 2007; Komatsu et al., 2008). These fabrics reflect a reoccurring collective morphology within assemblages rather than with individual traces. This collective morphology is expressed as a tendency towards avoidance of interpenetration of adjacent burrow structures in *M. segregatis* and, conversely, a tendency towards interpenetration of traces with *M. simplicatus* (Fig. 5.1). As such, the collective morphology is a direct expression of the systemized group interactions or behavior of the causative trace-makers. Variation in behavior reflects the secondary aspect of foraging optimization exhibited by *Macaronichnus*: a tendency towards interpenetration reflects no adaptations towards maximizing foraging efficiency while avoidance illustrates a more advanced foraging strategy. Bertling et al. (2006) suggested that criteria resulting from behavior formed the important ichnotaxobases while physical, chemical and sedimentological factors should be excluded. It is proposed here that behavior expressed in systematized group interactions produces a collective morphology that should also be considered a valid or pertinent ichnotaxobase for such examples of densely packed ichnofossils.

The above classification reflects a dynamic taxonomy in which most occurrences of *Macaronichnus* can be identified to the ichnospecies level in dense populations at the scale of core and outcrop. However, not every example of *Macaronichnus* is characterized by a dense association of traces. On bedding plane surfaces, *M. spiralis* occurs as distinctive planispiral configurations of variable perfection (Fig. 5.4) that may be localized amongst beds containing *M. segregatis* and/or *M. simplicatus*. This planispiral form exhibits the most advanced form of secondary foraging optimization whereby available space permits localized feeding of untouched sediment. Except in the case of *M. spiralis*, the identification of ichnospecies is problematic with sporadic occurrences of *Macaronichnus* as a result of a paucity in systematized group interactions (Fig. 5.5; e.g., Ranger et al., 1988, fig. 6a-d; Bergman, 1994, fig. 8; MacEachern, 1994, fig. VI-7g, h; Campbell and Nesbitt, 2000, fig. 7f, g; Savrda, 2002, figs. 1-3; Uchman and Krenmayr, 2004, fig. 7; MacEachern et al., 2005, figs. 4b, f, g, 6c, 9j). However, the distinctive mineralogical segregation is diagnostic, and it is proposed here, that isolated occurrences be identified as belonging to the *Macaronichnus* ichnogenus.

In addition to the *Macaronichnus* ichnogenus, another cylindrical, horizontal to inclined ichnofossil has been identified as a mineralogical

modification of the host sediment. This ichnofossil has been commonly identified as *Macaronichnus* or *Palaeophycus*, and was first recognized by Saunders et al. (1994) as a "unique form of *Macaronichnus*" that was unusually large with comparatively thick mantles. Despite the similarity of these biogenic structures to *Macaronichnus*, the proposed ichnotaxobases can be used to segregate this unique form from the *Macaronichnus* ichnogenus. This form is herein referred to as *Harenaparietis* n. ichnogen., which is also primarily defined upon segregation of host sediment components. This new ichnogenus is lined with darker mineral grains in conjunction with available silt and clay material. Segregation of fines in addition to heavy mineral grains and micas is an apparently minor distinction between *Harenaparietis* and *Macaronichnus*. However, it is the nature of the burrow components and systematic organization of the traces that separates this ichnogenus from *Macaronichnus*. Similar to *Macaronichnus*, *Harenaparietis* reflects subsurface deposit feeding and defecating; however, the burrows are lined rather than mantled and remain open for short periods of time prior to backfilling. In contrast, *Macaronichnus* is specifically defined as structures formed through active backfilling during deposit-feeding activities. The collective morphology also differs from that of *Macaronichnus*—traces tend to be clustered, cross-cut one another, and locally branch. Ethologically, *Harenaparietis* reflects a unique behavior in which successive probing of adjacent sediment packages occurs, such that a burrow is constructed and subsequently irregularly backfilled prior to being cross-cut by a later burrow.

The unorthodox means of delineating ichnofossils using mineralogical segregation and collective morphology falls outside the "uniform approach" suggested by Bertling et al. (2006). In addition, ethology cannot be fully segregated from this taxonomy as collective morphology is an integral expression of the organisms' behavior. In the case of the *Macaronichnus* and *Harenaparietis* ichnogenera, these newly proposed ichnotaxobases serve to identify the key components of these traces that distinguish them within the ichnotaxonomic system. The following systematic ichnology serves to: 1) present comprehensive revised diagnoses highlighting the complexity of the *Macaronichnus* ichnogenus and the distinguishing characteristics inherent to each ichnospecies; and 2) define the unique and varied expressions of the *Harenaparietis* ichnogenus.

SYSTEMATIC ICHNOLOGY

Macaronichnus Clifton and Thompson, 1978

Figures 5.2-5.6, 5.9, 5.12, 5.15

Macaronichnus Lockley, Rindsberg and Zeiler, 1987, fig. 2b; Moslow and Pemberton, 1988, fig. 7b; Saunders and Pemberton, 1988, p. 129-133, text-fig. 34; Fillion, 1989, text-fig. h; Saunders, 1989, p. 118-119, text-fig. 32; Ainsworth, 1992, fig. 46; Bradley and Pemberton, 1992, fig. 11d; Raychaudhuri and Pemberton, 1992, fig. 6f; Al-Rawahi, 1993, fig. 4.7b; Pollard, Goldring and Buck, 1993, fig. 8a, b; Walker and Bergman, 1993, figs. 17, 20, 22; Ainsworth, 1994, fig. 23b; Bergman, 1994, fig. 8; MacEachern, 1994, figs. IV-4b, V-8f, VI-7g, h, VI-10c, d; Saunders, MacEachern and Pemberton, 1994, p. 339, fig. 5b, f; Brekke, 1995, p. 83, figs. 21c, 22a; Keighley and Pickerill, 1995, text-fig. 2e; Ruffell and Wach 1998, table 1; Campbell and Nesbitt, 2000, fig. 7f, g; Obata, 2000, p. 34-35, fig. 4d, e; Bhattacharya and Willis, 2001, fig. 10f; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, text-figs. 93, 94, 107; Savrda, 2002, figs.1-3; Earle, 2003, p. 81, fig. 2.17b; Hobbs, 2003, figs. 3.2a, 3.3c, f, 5.1d; Savrda, 2003, paper no. 24-16; Bann and Fielding, 2004, p. 294, 299, figs. 7d, 8e, 13b, 14c; MacEachern and Hobbs, 2004, fig. 13b; Pemberton and Gingras, 2005, p. 1502, fig. 10; Savrda and Uddin, 2005, p. 3-4, fig. 1; Gibert, Netto, Tognoli and Grangeiro, 2006, p. 72, fig. 4b; Cavazza, DeCelles, Fellin and Paganelli, 2007, fig. 8h; Coates and MacEachern, 2007, figs. 13d-h, j, 18g, k; Fielding, Bann and Trueman, 2007, figs. 10d, 11d, 12c, 21a, 22a, c, e, 25a-c; Gingras, Pemberton, Henk, MacEachern, Mendoza, Rostron, O'Hare, Spila and Konhauser, 2007, fig. 8; Hansen and MacEachern, 2007, fig. 6a, d; Kotake, 2007, p. 498, figs. 30.5, 30.6; MacEachern, Pemberton, Bann and Gingras, 2007, figs. 7a, b, g, 10d, f; Pemberton, MacEachern, Gingras and Saunders, 2007, fig. 2a; Savrda, 2007, p. 102-103, fig. 6.11b; DesRoches, 2008, fig. 3.1.3g; Hoffman, 2008, figs. 2.9b-d, 2.12a, b; Komatsu, Ono, Naruse and Kumagae, 2008, fig. 6f; Pemberton, MacEachern, Gingras and Saunders, 2008, p. 278, figs. 2, 5.

Macaronichnus segregatis Clifton and Thompson, 1978, p. 1293-1295; Dupré, 1984, p. 441, fig. 3f; Hunter, Clifton, Hall, Császár, Richmond and Chin,

1984, p. 9, fig. 16; Clifton, 1988, p. 517, fig. 13; Saunders and Pemberton, 1988, p. 132-133, figs. 26b, 27a-c, e, text-fig. 29; Saunders, 1989, p. 124-125, fig. 24b, 25a-c, e; MacEachern and Pemberton, 1992, figs. 5d-f, 6c, e, f; Walker and Bergman, 1993, p. 844-845; MacEachern, 1994, figs. V-8d, e, V-9c, e, f, VI-10e, f, VI-11a-c, text-fig. VI-12; Nara, 1994, p. 9, text-fig. 3, fig. 4; Brekke, 1995, p. 83, fig. 32a-d; Martini, Cascella and Rau, 1995, fig. 11a, b; Bromley, 1996, p. 170, 204, 263; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103, figs. 104a-c, e, 106, 145, 152b; Gingras, MacMillan, Balcom, Saunders and Pemberton, 2002, p. 553, fig. 2; Hobbs, 2003, figs. 3.5a, b, e, 3.6a, c, 3.8c-e; Tamura, Masuda, Sakai and Fujiwara, 2003, fig. 7e; Schmidt and Pemberton, 2004, fig. 4a, b; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 7g; Pemberton and Gingras, 2005, fig. 9a; Dafoe, Gingras, Saunders and Pemberton, 2006, p. 78; Le Roux, Olivares, Nielsen, Smith, Middleton, Fenner and Ishman, 2006, p. 145; D'Alessandro and Uchman, 2007, p. 214-215, fig. 3b; DesRoches, Thompson and MacEachern, 2007, fig. 3c; Fielding, Bann and Trueman, 2007, fig. 12b, e; Hansen and MacEachern, 2007, fig. 6e; Pemberton, MacEachern, Gingras and Saunders, 2007, fig. 2c; Seike, 2007, p. 497-498; Dafoe, Gingras and Pemberton, 2008a, p. 91, fig. 1; Dafoe, Gingras and Pemberton, 2008b, p. 79, fig. 1; DesRoches, 2008, figs. 3.1.4f, 3.1.8e, f; Kamada, 2008, figs. 2-4; Pemberton, MacEachern, Gingras and Saunders, 2008, p. 278, figs. 6a, 7b; Tamura, Murakami, Nanayama, Watanabe and Saito, 2008, fig. 7c.

Macaronichnus segregatis lineiformis Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 117, fig. 4b (=*Macaronichnus segregatis*); Bromley, Milàn, Uchman and Hansen, 2009, figs. 4c, 5b, 6b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis maeandriformis Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 117, fig. 5a (=*Macaronichnus*); Bromley, Milàn, Uchman and Hansen, 2009, p. 105, figs. 5b, 6a, b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis segregatis Saunders, 1989, p. 124-125, text-fig. 27; Bromley, Milàn, Uchman and Hansen, 2009, p. 116-117 (=*Macaronichnus segregatis*).

Macaronichnus segregatis spiralis Saunders and Pemberton, 1988, p. 133, fig. 27b, d, f, g, text-fig. 29; Saunders, 1989, p. 125, fig. 25b, d, f, g, text-fig. 27

(=*Macaronichnus spiralis*).

Macaronichnus segregatis spiriformis Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 117, fig. 7 (=*Macaronichnus spiralis*).

Macaronichnus simplicatus Saunders and Pemberton, 1988, p. 133, text-fig. 29, pl. 11, figs. 1-5, 7; Saunders, 1989, p. 125, text-fig. 27, pl. 11, figs. 1-5, 7; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 3c.

Macaronichnus spiralis MacEachern and Pemberton, 1992, fig. 6d; MacEachern, 1994, fig. V-9d, text-fig. VI-12; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103, fig. 104b, d, f, g; Minter, Buatois, Lucas, Braddy and Smith, 2006, p. 1058.

non *Macaronichnus* MacEachern, 1994, fig. IV-4g, h; Saunders, MacEachern and Pemberton, 1994, p. 339, fig. 6b; Brekke, 1995, p. 83, figs. 18, 21d, 22a-d, 34a, 36a, b; Hubbard, 1999, fig. 2.18d; Hubbard, Pemberton and Howard, 1999, fig. 18d; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, figs. 95b, 106; Hobbs, 2003, figs. 3.2f, 6.2; Bann and Fielding, 2004, p. 291, 293, 294, 296, 299, figs. 7b, c, 8a-c, 9b, c, e, 10a, c-e, 13b, 14d; Hubbard, Gingras and Pemberton, 2004, fig. 8g; Fielding, Bann and Trueman, 2007, figs. 10a, 19e, 25g, h; MacEachern, Pemberton, Bann and Gingras, 2007, fig. 10b; Sadeque, Bhattacharya, MacEachern and Howell, 2007, fig. 10c (=*Harenaparietis*).

non *Macaronichnus* Fillion and Pickerill, 1990, p. 48 (=?), Caplan and Bustin, 2001, fig. 7d (=cryptobioturbation); Bann and Fielding, 2004, fig. 4c (=?*Asterosoma*); Fielding, Bann and Trueman, 2007, fig. 19a (=?*Palaeophycus*); Fielding, Bann and Trueman, 2007, fig. 19i (=?); Ocampo-Díaz, Jenchen and Guerrero-Suastegui, 2008, fig. 14d (=?).

non *Macaronichnus segregatis* Curran, 1985, p. 263-264, pl. 1, fig. b-d, pl. 2, fig. a; Maples and Suttner, 1990, p. 870, figs. 12.1, 12.9, text-fig. 13; Tamura and Masuda, 2005, p. 1383, fig. 7c (=*Harenaparietis*).

non *Macaronichnus segregatis* Hunter and Clifton, 1982, p. 135, fig. 4c; Orr, 1995, p. 272-274; Głuszek, 1998, p. 532-533, fig. 11a, b (=?*Harenaparietis*).

non *Macaronichnus segregatis* Clifton and Thompson, 1978, fig. 3; Fürsich and Heinberg, 1983, p. 95, text-fig. 7ii; DeCelles, 1987, p. 253, 255, fig. 5c; Ranger, Pemberton and Sharpe, 1988, p. 456, fig. 6a-d; Knaust, 2004, p. 14, fig. 6.5, 6.6; MacEachern and Hobbs, 2004, figs. 13a, 15b; Uchman

and Krenmayr, 2004, p. 238, fig. 7; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 4b; Tamura and Masuda, 2005, p. 1383, fig. 7e; D'Alessandro and Uchman, 2007, fig. 4c, d, f; Tamura, Nanayama, Saito, Murakami, Nakashima and Watanabe, 2007, fig. 6f; DesRoches, 2008, fig. 3.1.5d, g; Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 107, fig. 4a (=*Macaronichnus*).

non *Macaronichnus segregatis* Clifton and Thompson, 1978, p. 1293-1295, figs. 1, 2; Clifton, 1981, p. 170-171, fig. 9; DeCelles, 1987, p. 253, 255, fig. 5d; Bann and Fielding, 2004, fig. 6e; Johnstone, Mustard and MacEachern, 2006, fig. 6c (=*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Bromley, 1996, fig. 11.9 (=?*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Hunter, 1980, fig. 3b; Nadon, 1988, p. 49-50, fig. 25; Pollard, Goldring and Buck, 1993, p. 153, 161-162, fig. 4a-c; Carmona, Buatois, Mángano and Bromley, 2008, p. 101-102, figs. 4.6, 4.7 (=*Macaronichnus simplicatus-segregatis*).

non *Macaronichnus segregatis* Fürsich, 1984, p. 331, fig. 3b, text-fig. 10 (=?*Anconichnus*); Male, 1992, figs. 6a-c, 12c (=cryptobioturbation); Rigsby, 1994, fig. 12a (=?*Palaeophycus*); Orr and Howe, 1999, p. 37-38, fig. 3a, b (=?*Palaeophycus*); Bridges and Castle, 2003, table 2, fig. 4e (=?); Zhensheng, Xiaomin, Bin and Xilin, 2004, p. 207-208, fig. 3 (=*Palaeophycus*), figs. 4.1, 4.2, 4.4-4.6, 6 (=?*Chondrites*).

non *Macaronichnus simplicatus* Raychaudhuri and Pemberton, 1992, fig. 6e; Hobbs, 2003, figs. 3.4f; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 4e; DesRoches, 2008, figs. 3.1.2g, 3.1.4d (=*Harenaparietis*).

non *Macaronichnus simplicatus* MacEachern, Bann, Bhattacharya and Howell, 2005, figs. 3c, 4a, f, g, 6c, e, 9j (=*Macaronichnus*); MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 3b (=*Macaronichnus segregatis*).

transitional *Macaronichnus segregatis-simplicatus* Saunders, MacEachern and Pemberton, 1994, fig. 5g (=*Macaronichnus simplicatus-segregatis*).

?*Macaronichnus* Gingras, MacEachern and Pemberton, 1998, fig. 8d (=?*Macaronichnus*); Meyer, Krause and Braman, 1998, fig. 5 (=cryptobioturbation); Kumpulainen, Uchman, Woldehaimanot, Kreuser and Ghirmay, 2006, p. 414, fig. 10c (=?).

?*Palaeophycus* Boyer and Warme, 1975, p. 85, text-fig. 9d; King, 1987, p. 39, fig. 2g.

Planolites Fürsich and Heinberg, 1983, p. 95, fig. 9.
Scoyenia sp. Chamberlain, 1978, fig. 92.
Teichichnus Bustin and Palsgrove, 1997, fig. 9b.
"burrows of Milford type" Middlemiss, 1962, p. 33-35, text-fig. 1.
"curved non-branching bedding-plane burrows" Tillman and Martinsen, 1985, fig. 17c.
"*Excirolana chiltoni* burrows" Okazaki and Masuda, 1992, fig. 15b.
"*Excirolana chiltoni japonica*" Tokuhashi and Kondo, 1989, fig. 11.
"*Excirolana chiltoni japonica* burrows" Koyama, 1983, pl. I, fig. b-d, pl. II, fig. b.
"isopod traces" Kikuchi, 1972, p. 144, pl. 1, figs. 1-4.
"mottled burrows" Hakes, 1976, p. 38, pl. 12, fig. 2.

Type species—Macaronichnus segregatis Clifton and Thompson, 1978.

Emended Diagnosis—Unlined, non-branching, cylindrical burrows of small to moderate size and variable configuration. Infills consist of structureless to weakly defined spreiten, light colored sand, generally displaying depletion in darker colored grain constituents of the host sediment. Darker grains are concentrated at the infill periphery, which forms a mantle that may be subtle. The infill/mantle junction is sharp, and the mantle/host sediment junction is gradual.

Etymology—From the Italian "macaroni," which refers to the size and shape of the structures. Segregatis is from the Latin word "segregare," which refers to the segregation of minerals between the burrow mantle and infill.

Description—Intrastratal sinuous, meandering or planispiral configurations of cylindrical to tubular burrows that typically range from 1-25 mm in diameter (Figs. 5.2-5.4). In cross-section, smaller burrows are generally circular, while larger burrows may be circular to ovate. Burrows are predominantly horizontal, although inclined and rarer vertical structures are also observed. Burrows occurring in close proximity may tend towards interpenetration (sometimes displaying false branching; Fig. 5.3) or avoidance of interpenetration of structures (Fig. 5.2). Occurrences of *Macaronichnus* range from sparse or scattered burrows (Fig. 5.5) through to densely concentrated such that the original sedimentary fabric is completely reworked (Figs. 5.2, 5.3). In 3-dimensions, burrowing varies such that small burrows may be concentrated along laminae sets in a form of

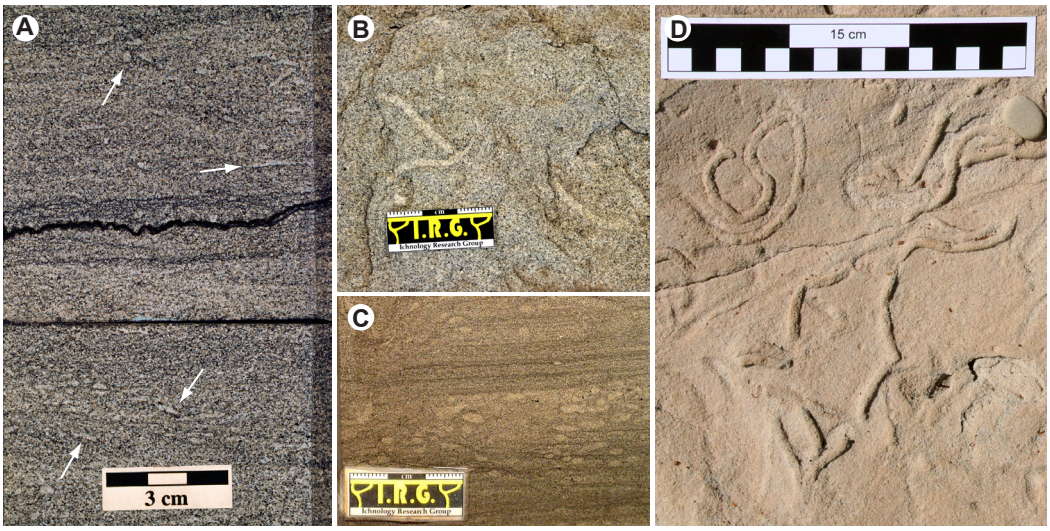

FIGURE 5.5—Low population densities of *Macaronichnus* in which isolation of the traces precludes assignment to an ichnospecies. **A:** Scattered, small *Macaronichnus* from the Cadotte Member of the Peace River Formation, northwestern Alberta. **B:** Isolated *Macaronichnus* from the Horseshoe Canyon Formation, Alberta, Canada. **C:** Small *Macaronichnus* in core with no clear tendency towards interpenetration or avoidance. From the Falher D Member of the Spirit River Formation (photo courtesy of Trevor Hoffman). **D:** Sparse *Macaronichnus* from the Freitag Formation of Queensland, Australia (photo courtesy of Kerrie L. Bann and Christopher R. Fielding).

2-dimensional foraging to preserve the general orientation of laminae through cryptobioturbation (Fig. 5.6). Burrows may also frequently penetrate multiple laminae through 3-dimensional foraging to develop a fabric reflecting a highly intertwined network (Fig. 5.4).

Macaronichnus reflects a characteristic modification of the host sediment whereby mineral grains are partitioned between the burrow infill and surrounding mantle. The infill is generally composed of quartz and may comprise lesser feldspar, chert and lithics. This burrow component may exhibit alignment of platy grains and/or contain meniscoid structures produced by backfilling. The mantle is generally comparatively dark with respect to the infill and the host sediment. Mineralogically, the mantle may be composed of a number of grain types including: micas, heavy minerals or mafics, lithics, glauconite, chert, feldspar, magnetite and limonite. The mineralogical composition of the host sediment and concordant mantle determines the prominence of the burrows, which may be subtle if the mantle and infill are similar in mineralogy or coloration. In some cases, dense *Macaronichnus* may result in obscured and amalgamated mantles such that contrasting infills and residual host sediment primarily defines the traces (Figs. 5.2, 5.3). Mantle thickness typically ranges from a few grains to

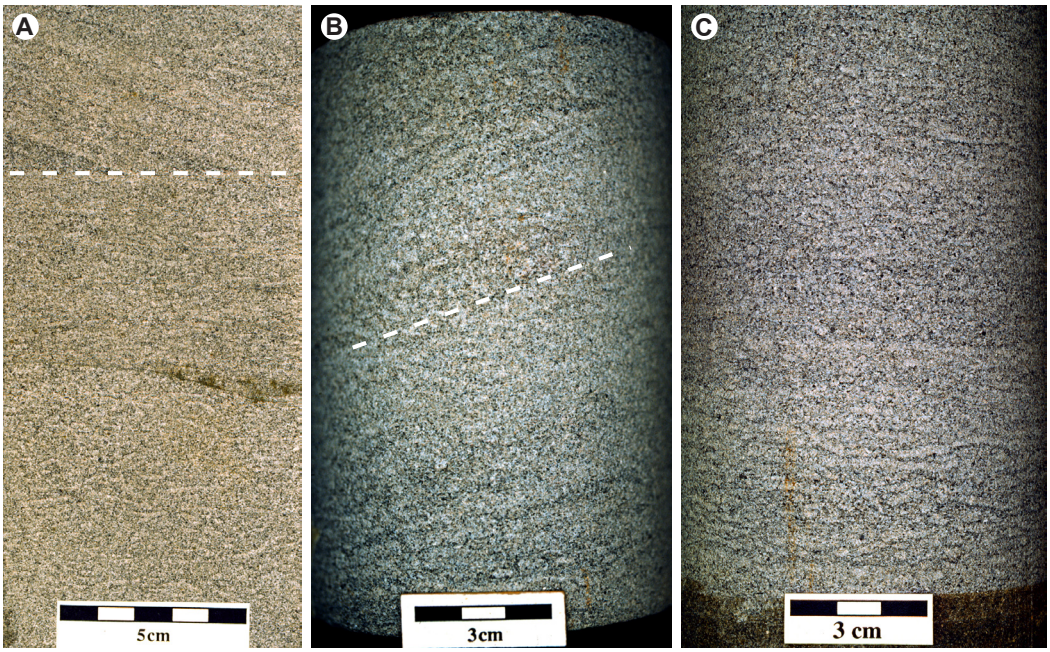

FIGURE 5.6—*Macaronichnus segregatis* exhibiting cryptobioturbation and sediment homogenization. **A:** Below the dashed line, sediment is homogenized by *M. segregatis*. Conversely, above the dashed line, cryptobioturbation by *M. segregatis* trace-makers has preserved the original cross-bedded fabric. (Bluesky Formation, well 06-32-074-12W6, 1800 m depth). **B:** Another example of cryptobioturbation in which cross beds (indicated by the dashed line) remain preserved despite the abundance of *M. segregatis*. Falher Member of the Spirit River Formation, northwestern Alberta. **C:** A less distinctive example of *M. segregatis* cryptobioturbation in which weak planar bedding is preserved. Notikewin Member of the Spirit River Formation, northwestern Alberta.

5 mm in thickness, and platy grains (especially micaceous minerals) may be tangentially aligned around burrow infills. In some instances, mantle grains may be preferentially concentrated on the underside of burrows. Typical lithological requirements for these burrows to be observed consists of coarse silt to medium-sized siliciclastic sand.

Discussion—The primary ichnotaxobase for the *Macaronichnus* ichnogenus is the distinctive mineralogical segregation between the burrow core and mantle, which reflects a modification of the host sediment. Accordingly, this ichnofossil is typically restricted to sandy sediment in which there is sufficient heterogeneities to allow for preservation of biogenic structures produced by mineralogical segregation (Saunders and Pemberton, 1988). The process of grain sorting is dependent upon ethological behaviors reflecting specialized deposit-feeding adaptations (cf. Clifton and Thompson, 1978; Saunders and Pemberton, 1988; Saunders, 1989; Nara, 1994; Gingras et al., 2002; Dafoe et al. 2008a). Fillion

and Pickerill (1990) suggested that traces possessing a lining and produced through active infilling be attributed to *Macaronichnus*. However, the mantle of *Macaronichnus* does not conform to the burrow lining of Pemberton and Frey (1982), which is associated with wall reinforcement of an open burrow structure. It is suggested here, that only traces mantled by distinctly mafic, micaceous or otherwise undesirable mineral grains, in which the mantle is formed concurrently with the infill during active backfilling, be considered within the *Macaronichnus* ichnogenus.

The presence of a compositionally distinct mantle and infill and the particular infill/mantle and mantle/host sediment junctions are sufficient to distinguish this ichnogenera from *Planolites*, *Palaeophycus*, *Muensteria*, *Ancorichnus*, and *Scoyenia*, which also possess a predominantly horizontal and cylindrical morphology. Differentiation between *Planolites*, *Palaeophycus* and *Macaronichnus* has been discussed by several authors (e.g., Clifton and Thompson, 1978; Curran, 1985; Fillion, 1989; Fillion and Pickerill, 1990; Bromley, 1996) and is briefly reviewed here. *Planolites* is an unlined trace with an infill that differs in texture from the host sediment. Sediment is processed by the trace-maker primarily through deposit-feeding activities (Pemberton and Frey, 1982). *Palaeophycus* is characterized by a distinctive burrow lining with an infill that is compositionally identical to the host sediment. This trace is typically formed through passive infilling by gravity-induced sedimentation in open, lined burrows (Pemberton and Frey, 1982). *Macaronichnus* differs from these structures in that the burrow fill is mantled rather than lined or unlined. In addition, the infill of *Macaronichnus* reflects a modification of the host sediment (Curran, 1985), which is in contrast to the infills of *Planolites* and *Palaeophycus*.

The presence of meniscate structures in some examples of *Macaronichnus* resembles other backfilled traces such as *Ancorichnus*, *Muensteria* and *Scoyenia*. The ichnofossil *Ancorichnus* reflects a distinctly lined, smooth-walled, meniscate burrow where menisci extend to, or into the wall lining (Frey et al., 1984). *Muensteria*, which is no longer considered a valid ichnogenera, was generally thought to include simple, unlined, unbranched meniscate burrows with a distinct mantle/host sediment junction and gradual mantle/infill boundary (Heinberg, 1974; D'Alessandro and Bromley, 1987). The ichnofossil *Scoyenia* was described by Frey et al. (1984) as irregularly walled and longitudinally striated burrows containing meniscus structures. *Macaronichnus* chiefly differs from these ichnofossils in the presence of a distinct infill/mantle boundary and a gradual

mantle/host sediment junction with no wall attributes.

The diagnostic mantle morphology of *Macaronichnus* depends upon four factors: 1) trace-maker size; 2) concentration of grains segregated from burrow infills; 3) grain mineralogy; and 4) the mechanism used to segregate grains (Saunders, personal commun., 2007). A larger trace-maker will tend to produce a thicker mantle as more sediment is invariably processed. In some instances, organisms will form comparatively thicker basal mantles or basal mantles encompassing a ridge-like morphology (e.g., Clifton and Thompson, 1978; Savrda and Uddin, 2005). In other examples, organisms may produce mantles that are generally consistent around the burrow infill (e.g., Saunders, 1989). An abundance of less desirable grains will also result in a thicker mantle as more sediment is processed in order to meet the nutritional requirements of the trace-makers.

Mineralogical composition of the initial host sediment also plays an important role in determining the morphology of *Macaronichnus*; however, it should not be considered a factor for subdividing ichnospecies based upon infinitesimal possibilities of sediment composition. In the Horseshoe Canyon Formation of Alberta, Canada, grey-colored chert and volcanic rock fragments form subtle *Macaronichnus* mantles (Saunders and Pemberton, 1988; Fig. 5.2) as compared to the mica and heavy mineral mantles from the Vaqueros Formation (Fig. 5.3). If the initial host sediment contained no dark grains and was relatively homogeneous, burrows would be indiscernible (Saunders and Pemberton, 1988; Bromley, 1996) or may resemble *Planolites* (Uchman and Krenmayr, 2004). In the case of modern *Macaronichnus*-like structures on Pachena Beach, mantles are comprised of white, opaque shell fragments that are lighter in color than the quartz-rich infills (Dafoe et al., 2008a; see Chapter 4). In the rock record, these shell fragments would most likely be dissolved during diagenesis. If dissolution occurred, the subordinate mafic mineral segregation would not be sufficient to accentuate the structures (Dafoe et al., 2008a; see Chapter 4).

The final factor associated with mantle morphology is the process used to segregate grains. These processes are largely unknown; however, the degree of mineralogical segregation is likely dependent upon: organism morphology, adaptations and behaviors, and the nature of the environment (sediment characteristics, distribution of food and population density).

The segregation of the mantle and infill in *Macaronichnus* occurs as a result of trace-makers preferentially ingesting felsic components of the host sediment and avoiding micas and mafic grains. Prior to the initial description

of *Macaronichnus* by Clifton and Thompson (1978), these structures were interpreted to have formed by various methods and organisms. "Burrows of Milford type" were interpreted by Middlemiss (1962) as structures created by worms in the Lower Greensand of Milford, Surrey. Kikuchi (1972) recognized unlined, cylindrical structures mantled by magnetite grains in the Upper Member of the Narita Formation of the Kanto Plain, Japan. These structures were interpreted to have formed by isopods hydraulically segregating heavy minerals from the sediment during burrowing in dense populations in beach sediment or the shallow sea.

In order to explain the mineral partitioning observed in *Macaronichnus*, Clifton and Thompson (1978) analyzed a modern analogue—*Ophelia limacina*. Based on observations of this polychaete, the authors proposed that the trace reflects selective ingestion of grains possessing a rough surface texture due to the associated bacterial abundance (food). On intertidal flats of Willapa Bay, Gingras et al. (1999) also observed *Ophelia* producing *Macaronichnus*-like structures. Studying another modern analogue, the polychaete *Euzonus mucronata*, Saunders (1989) suggested that rejection of darker grains was a function of lower nutritive value. The detection of these darker grains was suggested by Nara (1994) to be related to the specific gravity or shape of the grains. Gingras et al. (2002) suggested that these angular (darker) grains were rejected by feel. Based on quantitative analysis of *E. mucronata* activities, Dafoe et al. (2008a; see Chapter 4) suggested a possible mechanism used to segregate mineral grains—site-selective feeding at felsic-rich locales. This mechanism primarily resulted in the segregation of shell fragments from the burrow infills, and appeared unique to the sediment characteristics and species of polychaete used in the experiments. The function of the shell fragment segregation was inferred to be related to grain size and shape or surface texture and associated nutritive value (Dafoe et al., 2008a; see Chapter 4). Savrda and Uddin (2005) suggested that grain composition and shape are inherently linked, although the function these parameters play in mineral segregation is unknown. Further analysis is required to determine the methods of grain partitioning used in other sediments and by other species, and the purpose of the mineral segregation. Despite the limited understanding of mineralogical segregation, Saunders and Pemberton (1988) and Saunders (1989) alluded to the deposit-feeding strategy of *Macaronichnus* trace-makers as a primary form of optimal foraging. The selective ingestion of more desirable grains by the trace-makers enhances the net energy gain per unit of feeding (Saunders

and Pemberton, 1988).

With respect to the depositional environment, *Macaronichnus* is most commonly found in close proximity to the shoreface-foreshore transition (Pemberton et al., 2001). Initially Clifton and Thompson (1978) described *Macaronichnus* from a number of settings including: estuarine, beach, nearshore and shallow marine. More specifically, *Macaronichnus* has been identified from the nearshore-beach complex at the toe-of-the-beach (e.g., Saunders, 1989; Saunders et al., 1994), shallow shoreface (e.g., Ranger et al., 1988; Hoffman, 2008), and even tidal inlets (e.g., Savrda and Uddin, 2005). The presence of *Macaronichnus* is thought to be related to occurrences of "oxygen windows" that can occur within the shoreface as ephemeral, post-storm phenomena (Pemberton et al., 2001). Permanent, oxygenated sediment also can be found in the intertidal and innermost surf zone of wave-exposed beaches where oxygenated water can percolate several meters below the sediment surface (Riedl and Machan, 1972). *Macaronichnus* trace-makers were able to exploit these deep-zone habitats of high-energy shorefaces and beaches (Saunders and Pemberton, 1988). However, Saunders and Pemberton (1988) found that an oxygenated window was not a necessary condition for the habitation of modern, analogous *Macaronichnus* trace-makers. Evolution of the deposit-feeding activities of *Macaronichnus* trace-makers was likely a function of stable and predictable habitat and food resources (organic detritus and/or bacteria; Saunders and Pemberton, 1988). Variation in expression of the *Macaronichnus* ichnogenus reflects important adaptations of the trace-makers to local biomasses and environmental conditions that persisted during active burrowing within these nearshore to shoreface settings.

Macaronichnus segregatis Clifton and Thompson, 1978

Figures 5.2, 5.6, 5.9

Macaronichnus Moslow and Pemberton, 1988, fig. 7b; Ainsworth, 1992, fig. 46; Walker and Bergman, 1993, fig. 22; Ainsworth, 1994, fig. 23b; Saunders, MacEachern and Pemberton, 1994, fig. 5b, f; Bhattacharya and Willis, 2001, fig. 10f; MacEachern and Hobbs, 2004, fig. 13b; Gibert, Netto, Tognoli and Grangeiro, 2006, p. 72, fig. 4b; Coates and MacEachern, 2007, fig. 13h; Gingras, Pemberton, Henk, MacEachern, Mendoza, Rostron,

O'Hare, Spila and Konhauser, 2007, fig. 8; MacEachern, Pemberton, Bann and Gingras, 2007, fig. 10d (=*Macaronichnus segregatis*).

Macaronichnus Walker and Bergman, 1993, fig. 17; Fielding, Bann and Trueman, 2007, figs. 21a, 22e; Kotake, 2007, p. 498, figs. 30.5, 30.6; Komatsu, Ono, Naruse and Kumagae, 2008, fig. 6f (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis Clifton and Thompson, 1978, p. 1293-1295; Dupré, 1984, p. 441, fig. 3f; Hunter, Clifton, Hall, Császár, Richmond and Chin, 1984, p. 9, fig. 16; Clifton, 1988, p. 517, fig. 13; Saunders and Pemberton, 1988, p. 132-133, figs. 26b, 27a-c, e, text-fig. 29; Saunders, 1989, p. 124-125, fig. 24b, 25a-c, e; MacEachern and Pemberton, 1992, figs. 5d-f, 6c, e, f; Walker and Bergman, 1993, p. 844-845; MacEachern, 1994, figs. V-8d, e, V-9c, e, f, VI-10e, f, VI-11a-c, text-fig. VI-12; Nara, 1994, p. 9, text-fig. 3, fig. 4; Brekke, 1995, p. 83, fig. 32a-d; Martini, Cascella and Rau, 1995, fig. 11a, b; Bromley, 1996, p. 170, 204, 263; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103, figs. 104a-c, e, 106, 145, 152b; Gingras, MacMillan, Balcom, Saunders and Pemberton, 2002, p. 553, fig. 2; Hobbs, 2003, figs. 3.5a, b, e, 3.6a, c, 3.8c-e; Tamura, Masuda, Sakai and Fujiwara, 2003, fig. 7e; Schmidt and Pemberton, 2004, fig. 4a, b; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 7g; Pemberton and Gingras, 2005, fig. 9a; Dafoe, Gingras, Saunders and Pemberton, 2006, p. 78; Le Roux, Olivares, Nielsen, Smith, Middleton, Fenner and Ishman, 2006, p. 145; D'Alessandro and Uchman, 2007, p. 214-215, fig. 3b; DesRoches, Thompson and MacEachern, 2007, fig. 3c; Fielding, Bann and Trueman, 2007, fig. 12b, e; Hansen and MacEachern, 2007, fig. 6e; Pemberton, MacEachern, Gingras and Saunders, 2007, fig. 2c; Seike, 2007, p. 497-498; Dafoe, Gingras and Pemberton, 2008a, p. 91, fig. 1; Dafoe, Gingras and Pemberton, 2008b, p. 79, fig. 1; DesRoches, 2008, figs. 3.1.4f, 3.1.8e, f; Kamada, 2008, figs. 2-4; Pemberton, MacEachern, Gingras and Saunders, 2008, p. 278, figs. 6a, 7b; Tamura, Murakami, Nanayama, Watanabe and Saito, 2008, fig. 7c.

Macaronichnus segregatis lineiformis Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 117, fig. 4b (=*Macaronichnus segregatis*); Bromley, Milàn, Uchman and Hansen, 2009, figs. 4c, 5b, 6b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis maeandriformis Bromley, Milàn, Uchman and

Hansen, 2009, p. 105, 117, figs. 5b, 6a, b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis segregatis Saunders, 1989, p. 124-125, text-fig. 27; Bromley, Milàn, Uchman and Hansen, 2009, p. 116-117 (=*Macaronichnus segregatis*).

non *Macaronichnus segregatis* Curran, 1985, p. 263-264, pl. 1, fig. b-d, pl. 2, fig. a; Maples and Suttner, 1990, p. 870, figs. 12.1, 12.9, text-fig. 13; Tamura and Masuda, 2005, p. 1383, fig. 7c (=*Harenaparietis*).

non *Macaronichnus segregatis* Hunter and Clifton, 1982, p. 135, fig. 4c; Orr, 1995, p. 272-274; Głuszek, 1998, p. 532-533, fig. 11a, b (=?*Harenaparietis*).

non *Macaronichnus segregatis* Clifton and Thompson, 1978, fig. 2; Fürsich and Heinberg, 1983, p. 95, text-fig. 7ii; DeCelles, 1987, p. 253, 255, fig. 5c; Ranger, Pemberton and Sharpe, 1988, p. 456, fig. 6a-d; Knaust, 2004, p. 14, fig. 6.5, 6.6; MacEachern and Hobbs, 2004, figs. 13a, 15b; Uchman and Krenmayr, 2004, p. 238, fig. 7; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 4b; Tamura and Masuda, 2005, p. 1383, fig. 7e; D'Alessandro and Uchman, 2007, fig. 4c, d, f; Tamura, Nanayama, Saito, Murakami, Nakashima and Watanabe, 2007, fig. 6f; DesRoches, 2008, fig. 3.1.5d, g; Bromley, Milàn, Uchman and Hansen, 2009, p. 105, 107, fig. 4a (=*Macaronichnus*).

non *Macaronichnus segregatis* Clifton and Thompson, 1978, p. 1293-1295, figs. 1, 2; Clifton, 1981, p. 170-171, fig. 9; DeCelles, 1987, p. 253, 255, fig. 5d; Bann and Fielding, 2004, fig. 6e; Johnstone, Mustard and MacEachern, 2006, fig. 6c (=*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Bromley, 1996, fig. 11.9 (=?*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Hunter, 1980, fig. 3b; Nadon, 1988, p. 49-50, fig. 25; Pollard, Goldring and Buck, 1993, p. 153, 161-162, fig. 4a-c; Carmona, Buatois, Mángano and Bromley, 2008, p. 101-102, figs. 4.6, 4.7 (=*Macaronichnus simplicatus-segregatis*).

non *Macaronichnus segregatis* Fürsich, 1984, p. 331, fig. 3b, text-fig. 10 (=?*Anconichnus*); Male, 1992, figs. 6a-c, 12c (=cryptobioturbation); Rigsby, 1994, fig. 12a (=?*Palaeophycus*); Orr and Howe, 1999, p. 37-38, fig. 3a, b (=?*Palaeophycus*); Bridges and Castle, 2003, table 2, fig. 4e (=?);Zhensheng, Xiaomin, Bin and Xilin, 2004, p. 207-208, fig. 3 (=*Palaeophycus*), figs. 4.1, 4.2, 4.4-4.6, 6 (=?*Chondrites*).

non *Macaronichnus simplicatus* MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 3b (=*Macaronichnus segregatis*).

transitional *Macaronichnus segregatis-simplicatus* Saunders, MacEachern and Pemberton, 1994, fig. 5g (=*Macaronichnus simplicatus-segregatis*).

"*Excirolana chiltoni* burrows" Okazaki and Masuda, 1992, fig. 15b.

"*Excirolana chiltoni japonica*" Tokuhashi and Kondo, 1989, fig. 11.

Excirolana chiltoni japonica burrows" Koyama, 1983, pl. I, fig. b-d, pl. II, fig. b.

"isopod traces" Kikuchi, 1972, p. 144, pl. 1, figs. 1-4.

"mottled burrows" Hakes, 1976, p. 38, pl. 12, fig. 2.

Emended Diagnosis—Predominantly horizontal, randomly oriented burrows characterized by the tendency towards the avoidance of interpenetration of structures.

Description—Burrows are characterized by randomly curving and meandering paths generally occurring along bedding planes in moderate to high population densities. The structures are typically small with diameters ranging from 1-5 mm (characteristically 2-3 mm), and the mantle is on the order of one to several grains in thickness. Burrow infills are predominantly comprised of quartz and may include lesser feldspar and chert. Infills also may contain meniscate structures indicative of active backfilling. The mantle may be comprised of heavy minerals, micas, chert, plagioclase and/or magnetite. Burrows exhibit a propensity towards avoidance of interpenetration; however, localized cross-cutting may be observed. Recognition of avoidance can be identified as mantle material separating abutting traces, while intersections are demarcated by partial or complete removal of mantle material between adjoining structures. Where traces begin to converge, they tend to curve sharply away or become parallel with an approximately consistent separation distance. In the case of the latter, mantles between separate burrow infills may coalesce. Mantles may also be indistinct such that traces are defined by lighter colored burrow infills and a concentration of darker minerals in the surrounding host sediment. The overall behavior that produces *M. segregatis* was described by Saunders and Pemberton (1988) and Saunders (1989) as a "random avoidance" pattern of exploitation.

Etymology—Segregatis is from the Latin word "segregare," which refers to the segregation of minerals between the burrow mantle and infill.

Paratypes—Horseshoe Canyon Formation of Alberta, Canada, collected by T.D.A. Saunders in storage at the University of Alberta, Edmonton, Alberta, Canada (TF020 and TF021; Fig. 5.2).

Discussion—The ichnospecies diagnoses presented herein correspond to ichnofossil descriptions proposed by Saunders and Pemberton (1988) and Saunders (1989), and subsequent informal use of these trace fossil names. The original description of *Macaronichnus segregatis* (Clifton and Thompson, 1978) combines features of both *M. segregatis* and *M. simplicatus* (cf. Saunders and Pemberton, 1988). As a result, a specimen from the Painted Rock Sandstone Member of the Vaqueros Formation, from which the original holotype was collected, was analyzed in detail to assess proper ichnospecies designation. Ichnofossils in this specimen exhibit a tendency towards interpenetration of structures rather than avoidance (Fig. 5.3). Consequently, the informal holotype originally used to describe *M. segregatis* now describes the ichnospecies *M. simplicatus*. In place of the Painted Rock Sandstone Member, specimens from the Horseshoe Canyon Formation are now designated the paratypes for *M. segregatis*.

Recently, the *M. segregatis* ichnospecies has been formally diagnosed and subdivided (Bromley et al., 2009), and this recent work is assessed below. Based on occurrences of *Macaronichnus segregatis* from the east coast of Rhodes, Greece, Bromley et al. (2009) subdivided the trace fossil into three ichnosubspecies: *M. segregatis lineiformis*, *M. segregatis maeandriformis* and *M. segregatis spiriformis*. These ichnofossil distinctions were made on the general morphology as strongly oriented perpendicular to the shoreline (linear displaying phobotaxis and strong rheotaxis normal to the shoreline), winding and spiraled forms, respectively. These new forms of *M. segregatis* were interpreted to be associated with various porewater flow conditions (Bromley et al., 2009). Winter or high-energy conditions would result in strong porewater flow perpendicular to the shoreline resulting in rheotactic orientation of traces. In contrast, more stagnant waters lead to formation of spiraled burrows produced during summer months, and winding forms reflected intermediate conditions (Bromley et al., 2009).

Notable inconsistencies exist with the ichnosubspecies designations and concordant interpretations presented by Bromley et al. (2009). For instance, Bromley et al. (2009) indicated that subspecies can grade into one another, and

individual traces can be continuous from one form to another. Interpretation of a single burrow structure reflecting variation in seasonal conditions is improbable. Daily tidal fluctuations, however, influence the activities of a modern analogous worm—*Euzonus mucronata*—when tides and porewater pressure falls, the worms migrate to the sediment surface for respiration (Eikenberry, 1966). These daily fluctuations in porewater flow would not necessarily lead to changes in amplitude or degree of meandering or result in spiraling behaviors. It was also indicated that the three ichnosubspecies rarely occur together within the same laminae (cf. Bromley et al., 2009). However, specimens photographed by Bromley et al. (2009), display *M. segregatis lineiformis* and *maeandriformis* occurring together on the same bedding plane (Bromley et al., 2009, figs. 4c, 5b, 6a). Based on these examples, it appears that linear and meandering traces can be segregated only at a highly localized scale, further suggesting that variations in pore-water conditions (over mere centimeters) due to wave/wind charge do not fully explain the occurrence of the various ichnosubspecies. In addition, *M. segregatis maeandriformis* displays variation from simple meanders (Bromley et al., 2009, fig. 5a) to more complex, nested loops (Bromley et al., 2009, fig. 6a), which suggests that a continuum exists between linear and meandering forms in which meanders may increase in amplitude and complexity. Accordingly, the degree to which the amplitude and/or regularity of meanders becomes great enough to be called *maeandriformis* rather than *lineiformis* is subjective (e.g., Bromley et al., 2009, figs. 4c, 5b, 6b). *Macaronichnus segregatis lineiformis* and *maeandriformis* appear to reflect similar responses to environmental conditions and vary only in the degree of meander.

Despite the clear association of linear and meandering *Macaronichnus*, the general trend of some *Macaronichnus* occurrences do—as Bromley et al. (2009) assert—reflect shoreline-normal burrowing activities. However, winter (high energy) porewater conditions described by Bromley et al. (2009) for *lineiformis* do not correspond to observations of modern analogous burrowers that produce *Macaronichnus*-like structures. Shoreline-normal migrations near the sediment surface have been observed with modern *Euzonus mucronata* along Long Beach, Vancouver Island, Canada, during high energy summer conditions on the wind- and wave-eroded beach (Fig. 5.7; Saunders, 1989). Observations of *E. mucronata* by Saunders and Pemberton (1988) and Dafoe et al. (2008b) indicated that gradual onshore-offshore migrations of the *Euzonus* populations occur as a result of tidal drainage on dissipative foreshores (during which there were no major storms).

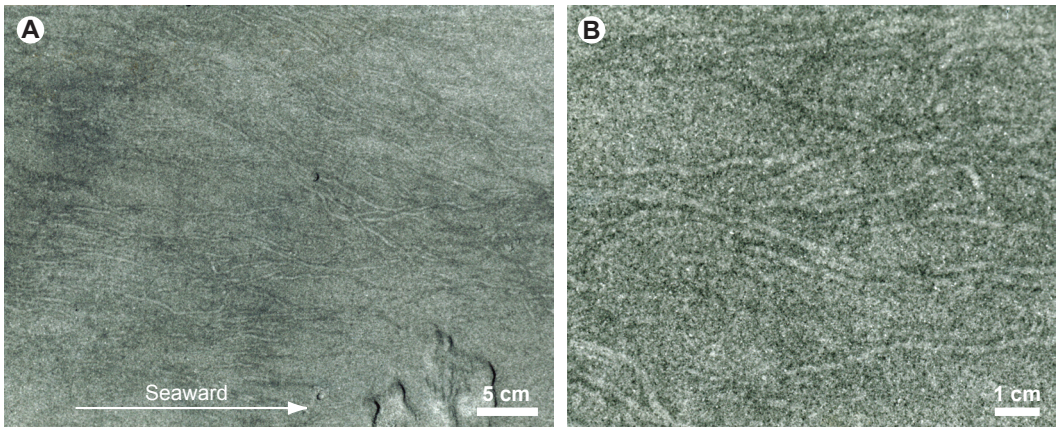

FIGURE 5.7—Onshore-offshore migrations of the polychaete *Euzonus mucronata* during summer on a wind- and wave-eroded beach. For scale, there is a footprint at the bottom of (A), and (B) shows a close-up view of the *Macaronichnus*-like burrows.

These polychaetes optimize their position within the sediment with respect to degree of water saturation and oxygenation (Saunders and Pemberton, 1988), necessitating semidiurnal onshore-offshore migrations despite the season or wave conditions. Seike (2008) also described shoreline-normal migrations of *Euzonus* sp. at greater depths within the substrate under storm conditions, which were also not restricted to the winter season. With regards to the association of spiraling behavior with stagnant summer conditions, winter storms can remove much of the reworked sediment on a beach face (e.g., Seike, 2008). However, preserved beds reflecting summer months should contain extensive burrow structures as conditions (temperature, food availability, stable beach conditions and population increases) are ideal at this time. However, dense spiraling *Macaronichnus* do not appear to occur in the Pefkos beachrock (e.g., Bromley et al., 2009) or in specimens from the Horseshoe Canyon Formation (e.g., Saunders, 1989). Indeed, spirals may reflect reduced porewater flow conditions (cf. Bromley et al., 2009) in which the trace-makers are not required to locomote perpendicular to the shoreline, but another factor must be related to the presence of these unique *Macaronichnus* (see *M. spiralis* section below).

Bromley et al. (2009) further suggested that the *M. segregatis* ichnosubspecies reflect varied foraging optimization as a function of pore-water movement. The filtering of seawater through pore spaces in the intertidal zone provides oxygen and dissolved particulate organic materials to infauna (McLachlan et al., 1985). Within high-energy beaches, current dynamics can retain a permanent "oxygen window" within the substrate (Riedl and Machan, 1972). For this reason, Saunders and Pemberton (1988) suggested that the

occurrence of *Macaronichnus* within the foreshore/shoreface setting is a result of "pumped" oxygen- and nutrient-rich waters within pore systems. Thus, the stagnant conditions proposed for *M. segregatis spiriformis* would result in decreased food resources and possibly suboxic conditions in the presence of organics. Whereas high-energy pore flow would enhance delivery of nutrients to infaunal organisms. The interpretation of Bromley et al. (2009) is also in contrast to the study of *Chiridotea coeca* (isopod) grazing trails by Hauck et al. (2008) in which increasing burrow tortuosity (from linear to looping to convolute) was associated with increased organic-carbon content of the sediment. Under stagnant (low nutrient) conditions, it is unclear what motivates the *Macaronichnus* trace-makers to continue foraging within a particular locality. More likely, under such conditions, *Macaronichnus* trace-makers would locomote to find more optimal living conditions. Accordingly, foraging optimization may not be directly linked to seasonal or long-term changes in pore-water movement. It is more likely that traces oriented normal to the shoreline (whether linear or meandering) reflect an affinity to particular porewater saturation levels that encourage the trace-making population to locomote and maintain a position within optimal sediment.

Following more traditional taxonomic protocols, the taxonomy presented by Bromley et al. (2009) is based on the morphological attributes of individual traces. However, the proposed taxonomic scheme fails to account for the most typical occurrence of *Macaronichnus*—abundant intertwined through to interpenetrating burrows (thus the connotation of "macaroni", bestowed by Clifton and Thompson, 1978). In this case, Bromley et al. (2009) relegated these forms of *Macaronichnus* to *M. segregatis segregatis*, which includes the original specimen described by Clifton and Thompson (1978). In the absence of bedding plane views, the ichnosubspecies presented by Bromley et al. (2009) cannot be positively identified in either low or high population densities of *Macaronichnus*. Furthermore, the reference to *M. segregatis lineiformis* by Carmona et al. (2008) demonstrates a possible misuse of this taxonomy. Carmona et al. (2008) interpreted randomly oriented *Macaronichnus* less than 10 cm in length as approaching *lineiformis*; however, the figure (Carmona et al., 2008, fig. 4.6) displays no preferred orientation of trace segments, which is an integral aspect of the trace diagnosis. Based on the above assessment, the ichnosubspecies presented by Bromley et al. (2009) do not capture the most important architectural aspects of *Macaronichnus* occurrences: a short fall that this paper attempts to address.

The ichnosubspecies of *M. segregatis* proposed by Bromley et al.

(2009) do not correspond with the diagnoses proposed herein: *M. segregatis* is distinguished by an avoidance of adjacent burrow structures. Examples presented by Bromley et al. (2009), largely reflect composite *M. simplicatus-segregatis* (see *M. simplicatus* discussion below) where localized avoidance occurs with localized interpenetration and cross-over of structures (Bromley et al., 2009, figs. 4c, 5b, 6). The remainder of examples depicted by Bromley et al. (2009) can be defined as *Macaronichnus* isp. where isolated (Bromley et al., 2009, figs. 4a, 5a) or *M. spiralis* where traces are planispiral (Bromley et al., 2009, fig. 7). The taxonomy presented in this paper serves to incorporate examples of *Macaronichnus* that are randomly and systematically oriented. Accordingly, it is left up to the ichnologist to interpret any organized patterns of burrowing as related to the particular strata being studied.

Macaronichnus segregatis is distinguished from other ichnospecies based on the collective morphology which is characterized by avoidance of other burrow structures. The traces generally occur in dense monospecific assemblages (Saunders and Pemberton, 1988), and tend to be pervasive throughout the sediment, which forms an ichnofabric rather than individual ichnofossils (Bromley, 1996). The pattern of burrowing is randomized and can be explained by three factors: 1) population densities; 2) the availability of food; and 3) the energy requirements of the trace-makers themselves (Saunders, 1989; Gingras et al., 2002). Dense populations result in intraspecific competition (Saunders, 1989), which forces individuals to continually migrate in 2 and 3 dimensions to locate untouched sediment. Food resources in intertidal settings may be patchily distributed (e.g., runnels versus beach berms) in addition to variation in porewater saturation and oxygenation, which also promotes random foraging to locate better food resources. As a result of the energy required to process previously burrowed sediment, simple, random foraging in conjunction with the primary grain-selective optimization likely proved insufficient to sustain dense trace-maker populations (Saunders and Pemberton, 1988). Accordingly, a more advanced deposit-feeding strategy in the form of avoidance of previously reworked sediment was adopted (Fig. 5.8; Saunders, 1989). This “random avoidance” strategy is a secondary optimal foraging strategy (Saunders and Pemberton, 1988) and is seen in detail with a surface-rendered MRI of *M. segregatis* from the Horseshoe Canyon Formation of Alberta, Canada in Figure 5.9. The “random” nature refers to the random orientations of ichnofossils that display a systematic refrain from intersection. The traces within this specimen display an obvious avoidance of

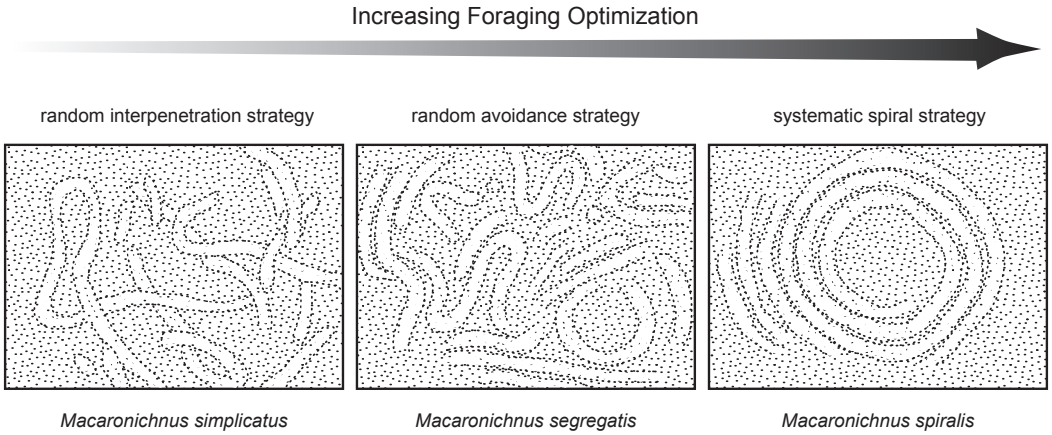

FIGURE 5.8—Plan view representation of *Macaronichnus simplicatus*, *M. segregatis* and *M. spiralis*. The foraging strategy becomes increasingly optimized in terms of efficient feeding behavior from *M. simplicatus* to *M. spiralis*. Foraging efficiency primarily changes due to population density pressures and food-resource distribution (see Figure 10). Modified from Saunders and Pemberton (1988) and Saunders (1989).

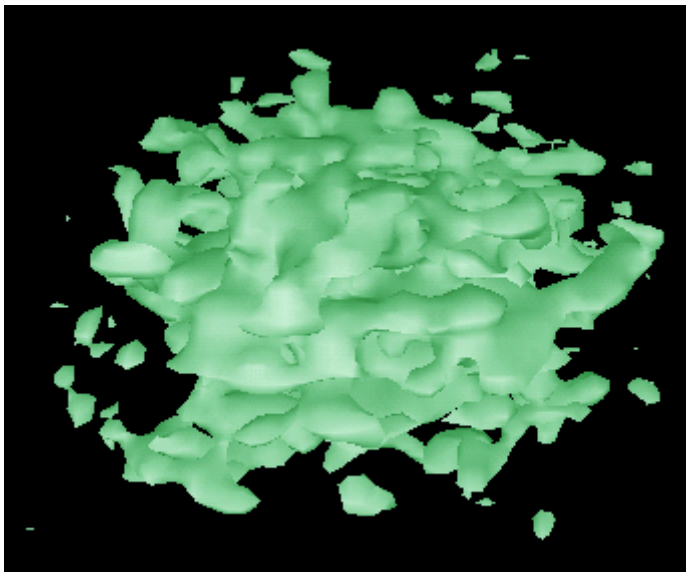

FIGURE 5.9—Three-dimensional surface rendering of a Magnetic Resonance Image (MRI) of a specimen containing *Macaronichnus segregatis* from the Horseshoe Canyon Formation of Alberta, Canada. Note the complex intertwining of burrow segments demonstrating the "random avoidance" strategy.

cross-cutting as structures tend to twist and intertwine around one another. Other traces exhibiting this random avoidance behavior include examples of *Nereites irregularis* documented by Uchman (2007).

This "random avoidance" pattern generally reflects the behaviors of smaller *Macaronichnus* trace-makers (based on the diameter of the traces). In general, smaller organisms inherently process less sediment per time frame as compared to larger burrowers. Accordingly, previously defecated sediment or a mantle of undesirable grains may be avoided by smaller organisms as the amount of energy required to reprocess this sediment is beyond a threshold of efficiency. These smaller organisms would be more inclined to avoid burrowed sediment and feed upon adjacent untouched sediment. In this case, avoidance of other structures provides an optimal advantage to these smaller trace-makers. The avoidance of interpenetration of traces reflects a moderate degree of foraging optimization (Fig. 5.8) whereby trace-makers are deposit feeding on sediment that is likely the most resource-rich based on the lack of previous reworking.

Alternatively, the shear density of modern *Euzonus* that construct *Macaronichnus*-like burrows can reach maxima of 14,000 individuals/m^2 (Dales, 1952) and even up to 98,000 individuals/m^2 (based on dry weight; Kemp, 1985). This suggests that biomass density may, in fact, be the driving force behind some examples of avoidance behavior due to limited available space within a narrow optimal sediment band along the foreshore. This relationship of *M. segregatis* trace-makers to vital environmental conditions is depicted in Figure 5.10. In instances in which dense trace-maker populations existed and available space was limited, avoidance was simply necessitated by worm-to-worm contact. However, with decreased population densities and enhanced availability of space, organisms had the opportunity to avoid other burrow structures, also producing random avoidance. Food resources were likely limited for *M. segregatis* trace-makers as avoidance suggests that: 1) energy cannot be expended by trace-makers to reburrow previously reworked sediment, or 2) dense populations rapidly depleted available food resources within the sediment. Sedimentation rates may also have been greater during construction of *M. segregatis.* As new sediment was deposited, nutritional resources were enriched, allowing for a more optimal foraging (avoidance rather than cross-cutting).

The activity of *Macaronichnus segregatis* trace-makers may obliterate primary stratification, or may form a type of cryptobioturbation in which bedding planes remain visible (Fig. 5.6; e.g., MacEachern and Pemberton, 1992;

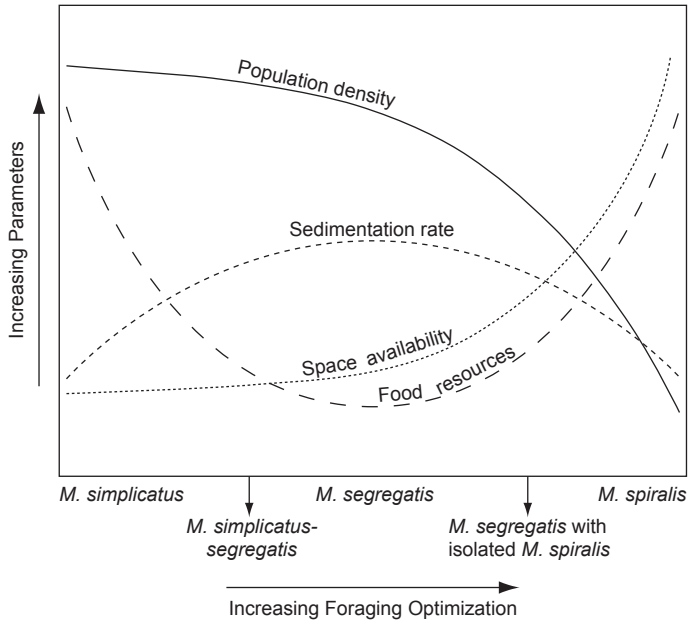

FIGURE 5.10—The relationships between the various ichnospecies of *Macaronichnus* and important environmental conditions (see text for further explanation).

Pemberton et al., 2001; Pemberton et al., 2008). The preservation of primary stratification may be related to: 1) optimal grains found in particular laminae sets; 2) increased food quality of particular laminae sets; or 3) laminae boundaries may act as guides for the trace-makers to permit feeding by dense populations (Saunders, personal commun., 2007). Within the realm of *M. segregatis* deposit-feeding, foraging is further optimized when trace-makers are vertically organized and exploit particular laminae (e.g., Figs. 5.2, 5.6). For instance, in Figure 5.6A, the upper portion of the core displays cryptobioturbation in which *M. segregatis* trace-makers were organized along laminae reducing the need to twist and intertwine around one another. In contrast, the lower portion of the core depicts 3-dimensional random foraging in which more energy is inevitably expended by traversing across laminae forcing trace-makers to more actively avoid other burrow structures and trace-makers.

Macaronichnus segregatis is generally found in monospecific assemblages (Brekke, 1995) in a variety of depositional settings including: the upper foreshore (e.g., Saunders, 1989; Saunders et al., 1990; MacEachern and Pemberton 1992; Hoffman, 2008; Bromley et al., 2009), foreshore-shoreface transition zone (e.g., Moslow and Pemberton, 1988; Walker and Bergman, 1993; MacEachern and Hobbs, 2004), upper shoreface (e.g., MacEachern and Pemberton 1992; Pemberton et al., 2001; Schmidt and Pemberton, 2004), delta front (e.g. Fielding

et al., 2007; Hansen and MacEachern 2007) and tidal channels (e.g., Schmidt and Pemberton, 2004). Variation in the environmental setting in which these traces are found may be associated with a number of factors including: the size, species, behavioral adaptations of the trace-makers and prevailing environmental conditions (oxygenation, food resources, sedimentation rate, erosional processes, and beach face morphology).

Macaronichnus simplicatus new ichnospecies

Figures 5.3, 5.8, 5.12

Macaronichnus Lockley, Rindsberg and Zeiler, 1987, fig. 2b; Bann and Fielding, 2004, p.294, fig. 14b; Fielding, Bann and Trueman, 2007, fig. 12c (=*Macaronichnus simplicatus*).

Macaronichnus Walker and Bergman, 1993, fig. 17; Fielding, Bann and Trueman, 2007, figs. 21a, 22e; Kotake, 2007, p. 498, figs. 30.5, 30.6; Komatsu, Ono, Naruse and Kumagae, 2008, fig. 6f (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis lineiformis Bromley, Milàn, Uchman and Hansen, 2009, figs. 4c, 5b, 6b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus segregatis maeandriformis Bromley, Milàn, Uchman and Hansen, 2009, p. 105, figs. 5b, 6a, b (=*Macaronichnus simplicatus-segregatis*).

Macaronichnus simplicatus Saunders and Pemberton, 1988, p. 133, text-fig. 29, pl. 11, figs. 1-5, 7; Saunders, 1989, p. 125, text-fig. 27, pl. 11, figs. 1-5, 7; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 3c.

non *Macaronichnus segregatis* Clifton and Thompson, 1978, p. 1293-1295, figs. 1, 2; Clifton, 1981, p. 170-171, fig. 9; DeCelles, 1987, p. 253, 255, fig. 5d; Bann and Fielding, 2004, fig. 6e; Johnstone, Mustard and MacEachern, 2006, fig. 6c (=*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Bromley, 1996, fig. 11.9 (=?*Macaronichnus simplicatus*).

non *Macaronichnus segregatis* Hunter, 1980, fig. 3b; Nadon, 1988, p. 49-50,

fig. 25; Pollard, Goldring and Buck, 1993, p. 153, 161-162, fig. 4a-c; Carmona, Buatois, Mángano and Bromley, 2008, p. 101-102, figs. 4.6, 4.7 (=*Macaronichnus simplicatus-segregatis*).

non *Macaronichnus simplicatus* Raychaudhuri and Pemberton, 1992, fig. 6e; Hobbs, 2003, figs. 3.4f; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 4e; DesRoches, 2008, figs. 3.1.2g, 3.1.4d (=*Harenaparietis*).

non *Macaronichnus simplicatus* MacEachern, Bann, Bhattacharya and Howell, 2005, figs. 3c, 4a, f, g, 6c, e, 9j (=*Macaronichnus*); MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 3b (=*Macaronichnus segregatis*).

transitional *Macaronichnus segregatis-simplicatus* Saunders, MacEachern and Pemberton, 1994, fig. 5g (=*Macaronichnus simplicatus-segregatis*).

?*Palaeophycus* Boyer and Warme, 1975, p. 85, text-fig. 9d; King, 1987, p. 39, fig. 2g.

Scoyenia sp. Chamberlain, 1978, fig. 92.

Diagnosis—Variably oriented and configured, predominantly horizontal burrows that are commonly randomly interpenetrating.

Description—Documented examples range in size from 1.5-10 mm in diameter, which is typically larger than *Macaronichnus segregatis*. *Macaronichnus simplicatus* is characterized by straight to randomly curving or meandering paths that are generally circular to ovate in cross section (Fig. 5.3). Burrows are predominantly horizontal to slightly inclined such that burrows may transect multiple laminae and are a few centimeters to a few decimeters in length. In some instances, burrow diameters may be characterized by a bimodal size distribution (e.g., Saunders and Pemberton, 1988). Infills are predominantly characterized by quartz and may contain meniscate structures indicative of active backfilling. The mantle is generally composed of darker mineral grains that may include: micas and heavy minerals. Mantle thickness ranges from 0.1 to 1 mm and may vary between individual traces or around the same structure. Some examples may display a thicker basal mantle that may or may not be irregular in nature. In some cases, the distinction between mantle and host sediment may be difficult to ascertain especially with dense ichnofossils (Fig. 5.3).

Interpenetration of *Macaronichnus simplicatus* is observed in cross section as the cross-cutting of burrows intersecting at random. Intersections or cross-cutting of adjacent traces is recognized through partial or complete

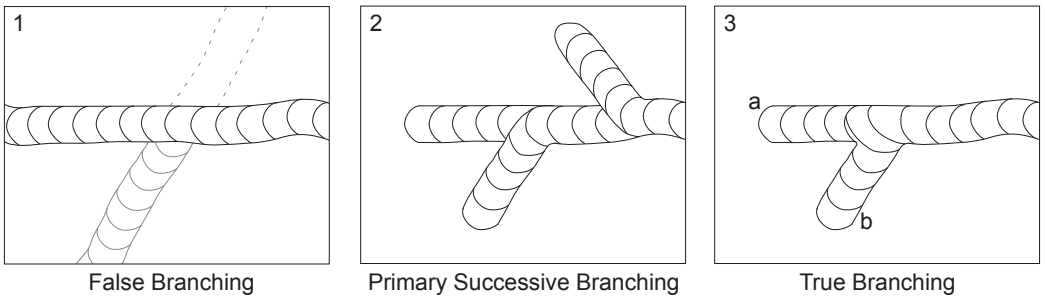

FIGURE 5.11—Various forms of branching. **A:** False branching formed by intersecting burrows constructed at different levels within the sediment. **B:** Primary successive branching formed by an animal systematically probing and backfilling branching burrow components. **C:** true branching in which backfilling of branch (a) is succeeded by backfilling of (b) rather than simultaneous infilling. Modified from D'Alessandro and Bromley (1987).

removal of mantle material. In plan view, the configuration of structures includes overlapping, cross-cutting and false branching (Figs. 5.3, 5.11). False branching is identified where there is no mantle or a partial mantle preserved between intersecting burrows. The angle of intersection of false branches ranges due to the random configuration of burrows. Despite the characteristic occurrence of these interpenetrations, examples where adjacent traces display avoidance are also present.

Etymology—Describes the simplistic form of foraging in which trace-makers display no adaptations towards maximizing foraging efficiency.

Holotype—Painted Rock Sandstone Member of the Vaqueros Formation (Miocene) in storage at the University of Alberta, Edmonton, Alberta, Canada – TF023 (Fig. 5.3).

Paratype—Painted Rock Sandstone Member of the Vaqueros Formation (Miocene); sample collected by D.L. Durham on repository at the U.S. Geological Survey, Menlo Park, California. (Original informal *Macaronichnus segregatis* holotype from Clifton and Thompson (1978)).

Discussion—The defining characteristic of *Macaronichnus simplicatus* is the tendency towards interpenetration of burrows, which forms an overall collective morphology. The paucity of interpenetrations observed in *M. segregatis* as compared to *M. simplicatus* may, in some instances, be a function of the size of the trace-makers and their ability to process sediment. Based on the dimensions

of *M. simplicatus*, these traces are generally constructed by larger organisms as compared to *M. segregatis*. In dense populations, it would be difficult for large organisms to maneuver around previously constructed burrows in a limited interval of exploitable sediment. In addition, the ease and rapidity of sediment processing is an advantage to these larger trace-makers. The energy expended to feed upon previously reworked sediment would unlikely affect their efficiency of balancing expended and acquired energy resources. Accordingly, larger organisms would more frequently ingest previously reworked sediment, resulting in a tendency towards interpenetration of structures. In some cases, the methods of deposit feeding employed by *M. segregatis* and *M. simplicatus* trace-makers also may be significantly divergent to produce the varied interactions. Overall, the tendency towards interpenetration and less organized foraging suggests a simplistic form of deposit feeding that exhibits no secondary adaptations towards efficiency beyond primary grain selectivity (Saunders and Pemberton, 1988; Fig. 5.9).

Strata characterized by *Macaronichnus simplicatus* also contain structures exhibiting avoidance of interpenetration, which is expected as the random orientation of burrows does not guarantee the interpenetration or cross-cutting of every structure. The degree of interpenetration of burrows depends upon: 1) the population density; 2) availability of space; 3) abundance of food; 4) the amount of time available for reworking (e.g., reduced in storm beds) or sedimentation rate; and 5) trace-maker morphology and deposit-feeding strategy (Fig. 5.10). In order for *M. simplicatus* to be constructed, abundant cross-cutting and interpenetration of burrows generally requires high population densities, either widespread or localized, and limited available space. Food resources are generally plentiful such that the population can be sustained despite the degree of reburrowing of previously ingested sediment (Saunders and Pemberton, 1988). On the scale of a bedding plane, resource-rich patches may lead to concentrated areas of burrow intersection. Sedimentation rates are generally low, which necessitates continual reworking of the same interval of optimal sediment for prolonged periods of time. These factors progressively influence the degree of cross-cutting of *Macaronichnus* traces, which results in a continuum of structures ranging from predominantly intersecting to predominantly avoiding. Accordingly, the identification and distinction between *M. segregatis* and *M. simplicatus* may not always be clear especially in moderate population densities where interactions are minimized.

Macaronichnus segregatis and *M. simplicatus* represent near end-member community interactions. These ichnofossils reflect the preservation of natural behaviors, and the likelihood of observing complete avoidance of interpenetration or complete interpenetration of all structures is infinitesimally low. Examples of *Macaronichnus* may clearly characterize one near end-member of the continuum (especially at the scale of core), or strata may contain mixed elements of both behaviors with no clear tendencies towards avoidance or interpenetration. This transitional foraging strategy was first recognized by Saunders et al. (1994) from the Cadotte Member of the Peace River Formation of Alberta in which mixed elements of *M. segregatis* and *M. simplicatus* were identified. This mixing of elements of both end-members is presumably observed at outcrop scale (rather than core) where isolated intervals or even adjacent grouping of structures may be characterized by different forms. In such cases, the assemblage should be described as containing elements of both *M. segregatis* and *M. simplicatus* and should be referred to as the composite ichnofossil: *M. simplicatus-segregatis* (Fig. 5.12). This mixed expression of *Macaronichnus* may be associated with localized variations in population densities of trace-makers. Where population densities are low, trace-makers have the ability to avoid other burrow structures producing *M. segregatis*. Where localized higher population densities exist, *M. simplicatus* may be constructed if the availability of space is low enough that organisms are required to burrow within previously reworked sediment. In instances where population densities vary laterally or vertically through time, both forms of

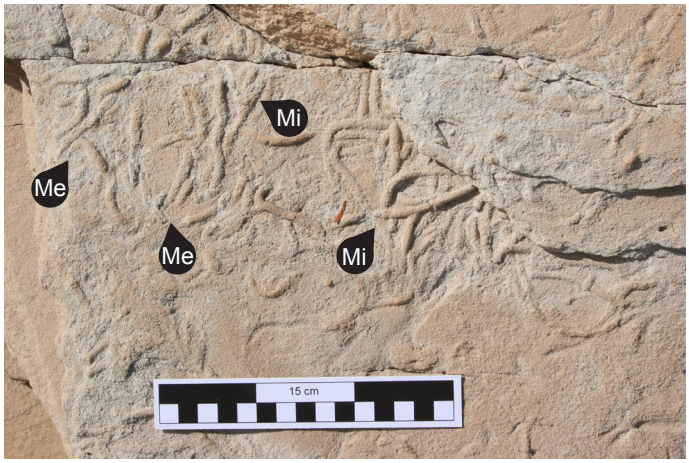

FIGURE 5.12—*Macaronichnus simplicatus-segregatis* in which elements of "random avoidance" of *M. segregatis* (Me) are mixed with elements of cross cutting of *M. simplicatus* (Mi). Plan view from the Freitag Formation of Queensland, Australia. Photo courtesy of Kerrie L. Bann and Christopher R. Fielding.

Macaronichnus also may be present.

With regards to the depositional environment, *Macaronichnus simplicatus* has been observed in settings similar to that of *M. segregatis*: the upper foreshore (e.g., Bromley et al., 2009); nearshore-beach complex at the toe-of-the-beach (e.g., Clifton and Thompson, 1978; Saunders et al., 1994); middle shoreface (e.g., Bann and Fielding, 2004); and lowermost upper shoreface to distal lower shoreface (Saunders and Pemberton, 1988).

Macaronichnus spiralis new ichnospecies

Figures 5.4, 5.9

Macaronichnus segregatis spiralis Saunders and Pemberton, 1988, p. 133, fig. 27b, d, f, g, text-fig. 29; Saunders, 1989, p. 125, fig. 25b, d, f, g, text-fig. 27 (=*Macaronichnus spiralis*).

Macaronichnus segregatis spiriformis BROMLEY, Milàn, Uchman and Hansen, 2009, p. 105, 117, fig. 7 (=*Macaronichnus spiralis*).

Macaronichnus spiralis MacEachern and Pemberton, 1992, fig. 6d; MacEachern, 1994, fig. V-9d, text-fig. VI-12; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, p. 127, text-fig. 103, fig. 104b, d, f, g; Minter, Buatois, Lucas, Braddy and Smith, 2006, p. 1058.

Diagnosis—Burrows display planispiral configurations on bedding planes with varying levels of perfection including: single irregular loops, nested partial loops, single perfect coils, and perfect coiled spirals.

Description—Planispiral configurations are generally constructed outwards (dextral or sinistral) from an initial circular to sub-circular burrow 1.5-2.5 cm in diameter (Saunders and Pemberton, 1988; Saunders, 1989). The cross-sectional diameter of the burrow ranges from 1.5-3 mm. Coil spacing tends to be constant (0.5-2 mm) with minor irregularities, and a maximum of up to 12 coils has been observed (Saunders and Pemberton, 1988).

This ichnospecies is generally observed with low population densities at various scales. *Macaronichnus spiralis* exhibits varying degrees of systemization and is often characterized by disorganized and irregularly curved structures

confined to a specific area (Fig. 5.4B). In rare instances, perfect planispiral configurations may be observed (Fig. 5.4A, C). Irregular singular spirals (Fig. 5.4D) or clusters of nearly complete spirals (Fig. 5.4B) are more common and may be observed in conjunction with *M. segregatis* (Fig. 5.4D).

Etymology—Describes the spiraled nature of the burrows in plan view.

Holotypes—Horseshoe Canyon Formation of Alberta, Canada, collected by T.D.A. Saunders in storage at the University of Alberta, Edmonton, Alberta, Canada (TF024 and TF025; Fig. 5.4A, C).

Discussion—The planispiral configurations of *Macaronichnus spiralis* are rare and have been identified from the Horseshoe Canyon Formation of Alberta (Saunders and Pemberton, 1988; Saunders, 1989; MacEachern and Pemberton, 1992; MacEachern, 1994; Pemberton et al., 2001; Gingras et al., 2002) and the Pefkos beachrock of Rhodes Island (Bromley et al., 2009). Specific environmental requirements that permit the construction of *M. spiralis* include: 1) low population densities (Saunders and Pemberton, 1988); 2) abundance of available space (Saunders and Pemberton, 1988); 3) plentiful food resources; and 4) low sedimentation rates (Fig. 5.10). *M. spiralis* occurs in regional to highly localized low population densities in which there is an abundance of available space such that interference from other burrow structures or individuals is minimized. In localized available spaces, *M. spiralis* may occur on bedding planes with other forms of *Macaronichnus*. In these instances, the trace-maker exploited a small patch of available sediment without interference from other individuals (Fig. 5.4D). Regardless of how resource-rich the sediment may have been, the organism had the opportunity to exploit unbioturbated sediment that was likely more nutrient-rich as the sediment had not been previously processed by other burrowing individuals. Kitchell (1979) stated that differential predation and competition pressures could explain the presence of both random and non-random feeding strategies within the same area. Where populations of trace-makers are dense, a random foraging pattern (in regards to trace orientation) is expected (i.e., *M. segregatis or M. simplicatus*), and where competition for food resources is low, a non-random foraging pattern (in regards to predictable orientation) is expected (i.e., *M. spiralis*). Abundant food resources also plays a major role in the formation of *M. spiralis* as focused deposit feeding within a particular locale

suggests the presence of optimal sediment. Sedimentation rates would typically be low to allow for the construction of *M. spiralis* without necessitating vertical adjustment to maintain a position within optimal substrate.

The modern spiraled burrows of *Paraonis* found in intertidal settings resemble that of *Macaronichnus spiralis*. These polychaetes feed on diatoms (rather than sediment) and form spirals 4 to 8 cm in diameter and less than 1 mm in cross-sectional diameter. Risk and Tunnicliffe (1978) reported that food resources of *Paraonis* are concentrated along bedding planes such that systematic mining increases feeding efficiency. In a computer simulation of *Paraonis fulgens* spiraling behavior, Papentin (1973) suggested that avoiding cross-over of other burrow paths in high population densities may have led to the evolution of meandering and spiraling. However, *P. fulgens* can migrate to other bedding surfaces, similar to *M. spiralis* trace-makers, so the worms are seldom required to cross-over previously constructed burrows.

Similar rationale can be used to explain the evolution of *Macaronichnus spiralis*. The occurrence of small, irregular *M. spiralis* in association with *M. segregatis* (Fig. 5.4D) may have initially evolved as a result of limited food resources. Under intraspecific competition, resource-rich patches were exploited in a more efficient manner through planispiral burrowing. The spiraling nature of these traces minimized the probability of the burrower intersecting other burrow structures due to the areal clustering, thereby enhancing nutrient intake (Saunders and Pemberton, 1988). Once this behavior was established, a trace-maker that encountered a widespread open space could form larger, more complex planispiral configurations. Despite the evolution of this spiraling behavior, *M. spiralis* is rarely observed, although this scarcity can be explained by a few factors. In most densely populated successions, pronounced intraspecific competition could explain the lack of *M. spiralis* traces (Saunders and Pemberton, 1988). Limited bedding-plane exposures in core and outcrop also preclude identification of these ichnofossils. In some successions where bedding planes are visible, curved traces may approach the spiraled form of *M. spiralis* (e.g., Hobbs, 2003). Similar to *Paraonis*, the *M. spiralis* trace-maker is able to forage in 3 dimensions, which may further explain the rare preservation of these structures. Coiling in 3 dimensions may explain the spiraling upwards *Macaronichnus* identified from the Freitag Formation by Bann and Fielding (2004) and Fielding et al. (2007). Bann and Fielding (2004) suggested that this ichnofossil was formed under high sedimentation rates as a form of escape structure.

The planispiral configurations of *M. spiralis* also resemble deep-sea trace patterns such as *Spirorhaphe* (Seilacher, 1977) and *Nereites irregularis* (e.g., Uchman, 2007). Richter (1924) was the first to suggest that spiraling and meandering burrow paths reflect optimal utilization of food resources present within the sediment. A uniform distribution of food, such as in the deep sea, favors the construction of complex grazing patterns that maximize coverage of the area while minimizing cross-cutting of other structures (Raup and Seilacher, 1969). In the deep sea, avoidance of other burrow paths is advantageous in a similar fashion to the shallow marine where food resources may be more abundant, but populations are denser (Kitchell, 1979). Seilacher (1974) interpreted complex flysch traces in terms of evolutionary optimization where more regular, patterned structures generally reflect a more advanced behavior. Based on analogous *Paraonis* burrows and deep-sea traces, *M. spiralis* exhibits a more advanced foraging strategy in comparison to *M. segregatis* and *M. simplicatus* (Fig. 5.9). The random interpenetrations of *M. simplicatus* exhibit no adaptations towards optimizing foraging efficiency, whereas the random avoidance of *M. segregatis* illustrates a moderate degree of foraging optimization. In planispiral form, the length of *M. spiralis* is maximized and the aerial utilization is minimized, which reflects the most advanced or efficient foraging strategy (Fig. 5.9; Saunders and Pemberton, 1988; Saunders, 1989). Preservation of these spiraled traces generally occurs within the foreshore where quiescent conditions (as compared to the shoreface) permit more systematic foraging (e.g., Saunders, 1989; MacEachern and Pemberton, 1992; Bromley et al., 2009).

Harenaparietis n. ichnogen.

Figures 5.13-5.16

Palaeophycus Cant, 1984, p. 547, fig. 8; O'Connell, 1988, p. 389, fig. 5b, d; Pemberton, Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, figs. 97, 98; Sadeque, Bhattacharya, MacEachern and Howell, 2007, fig. 13b.

Palaeophycus haberti Fielding, Bann and Trueman, 2007, fig. 25c.

Palaeophycus tubularis Fielding, Bann and Trueman, 2007, fig. 25c.

Palaeophycus tubularis Rouble and Walker, 1997, fig. 10 (=?*Harenaparietis*).

Planolites sp. Chisholm, 1970, p. 24, pl. 1, figs. 1-4; Handford, 1986, fig. 7c, text-fig. 8c.

Planolites sp. Heinberg, 1974, p. 15, text-fig. 9b (=?*Harenaparietis*)

non *Macaronichnus* MacEachern, 1994, fig. IV-4g, h; Saunders, MacEachern and Pemberton, 1994, p. 339, fig. 6b; Brekke, 1995, p. 83, figs. 18, 21d, 22a-d, 34a, 36a, b; Hubbard, Pemberton and Howard, 1999, fig. 18d; Spila, Pulham, Saunders, MacEachern, Robbins and Sinclair, 2001, figs. 95b, 106; Hobbs, 2003, figs. 3.2f, 6.2; Bann and Fielding, 2004, p. 291, 293, 294, 296, 299, figs. 7b, c, 8a-c, 9b, c, e, 10a, c-e, 13b, 14d; Hubbard, Gingras and Pemberton, 2004, fig. 8g; Fielding, Bann and Trueman, 2007, figs. 10a, 19e, 25g, h; MacEachern, Pemberton, Bann and Gingras, 2007, fig. 10b; Sadeque, Bhattacharya, MacEachern and Howell, 2007, fig. 10c (=*Harenaparietis*).

non *Macaronichnus segregatis* Curran, 1985, p. 263-264, pl. 1, fig. b-d, pl. 2, fig. a; Maples and Suttner, 1990, p. 870, figs. 12.1, 12.9, text-fig. 13; Tamura and Masuda, 2005, p. 1383, fig. 7c; (=*Harenaparietis*).

non *Macaronichnus segregatis* Hunter and Clifton, 1982, p. 135, fig. 4c; Głuszek, 1998, p. 532-533, fig. 11a, b (=?*Harenaparietis*).

non *Macaronichnus simplicatus* Raychaudhuri and Pemberton, 1992, fig. 6e; MacEachern, Bann, Bhattacharya and Howell, 2005, fig. 4e; DesRoches, 2008, figs. 3.1.2g, 3.1.4d (=*Harenaparietis*).

Para-*Macaronichnus* Hoffman, 2008, p. 49, figs. 2.8a, e, 2.9a-c, 2.10, 2.11a, 2.12b, c.

"burrows of ?Haustoriid amphipods" Radwanski, Friis and Larsen 1975, p. 237-239, fig. 10.

"Horizontalschliff" Häntzschel and Reineck, 1968, tafel 14, fig. 1.

"irregular horizontal pipes" Chisholm, 1968, p. 116 (=?*Harenaparietis*).

"small meniscus filled tunnels" Heinberg, 1974, p. 15-17, text-figs. 1e, 3c, d, 7, 8 (=?*Harenaparietis*).

Type species—Harenaparietis reprobus n. ichnosp.

Diagnosis—Cylindrical, commonly interpenetrating, locally branching, predominantly horizontal to slightly inclined burrows concentrically lined with darker mineral grains in conjunction with available fines (silt and clay). Infills closely resemble host sediment or may display a reduction in darker mineral grains and fine grained material and may contain irregular backfills. The junction

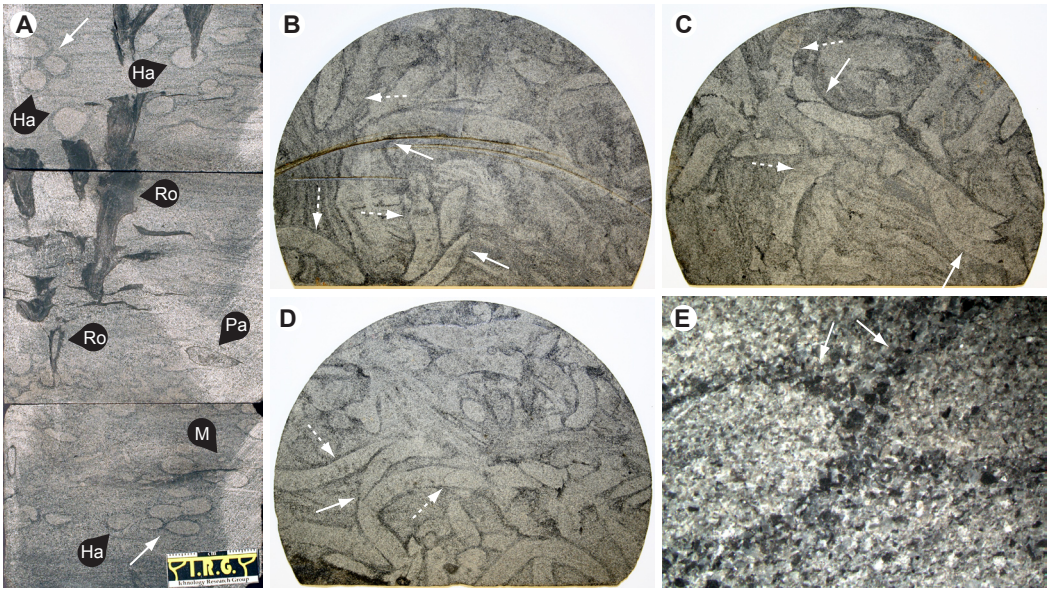

FIGURE 5.13—Holotype specimens of *Harenaparietis* from the Bluesky Formation well 07-27-072-13W6 in Alberta, Canada. **A:** Slabbed core containing *Harenaparietis* (Ha), *Rosselia* (R), *Macaronichnus* (M) and *Palaeophycus* (Pa). Note the circular to ovate cross section and thick concentric lining of *Harenaparietis*. **B-D:** Core slices displaying the successive probes of *Harenaparietis* (solid arrows) and meniscate backfills (dashed arrows). **E:** Close-up view of two abutting *Harenaparietis* from the slabbed core. Note the concentration of dark mineral grains and small degree of fines in the lining and similarity of the infill and host sediment composition.

between the infill and lining is sharp and the lining to host sediment junction ranges from moderately diffuse to sharp.

Etymology—From the Latin words “harena” for sand and “parietis” for wall, which is in reference to the sandy burrow wall lining. Reprobus is in reference to the probing nature of the burrow structures whereby successive probes cross-cut earlier formed tubes.

Holotypes—Collected by Tom Saunders from the Bluesky Formation (07-27-072-13W6), Sinclair Field area, West Central Alberta, in storage at the University of Alberta, Edmonton, Alberta, Canada – TF026 (Fig. 5.13A, E) and TF027 (Fig. 5.13B, D).

Description—In cross section, burrows are typically circular to slightly ovate depending on the degree of compaction. The diameter of structures is variable (2-15 mm), but is generally 5-10 mm. Traces are often clustered locally (Figs. 5.13A, 5.14E, F, 5.15A, C), and may show evidence of collapse prior to infill such

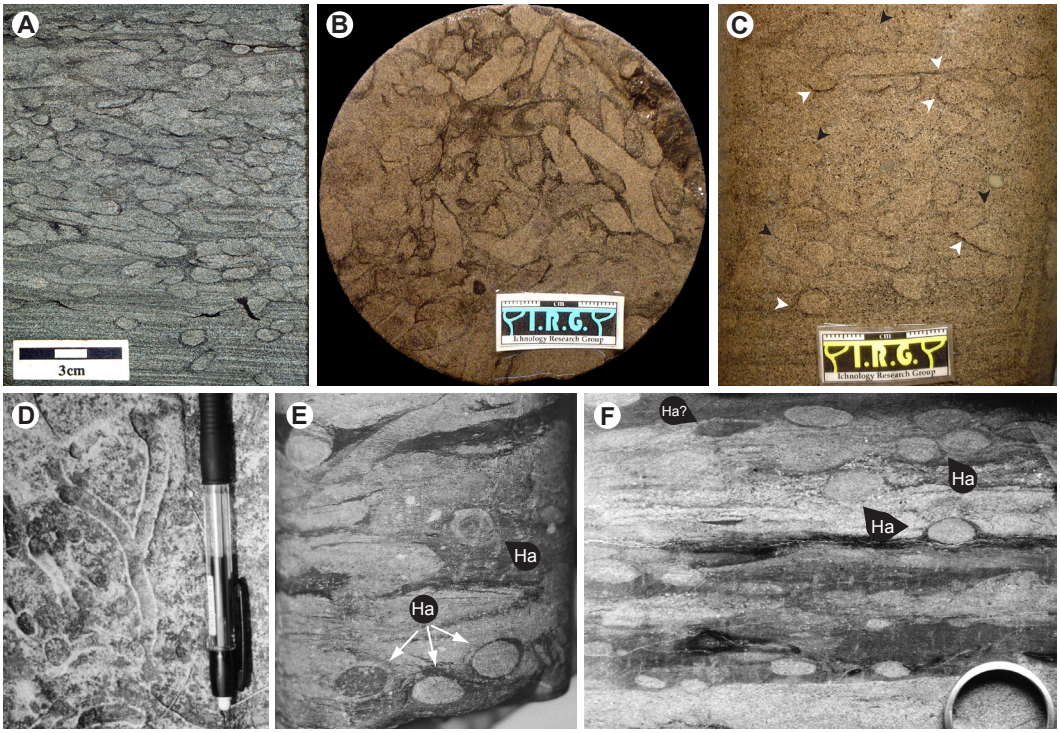

FIGURE 5.14—*Harenaparietis* examples from various units. **A:** Traces display distinctive interpenetration of structures, and some examples display relatively sharp lining/host sediment boundaries while other traces exhibit more diffuse lining/host sediment junctions. Trace infills display a low to moderate degree of segregation of minerals as compared to the host sediment (Bluesky Formation, well 06-10-075-08W6). **B:** Plan view demonstrating the interpenetration and backfilling of *Harenaparietis* from the Falher D Member of the Spirit River Formation (photo courtesy of Trevor Hoffman; 06-13-068-11W6, depth 2280.5 m). The traces display variation in burrow infill composition including well segregated felsic infills, infills resembling surrounding host sediment and infills containing slightly darker infills as compared to the host rock. **C:** *Harenaparietis* in cross section from the Falher D Member of the Spirit River Formation (photo courtesy of Trevor Hoffman; 11-07-068-12W6, depth 2507.6 m). These examples show weakly defined ichnofossil walls (black arrows) with some examples showing more distinct walls in which concentrations of more mafic minerals or fines are present (white arrows). Infills also closely resemble the composition of the host sediment where linings are less distinctive. **D:** Branching *Harenaparietis* from Cattle Creek Nianda, Queensland (photo courtesy of Kerrie L. Bann and Christopher R. Fielding). **E:** *Harenaparietis* (Ha) exhibiting variation in infill and lining based on local lithology. Core (approximately 8 cm in diameter) from the Freitag Formation, GSQ Springsure –17 (photo courtesy of Kerrie L. Bann and Christopher R. Fielding). **F:** *Harenaparietis* (Ha) exhibiting variation in trace infill and lining based on nearby lithology. Note the subtly of some traces and the clarity of other structures which contain more fines in the lining. Core from the Freitag Formation, Rolleston Core –11:2 (photo courtesy of Kerrie L. Bann and Christopher R. Fielding).

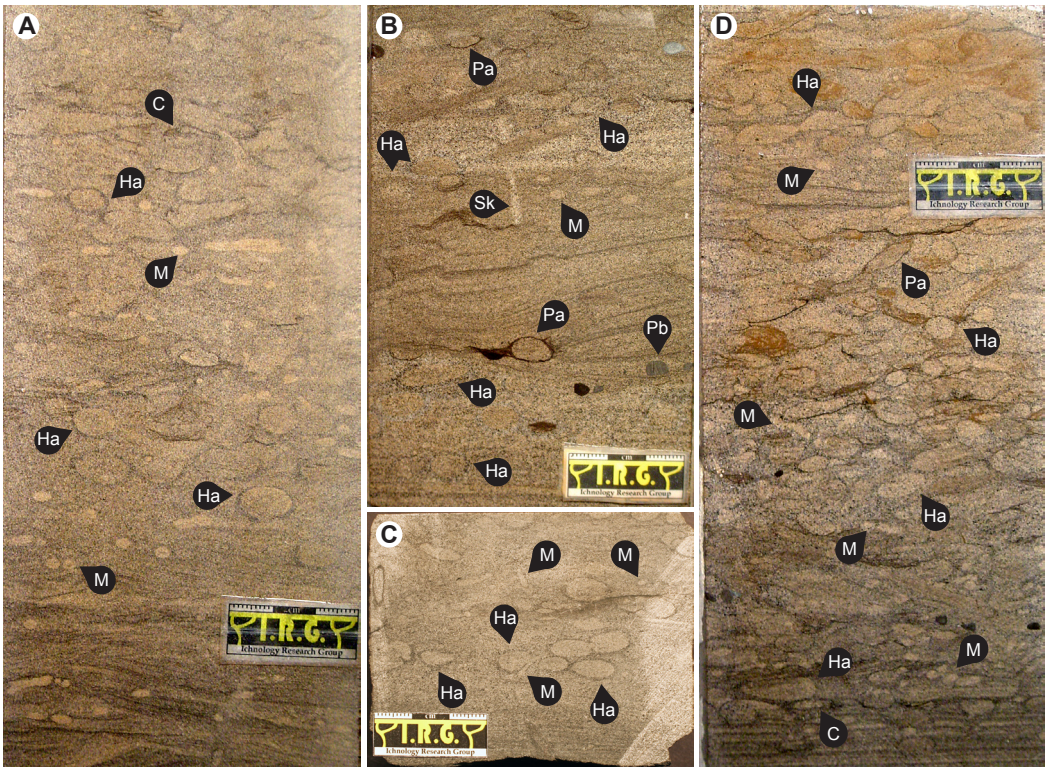

FIGURE 5.15—*Macaronichnus* (M) occurring in conjunction with *Harenaparietis* (Ha) in core. **A:** Small *Macaronichnus* occurring with *Harenaparietis* from the Falher D Member of the Spirit River Formation, Alberta (photo courtesy of Trevor Hoffman). Note the variation in degree of mineral segregation where *Macaronichnus* shows strong segregation while *Harenaparietis* shows weak or no segregation of the infill in comparison to the host sediment. *Harenaparietis* also displays distinct linings whereas *Macaronichnus* mantles range from distinct (at the base of the core) to indiscernible from the host sediment at the top of the core. Collapsed *Harenaparietis* (C) are also present. **B:** Small *Macaronichnus* occurring with subtle *Harenaparietis*, which may be a function of a lack of fines within sandier intervals from the Falher D Member of the Spirit River Formation, Alberta (photo courtesy of Trevor Hoffman). There are also scattered *Palaeophycus* (Pa), small pebbles (Pb), and *Skolithos* (Sk). Note the difference in linings between *Harenaparietis* and *Palaeophycus*. **C:** scattered *Macaronichnus* cross cutting *Harenaparietis* from the holotype (TF=026). Unlike the scattered *Macaronichnus*, *Harenaparietis* displays obvious clustering. **D:** Pervasively burrowed sediment containing *Harenaparietis* (Ha), *Macaronichnus* (M), *Palaeophycus* (Pa), and collapsed *Harenaparietis* (C) from the Falher D Member of the Spirit River Formation, Alberta (photo courtesy of Trevor Hoffman). The abundance and mixing of trace fossils makes it difficult to discern individual structures.

that there is only a lining preserved (Fig. 5.15A, C). Cross-cutting and abutting of tubes is common and depends upon the density of structures. In plan view, rare branching is observed (Fig. 5.14B, D), and burrows display tapered terminations especially with associated clustering of tubes (Fig. 5.13B, C). These ichnofossils tend to occur in fine-grained sands that also may contain a small fraction of silt and clay. However, one occurrence has been observed from a limestone in which light carbonate grains formed the infill and darker peloids were used to form the lining (cf. Handford, 1986).

Harenaparietis is primarily characterized by a lining and infill exhibiting mineralogical and often lithological segregation. The lining is generally thick (0.1 to 2 mm) and evenly distributed around the burrow with evidence suggesting concentric lamination within the lining (Fig. 5.13E). Composition of the lining can include: micas (biotite, muscovite), heavy minerals, and fine-grained or carbonaceous material. With increasing incorporation of fines, the lining appears darker in colour and is generally thinner (Fig. 5.14A) as compared to sandier wall linings (Fig. 5.13A). The lining may possess tangential orientation of grains (primarily micas) throughout the lining (from the host sediment to infill boundary) suggestive of formation over a period of time. The infill can resemble the host sediment closely (Figs. 5.13E, 5.14C, 5.15A) or exhibit substantial mineralogical segregation in which the infill is lighter in colour than the host sediment (Figs. 5.13A, 5.14B). Infills are commonly dominated by quartz with a paucity of micaceous material and may contain a higher proportion of coarser grained material as compared to the host sediment. The infill commonly contains meniscate structures that sharply truncate against the inner lining boundary and display variable thickness, distribution, and mineralogy (Fig. 5.13B-D, 5.14B). The composition of infills may vary lithologically between adjacent individual tubes (Fig. 5.14B, E, F; e.g., Chisholm, 1970, plate 1, figs. 1-4; Bann and Fielding, 2004, figs. 9b, c, 10d). The lining also can vary vertically as the lithology and concordant available sediment varies (e.g., Handford, 1986, fig. 7c). Burrows may also contain "tubular tempestites" or laminae deposited from passive sedimentation.

Discussion—This newly defined ichnogenus was first documented by Häntzschel and Reineck (1968) as "Horizontalschliff," which displayed obvious reprobing and branching of clustered tubes. Subsequently, Chisholm (1970) identified an "annfield form of *Planolites*" described as backfilled and lined by mica and

carbonaceous material, and specimens also displayed successive probing with variable infill composition. *Planolites* with a concentration of tangentially oriented mica surrounding the burrow fill and related "small meniscus filled tunnels" lined with tangential mica grains were described by Heinberg (1974). In this study, Heinberg (1974) suggested that mica was excluded prior to ingestion of sediment and then pressed into the burrow wall to produce the vague mica zone/host boundary. The sharp mica zone/infill boundary was interpreted as reflecting a depositional time gap, which suggests that Heinberg was possibly describing *Harenaparietis*. Radwanski et al. (1975) identified *Harenaparietis* as "burrows of ?haustoriid amphipods" and interpreted the structures as formed by active vagile animals that burrowed rapidly through the sediment.

Following establishment of the *Macaronichnus* ichnogenus by Clifton and Thompson (1978), *Harenaparietis* was most commonly identified as *Macaronichnus* and to a lesser extent *Palaeophycus*. A few notable examples include those documented by Hunter and Clifton (1982) in carbonaceous-micaceous sandstone that were reported as resembling *M. segregatis*. The resemblance to *Macaronichnus* in combination with finer-grained sediment indicates that these traces may have in fact been *Harenaparietis*. The Y-shaped structure observed by Curran (1985) reflects the rare branching nature of *Harenaparietis*. Examples presented by Handford (1986) displayed variation in infill and lining through a sandier-upwards bed such that linings became thinner and less distinct upwards as the proportion of fine-grained sediment decreased. Saunders et al. (1994) also recognized this trace as a "unique form of *Macaronichnus*" constructed by grain-selective deposit-feeders, in which the traces appeared to be closely associated with *Palaeophycus tubularis*. Regardless, Saunders et al. (1994) suggested that this trace reflected the activity of organisms separate from the *Macaronichnus* trace-makers that colonized the toe-of-the-beach.

Bromley (1996) indicated that structures containing a "zoned fill" can be categorized as one of the following: (1) open burrows that are inhabited and irrigated over long periods of time; and (2) structures formed through sediment processing by mobile deposit feeders undergoing continuous locomotion within the substratum. The structures of *Harenaparietis* reflect aspects of both behaviors in such a way that feeding and defecating occurs within the subsurface (Fig. 5.16). Burrows remain open for short periods of time and also are formed through sediment processing whereby burrow linings contain segregated heavy

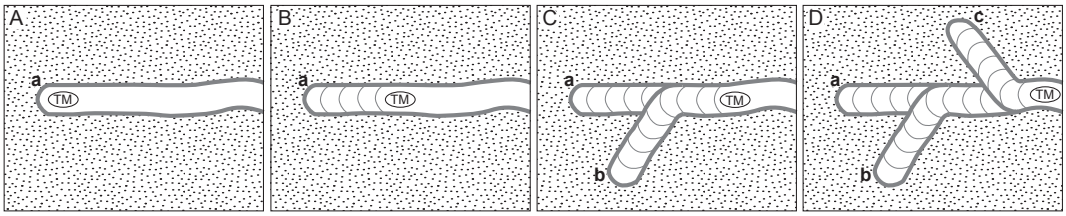

FIGURE 5.16—Formation of *Harenaparietis*. TM=Trace-maker. **A:** Segregation of mafic and micaceous grains in addition to fines forms the wall lining (a), which occurs with concordant ingestion of felsic mineral grains. **B:** Backfilling of the initial burrow (a) with ingested and processed felsic material. **C:** Formation of wall lining (b), ingestion of felsic mineral grains, and subsequent backfilling of burrow (b). **D:** Formation of wall lining (c), ingestion of felsic mineral grains, and subsequent backfilling of burrow (c).

and micaceous mineral grains and even silt and clay. Evidence suggesting the formation of a lining rather than a mantle includes: the presence of collapsed burrows, branching structures and meniscate structures that sharply truncate against the burrow wall which indicate a depositional time gap between the two features. Bromley (1996) recognized the branching Y-shaped trace documented by Curran (1985, pl. 1, fig. C) to be similar to that of *M. segregatis*. However, based on the branching morphology, Bromley (1996) suggested that the trace could not be trophically or ichnotaxonomically equivalent to any form of *Macaronichnus*. As *Macaronichnus* is defined as structures in which the mantle is formed concurrently with the infill during active backfilling of the infill. This Y-shaped structure may reflect actual branching (Fig. 5.11C) or possibly false branching produced by the intersection of two traces (Fig. 5.11A). Most likely, infrequent branching of *Harenaparietis* was preserved as the Y-shaped structure from Curran (1985) as it resembles intersections seen in the *Harenaparietis* holotype (Fig. 5.13), the Falher D Member (Fig. 5.14B; Hoffman, 2008), the Freitag Formation (Fig. 5.14D; Bann and Fielding, 2004), and in Maples and Suttner (1990, fig. 12.1).

The characteristics that distinguish *Harenaparietis* reflect aspects of both *Palaeophycus* and *Macaronichnus*. Bann and Fielding (2004) also found that these traces encompassed features of multiple ichnofossils (*Palaeophycus*, *Planolites*, and *Macaronichnus*), as did Hoffman (2008; *Palaeophycus* and *M. segregatis*). The distinguishing attributes that suggest a time gap between formation of the lining and infill (e.g., sharply truncating meniscate fill, burrow collapse and branching) are not always present or discernible in cross-section. Accordingly, the collective morphology—abundant trace interpenetrations and clustering—in conjunction with mineralogical segregation closely resembles

that of *M. simplicatus*. However, the nature of the burrow components can be used to differentiate this ichnogenus from *Macaronichnus*. *Harenaparietis* tends to be more circular in cross section as compared to *Macaronichnus*; however, *Harenaparietis* may also be ovate depending on the sediment properties, lining characteristics, and degree of compaction. The lining of *Harenaparietis* is also thicker and evenly distributed concentric around the burrow infill with tangential orientation of platy minerals throughout the lining suggesting concentric lamination. In addition, *Harenaparietis* generally displays a lower degree of segregation of light colored, felsic minerals in the infill as compared to typical *Macaronichnus* (Hoffman, 2008). This relationship is especially apparent where the two ichnogenera are found within the same unit (Fig. 5.15A, B, D). The coexistence of *Harenaparietis* and *Macaronichnus* was also observed in the Upper Falher of the Spirit River Formation by Hobbs (1999). Infills of *Harenaparietis* also contain irregular meniscate structures that contrast the more regular meniscate structures found within *Macaronichnus*. The prominence of *Harenaparietis* linings also contrasts the indistinct mantles that may be found with some examples of *M. simplicatus* and *M. segregatis* (Figs. 5.1, 5.2), and the diameter of *Harenaparietis* tends to be greater than most occurrences of *Macaronichnus*. The presence of a lining containing fine-grained material resembles that of *Palaeophycus*; however, the presence of actively segregated minerals within the lining suggests separation from the *Palaeophycus* ichnogenus. In addition, *Harenaparietis* also displays clustering of structures and cross-cutting of adjacent tubes, which is not characteristic of *Palaeophycus*. The uniqueness of this new ichnogenus can only be properly ascertained through careful analysis of the grain sorting, burrow components and collective trace morphology.

In describing traces interpreted as *Macaronichnus*, Bann and Fielding (2004) reported a range of infills including: passive, active and meniscate. These structures are, in fact, *Harenaparietis* as *Macaronichnus* is, by definition, actively rather than passively infilled. The infills of these *Harenaparietis* also vary in coloration and mineralogy (Fig. 5.14E, F; Bann and Fielding, 2004, figs. 9c, 10d, 13b). Variation in infill mineralogy/coloration of adjacent or even overlapping tubes suggests that sediment was sourced from different localities. Some tubes may have been passively infilled with different surface sediment, or pockets or laminae of differing lithology may have been preferentially mined by the trace-maker and later backfilled into tubes. Especially in the case of Figure 5.14E, variation in burrow infill mineralogy/lithology is likely due to sediment sourced

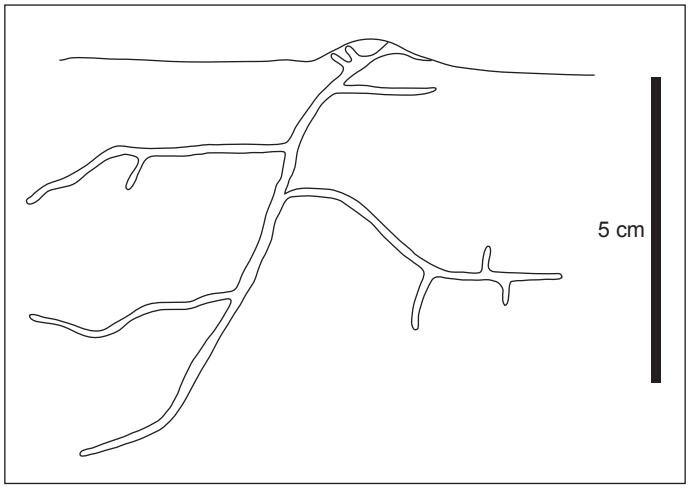

FIGURE 5.17—A typical *Lumbrineris* cf. *latreilli* burrow constructed under laboratory conditions in a thin-walled aquarium. Modified from Petch (1986).

from different localities within the interbedded sandstone and mudstone.

Based on the core slices from the Bluesky Formation (Fig. 5.13B-D), *Harenaparietis* is interpreted to reflect probing of adjacent sediment packages (Fig. 5.16). Mineralogical and lithological segregation occurs during the formation of an open tube, which remains open until the trace-maker backfills egested sediment into this newly constructed burrow (Fig. 5.16B). The overlapping or cross-cutting of individual tubes suggests that infilling occurs relatively rapidly such that older burrows can be cross-cut by newly formed tubes (Fig. 5.16C, D). The formation of these burrows involves segregation of sediment such that mafic and micaceous grains in addition to fines are segregated and used to form the burrow wall while the felsic component of the host sediment is ingested (Fig. 5.16B). The addition of fines to the burrow wall serves to enhance stabilization by filling in pore spaces between segregated mineral grains. Ingested grains are then processed by the animal and egested as backfilled sediment into the newly constructed open burrow. This allows for subsequent cross-cutting of adjacent burrow structures as the organism successively probes the sediment. In the formation of these burrows, branching is possible (e.g., Fig. 5.14D) as well as passive infilling (e.g., Bann and Fielding, 2004).

A possible analogous modern burrower, *Lumbrineris* cf. *latreilli*, was described by Petch (1986) as a deposit-feeder that ingests subsurface sediment while constructing semi-permanent burrows (Fig. 5.17). The burrows are mucous-lined and branch off of a main tunnel (Petch, 1986). Worms first construct the main tunnel that is generally connected to the sediment-water interface. Feeding

then takes place in the side branches where the worms selectively ingest smaller particles likely due to greater surface area per unit of volume ingested (Petch, 1986). This polychaete appears to display the deposit-feeding, branching, and probing behavior interpreted from *Harenaparietis*; however, this modern polychaete is relatively small, and it is uncertain whether it backfills older side tunnels.

Very little is known about *Harenaparietis*; however, the process of successively probing, or reprobing, best explains the common cross-cutting nature of the traces. If the ichnofossils reflected a large network of open burrows, cross-cutting of open tubes would result in burrow collapse. Rather, cross-cutting of successive sediment probes following backfilling of earlier formed tubes, produces structures that neatly cross-cut one another. In plan view, this reprobing appears as overlapping of adjacent burrow structures that simultaneously terminate (i.e., display tapered ends) within a particular locality (Figs. 5.13B, D, 5.14B). This form of branching was called "primary successive branching" (Fig. 5.11) by D'Alessandro and Bromley (1987). A possible explanation for this reprobing behavior is the need for the trace-maker to maintain open irrigated burrows in conjunction with deposit-feeding activities. Burrows may be connected to the sediment surface while trace-makers actively mine sediment within a particular locale. If this is the case, reprobing of sediment adjacent to a semi-permanent burrow open to the surface would provide a relatively efficient feeding strategy whereby available sediment is systematically mined despite overlap of structures.

The other aspect of these traces that requires some explanation is the formation of a wall lining in addition to deposit-feeding activities. There may have been an adequate time gap between the ingestion and egestion of processed sediment which required open burrows to be constructed for later waste disposal. Most likely, unstable and shifting sediment required trace-makers to stabilize burrow walls. In Figure 5.15B, C, and D, *Harenaparietis* is clearly cross-cut by *Macaronichnus*. Knowing that *Macaronichnus* is a deeper-tier ichnofossil (cf. Pemberton et al., 2001), this suggests that *Harenaparietis* is formed within a shallower tier and is successively cross cut by deeper-tier *Macaronichnus*. If *Harenaparietis* exists within a mid-tier setting (i.e., centimeters from the sediment surface), burrow-wall stabilization would be an ideal adaptation to prevent burrow collapse. In contrast, deep-tier *Macaronichnus* colonized the sediment at a depth in which shifting sediment did not influence their deposit-feeding activities. This

would explain the occurrences of *Macaronichnus* and *Harenaparietis* described by Hoffman (2008) from the Falher D Member of the Spirit River Formation. Hoffman (2008) observed the abundance of *M. segregatis* to decrease upwards while *Harenaparietis* (described as Para-*Macaronichnus*) increased upwards through the same interval. The presence of *Harenaparietis* demarcates the upper portion of the bed while *Macaronichnus* reflects the successive deeper-tier colonization of the same sediment.

The co-occurrence of *Macaronichnus* and *Harenaparietis* in the Falher D Member lead Hoffman (2008) to interpret the traces to have been constructed by the same organism (likely a polychaete) in which *Macaronichnus* reflected activity of juvenile forms (based on trace diameters). It is unlikely that these traces were formed by the same animal as the two traces reflect activity within separate tiers. In the study by Dafoe et al. (2008b), juvenile *Euzonus mucronata*, which form modern *Macaronichnus*-like biogenic structures, were actually found closer to the sediment surface as compared to the adult population. These polychaetes require respiration at the sediment surface, and juveniles burrow more slowly than the adult counterparts, as such, juveniles maintain a position closer to the sediment surface. Based on these analogous modern polychaetes, it is unlikely that juvenile forms of the same animal would burrow beneath the adult population to cross-cut the larger biogenic structures. Furthermore, the two ichnogenera reflect inherently different behavioral adaptations—one probing the sediment with lined structures and the other segregating minerals during continuous deposit-feeding activities.

The sedimentary environment in which *Harenaparietis* typically occurs corresponds to shoreface deposition and in association with *Rosselia* (Fig. 5.13A), *Palaeophycus* (Fig. 5.15A, B, D) and wave rippled or HCS sandstone (cf. *Macaronichnus* sp., Brekke, 1995; Maples and Suttner, 1990). *Harenaparietis* can be found in the lower to middle shoreface (e.g., O'Connell, 1988), the upper shoreface or barrier setting (e.g., Hubbard et al., 2004; Hoffman, 2008), wave-reworked mouth bar deposits (e.g., Bann and Fielding, 2004), delta front (e.g., Bann and Fielding, 2004; Fielding et al., 2007; Hoffman, 2008), and prodeltaic tempestites (Fielding et al., 2007). Unlike many occurrences of *Macaronichnus*, *Harenaparietis* is generally found in water depths below the shoreface-foreshore transition. Under such high-energy shoreface conditions, burrow linings are an optimal adaptation to maintain burrow stability of temporary open tubes.

DISCUSSION

Reservoir Properties

Distinguishing between traces that display mineralogical segregation can enhance the understanding of trace-maker behaviors and adaptations that developed in response to the local environmental conditions. In addition, recognition of *Macaronichnus* and *Harenaparietis* plays an important role in determining potential reservoir properties of the rock. Schmidt (2002) suggested that the degree of *Macaronichnus* burrowing and diagenetic history can act to either enhance or decrease overall permeability. For instance, Lerette and MacEachern (2004) determined that the grain selectivity of *Macaronichnus* trace-makers initially enhanced porosity, but also led to diagenetic quartz overgrowths which degraded reservoir productivity. Conversely, *Macaronichnus* in the Bluesky Formation consist of dark chert-mantled traces in which the mantle acts as a "compaction shelter," and the lack of quartz overgrowths also enhanced reservoir properties (Gordon et al., 2008). With regards to mineralogical segregation, Pemberton et al. (2008) found that *Macaronichnus* cryptobioturbation enhanced permeability (Kha) by up to 10 times in the Early Cretaceous Sandstones in Papua, New Guinea by segregating out glauconite. Using MRI images of *M. segregatis* from the Horseshoe Canyon Formation of Alberta, Gingras et al. (2002) concluded that the traces formed a dual porosity-permeability system.

Variation in reservoir enhancement or degradation would also depend on the form of *Macaronichnus* found in the rock. Isolated *Macaronichnus* or *M. spiralis* would unlikely affect the overall characteristics of the sandstone. However, *M. simplicatus* could potentially enhance permeability and porosity as compared to *M. segregatis*. The pathways (burrows) in *M. simplicatus* are more commonly interconnected rather than intertwined as in *M. segregatis*. In comparison to *Macaronichnus*, one would expect variation in reservoir properties with rocks containing *Harenaparietis*. With *Harenaparietis*, the organisms have concentrated fines within burrow walls, producing networks that are potentially sealed off from the host rock. In addition, the reprobed nature suggests that terminations could act as areas for hydrocarbons to pool. Despite the cross-cutting nature of *Harenaparietis*, the degree of inclusion of fine-grained sediment and density of structures would influence the potential to enhance (decreased fine-grained sediment and dense traces) or degrade (abundant fine-grained sediment and low density of traces) reservoir properties. Clearly, recognition and

assessment of traces displaying mineralogical segregation plays an important role in determining the reservoir potential of the rock.

The Future of Ichnotaxonomy

A "uniform approach" to ichnotaxonomy (cf. Bertling et al., 2006) in which ichnotaxobases lie within a predisposed hierarchy may not be the most ideal means of enhancing this key aspect of ichnology. Ichnologists should be open to more dynamic taxonomy in which traces may not always be classified via the traditional means (i.e., typical morphological criteria). Ichnofossils record the preservation of animal activities within a natural system and may not always be neatly categorized. This paper demonstrated the use of unconventional ichnotaxobases—grain sorting and collective trace morphology—in the classification of *Macaronichnus* and *Harenaparietis*. In the case of *Macaronichnus*, grain sorting defines the ichnogenus while collective morphology is inherently tied to ethology and defines the ichnospecies. In contrast, the ichnogenus *Harenaparietis*, often mistaken for *Macaronichnus* in previous literature, is defined on both grain sorting and collective morphology. Bertling et al. (2006) suggested that ichnotaxobases have been given different levels of priority in previous taxonomic assessments based on the subjectivity of the ichnotaxonomist. If we try to develop a consensus over what makes ichnogenera or ichnospecies different from one another, we are likely to miss other, more significant, criteria.

Ichnotaxobases presented within this study have the potential to be applicable to the classification of other ichnogenera and ichnospecies. It was also shown that inherent ethological elements may not always be separated from the description of ichnofossils. Despite the incorporation of ethological elements in the presented ichnotaxonomy the definition of traces based on a single trace-maker remains an unacceptable approach to ichnotaxonomy. Ichnofossils cannot be necessarily attributed to particular trace-makers, as Ekdale et al. (1984) noted, there are basic ichnological principles at work:

1) The same individual or species of animal can produce different structures depending on the expression of behavior.
2) The same individual or species of animal can produce different structures resulting from the same behavior, but in different substrates.
3) Different animals can produce the same structures through similar

behaviors.

4) A structure may be formed by two or more different animals living together or in succession.

There are likely numerous undiscovered biogenic structures, and it is our job, as ichnologists to describe these structures in the most communicable way as to further our understanding of the traces, the exhibited behavior, potential trace-makers and the significance of the structure in an evolutionary and environmental sense.

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CHAPTER 6 – ICHNOLOGICAL ASPECTS OF A NEW FORM OF *PISCICHNUS* IN THE SNAPPER POINT FORMATION, NEW SOUTH WALES, AUSTRALIA

INTRODUCTION

In the Snapper Point Formation (SPF) of the southern Sydney Basin of southeastern Australia, large depressions, interpreted as biogenic in origin, demarcate particular stratigraphic horizons (Fig. 6.1). These ichnofossils are dimensionally and morphologically comparable to the trace fossil *Piscichnus* (Tables 6.1, 6.2). Other plug-shaped trace fossils – *Conostichnus*, *Bergaueria*, *Conichnus*, and *Dolopichnus* – are more regular, ornamented, and generally possess different width-to-depth ratios than the traces observed in the SPF (cf. Pemberton et al., 1988). This study presents an ichnotaxonomic diagnosis for a currently unrecognized form of *Piscichnus* and suggests possible trace-makers and exhibited behaviors associated to construction of *Piscichnus* within the Permian deposits.

Mechanisms of *Piscichnus* Generation

Interpretation of the *Piscichnus* ichnofossil is based upon modern observations of morphologically and dimensionally analogous structures (Table 6.3). Various forms of *Piscichnus* are considered to reflect different: 1) animal behaviors; 2) phylogenetic attributes; and 3) methods of generation. The behaviors exhibited in the formation of *Piscichnus* include protection from predators, nesting, and the pursuit of food resources (Cook, 1971; Feibel, 1987). There are clear indications from the rock record, however, that most *Piscichnus* are associated with predation of infaunal organisms (e.g., Kamola, 1984; Ekdale and Lewis, 1991; Gregory, 1991; Martinell et al., 2001; Gingras and Armitage, 2004; Gingras et al., 2007). Similar feeding relationships have been reported from the present day (e.g., Cook, 1971; Howard et al., 1977; Gregory et al., 1979; Grant, 1983; Oliver et al., 1983b; Nelson et al., 1987; Hines et al., 1997; Levermann et al., 2003; Pearson et al., 2007).

The size and morphology of the causative organism influences the

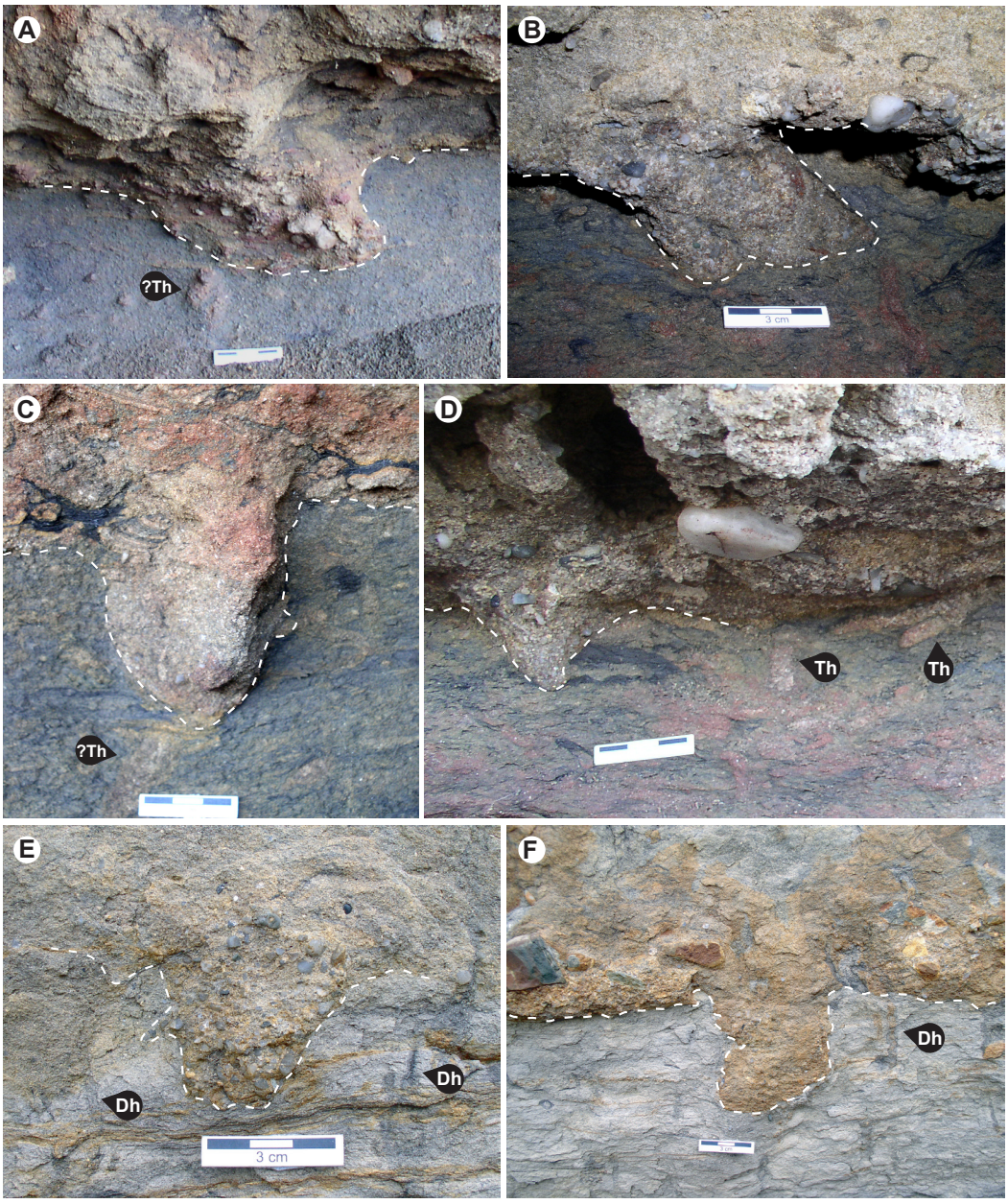

FIGURE 6.1—*Piscichnus* in the Permian Snapper Point Formation, SE Australia. **A, B, D:** Photos from Snapper Point North (near Merry Beach, SE Australia). These traces represent colonization of the same palimpsest surface. **C:** Photo from Snapper Point South reflecting colonization of another palimpsest surface. **E-F:** Photos of traces along a surface from the Clear Point outcrop locality. **A:** An inclined and hooked-shaped depression identified as *P. gregorii*. The trace may be associated with a possible *Thalassinoides* directly below the *Piscichnus*. **B:** An inclined and hooked-shaped *Piscichnus* with two overlapping depressions also regarded as *P. gregorii*. **C:** A conical form of *P. waitemata* that may also be associated with an underlying *Thalassinoides*. **D:** *P. gregorii* occurring with *Thalassinoides* along a stratigraphic horizon. **E:** Columnar-shaped *P. waitemata* infilled with sand and small pebbles. **F:** *P. gregorii* within deposits containing *Diplocraterion habichi*.

Example	Morphology	Width, W (cm)	Depth, D (cm)	W:D ratio	Inclination from horizontal (°) Left side	Right side
1	Cone shaped	7.6	7.9	0.95	70	76
2	Cylindrical	5.5	3.4	1.62	80	54
3	Hooked shaped	11.6	5.9	1.98	30	53
4	Hooked shaped	6.6	5.1	1.29	47	43
5	Hooked shaped	6.5	2.9	2.23	50	45
6	Hooked shaped	8.4	7.6	1.11	86	89
Overall Average		7.7	5.5	1.53	60.5	60.0
Hooked Shaped Average		8.3	5.4	1.65	53.3	57.5

TABLE 6.1—Measurements corresponding to *Piscichnus* documented from the Permian Snapper Point Formation. The measurements were approximated from photographs of the trace fossils, using the scales shown in the photos for reference. The measurements represent the maximum width (diameter) and depth of the trace fossils. Widths are measured at the tops of the traces, and abnormalities in the ichnofossil boundaries are not considered. The maximum width is taken where there is a clear transition from the approximately horizontal surface to the sloped surface of the trace fossil margin. In most cases, the top of the trace fossil is asymmetrical, in that one side of the trace lies above the other. In such cases, the width is estimated along a horizontal line that intersects the vertical position equivalent to both sides of the trace. The width-to-depth ratios are also presented along with the overall inclinations of the trace fossil boundary walls from horizontal.

	Width			Depth			W:D Ratio			
Publication	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Trace fossil
Feibel (1987)	45	135	90	5	15	10	3.00	27.00	9.00	*Piscichnus brownii*
Kamola (1984)			15			20			0.75	*unnamed*
Ekale and Lewis (1991)	20	40	30		50	50	0.40	0.80	0.60	*Piscichnus isp.*
Gregory (1991)	15	30	22.5	15	50	32.5	0.30	2.00	0.69	*Piscichnus waitemata*
Martinell et al. (2001)	9	53	31	32	70	51	0.13	1.66	0.61	*Piscichnus isp.*
Gingras et al. (2007)	20	30	25	10	40	25	0.50	3.00	1.00	*Piscichnus isp.*
Frey and Howard (1981)	3	8	5.5	12	20	16	0.15	0.67	0.34	*Conichnus conicus*
Pemberton et al. (1988)	3.6	8	5.8		20	20	0.18	0.40	0.29	*Conichnus conicus*
Pemberton et al. (1988)	1.8	4	2.9		8	8	0.23	0.50	0.36	*Conichnus papillatus*
This publication	5.5	11.6	7.7	2.9	7.9	5.5	0.95	2.23	1.53	*Piscichnus*

TABLE 6.2—A comparison of width-to-depth ratios of traces from various publications and this study. The minimum width-to-depth ratio reflects the minimum width to maximum depth, and the maximum width-to-depth ratio corresponds to the maximum width to minimum depth ratio. The mean width–to-depth ratio is calculated using the mean width and depth.

	Organism or Structure	Morphology of Structure	Interpreted Behavior	Depositional Setting	Reference(s)	Possibility of Generating SPF Depressions
BIOGENIC	Cephalopods					
	Octopus and squid	Undescribed	Mechanical excavation with arms to uncover prey	Shallow marine	Lane (1960), Hartwick et al. (1978), Hanlon and Messenger (1999)	NO–Mechanical excavation could not have formed the depressions
	Cuttlefish	Undescribed	Water jetting to stir up bottom sediments and expose buried prey	Shallow marine	Wells (1962)	YES--Coleoids and nautiloids both employ jetting and existed in the Permian and ammonoids may also have jetted
	Fish					
	Atlantic Sturgeon	Crescent-shaped depression and adjacent cylindrical hole with a diameter of 5-15 cm and depth of 2-6 cm	Snout forms the crescent-shaped depression and the cylindrical hole is formed by rapid sediment biting for predation	Intertidal mud flat	Pearson et al. (2007)	NO–Morphology is incompatible
	Eelpouts	Small, round, often steep-walled depressions that are up to 10 cm in depth	Fish partially bury themselves anterior end downward	Continental slope	Stanley (1971)	NO--Depressions are mechanically excavated
	Flounder and skates	Pits are 2-3 cm wide and 3-5 cm deep with a shallow entry mark	Sediment biting to forage upon amphipods and bivalves by striking forward and down at the sediment	Intertidal sand and mud flats	Risk and Craig (1976), McCurdy et al. (2005)	NO--Morphology and mechanism of formation are incompatible
	Tetraodontiformes (triggerfish and allies)	Undescribed	Water jetting to uncover buried prey from an inverted, vertical position	Shallow seafloor near reef	Hobson (1965), Reinthal et al. (1984), Fraser et al. (1991), Turingan and Wainwright (1993), Helfman et al. (1997), Chen et al. (2001)	YES--Fishes of Class Actinopterygii resemble ancestral fishes which originated in the Lower Devonian
	Tilefish	Simple vertical shafts 10-60 cm in diameter and 45-60 cm deep, to funnel-shaped burrows 1-5 m diameter and 1-3 m deep. Also contains other invertebrate burrows near the sediment surface	Fish first occupies an invertebrate burrow, further excavated by fin and body movements and invertebrate burrowing	Submarine canyon, shallow seafloor	Able et al. (1982), Twitchell et al. (1985), Able et al. (1987)	NO–Morphologically incompatible and mechanically excavated in stiff clay
	Rays, Skates, Flatfish	Shallow, typically rounded to ovate depressions 6-100 cm in diameter and 2-10 cm in depth, and may possess a surrounding sand ridge 3-4 cm high	Produced by organisms using undulatory movements (wing flapping in rays) to burying themselves within the sediment or expose prey	Nearshore, tidal flats, estuarine sand bars and channels, and continental slopes	Cook (1971), Stanley (1971) Howard et al. (1977), Grant (1983), Martinell et al. (2001)	NO--Depressions are too shallow and modern rays and skates did not evolve until the Jurassic
	Eagle Rays	Approximately cylindrical excavations with a steeper side to the front of the excavation which is 14-30 cm in diameter and 30 cm or less in depth	Excavation through hydraulic water jetting from the mouth or gill clefts for predation.	Intertidal and sub-tidal sand flats	Gregory et al. (1979), Hines et al. (1997)	POSSIBLE--Modern rays did not evolve until the Jurassic; however related holocephalans filled the niche of rays from the Devonian to Jurassic (unknown if holocephalans jetted water)
	Grey Whale	Oblong, bowl-shaped depressions 100 by 200 cm in size and 50 cm deep	Sediment biting to feed on benthic invertebrates	Shallow sea floor	Oliver et al. (1983a)	NO--Dimensions are too great and the structure is oblong in shape
	Turtles (Loggerhead)	Circular pits to straight, meandering, hooked and horseshoe-shaped paths typically 1.5 m wide and 30-45 cm deep at the front	Excavation through use of foreflippers to carve the wall in front in order to feed upon infauna	Bay	Preen (1996)	NO–Morphology does not resemble Snapper Point Formation pits
	Walrus	Cone-shaped depressions with or without a central shaft. Depth ranges from 11-32 cm and width ranges from 14-45 cm	Excavation occurs through "rooting" by the snout followed by hydraulic jetting to uncover molluscs.	Shallow sea floor	Oliver et al. (1983b), Kastelein and Mosterd (1989), Levermann et al. (2003)	NO–Walruses evolved in the Late Miocene
PHYSICAL	Gutter cast	Typically elongate, sharp-walled excavations generally more than 1 m in length and centimeters to decimeters in depth. May be symmetrical to asymmetrical, with local flat bases, overhanging sides and rarely deform underlying laminae	Form in cohesive mud by water flowing in helicoidal paths with horizontal axes	Storm dominated shallow marine	Whitaker (1973), Myrow (1992a)	NO–Formed in cohesive mud and no evidence of linearity in Snapper Point Formation structures
	Pot cast	Cup-shaped to cylindrical sandstone pillars from infilling of rounded erosional depressions 1-20 cm in diameter with a raised central point in the base	Formed by spiraling eddy of water that exits up through the center of the vortex	Storm dominated shallow marine	Myrow (1992b, 2003)	NO–Likely formed in cohesive sediment, and none of the Snapper Point Formation structures show the raised central high

TABLE 6.3 (Previous page)—Complied descriptions and interpretations of excavations constructed by modern organisms and processes. The possibility of analogous ancient organisms or similar physical processes producing the structures in the Snapper Point Formation (SPF) is briefly explained, and expanded upon in the text.

Piscichnus or *Piscichnus*-like structures that are ultimately formed (Cook, 1971). Organisms known to produce modern *Piscichnus*-like burrows (Fig. 6.2; Table 6.3) include: rays (Cook, 1971; Howard et al., 1977; Gregory et al., 1979; Grant, 1983; Martinell et al., 2001); skates, flatfish and flounder (Cook, 1971; Stanley, 1971; Risk and Craig, 1976; McCurdy et al., 2005); sturgeon (Gingras and Armitage, 2004; Pearson et al., 2007); eelpouts (Stanley, 1971); tilefish (Able et al., 1982, 1987; Twitchell et al., 1985) and walrus (Oliver et al., 1983b; Nelson et al., 1987; Gingras et al., 2007). The principal methods used by these organisms to form *Piscichnus* include: 1) hydraulic jetting into the substrate to induce resuspension of sediment, sediment winnowing and lamination (Fig. 6.2A, D; e.g., Gregory et al., 1979; Kastelein and Mosterd, 1989; Gregory, 1991; Hines et al., 1997; Levermann et al., 2003; Gingras and Armitage, 2004; Pearson et al., 2005; Gingras et al., 2007); and 2) mechanical excavation of the substrate through intrusion, sediment biting, undulatory movements, "wing-flapping" (e.g., rays), or digging, where infill occurs through pit-margin collapse and passive sedimentation (Fig. 6.2B, C; e.g., Risk and Craig, 1976; Howard et al., 1977; Able et al., 1982; Feibel, 1987; Martinell et al., 2001; Levermann et al., 2003; Gingras and Armitage, 2004; McCurdy et al., 2005; Pearson et al., 2005; Pearson et al., 2007; Gingras et al., 2007).

This study concerning *Piscichnus* from the Permian Snapper Point Formation of SE Australia, aims to: 1) classify the observed traces; 2) interpret the behavior(s) exhibited by the trace-maker(s); 3) evaluate the unusual, stratigraphically limited preservation of these traces; 4) postulate the method of formation of the *Piscichnus*; and 5) identify possible trace-makers.

Geological Setting

The SPF comprises part of the Shoalhaven Group and is Tastubian to Sterlitamakian (Early Permian) in age (Fig. 6.3; Bann et al., 2004). The formation stratigraphically overlies the Pebbley Beach Formation and outcrops along the SE coast of New South Wales, Australia (Fig. 6.4). The SPF was deposited in the southern Sydney Basin (Carey, 1978), which comprises part of the larger Sydney-

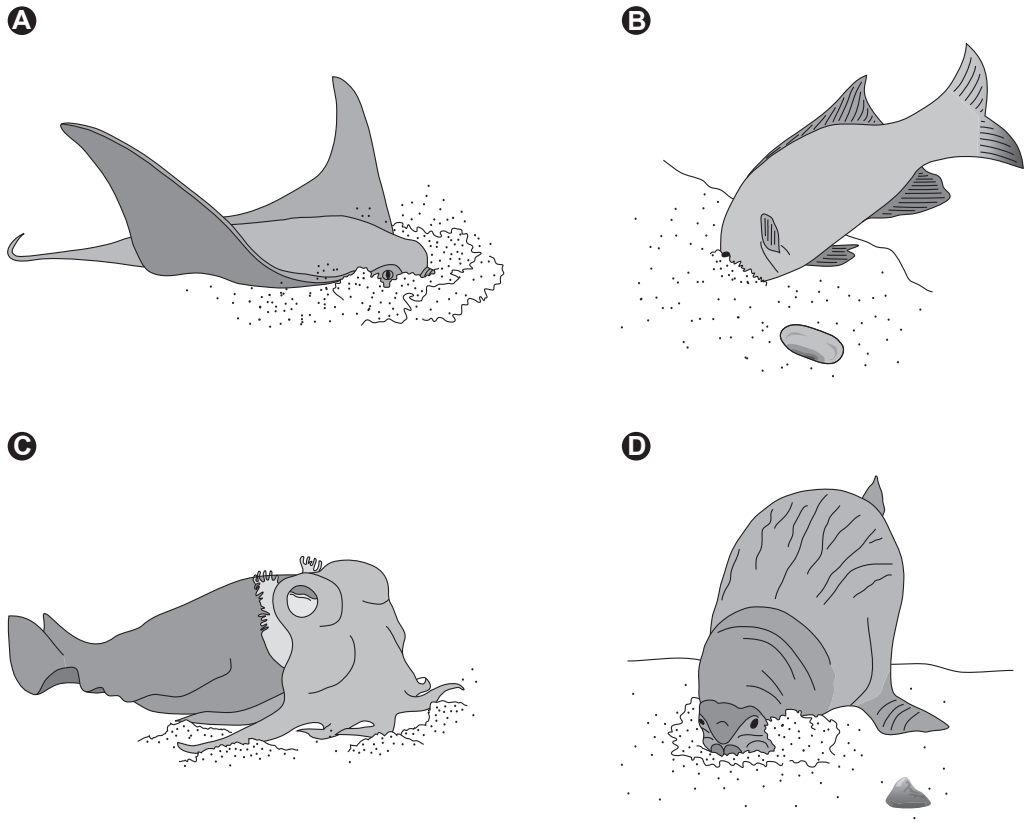

FIGURE 6.2—Modern animals capable of forming *Piscichnus*-like structures. The animals include: **A:** rays; **B:** fish; **C:** cephalopods; and **D:** walrus. All of the modern animals can form *Piscichnus*-like structures through mechanical means (depicted in B and C) and through hydraulic jetting (depicted in A and D).

Gunnedah-Bowen Basin, in which sedimentary successions are closely associated with tectonic events (Tye et al., 1996).

The Shoalhaven Group reflects overall relative sea-level rise (Tye et al., 1996), punctuated by periods of short-lived progradation. The SPF consists mainly of sandstone with interbedded siltstone and conglomerate and corresponds to an overall transgressive cycle with intervening regressive packages (e.g., Gostin and Herbert, 1973; Carey, 1978; Runnegar, 1980; Tye et al., 1996). The early SPF (Tastubian) transgression may have been associated with deglaciation, whereas the subsequent Sterlitamakian regression was possibly related to post-glacial isostatic rebound (Veevers and Powell, 1987).

Ice sheets over Eastern Antarctica and Eastern Australia played an integral role in the deposition of Permian continental margin strata (Crowell and Frakes, 1975; Veevers and Powell, 1987). The climate during deposition of the Wasp Head and overlying Shoalhaven Group is thought to have been glacially

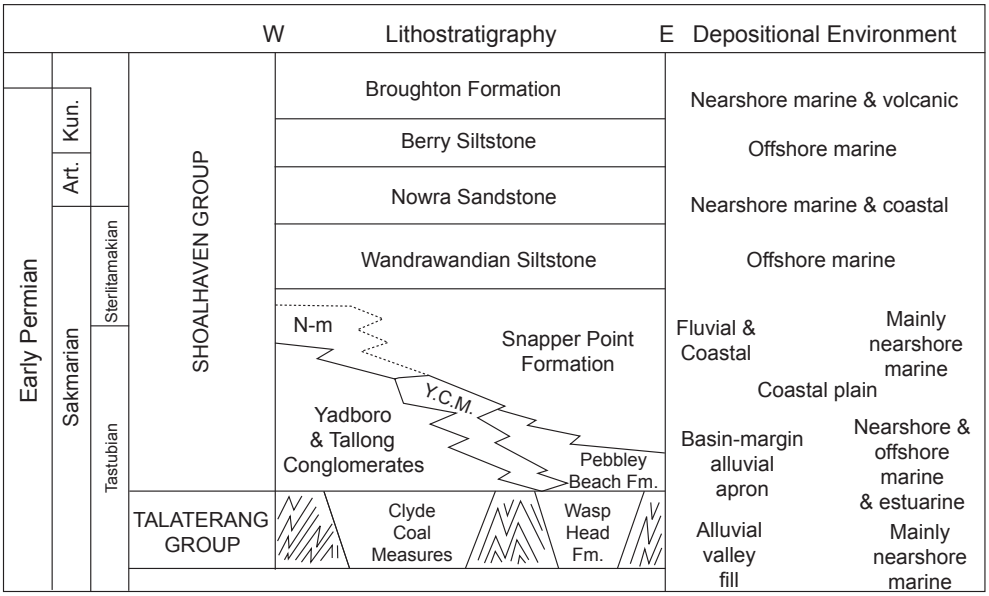

FIGURE 6.3—Stratigraphic chart of the Early Permian from New South Wales, Australia. Modified from Bann et al. (2004). Art=Artinskian, Kun.=Kungurian, N-m=non-marine, Y.C.M.=Yurrunga Coal Measures.

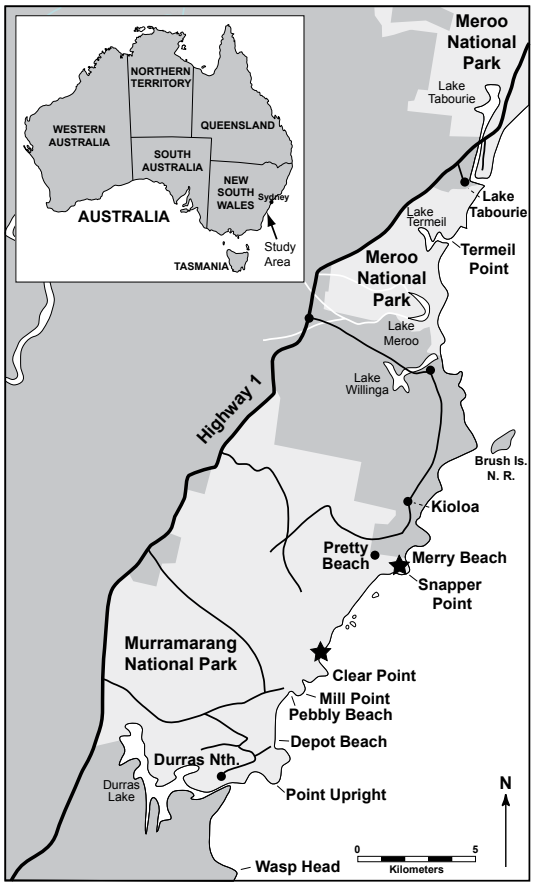

FIGURE 6.4—The study area showing detail of a section of the New South Wales coastline. The stars indicate studied sections, and the arrow in the inset map indicates the location of the study area, south of Sydney, Australia.

influenced, based on the presence of distinctive cold-climate indicators (Fig. 6.5; e.g. Raggatt, 1938). Lonestones, dropstones, and lenses or layers consisting of angular clasts record probable ice-rafted debris from sea-ice or released river ice (Fig. 6.5A; Raggatt, 1938; Gostin and Herbert, 1973; Crowell and Frakes, 1975; Carey, 1978; Veevers and Powell, 1987; Tye et al., 1996; Frank et al., 2004; Thomas et al., 2004; Fielding et al., 2006). Fossils further emphasize cold-water conditions during the Sakmarian. They are associated with glacial deposits, low diversity assemblages, and the presence of thick-walled *Eurydesma*, a distinctive component of Permian southern cool-temperature biota (Fig. 6.5B; Dickins, 1978, 1996; Runnegar, 1979, 1980). Additional evidence of cold-climate conditions includes post-depositional folding and mechanical mixing, believed to have been produced by iceberg keels grounding on the sea floor (Fig. 6.5C; cf. Eyles et al., 1997).

Glacial influence is also supported by the presence of glendonite crystals in the Shoalhaven Group, taken to indicate that near-freezing conditions persisted at the sea floor during deposition (Fig. 6.5D; Raggatt, 1938; Kaplan, 1979; Carr et al., 1989; Eyles et al., 1998; De Lurio and Frakes, 1999; Swainson and Hammon, 2001; Frank et al., 2004; Thomas et al., 2004; James et al., 2005). Finally, large *Rhizocorallium* and *Diplocraterion* in the Shoalhaven Group are interpreted to reflect cold-climate conditions, based on the unusual gigantism of the traces and Bergman's Rule (Fig. 6.5E, F; cf. Pemberton et al., 2001, 2006a, b).

Study Area and Methods

Cliffs along the coast of New South Wales yield near-pristine exposures of Permian strata. The SPF crops out between Clear Point and Merry Beach and exposures examined for this study include sections of outcrop north of Clear Point and at Snapper Point (Fig. 6.4). At these outcrops, *Piscichnus* were photographed and general sedimentological and ichnological attributes were recorded. Intensities of bioturbation within facies were reported using Bioturbation Index (BI; cf. Reineck, 1967; Taylor and Goldring, 1993; Bann et al., 2004). Units within the formation show variations from BI 0-6. Trace fossil width and depth measurements were obtained from the photographs using the scale bars for reference (Table 6.1). The widths were measured from the point where the steep inclination of the trace boundaries intersect the shallow slope of the stratigraphic surface. The maximum height of the trace fossils was measured from the

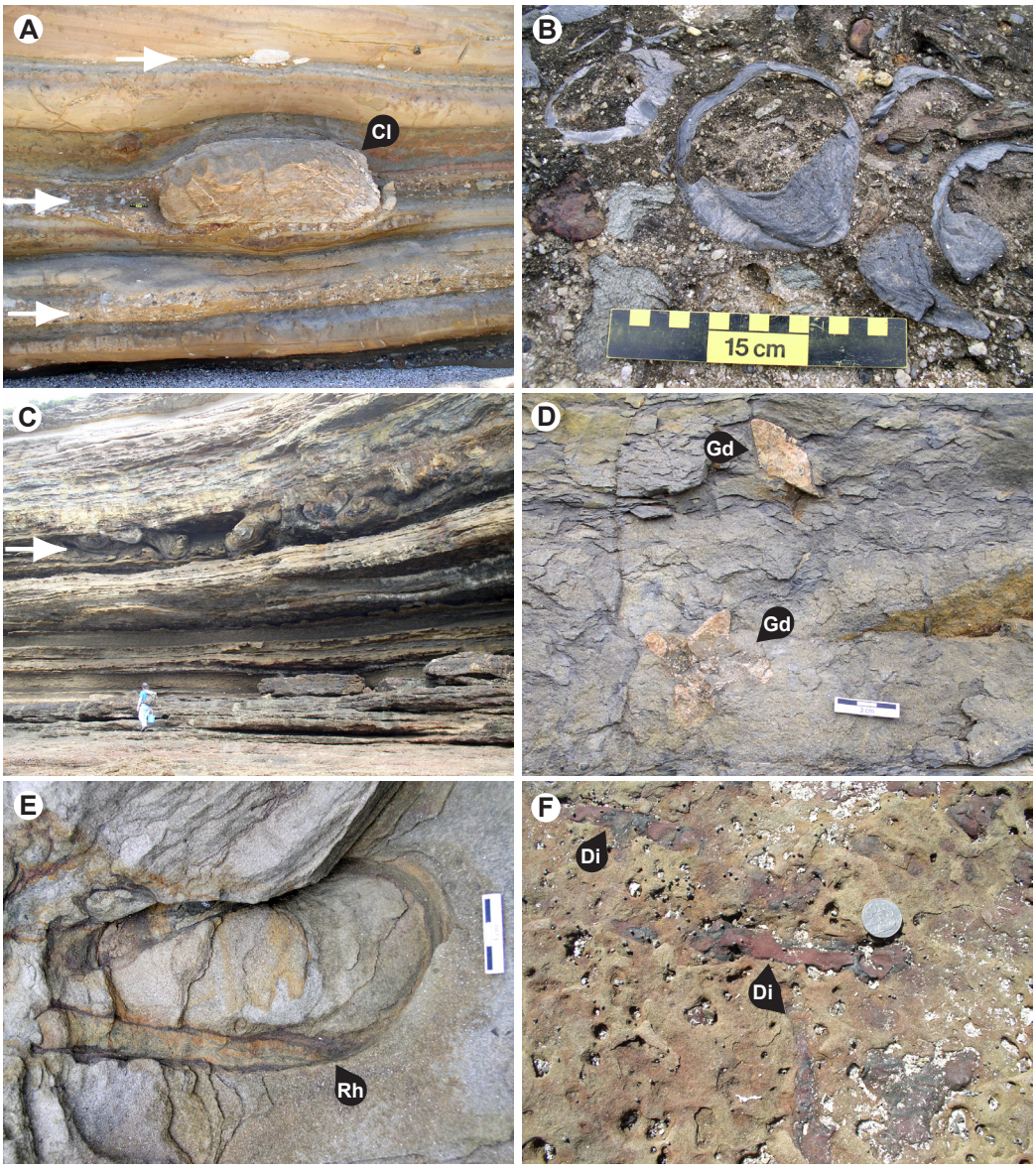

FIGURE 6.5—Evidence of cold-climate conditions during deposition of the Shoalhaven Group. **A:** Large outsized clast (Cl) in the Wasp Head Formation, which has depressed the underlying strata, and is consistent with ice rafting rather than erosion. Multiple pebbly to brecciated clast layers suggest abundant sediment transport into the area (white arrows). **B:** *Eurydesma* pavement at the base of the Snapper Point Formation, corresponding to a major transgressive event. **C:** Large-scale deformation structures in the Snapper Point Formation, produced by icebergs grounding on the sea floor. **D:** Glendonite (Gd) crystals in the Pebbly Beach Formation. These minerals are pseudomorphs of calcite and replaced the mineral ikaite, which requires waters below 5°C in order to form. **E:** Exceptionally large *Rhizocorallium* (Rh; plan view) in the Pebbley Beach Formation (the scale is 3 cm). **F:** Robust *Diplocraterion parallelum* (Di) in plan view from the Pebbley Beach Formation (coin is approximately 32 mm in diameter).

stratigraphically lowest point of the traces to the uppermost boundary of the trace fossils. These values were used to calculate width-to-depth ratios of the structures. The overall inclinations of the ichnofossil boundaries from the horizontal were also calculated using the photographic data set (Table 6.1).

OBSERVATIONS

Snapper Point

The SPF at the Snapper Point locality (Fig. 6.5) contains surfaces characterized by *Piscichnus* overlain by gritty and pebbly deposits (Fig. 6.1A-D). These ichnofossils occur within thoroughly homogenized (BI 5) sandy mudstones, characterized by common *Helminthopsis*; moderate to common *Planolites*; rare to moderate *Palaeophycus tubularis* and *Rosselia*; and rare *Asterosoma*. Material infilling the cross-cutting *Piscichnus* typically consists of coarse-grained sandstone with abundant to sparse, subangular to subrounded quartz, chert and lithic granules, and small (typically less than 2 cm diameter) pebbles. Locally, clasts up to 6 cm in diameter are intercalated. This coarse clastic material infills *Piscichnus,* which are characterized by a single depression with a hooked end (Fig. 6.1A, D), overlapping hook-ended depressions (Fig. 6.1B), and a cone-shaped structure (Fig. 6.1C). *Thalassinoides* infilled with coarse clastic debris also occur along the surface (Fig. 6.1D), and some of the traces are potentially associated with *Piscichnus* (Fig. 6.1A, C). Overlying this ichnologically demarcated surface, the strata consists of massive muddy sandstones (BI 3) with moderate numbers of *Rosselia* and *Palaeophycus tubularis*; rare to moderate *Planolites*; and rare *Teichichnus* and *Rhizocorallium*.

Clear Point

Near Clear Point, exposures of the SPF contain large, gritty sandstone-filled *Piscichnus*, characterizing a surface separating muddy sandstone from an overlying sandstone unit (Fig. 6.1E, F). The underlying strata comprises bioturbated (BI 3) muddy sandstone with moderate to common *Rosselia* and *Diplocraterion habichi*, rare to moderate *Palaeophycus tubularis,* and rare *Asterosoma*. The sedimentary media infilling the *Piscichnus* consist of sand, with scattered clasts that are generally less than 3 cm in length and are subangular

to subrounded. The *Piscichnus* at this locality includes a cylindrical form (Fig. 6.1E) and a steep-walled, hook-shaped form (Fig. 6.1F). The trace fossil suite and coarse clastics along the surface are overlain by apparently massive sandstone with scattered reworking (BI 1) containing rare *Rosselia* and *Diplocraterion habichi*.

SYSTEMATIC ICHNOLOGY

Piscichnus Feibel 1987

Figure 6.6A

Emended Diagnosis—A shallow, circular, bowl-shaped structure to a more steeply-sided, cylindrical, plug-like, or hook-shaped excavation. These structures are concave upward and perpendicular to a horizontal plane (Fig. 6.6A; Feibel, 1987; Gregory, 1991).

Discussion—The *Piscichnus* ichnogenus was originally described by Feibel (1987) from specimens in the Koobi Fora Formation of northern Kenya. The original ichnogenus was intended to describe shallow, dish-shaped structures that were interpreted to have been formed by nesting fish (Feibel, 1987). Gregory (1991) expanded this description to include more steeply-sided traces from the Waitemata Group of Northland, New Zealand, which are interpreted

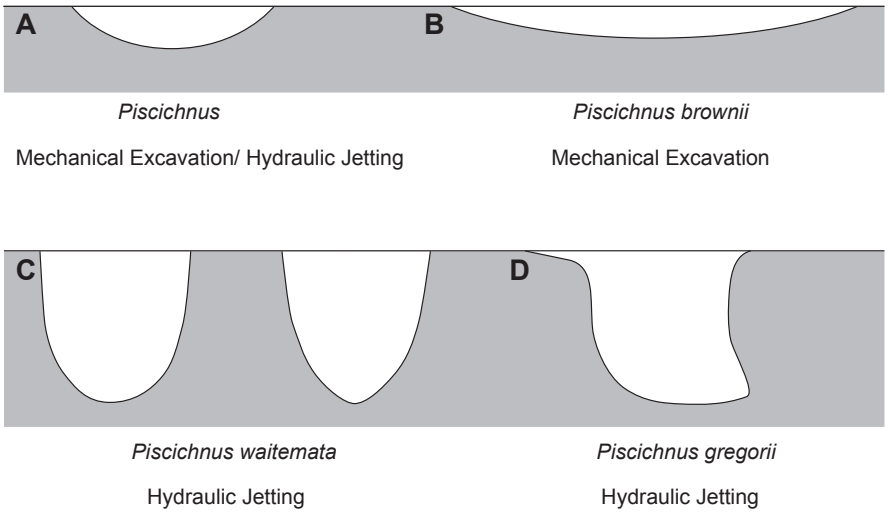

FIGURE 6.6—Various forms of *Piscichnus* and the likely methods of formation.

as pits formed through hydraulic jetting by rays. More recent descriptions have incorporated asymmetrical conical depressions, concave depressions, and dish- or bowl-shaped depressions (Fig. 6.2; Table 6.1; e.g., Ekdale and Lewis, 1991; Martinell et al., 2001; Gingras and Armitage, 2004; Gingras et al., 2007).

Piscichnus brownii **Feibel 1987**

Figure 6.6B

Diagnosis—a smooth, shallow, unornamented form of *Piscichnus* in which the diameter typically ranges from 0.45-1.35 m, and the depth is generally 5-15 cm (Fig. 6.6B; Feibel, 1987).

Description—These traces typically possess a width-to-depth ratio of 10:1 and are normally scattered in outcrop (Feibel, 1987). Important aspects of these traces are the distinctive circular shape in plan view and absence of cross-cutting of individual structures. The infill of *P. brownii* varies from massive to weakly bedded units. The surface of the structure also can be draped by a veneer of coarser-grained material as compared to the underlying deposit.

Discussion—This ichnospecies is interpreted to reflect the nesting structures of fish. Such nesting structures are excavated by mouth, similar to extant African cichlids (Feibel, 1987). These fish generally spawn within 1-2 m of water depth; however, other modern nesting burrows have been observed at much greater depths (e.g., Stanley, 1971).

Piscichnus waitemata **Gregory 1991**

Figures 6.1C, E, 6.6

Diagnosis—A large, epichnial, subcylindrical, pit- or pothole-like excavation (Fig. 6.6C).

Description—The pits are, on average, 15-20 cm in diameter and 15 cm in depth, with a maximum of 30 cm and 50 cm, respectively. The traces occur along bedding planes and are oriented perpendicular to the bedding-plane surfaces. In plan view, the traces have a circular outline, are roughly clustered, and locally inter-nested. In cross-section, the traces can display asymmetry, and can be locally related to narrow, shaft-like protuberances that are an additional 10-15 cm deep.

The infill comprises conglomeratic units that are generally structureless, although imbrication of cobbles is locally observed. The defining characteristics of this ichnospecies includes: 1) the similarity in the dimensions of the diameter and depth; 2) steep-sided trace boundaries; and 3) approximate circular cross-sections.

Discussion—This trace fossil is larger than those typically attributed to burrowing activities or escape by sea anemones (e.g., *Conichnus*). The paucity of symmetry also precludes an actinian anemone origin like that of resting or dwelling structures of *Bergaueria* (cf. Pemberton et al., 1988). Gregory (1991) interpreted *P. waitemata* as a structure formed through hydraulic jetting, similar to that of modern rays. The protruding shafts were likely formed by infaunal bivalves buried within the sediment (producing *Siphonichnus*), which served as prey for the *Piscichnus* trace-maker (Gregory, 1991).

The cylindrical and cone-shaped depressions in the SPF (Fig. 6.1C, E) are interpreted as *Piscichnus waitemata,* as the width-to-depth ratios and overall trace-fossil morphologies correspond most closely to structures described by Gregory (1991; Table 6.2). The trace *Conichnus* morphologically resembles the structures from the SPF; however, *Conichnus* generally has a width-to-depth ratio of less than 0.40 (cf. Pemberton et al., 1988), which is inconsistent with ratios measured from traces in the Snapper Point (Table 6.2, 6.3). Pemberton et al. (1988) reported that *Bergaueria* width-to-depth measurements tend to range from 0.67 to 3.93, with a mean of 1.91. These values resemble those from the SPF; however, the trace *Bergaueria* is described as cylindrical to hemispherical with a rounded base, with or without a shallow, central depression. The traces in the SPF, however, do not possess the rounded bases described by Pemberton et al. (1988; Fig. 6.1). Accordingly, the anomalously large cone-shaped and cylindrical biogenic structures in the SPF are best described as various forms of *Piscichnus waitemata*.

The use of hydraulic jetting to construct *Piscichnus* (especially *P. waitemata*) has been inferred from modern observations of rays and walruses constructing analogous structures (Fig. 6.3; Gregory et al., 1979; Oliver et al., 1983b; Levermann et al., 2003), and from the morphology and internal fabric of the traces themselves (Gregory, 1991; Gingras et al., 2007). Deep, steep-sided traces suggest a focused method of excavation. Furthermore, weak to well-defined imbrication has been noted in some examples of *Piscichnus* (Gregory, 1991; Gingras et al., 2007), as well as centralized cores (Oliver et al., 1983b; Gingras

et al., 2007). *Piscichnus waitemata* in the SPF (Fig. 6.4C, E) are also interpreted to have formed through hydraulic jetting, based predominantly on the overall morphology, as the trace fossil infills have been obscured by reburrowing or possess a disorganized fabric.

***Piscichnus gregorii* n. ichnosp.**

Figures 6.1A, B, D, F, 6.6D

Diagnosis—A concave-upwards depression that is perpendicular to a horizontal plane and, in cross-section, possesses a hooked-shaped end and may comprise an overhang along one side of the vertical trace fossil boundaries (Fig. 6.6D).

Description—The sides of the depression may be shallow to steep, and the axes of the trace is typically inclined. The traces may be inclined from the horizontal between 30° and 90°. These structures range from 6.5 to 11.6 cm in width and 2.9 to 7.6 cm in depth. Width-to-depth ratios vary from 1.11 to 2.23 and average 1.65. *Piscichnus gregorii* are generally composed of a single depression; however, in rare cases, the trace reflects overlapping depressions (Fig. 6.1B). Traces locally display variation in the height (on the order of millimeters to centimeters) of the depression boundaries. In addition, the traces tend to flare towards the top, which accounts for the large width-to-depth ratios.

Discussion—Inclined and asymmetrical *Piscichnus* have been described in earlier studies (e.g., Gregory, 1991; Ekdale and Lewis, 1991; Martinell et al., 2001; Gingras et al., 2007). However, a hooked-end structure (or some form of overhang) has not been formally described, and constitutes a unique feature of this ichnofossil. The absolute sizes of traces are generally not acceptable criteria for identifying ichnogenera; however, the overall morphology and width-to-depth ratios of plug-shaped traces can be used to establish an ichnogenus (cf. Pemberton et al., 1988). The reported width-to-depth ratios of the hook-shaped traces from Table 6.1 are comparable to the trace fossil *Piscichnus* (Table 6.2). Previously documented *Piscichnus* possess width-to-depth ratios that typically range from 0.60 to approximately 9.00. The range seen in the hook-shaped biogenic structures is limited, and varies from 1.11-2.23.

The hooked nature of *P. gregorii* indicates that mechanical excavation is not the most plausible method of construction. The *Piscichnus* lack evidence of pit-

margin collapse or passive sedimentation into open excavations (e.g., Howard et al., 1977; Feibel, 1987; Martinell et al., 2001; Levermann et al., 2003; Gingras and Armitage, 2004; Pearson et al., 2005; Pearson et al., 2007; Gingras et al., 2007). Furthermore, mechanical excavation would most likely result in burrow collapse of the overhang structure. The most logical method of formation of these structures would be some form of water jetting that occurred at an angle to the substrate. This hydraulic jetting would allow for the rapid removal of a plug of sediment to preserve an overhang structure. The *P. gregorii* with overlapping depressions (Fig. 6.1B) possibly reflects multiple jetting events, which also has been observed with *P. waitemata* by Gregory (1991).

Hydraulic jetting may be used to form both *P*. *waitemata* and *P. gregorii*, but the morphology suggests variation in the mechanism of formation. The hook-shaped nature of *P. gregorii* can be explained by either a biological or physical process. Mouths of the trace-makers could have been ventrally positioned such that the animal rested on the sediment surface, or that the causative organism could have been oriented at an angle to the substrate with an anterior-located mouth. The depressed boundaries found along one side of some *Piscichnus* examples (Fig. 6.1A-C) suggest that trace-makers may have rested at the edge of the excavation. *Piscichnus waitemata* within larger, shallow depressions were observed by Gregory (1991). Alternatively, jetting may have carved a steep-sided excavation with additional "down-drift" erosion at the sediment-water interface. Since the depressed edge opposes the hooked end in *P. gregorii*, the angle of jetting would have to be oriented forward at a shallow angle in order to form the hook shape while the organism depressed the substrate. If the lowered sediment surface was simply due to related erosion, then a particular snout shape of the trace-maker may have deflected the water jet to develop a more turbulent flow.

DISCUSSION

Stratigraphic Interpretations

The surfaces characterized by *Piscichnus* from Snapper Point North (Fig. 6.1A, B, D) and Snapper Point South (Fig. 6.1C) suggest a change in depositional conditions across the surface. The underlying sandy mudstone to muddy sandstone contains suites dominated by deposit-feeding structures with lesser grazing traces and dwelling structures of inferred suspension-feeders. This

trace-fossil suite is consistent with an archetypal expression of the *Cruziana* Ichnofacies, and is interpreted to reflect deposition in upper offshore conditions. Stratum overlying the surfaces is sandier, contains fewer traces, and displays reduced ichnofossil diversities. Ethological assessments of the suites indicate that they predominantly consist of deposit-feeding structures and fewer dwelling structures of inferred suspension-feeding organisms. This suite reflects a stressed and proximal expression of the *Cruziana* Ichnofacies, which is consistent with conditions of the lower to middle shoreface; however, the stressed trace fossil suite possibly indicates deltaic deposition.

From outcrops near Clear Point, the stratum underlying the surface characterized by *Piscichnus* is dominated by deposit-feeding structures and dwelling structures of inferred suspension-feeders with rarer dwelling structures. This suite is interpreted as a proximal expression of the *Cruziana* Ichnofacies reflecting lower shoreface deposition. The overlying stratum consists of sandstone dominated by deposit-feeding traces with structures of inferred suspension-feeding organisms reflecting a stressed expression of the *Cruziana* Ichnofacies, mixed with elements of the *Skolithos* Ichnofacies. This suite reflects shallower-water conditions, possibly related to stressed middle shoreface (deltaic?) deposition. Accordingly, the surface at Clear Point does not reflect a significant facies change; however, the accumulation of coarse clastics suggests a change in depositional conditions.

The abrupt transition from the upper offshore to lower/middle shoreface at Snapper Point suggests that a minor drop in relative sea level is associated with the surface, which was evidently less significant at Clear Point. Decreased trace fossil abundances and diversities above the stratigraphic surface, in conjunction with the coarse clastic material suggests that environmentally stressful conditions persisted during deposition. Possibly, increased riverine output suppressed infaunal colonization, and the coarse clastic material may have been sourced from contemporaneous released river ice (cf. Tye et al., 1996).

Substrate Properties and *Piscichnus* Preservation

Preservation of the hook-shaped *Piscichnus* is likely attributed to one of two factors: 1) the sediment possessed some degree of cohesion (i.e., it approached stiffground conditions) and the excavations were infilled over time; or 2) the structures were rapidly infilled at the time of formation by the disturbed

sediment. Mechanical excavation of fish burrows into stiff substrate via sediment biting or body/fin movements has been documented previously (e.g., Voorhies, 1975; Stanley, 1971; Able et al., 1982, 1987). However, there is a paucity of evidence from modern settings indicating that animals are capable of excavating into stiffground through hydraulic jetting. Most likely, under such conditions, sediment would be eroded in clumps rather than uniform dispersal of sediment into the water column. In contrast, Gregory (1991) theorized that the presence of *P. waitemata* indicated that the substrate possessed some degree of cohesion possibly due to enhanced microbial activity.

Despite Gregory's (1991) interpretation, the SPF *Piscichnus* are interpreted to demarcate a palimpsest softground suite (Fig. 6.7) based upon the following criteria: 1) the surface-constrained ichnofossils cross-cut the underlying trace fossil suite; 2) traces display diffuse boundaries (i.e., not sharp as in a typical firmground); 3) some examples possess a surrounding halo of disturbance in the host sediment (Fig. 6.1B, C); 4) some examples show mixing of lag deposits within adjacent host sediment (Fig. 6.1E, F); 5) emplacement of palimpsest structures deformed the underlying fabric or lamination (Fig. 6.1C, E, F); 6) loading may be present along the surface (Fig. 6.1F); 7) concentration of coarse clastics suggests that palimpsest burrows were passively infilled; and 8) biogenic structures may exhibit evidence of subsequent reburrowing (Fig. 6.1A, C; see Chapter 9).

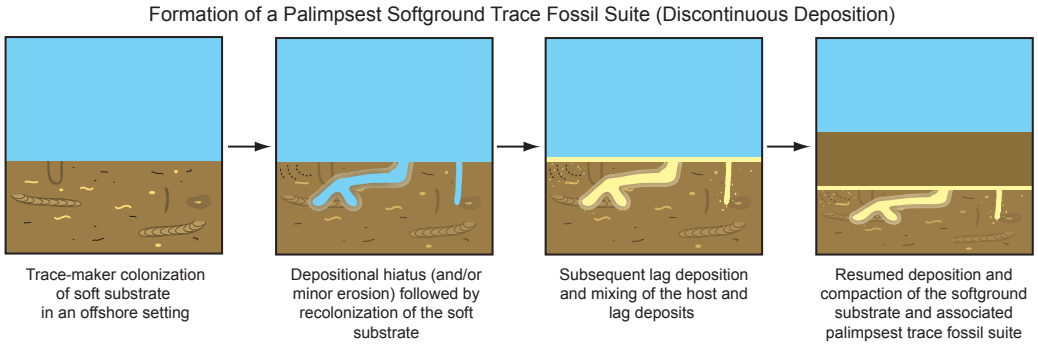

FIGURE 6.7—The generation of softground palimpsest trace fossil suites. Initially, the resident infaunal elements bioturbate the sediment, producing an initial softground trace fossil suite. Subsequently, a depositional hiatus and/or minor erosion occurs, which is followed by recolonization of the palimpsest softground substrate. These traces truncate the underlying trace fossil suite and are typically passively or actively infilled with a depositional lag. In the case of *Piscichnus*, the traces are immediately infilled following hydraulic jetting. Finally, deposition resumes, and there is compaction of the softground substrate and palimpsest trace fossil suite.

If the substrate lacked a significant degree of cohesion, excavations must have been rapidly infilled at the time of formation to permit preservation of the deep, steep-sided depressions within softground sediment. If infilling occurred rapidly, the presence of coarse clastic lag material within the *Piscichnus* must be explained. In order for the lag to be present within the traces, the trace-makers most likely hydraulically jetted through a lag that mantled the surface, which remobilized the lag and allowed it to be re-deposited into the depressions. Jetting into muddy sandstone through a pebbly veneer would stir up the underlying sand and mud, forming a cloud of sediment and allowing pebbly material to fall into open excavations concurrently with the coarser fraction of jetted sediment. This would account for coarse clastics within, but not directly located at the base of all *Piscichnus* (except for Figure 6.1E). In contrast, passive infill of open excavations would likely have concentrated more of the coarser clastic fraction at the base of the structures, as larger clasts rolled or slid along the sediment surface.

The occurrence of *Piscichnus* in the SPF is restricted to palimpsest stratigraphic horizons, and their occurrence and/or preservation may be a function of a few factors. Possibly, the contrasting infill (sandy coarse clastic material) provided a more effective means of preserving the traces in addition to a general paucity of reburrowing. Most likely, the longer period of time reflected by the palimpsest surface led to increased numbers of *Piscichnus* forming along the same surface, enhancing their preservational potential.

Nature of the Trace-maker

Based on the overall morphology of the *Piscichnus*, coupled with the width-to-depth ratios, a probable behavior and trace-maker can be inferred for the SPF occurrences. The depth of penetration is suggestive of feeding or foraging behaviors, and association with nearby traces may indicate a predator-prey relationship. In the Snapper Point area, palimpsest *Thalassinoides* locally occur along the same surface as *Piscichnus* (Fig. 6.1D), and some examples potentially display *Piscichnus* cross-cutting possible softground *Thalassinoides* (Fig. 6.1A, C). *Diplocraterion* are also found along the same stratigraphic surface in the Clear Point area (Fig. 6.1E, F); however, no clear cross-cutting relationships were observed. Palimpsest surfaces reflect extended periods of time compared to typical bedding planes within softground sediment; however, shallow-tier *Piscichnus* were most likely constructed following extensive bioturbation of deep-

tier structures (*Thalassinoides* and *Diplocraterion*). In the Upper Cretaceous of La Posa, Spain, *Piscichnus* were also found in association with both *Thalassinoides* and *Ophiomorpha* (Martinell et al., 2001). Based on a potential cross-cutting relationship, *Piscichnus* trace-makers may have preyed upon *Thalassinoides* trace-makers during search for infaunal food resources.

Foraging behaviors inferred from *Piscichnus* are consistent with activities of rays, walrus, fish and cephalopods in modern-day settings (Table 6.3). Walruses evolved in the Late Miocene (Levin, 1996), and are therefore excluded as a possible trace-maker of the SPF *Piscichnus*. Modern chondrichthyan fishes include sharks, rays and chimaeras, which have a cartilaginous skeleton. These fishes, which include elasmobranchs and holocephalans in the fossil record, appeared during the late Lower Devonian (Moy-Thomas, 1971). However, forms resembling modern-day rays and skates did not appear until the Jurassic, and this niche was filled by durophagous holocephalans (adapted to consuming hard-shelled organisms) following the Devonian and prior to the Jurassic (Moy-Thomas, 1971). The Snapper Point Formation is Permian in age, and therefore, the *Piscichnus* structures were not formed by rays, but possibly by forms of holocephalan fish. Holocephalan fishes include chimaeras, which in the present day feed primarily on bottom-dwelling invertebrates (Helfman et al., 1997; Last and Stevens, 2009). The ability of these fish to jet into the substrate is, however, unknown. As mentioned earlier, a particular snout shape of the causative organism may have deflected the water jet to form the hook shape of *P. gregorii*. Modern elephant fishes or plough-nose chimaeras possess such a snout, which provides additional evidence implicating equivalent ancestral species as potential trace-makers of the SPF *Piscichnus*.

Modern fish that have the ability to gulp and expel water include the Tetraodontiformes from the Actinopterygii Class which includes: spikefishes, triplespines, triggerfishes, filefishes, boxfishes, cowfishes, trunkfishes, puffers, and porcupinefishes (Nelson, 2006). These fishes can jet small amounts of water to uncover invertebrate prey buried within the sediment (e.g., Hobson, 1965; Reinthal et al., 1984; Fraser et al., 1991; Turingan and Wainwright, 1993; Helfman et al., 1997; Chen et al., 2001). In some instances, these fish have been observed to expose prey by jetting from an inverted, vertical position due to the anterior position of the mouth (Hobson, 1965; Fraser et al., 1991). Extant fishes of the Class Actinopterygii are similar in size and shape to ancestral fishes, such that fossil and modern antinopterygians can be equated with regards to descendancy,

form and possibly even function (Helfman et al., 1997). Moy-Thomas (1971) suggested that irrefutable evidence of the first appearance of actinopterygian fish is from the Lower Devonian. Accordingly, ancestral forms of tetraodontiformes also may have been able to jet into the sediment to forage for invertebrates during Permian time.

Cephalopods have been reported to uncover prey within the substrate through mechanical excavation using their arms (e.g., Hanlon and Messenger, 1999) and water jetting (e.g., Wells, 1962). The cuttlefish *Sepia* can blow jets of water to stir up bottom sediment to uncover buried shrimp and other crustacean prey (Wells, 1962). Cuttlefish are part of the group of cephalopods known as coleoids, which includes squid and octopuses. Coleoids make up one of the subclasses of cephalopods that, in addition to the subclasses Ammonoidea and Nautiloidea, arose from a Late Cambrian shelled mollusc that evolved a mechanism for buoyancy (Boyle and Rodhouse, 2005). Coleoids first appeared in the Devonian, but major radiation (except for belemnites) did not occur until the Tertiary (Boyle and Rodhouse, 2005). Ammonoids appeared in the late Silurian and became extinct at the end of the Cretaceous, while nautiloids evolved in the Ordovician and are extant today. It is unknown whether ammonoids used jet propulsion (cf. Donovan, 1993); however, present day nautiloids do employ jet propulsion (Lehmann, 1981) like that of coleoids. The mechanism used for jet propulsion by nautiloids could easily have been used to uncover prey within the substrate. Ancestral species of coleoids or potentially nautiloids and/or ammonoids may have been sufficiently large to jet the substantial volumes of water needed to form *Piscichnus*.

Accordingly, causative organisms that formed the SPF *Piscichnus* may have been some form of holocephalan or actinopterygian fish, or possibly a form of cephalopod tolerant of cold-climate conditions. In any event, the trace-makers would have had to have been sufficiently large to expel the volume of water required to produce a jetting action. *Piscichnus* from the SPF are relatively small compared to structures inferred to have been formed by rays (e.g., Gregory, 1991) and walrus (e.g., Gingras et al., 2007). Accordingly, the likelihood of a comparatively smaller fish or cephalopod forming the structures is plausible. Variation in *Piscichnus* morphology seen in the SPF and potentially other occurrences is likely a function of a number of factors including: causative organism; species; organism size (e.g., adult vs. juvenile); angle of jetting relative to the sediment surface; style of jetting (e.g., rapid or short bursts); substrate

properties (lithology, degree of cohesion); infill material (pebbles vs. sandy sediment); outcrop exposure and orientation of asymmetrical structures; and initial substrate morphology.

Gutter and Pot Casts

The resemblance of fish-formed features to physical structures has been previously discussed by Stanley (1971) and Risk and Craig (1976). For example, Hunter et al. (1984) identified *Piscichnus*-like depressions as "surf-zone potholes;" however, Gregory (1991) suggested that the structures were most likely biogenic in origin due to their association with other ichnofossils. The depressions observed in the SPF broadly resemble gutter and pot casts formed through erosional processes. Gutter casts are sharp-walled, current-generated excavations at the bases of high-energy beds. Such features tend to be elongate (typically a meter or more in length) and a few centimeters to several decimeters deep (Whitaker, 1973). These structures vary from symmetrical to asymmetrical, locally display flat bases, vertical to overhanging sides, and rarely deform underlying laminae (Whitaker, 1973). Gutter casts were interpreted by Whitaker (1973) to form in firm cohesive mud, wherein erosion takes place by water moving in helicoidal paths with horizontal axes. Pot casts are cup-shaped to cylindrical pillars of sandstone, recording the depositional fill of pot holes or rounded, nonlinear erosional features. Pot holes are typically 1-20 cm in diameter, and there is commonly a central erosional high at the base of the pot cast (Myrow, 2003). Pot holes are formed by a spiraling eddy of water that flows downward along the outer wall of the structure, and exits up through the center of the vortex (Myrow, 1992b).

Compelling evidence of the biogenic origin of *Piscichnus* within the SPF includes: 1) the uniformity of shape; 2) plausibility of traces to cross-cut one another; 3) association with softground conditions; 4) environmental occurrence; 5) paucity of other physical structures; 6) potential association with *Thalassinoides*; and 7) analogous modern pits formed by rays, walrus and fish. Dimensions of the *Piscichnus* superficially resemble gutter and pot casts (e.g., Myrow, 1992b; Browne, 1994; Chakraborty, 1995; Leeder, 1999; Pérez-López, 2001); however, the structures do not display any evidence of the linearity typical of gutter casts. The predominance of two-dimensional exposures in the outcrop, however, may account for this. The biogenic structures also do not possess the

typical raised center characteristic of pot casts. Overall, the general uniformity of width-to-depth ratios indicates a similar mechanism of formation with steep sides suggesting focused excavation. In addition, the overhanging boundaries observed in some examples (Fig. 6.1A, B) are difficult to account for with a downward spiraling eddy mechanism of formation. The overprinted nature of *Piscichnus* in Figure 6.1B suggests biogenic generation, as gutter and pot casts are typically infilled following resumed deposition. If deposition occurred to infill an earlier physically formed excavation, subsequent current activity would unlikely scour the substrate to cross-cut the initial scour.

Researchers generally agree that gutter casts are formed in firm cohesive mud (e.g., Bridges, 1972; Whitaker, 1973; Pérez-López, 2001; Myrow, 2003). Conversely, *Piscichnus* from the SPF exhibit clear evidence of softground conditions during formation of the structures. Erosion of pot casts and gutter casts within non-cohesive particulate softground sediment rather than in firmground conditions or cohesive mud would most likely produce rounded, flat-bottomed features. Furthermore, *P. gregorii* structures can possess an overhang along one side of the trace. Whitaker (1973) suggested that helical flow could result in the formation of overhangs in gutter casts; however, these require firm cohesive mud in order to form during progressive erosion.

Most gutter casts are found in shallow-marine deposits, and are interpreted to have been formed by storms (Myrow, 1992a, b, 2003; Chakraborty, 1995; Pérez-López, 2001). There is no evidence of associated storm reworking or deposition in the units above or below the palimpsest surface (e.g., the presence of HCS). In addition, there are no associated physical structures associated with the palimpsest surface. The *Piscichnus* also lack the sole markings that typically occur at the bases and sides of gutter casts. In contrast, the *Piscichnus* occur between highly to weakly bioturbated units and are potentially associated with other ichnofossils. The features are also analogous to modern, biogenically generated pits. The weight of evidence demonstrates that the structures in question are biogenic and attributable to the ichnogenus *Piscichnus*.

SUMMARY

The Permian Snapper Point Formation of southeastern Australia contains unique and well-preserved *Piscichnus*. These cone-shaped and cylindrical traces are dimensionally and morphologically attributable to *P. waitemata*, originally described by Gregory (1991). The inclined hook-shaped structures in the SPF have not been previously documented, and are designated as a new form – *P. gregorii*. The depth of penetration of *Piscichnus* suggests feeding or foraging behaviors that may be associated with predation, possibly upon *Thalassinoides* trace-makers. The morphology, depth of penetration, and occurrence within softground sediment suggests that both ichnospecies of *Piscichnus* were generated by hydraulic jetting. The presence of coarse clastic material within the excavations suggests that jetting occurred through a lag deposit and was succeeded by rapid infilling of the depressions.

Strong evidence suggests that softground conditions persisted during *Piscichnus* generation along surfaces that separate offshore-lower shoreface deposits from lower-middle shoreface strata. The occurrence of *Piscichnus* along these palimpsest softground stratigraphic horizons and their paucity within the over- and underlying strata is most likely explained by prolonged exposure of the surface during depositional hiatus combined with a low degree of reburrowing and contrasting infill.

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CHAPTER 7 – ICHNOLOGICAL ASSEMBLAGES OF WAVE-INFLUENCED AND MIXED RIVER- AND WAVE-INFLUENCED DELTAIC DEPOSITS IN THE LOWER CRETACEOUS VIKING FORMATION, ALBERTA, CANADA

INTRODUCTION

The Lower Cretaceous (Albian) Viking Formation (Fig. 7.1) consists of a series of regionally coarsening-upward parasequences, capped by a complex succession of erosionally amalgamated deposits reflecting deposition in incised valley fills (Pemberton et al., 1992; Pattison and Walker, 1994), incised shorefaces (Downing and Walker, 1988; Raddysh, 1988; Boreen and Walker, 1991; Davies and Walker, 1993; Posamentier and Chamberlain, 1993; and Walker and Wiseman, 1995; MacEachern et al., 1999a), and deltaic complexes (Raychaudhuri and Pemberton, 1992; Raychaudhuri, 1994). Initially, these sandy Viking reservoirs were interpreted as offshore bars (submerged sand ridges built some distance from the shoreline) or tidal bars (e.g., Evans, 1970; Beaumont, 1984; Amajor, 1986; Cant and Hein, 1986; Hein et al., 1986; Leckie, 1986; Amajor and Lerbeckmo, 1990a, b). These interpretations are problematic, as questions arise regarding transport mechanisms and the processes responsible for concentrating sediment into linear, coarsening-upward bodies (cf. Downing and Walker, 1988). More recent interpretations of the Viking sands appeared after Beaumont (1984), who proposed shoreface erosion of older regressive deposits during stillstands, subsequently followed by reworking of sediment into linear sandstone bodies. Interpretations such as lowstand shorefaces (e.g., Walker and Wiseman, 1995), forced regressive deposits (Davies and Walker, 1993; MacEachern et al., 1999a), and transgressively incised shorefaces (Downing and Walker, 1988; Raddysh, 1988; Boreen and Walker, 1991; Davies and Walker, 1993; Posamentier and Chamberlain, 1993; and Walker and Wiseman, 1995; MacEachern et al., 1999a) became commonplace in the late 1980s and throughout the 1990s. However, only two publications document deltaic Viking and equivalent Bow Island deposits

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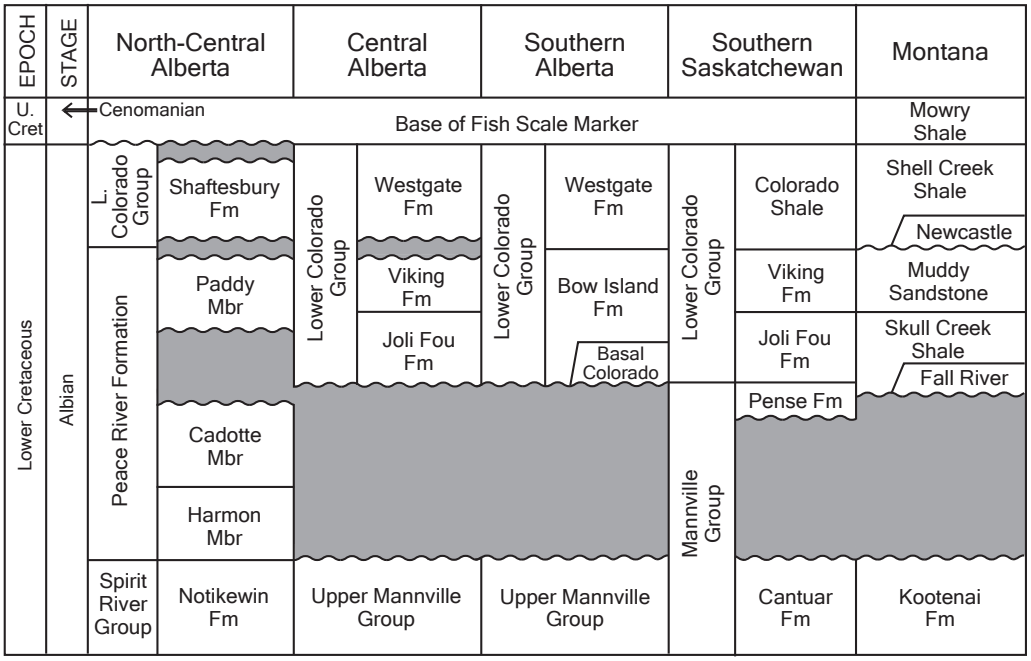

FIGURE 7.1—Stratigraphic correlation chart for the Viking Formation and equivalents (modified from MacEachern et al., 1999a).

that are interpreted as storm-dominated (Raychaudhuri and Pemberton, 1992) and wave-dominated (Raychaudhuri, 1994) complexes. This study incorporates detailed ichnological and sedimentological analyses of Viking Formation strata that reveals wave-influenced and mixed river- and wave-influenced deltaic deposition.

Study area

The studied Viking Formation includes two adjacent study areas in south-central Alberta (Fig. 7.2). The first study area encompasses the Hamilton Lake (HL) field and surrounding area between townships 32 to 38 and ranges 6W4 to 14W4 (Fig. 7.3). A total of 24 cores were examined from this area. The second study area is located southwest of HL and is encompassed by townships 26 to 33 and ranges 11W4 to 26W4 (Fig. 7.3). This area is located between the Wayne-Rosedale and Chain (WRC) fields, from which 22 cores were inspected.

Previous work

In the HL area, earlier interpretations of the sand bodies included offshore

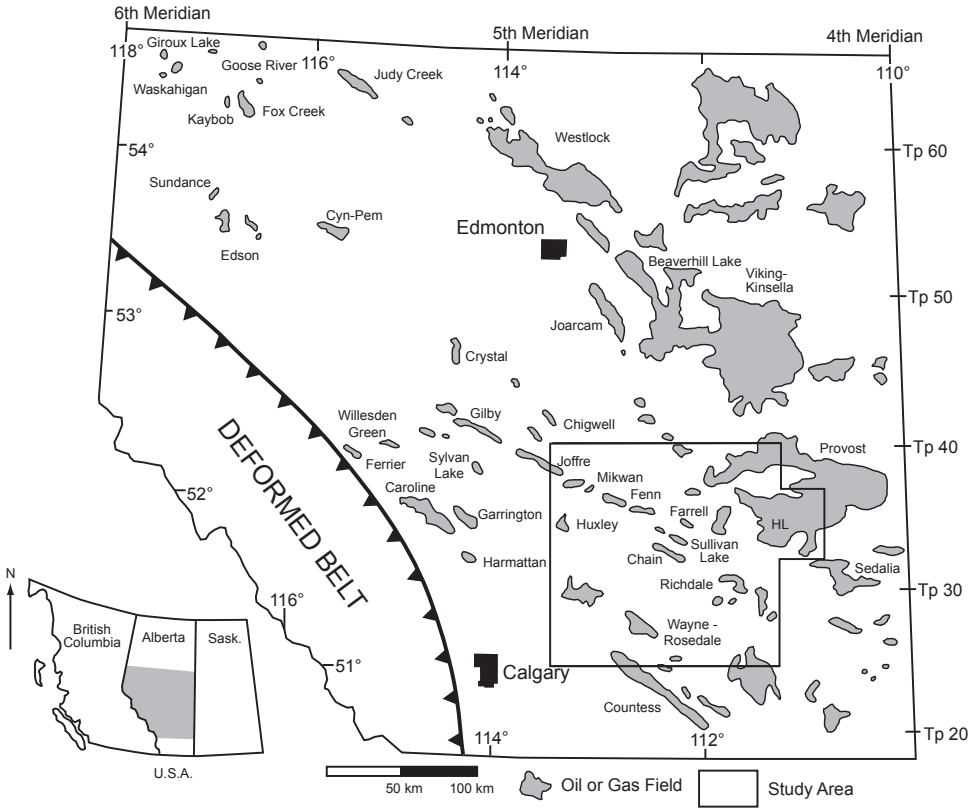

FIGURE 7.2—The Hamilton Lake (HL) and Wayne-Rosedale-Chain (WRC) study areas in Alberta (modified after MacEachern et al., 1999a).

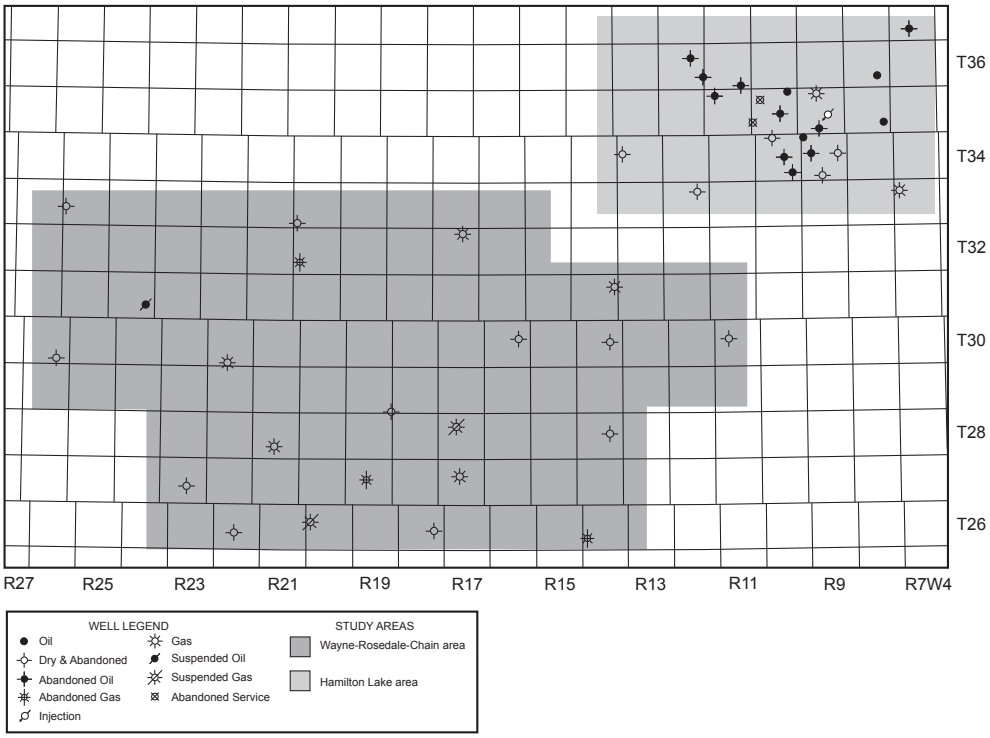

FIGURE 7.3—Logged Viking core from the Hamilton Lake and Wayne-Rosedale-Chain study areas.

bar deposition below fair-weather wave base in a tide-dominated setting (Amajor and Lerbeckmo, 1990b). The sand bodies were thought to have formed at stable or shallowing water depths with a ridge-and-swale morphology. To explain the formation of these sand bodies, Amajor and Lerbeckmo (1990b) suggested the redistribution of gravity flows or older deltaic deposits into sand ridges. Subsequently, Burton (1997) interpreted the HL strata as lower to upper offshore deposits capped by transitional to lower shoreface deposits. This interpretation was based on the dominance of hummocky cross-stratification and an ichnological suite characteristic of the *Cruziana* Ichnofacies (Burton, 1997). More recently, MacEachern and Burton (2000) described the transgressively modified sequence boundary from the top of the Viking Formation (bounding discontinuity 4) at HL. This surface is uniquely characterized by the colonization of firmground suites attributable to distal expressions of the *Glossifungites* Ichnofacies (see Chapters 8 and 9).

A shortage of cored Viking intervals between the Wayne-Rosedale and Chain fields has resulted in few publications detailing the Viking facies. Brief discussions by Amajor and Lerbeckmo (1990a, b) concluded that sandstone bodies in the area were deposited as offshore bars. The ichnology and sedimentology of the Bow Island/Viking Formations in the Wayne-Rosedale, Standard, Wintering Hill and some of the Carbon and Hussar-Countess fields were examined by Raychaudhuri and Pemberton (1992) and Raychaudhuri (1994). Thickly bedded, low-angle laminated sandstones in this area were interpreted as storm-dominated deltaic deposits (Raychaudhuri and Pemberton, 1992) and wave-dominated delta front or lower to middle shoreface deposits (Raychaudhuri, 1994). Viking successions to the north of the study area have been well documented (Downing and Walker, 1988; Peterson, 1995; MacEachern et al., 1998; Burton and Walker, 1999; MacEachern et al., 1999a, b). Sand bodies in this area are interpreted as incised shorefaces (Downing and Walker, 1988); transgressively incised shorefaces (Peterson, 1995; MacEachern et al., 1999a); progradational shorefaces deposited during stillstand (Burton and Walker, 1999); and an embayment complex filled through bayhead-delta progradation during stillstand (Peterson, 1995; MacEachern et al., 1998, 1999b). This study integrates detailed sedimentological and ichnological observations to further refine facies analysis of the Viking Formation in south-central Alberta.

FACIES DESCRIPTIONS

Deposits from the two study areas can be grouped into two facies associations based on recurring lithological, sedimentological, and ichnological characteristics. Each facies association encompasses a vertical succession of genetically related deposits that are intergradational with respect to lithology, degree of biogenic disruption, and ichnofossil suites. Grouping facies into facies associations permits the development of more comprehensive interpretations within the depositional system. Within each study area, 4 related facies have been defined and grouped into two separate facies associations. The degree of bioturbation within the facies is described using the bioturbation index (BI), with grades from 0 to 6. BI 0 reflects unbioturbated units and BI 6 indicates complete homogenization (cf. Reineck, 1967; Taylor and Goldring, 1993). Trace fossils are listed in order of decreasing abundance. In the following sections, the lithology, sedimentology and ichnology of each facies is described and interpreted within the facies associations.

FACIES ASSOCIATION 1: HAMILTON LAKE AREA

Deposits of Facies Association 1 (FAS1) display a gradual decrease in mud content and bioturbation intensity, with a corresponding increase in the preservation of sedimentary structures from facies A through D.

Facies A: *Burrowed Muddy Sandstone to Sandy Mudstone*

Sedimentology

Lithologically, Facies A (FA) is highly variable and includes burrowed muddy sandstone with 30-45% mud, sandy mudstone with 15-50% sand, and/or interbedded sandstone and mudstone intervals (Fig. 7.4A-E). Dark, carbonaceous mudstone laminae and interbeds are also intermittently present, and typically drape underlying deposits. Sandstone beds in FA are typically less than 5 cm thick and are sharp-based. Sedimentary structures in the sandstone beds include common wavy parallel and planar parallel lamination with lesser oscillation ripples and rare aggradational oscillation ripples. Soft-sediment deformation

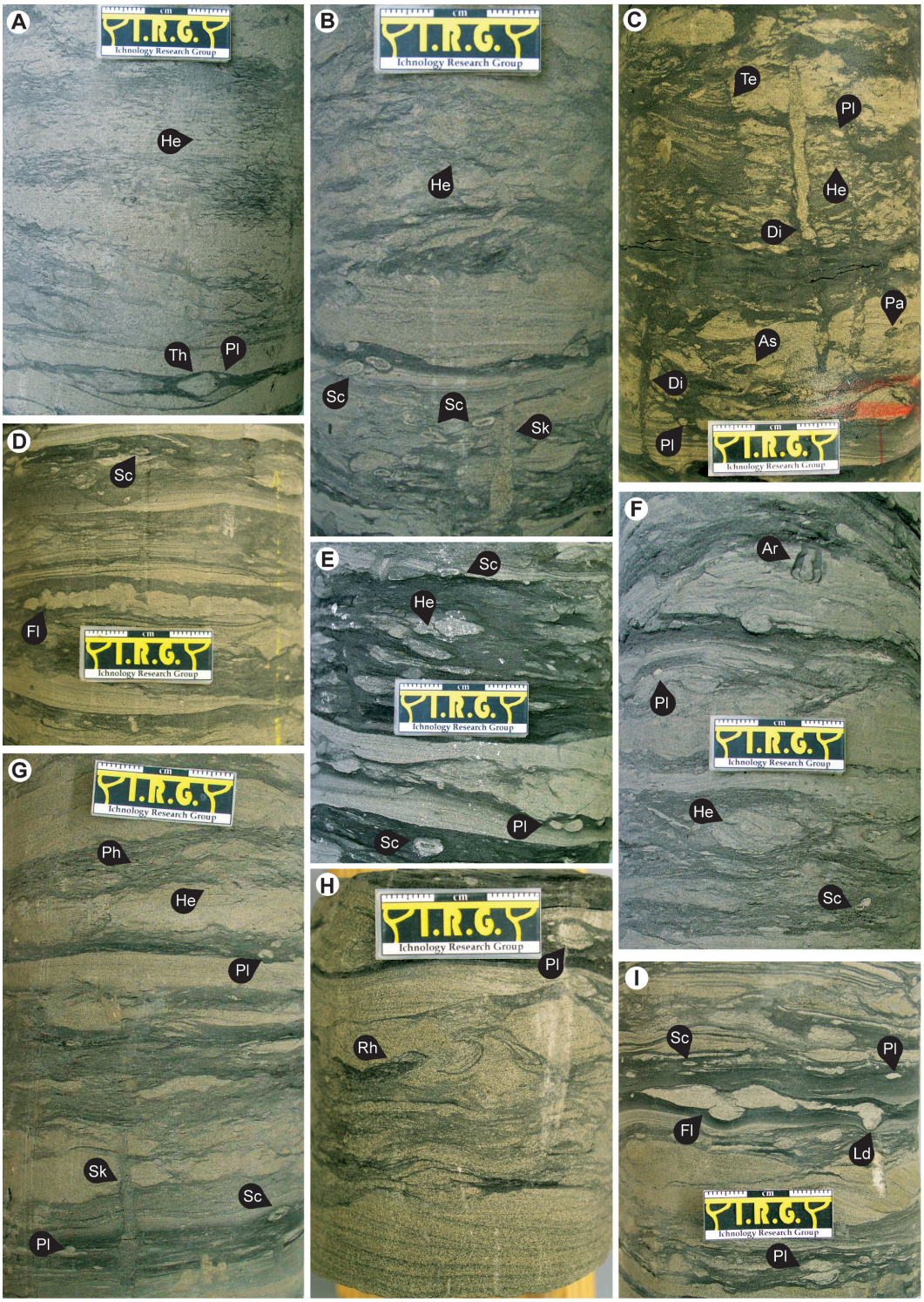

FIGURE 7.4—Hamilton Lake Deposits. **A-E:** Facies A. **A:** A sharp-based mudstone lamina with *Thalassinoides* (Th) and *Planolites* (Pl), overlain by sandstone with pervasive *Helminthopsis* (He) in muddy sandstone, well 10-09-037-07W4 (820.7 m). **B:** Highly burrowed muddy sandstone, with *Schaubcylindrichnus* (Sc), *Helminthopsis* (He) and *Skolithos* (Sk), well 09-15-035-09W4 (905.5 m). **C:** Burrowed muddy sandstone with *Diplocraterion* (Di), *Asterosoma* (As), *Palaeophycus* (Pa), *Teichichnus* (Te), *Planolites* (Pl), and *Helminthopsis* (He), well 11-11-036-08W4 (852.3 m). **D:** Interbedded sandstone and mudstone with a low bioturbation intensity (BI 2),

FIGURE 7.4 (Continued)—flame structures (Fl), normally graded beds and *Schaubcylindrichnus* (Sc), well 02/06-33-035-09W4 (900.0 m). **E:** Wave-rippled sandy mudstone with *Schaubcylindrichnus* (Sc), *Helminthopsis* (He), and *Planolites* (Pl), well 10-12-036-12W4 (935.1 m). **F-I:** Facies B. **F:** Relatively thick, partially reworked sandstone beds interbedded with muddier deposits, with *Planolites* (Pl), *Helminthopsis* (He), and *Schaubcylindrichnus* (Sc). *Arenicolites* (Ar) is interpreted to represent opportunistic colonization of a sandstone bed, well 10-12-036-12W4 (923.9 m). **G:** Interbedded wavy parallel laminated sandstone and mudstone with bioturbated units containing *Phycosiphon* (Ph), *Helminthopsis* (He), *Skolithos* (Sk), and *Planolites* (Pl), well 10-02-036-11W4 (904.4 m). **H:** Wavy laminated sandstone with *Rhizocorallium* (Rh) and *Planolites* (Pl), well 12-29-035-10W4 (901.0 m). **I:** Interbedded sandstone and mudstone with flame (Fl) and loading (Ld) structures, as well as *Planolites* (Pl) and *Schaubcylindrichnus* (Sc), well 10-23-034-09W4 (892.9 m).

features and synaeresis cracks are very rarely observed. Lithological accessories are rare and include siderite, glaucony, organic fragments, shell fragments, and pyrite.

Ichnology

The biogenic disruption in FA is intense in comparison to the other facies of FAS1. Bioturbation is typically common (BI 4-5), though units with a BI ranging from 2-6 are observed. Carbonaceous mudstone laminae generally display low degrees of burrowing (Fig. 7.4D). Sandstone beds are locally partially reworked with traces persistent from muddier intervals, but locally remain unburrowed (Fig. 7.4B). The ichnological suite includes: moderate *Helminthopsis*; rare to moderate *Planolites*, *Schaubcylindrichnus*, *Rhizocorallium*, *Skolithos*, and *Asterosoma*; rare *Diplocraterion*, *Palaeophycus*, *Teichichnus*, *Zoophycos*, *Arenicolites*, *Thalassinoides*, and *Rosselia*; and very rare fugichnia, *Chondrites*, *Siphonichnus*, *Phycosiphon*, and *Cylindrichnus*.

Interpretation

Sedimentological features such as aggradational wave ripples and soft-sediment deformation structures imply high sedimentation rates during deposition. Carbonaceous, sharply bounded mudstone laminae with low bioturbation intensities are suggestive of subaqueous fluid mud deposition, in which its rapid emplacement hampers infaunal colonization of the substrate (MacEachern et al., 2005). The presence of synaeresis cracks is suggestive of salinity variations through the introduction of freshwater into a marine body of water (Burst, 1965). Alternately, Plummer and Gostin (1981) suggest that synaeresis can be related to

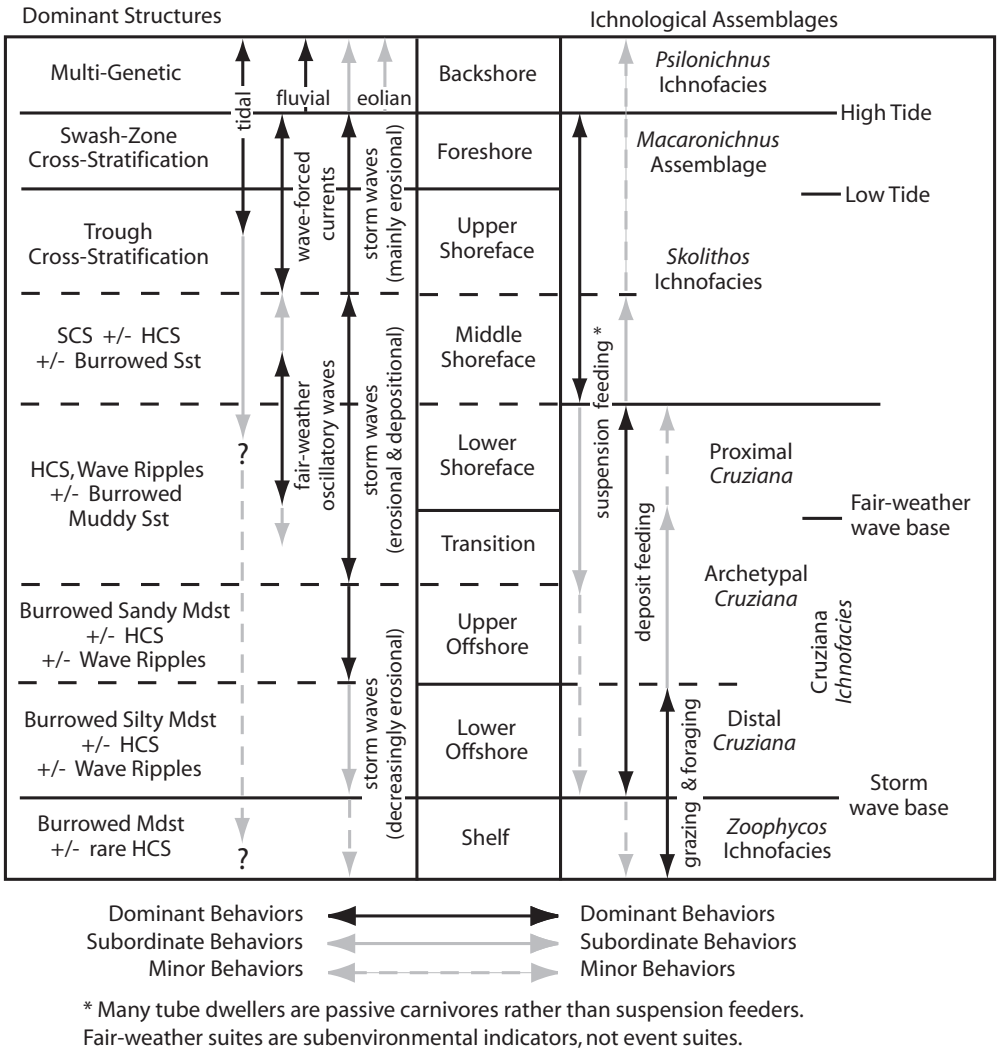

FIGURE 7.5—Shoreface model for ichnological assemblages in the Western Canada Sedimentary Basin (modified from MacEachern et al. 1999a).

rapid dewatering due to high sedimentation rates. Regardless of the formational mechanism, salinity fluctuations and high sedimentation rates (or both) are suggestive of deltaic influence.

The degree of bioturbation in units of FA reflects burrowing in a distal setting. The ichnological suite is dominated by grazing traces and deposit-feeding traces, with subordinate dwellings of inferred suspension-feeding organisms, representative of the archetypal *Cruziana* Ichnofacies. Reduced abundance and diversity of traces may be attributed to weak environmental stresses (Fig. 7.5; cf. Pemberton and MacEachern, 1995; MacEachern et al., 1999; Pemberton et al., 2001). Facies A is therefore characterized by a subtly stressed expression of the archetypal *Cruziana* Ichnofacies. Accordingly, this facies is interpreted as a distal

prodelta deposit, based on the fine-grained nature of the deposit, indications of high sedimentation rates, salinity variations, and riverine influx suggested by fluid mud emplacement, and the subtly stressed nature of the trace fossil suite.

Facies B: *Burrowed Muddy Sandstone*

Sedimentology

Facies B (FB) is characterized by burrowed muddy sandstone with 20-35% mud content (Fig. 7.4F-I). This facies contains intercalated thin sandstone beds that are generally less than 10 cm thick and sharp-based. These beds display common wavy parallel and planar parallel lamination, lesser oscillation ripples, and rare aggradational wave ripples and hummocky cross-stratification. Carbonaceous mudstone laminae and interbeds are rare to common and typically less than 1 cm thick. Accessory elements include rare to moderate mudstone rip-up clasts, and rare convolute bedding, soft-sediment deformation features (Fig. 7.4I), synaeresis cracks, glaucony, and wood fragments.

Ichnology

Bioturbation intensities in FB range from BI 0 to 4, with a BI of 3-4 prevailing. The trace fossil suite consists of moderate *Helminthopsis* and *Planolites*; rare to moderate *Schaubcylindrichnus*, *Asterosoma*, *Rhizocorallium*, and *Skolithos*; rare *Diplocraterion*, *Palaeophycus*, *Arenicolites*, *Teichichnus*, fugichnia, and *Zoophycos*; and very rare *Thalassinoides*, *Phycosiphon*, *Ophiomorpha*, and *Rosselia*. *Diplocraterion*, *Skolithos*, *Arenicolites* and *Phycosiphon* locally subtend into sandstones beds from higher levels (Fig. 7.4F). Some sharp-based mudstone laminae are partially reworked with deposit-feeding or grazing traces, while others are unburrowed.

Interpretation

Carbonaceous mudstone laminae, wood fragments, and synaeresis cracks support interpretation of a close proximity to a riverine source. The presence of sharp-based mudstone laminae, likely deposited as fluid mud, and soft sediment deformational features are suggestive of high sedimentation rates. The ichnofossil suite is dominated by deposit-feeding and grazing traces with fewer dwellings of inferred suspension-feeders. This type of suite is consistent with the

archetypal *Cruziana* Ichnofacies (Fig. 7.5). Although the suite appears diverse, traces designated as "very rare" reflect single occurrences in units of FB. In general, the ichnofossil suite is dominated by 8 to 9 ichnotaxa signifying some environmental stress during deposition. Bioturbation intensities are also reduced relative to FA and typical upper offshore deposits characterized by the archetypal *Cruziana* Ichnofacies (Fig. 7.5). Accordingly, the trace fossil suite corresponds to a moderately stressed expression of the archetypal *Cruziana* Ichnofacies. This facies was deposited in a more proximal setting than FA, as bioturbation intensities and mud contents are reduced. Indications of fluvial influx, the fine-grained nature of the sediment, and the moderately stressed archetypal *Cruziana* Ichnofacies are interpreted to represent deposition in a proximal prodelta setting.

Facies C: *Moderately Burrowed Sandstone*

Sedimentology

Facies C (FC) consists of sandstone with common mudstone laminae and thin beds, as well as muddy sandstone with up to 20% dispersed mud (Fig. 7.6A-D). Physical structures dominate units of FC and encompass moderate occurrences of oscillation ripples, low-angle cross lamination and planar parallel lamination, with rarer aggradational wave ripples and hummocky cross-stratification. Mudstone laminae and beds are dark, carbonaceous, up to 4 cm thick, and locally burrowed (Fig. 7.6C). Coal fragments, mudstone rip-up clasts, glaucony and sideritized mudstone intervals occur rarely in this facies.

Ichnology

Bioturbation intensities range from BI 1 to 4 and, on average, bioturbation is consistent with a BI of 2-3. Bioturbation intensities are high in the muddy sandstone and locally within mudstone laminae (Fig. 7.6A). The ichnological suite consists of rare to moderate *Planolites*, *Helminthopsis*, *Schaubcylindrichnus*, and *Diplocraterion*; rare *Asterosoma*, *Skolithos*, *Palaeophycus*, and *Thalassinoides*; and very rare *Rhizocorallium*, *Chondrites*, *Arenicolites*, *Rosselia*, and *Phycosiphon*. Carbonaceous mudstone deposits are typically penetrated by vertical *Diplocraterion* and *Skolithos* (Fig. 7.6B) or the deposit-feeding structures *Planolites* and *Thalassinoides*.

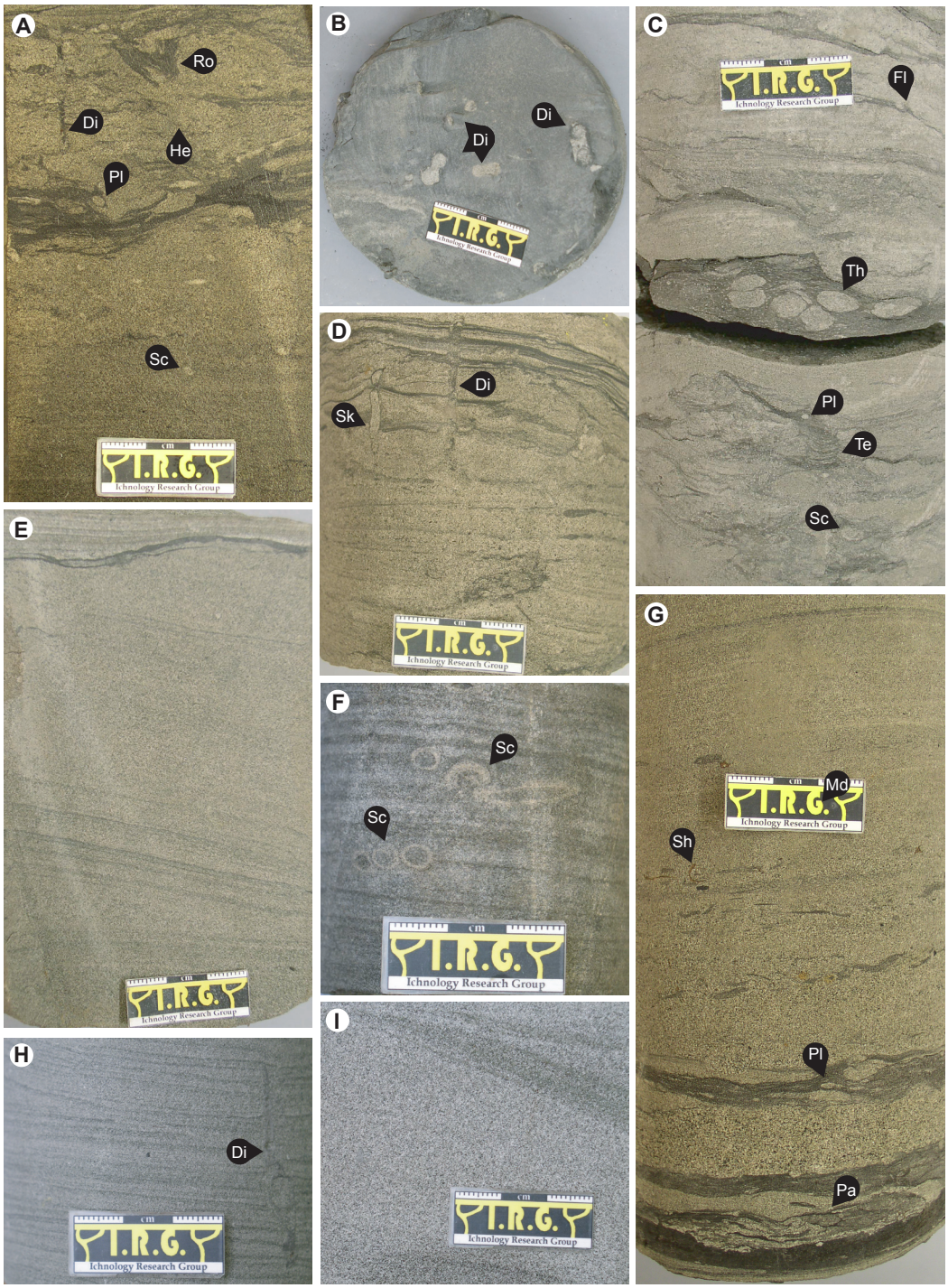

FIGURE 7.6—Hamilton Lake Deposits. **A-D:** Facies C. **A:** Partially reworked mudstone laminations with *Rosselia* (Ro), *Schaubcylindrichnus* (Sc), *Planolites* (Pl), *Helminthopsis* (He) and *Diplocraterion* (Di), well 12-31-034-09W4 (884.9 m). **B:** Sand-infilled *Diplocraterion* (Di) in plan view, well 04-26-036-12W4 (924.9 m). **C:** Wave-rippled sandstone and thin carbonaceous mudstone bed burrowed with *Thalassinoides* (Th). Traces in the sandstone include *Teichichnus* (Te), *Planolites* (Pl), and *Schaubcylindrichnus* (Sc). The top of the core has reduced burrowing, and flame structures (Fl) can be seen at the top of a thin mudstone laminae, well 04-32-035-11W4 (930.4 m). **D:** *Skolithos* (Sk) and possible *Diplocraterion* (Di) penetrating mudstone laminae; underlying planar laminations contain organic detritus, well 10-02-036-11W4 (902.9m).

FIGURE 7.6 (Continued)—E-I: Facies D. **E:** Planar to low-angle parallel lamination interpreted as HCS and capped by a thin carbonaceous mudstone laminae and overlying wave rippled sandstone, well 12-20-034-09W4 (902.8 m). **F:** Large, robust, thick-walled *Schaubcylindrichnus* (Sc) in low-angle parallel laminated sandstone, well 10-30-033-07W4 (873.2 m). **G:** Thin mudstone laminae with small *Planolites* (Pl) and *Palaeophycus* (Pa) at the base of a sandy unit, with small shell fragments and mudstone rip-up clasts, well 10-35-35-10W4 (880.3 m). **H:** Possible *Diplocraterion* (Di) in planar to low-angle to parallel laminated (HCS) sandstone, well 10-04-034-09W4 (898.2 m). **I:** Apparently massive to wave rippled sandstone, well 10-04-034-09W4 (896.6 m).

Interpretation

Sedimentologically, the sandy nature of FC suggests a nearshore setting relative to FB. Aggradational wave ripples indicate high sedimentation rates, and the presence of coal fragments, carbonaceous mudstone deposits, and siderite cements are consistent with a nearby fluvial source. Sideritized mudstones in a deltaic setting likely form due to the organic nature of the river-sourced muds, which are conducive to bacterially facilitated precipitation of siderite by processes similar to those in operation today (Coleman, 1993). High sedimentation rates result in shorter durations of sediment in the aerobic oxidation and sulfate reduction zones. This curtails consumption of organic matter by sulfate-reducing bacteria, and promotes siderite precipitation (Gautier, 1982). High-energy conditions are indicated by the presence of mudstone rip-up clasts and structures suggestive of unidirectional current flow.

The ichnological suite is characterized by prevailing deposit-feeding and dwellings of inferred suspension-feeding animals with fewer grazing traces. This suite is generally consistent with a proximal expression of the *Cruziana* Ichnofacies typical of lower shoreface deposits (Fig. 7.5; Pemberton and MacEachern, 1995; MacEachern et al., 1999; Pemberton et al., 2001). The suite is, however, reduced in diversity and abundance in comparison to these successions. Accordingly, some degree of environmental stress influenced deposition of FC, and the trace fossil suite corresponds to a moderately stressed proximal expression of the *Cruziana* Ichnofacies. The sandy nature of this facies, indications of fluvial input and high energy conditions, and the moderately stressed trace fossil suite are interpreted to reflect deposition in the distal delta front.

Facies D*: Sparsely Burrowed Sandstone*

Sedimentology

Sandstone with rare to moderate occurrences of mudstone laminae

characterizes Facies D (FD; Fig. 7.6E-H). Units are dominated by very low-angle laminations with increasing thicknesses upwards interpreted as hummocky cross-stratification (HCS; Fig. 7.6A). Other sedimentary structures include planar parallel lamination and oscillation ripples with rarer wavy parallel lamination, aggradational wave ripples and low-angle cross lamination. In a few instances, units are characterized by massive (apparently structureless) bedding. Mudstone laminae are typically less than 1 cm thick, sharp-based, carbonaceous, and drape underlying sedimentary structures (Fig. 7.6G). Mudstone rip-up clasts are rare to common, whereas occurrences of glaucony, sideritized mudstone laminae, wood fragments and coal fragments are rare.

Ichnology

Units of FD locally range from BI 0 to BI 2; however, deposits are typically characterized by a BI 1. Mudstone laminae are commonly the sites of increased bioturbation (*Planolites*, especially). Trace fossils include rare to moderate numbers of *Planolites*, *Palaeophycus*, *Diplocraterion*, *Skolithos*, and *Schaubcylindrichnus*; rare *Asterosoma*, *Helminthopsis*, *Thalassinoides*, *Rhizocorallium*, *Chondrites*; and very rare *Ophiomorpha*, *Rosselia*, *Teichichnus*, and fugichnia. In some instances, *Schaubcylindrichnus* in sandstone beds are enlarged, thick-walled, and robust, possibly reflecting harsh environmental conditions.

Interpretation

Sedimentologically, FD is similar to the lower shoreface described by Pemberton et al. (2001), except for the presence of sharp-based, carbonaceous mudstone laminae and beds. These mudstones are possibly the result of rapid outflows of riverine discharge, and would not be observed in a typical shoreface succession (cf. MacEachern et al., 2005). Indications of rapid sedimentation include aggradational wave ripples and massive bedding. Mudstone rip-up clasts, hummocky cross-stratification, and low-angle cross laminations indicate high-energy conditions during deposition. Occurrences of wood and coal fragments are suggestive of proximity to a fluvial source, and sideritized mudstone deposits may signify salinity fluctuations (Coleman, 1993).

The ichnological suite is dominated by a few deposit-feeding and dwellings of inferred suspension-feeders. The suite consists of elements

attributable to a proximal expression of the *Cruziana* Ichnofacies and/or the *Skolithos* Ichnofacies (Fig. 7.5; Pemberton and MacEachern, 1995; MacEachern et al., 1999; Pemberton et al., 2001). However, within a particular unit, the abundance and diversity of traces is substantially diminished in comparison with a typical shoreface succession characterized by these suites (e.g., Moslow and Pemberton, 1988). As a result, the ichnological suite is interpreted as a stressed and proximal expression of the *Cruziana* Ichnofacies with storm beds exemplifying a stressed *Skolithos* Ichnofacies. Evidence of rapid sedimentation, high-energy conditions, proximity to a fluvial source, and a stressed ichnological suite are interpreted to reflect deposition in the proximal delta front.

Facies Association 1: Summary

Facies of FAS1 range from sandstones containing isolated mudstone laminae with rare bioturbation to sandy mudstones with intense burrowing. Facies contain sparse occurrences of sedimentological features suggestive of high sedimentation rates, such as soft-sediment deformation features and aggradational wave ripples. Dispersed synaeresis cracks, locally burrowed carbonaceous mudstone laminae, coal and wood fragments, mudstone rip-up clasts, and sideritized mudstone are interpreted to reflect subtle riverine influx (cf. MacEachern et al., 2005). From facies A through to D, the ichnological succession becomes increasingly stressed and reflects expressions of increasingly proximal ichnofacies. In addition, biostratigraphic analysis of mudstone deposits within the deltaic units of FAS1 revealed a paucity of foraminifera suggestive of environmental stress as compared to typical Viking mudstones (cf. MacEachern et al., 1999c). Subtle indications of high sedimentation rates, high energy conditions and riverine influx are in contrast to deposits from the Wayne-Rosedale-Chain area in which such attributes are more common.

The minor and sporadic distribution of river-generated features is suggestive of mitigation of deltaic influence by waves, and the dominance of HCS in the proximal delta front is suggestive of storm influence. Wave-dominated deltas typically consist of hummocky cross-stratified and wave rippled successions (Bhattacharya and Walker, 1992). In comparison to typical wave-dominated deltaic successions (e.g., Weise, 1979; Balsley, 1980; Tankard and Barwis, 1982; Bhattacharya, 1988; Bhattacharya and Walker, 1992; Siedler and Steel, 2001; Nouidar and Chellai, 2002), the HL deposits comprise fewer

amalgamated storm beds and scattered sedimentary features typical of river-dominated deltas. The presence of carbonaceous mudstone separating storm beds may signify deposition in a wave-influenced deltaic system (cf. Bhattacharya and Walker, 1991, 1992; Bhattacharya and Giosan, 2003).

Units of FAS1 contain trace fossil suites comparable to that of wave-dominated deltas of the Dunvegan Formation (Gingras et al., 1998; Coates and MacEachern, 1999). However, the suites from the HL area contain fewer dwellings of inferred suspension-feeding animals and reflect deposition in settings affected by harsher environmental stresses. Suspension-feeding behaviors are common on some wave-dominated delta fronts as water turbidity is minimized by active wave reworking (Gingras et al., 1998; Coates and MacEachern, 1999). Under moderate degrees of wave influence, a noticeable reduction in the diversity and abundance of traces occurs due to reduced mitigation of the effects of riverine discharge (turbidity, high concentration of suspended sediment, and decreased marine salinity). In comparison to a wave-dominated delta, turbidity is enhanced in a wave-influenced delta, which inhibits suspension-feeding behaviors (MacEachern et al., 2005). The above sedimentological and ichnological characteristics of FAS1 are interpreted to reflect deposition in a wave-influenced deltaic system.

FACIES ASSOCIATION 2: WAYNE-ROSEDALE TO CHAIN AREA

The second facies association comprises deposits from the WRC study area. The four facies (E-H) of FAS2 are typified by an upward decrease in mud content, an overall decrease in the abundance and diversity of biogenic structures, and a corresponding increase in the prevalence of physical sedimentary structures from facies E through H.

Facies E: *Burrowed Sandy Mudstone*

Sedimentology

Facies E is diverse lithologically, and primarily comprises sandy siltstone with 30-50% sand grains and sandy mudstone with 20%-40% sand content. To a lesser extent, muddy or silty sandstone with 40-50% mud/silt, or interbedded

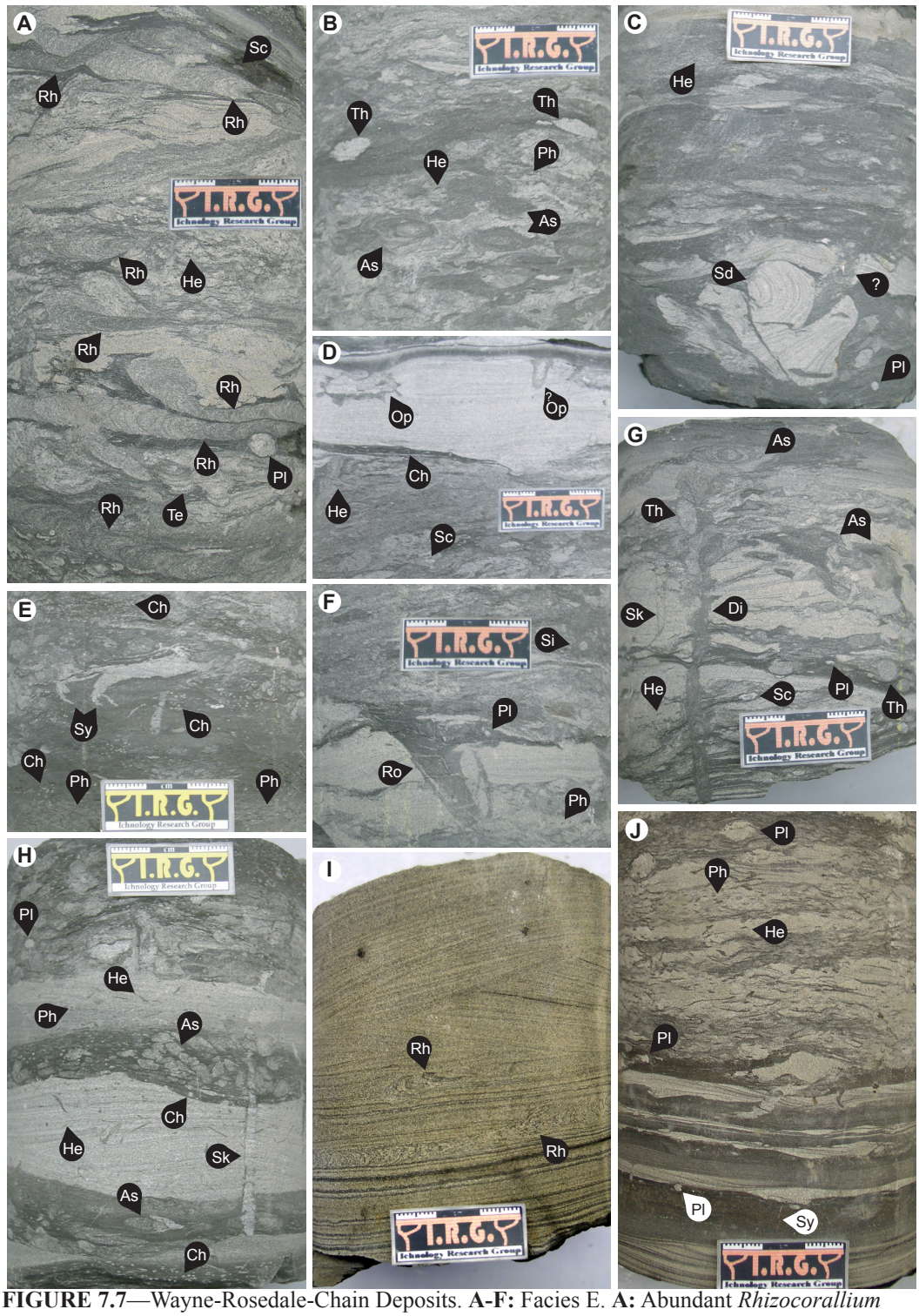

FIGURE 7.7—Wayne-Rosedale-Chain Deposits. **A-F:** Facies E. **A:** Abundant *Rhizocorallium* (Rh) with *Helminthopsis* (He), *Planolites* (Pl), and *Schaubcylindrichnus* (Sc), well 10-03-032-17W4 (1072.8 m). **B:** Burrowed muddy sandstone with *Asterosoma* (As), *Thalassinoides* (Th), *Phycosiphon* (Ph), and *Helminthopsis* (He), well 02/10-14-026-18W4 (1185.0 m). **C:** Soft-sediment deformation (Sd) with possible escape structure (?), as well as *Planolites* (Pl) and *Helminthopsis* (He), well 10-03-032-17W4 (1080.7 m). **D:** Thin sandstone bed with subtending *Ophiomorpha* (Op) and background traces which include *Helminthopsis* (He), *Chondrites* (Ch), and *Schaubcylindrichnus* (Sc), well 16-11-031-24W4 (1115.6 m). **E:** Synaeresis cracks (Sy) in

FIGURE 7.7 (Continued)—sandy mudstone with abundant *Chondrites* (Ch) and *Phycosiphon* (Ph), well 06-15-027-23W4 (1311.3 m). **F:** Opportunistic behavior displayed by *Rosselia* (Ro) in a thin sandstone bed. Other traces include *Planolites* (Pl), *Phycosiphon* (Ph), and *Siphonichnus* (Si), well 02/10-14-026-18W4 (1178.4 m). **G-J:** Facies F. **G:** *Asterosoma* (As), *Planolites* (Pl), *Schaubcylindrichnus* (Sc), *Diplocraterion* (Di), *Helminthopsis* (He), *Thalassinoides* (Th), and *Skolithos* (Sk), well 10-07-032-20W4 (1208.3 m). **H:** Wave-rippled sandstone beds with *Helminthopsis* (He), *Phycosiphon* (Ph) and *Skolithos* (Sk) interbedded with a fair-weather assemblage of *Chondrites* (Ch), possible *Asterosoma* (As), and *Planolites* (Pl), well 11-02-030-26W4 (1557.4 m). **I:** *Rhizocorallium* (Rh) in a low-angle laminated to wave-rippled sandstone bed, well 06-23-028-14W4 (944.2 m). **J:** *Planolites* (Pl), *Helminthopsis* (He), and *Phycosiphon* (Ph) overlying fining-upward, wave-rippled beds with carbonaceous mudstone deposits, *Planolites* (Pl), and synaeresis cracks (Sy), well 10-07-026-14W4 (935.3 m).

sandstone and mudstone with 50-80% mud are also included in Facies E (Fig. 7.7A-F). The principal difference between the lithologies is the extent to which biogenic homogenization has taken place. Where sandstone interbeds are well preserved, the facies is more heterolithic. Sharp-based, locally fining-upward, sandstone beds are generally a few centimeters thick and up to 20 cm in thickness (Fig. 7.7D). These sandstone interbeds contain common oscillation ripples, and rare aggradational wave ripples, hummocky cross-stratification, and planar parallel lamination. Unbioturbated, carbonaceous, sharp-based, dark mudstone laminae and beds are generally thin (1 cm in thickness or less). Mudstone laminae may drape underlying structures or be partially burrowed. Convolute bedding and loading structures also occur, but are typically rare. Accessory elements include rare to moderate occurrences of pyrite and siderite, with siderite beds reaching 12 cm in thickness. Rare coal fragments, mudstone rip-up clasts, and synaeresis cracks are also present (Fig. 7.7E).

Ichnology

Facies E (FE) contains the highest bioturbation intensities of FAS2. It is pervasively bioturbated (BI 4-5), but units include bioturbation intensities ranging from BI 1-6. Generally, sandstone beds have low degrees of bioturbation, with some unburrowed and others preserved as lenses indicative of partial reworking. Facies E contains a diverse suite of traces including: moderate to common *Helminthopsis* and *Planolites*; moderate *Chondrites*, *Phycosiphon*, *Asterosoma*, *Schaubcylindrichnus*, *Palaeophycus*, *Rhizocorallium*, and *Teichichnus*; rare, *Skolithos*, *Diplocraterion*, *Rosselia*, *Thalassinoides*, and *Ophiomorpha*; and very rare *Siphonichnus* and *Scolicia. Ophiomorpha* and *Rosselia*, as well as some *Skolithos*, *Diplocraterion*, *Helminthopsis*, and *Phycosiphon* are associated

with weakly-burrowed, sharp-based sandstone beds (Fig. 7.7D, E). These traces generally subtend from the tops of sandstone beds. Common traces associated with the carbonaceous mudstone deposits include *Chondrites*, *Planolites*, and *Thalassinoides* (Fig. 7.7E).

Interpretation

The fine-grained nature and burrowing intensities in FE are suggestive of a distal marine setting. Sedimentary structures in the sandstone beds are dominated by wave-formed structures, but are preserved as remnants due to a high degree of bioturbation. Similar to deposits of FAS1, carbonaceous mudstone layers are interpreted to have been deposited as fluid mud sourced from riverine influx. Rare occurrences of sediment loading structures, convolute bedding, and aggradational wave ripples indicate periods of high sedimentation during deposition. Riverine influx may be indicated by occurrences of sideritized mudstone, coal fragments, mudstone rip-up clasts, and synaeresis cracks.

The diverse trace fossil suite is dominated by deposit-feeding structures and grazing traces, with few dwellings of inferred suspension-feeding organisms. Traces associated with sharp-based, rarely to moderately bioturbated sandstone beds are interpreted to reflect opportunistic colonization of tempestite beds (Pemberton et al., 1992b). The diversity of the suite and ethological groupings are consistent with the archetypal *Cruziana* Ichnofacies (Fig. 7.5). However, the intensity of bioturbation is somewhat subdued. Accordingly, the trace fossil suite is consistent with a subtly stressed expression of the archetypal *Cruziana* Ichnofacies. The high proportion of clay and silt particles, indications of high sedimentation rates and fluvial input, and subtly stressed expression of the archetypal *Cruziana* Ichnofacies are interpreted to reflect deposition in the distal prodelta.

Facies F: *Burrowed Interbedded Sandstone and Mudstone*

Sedimentology

Lithologically, Facies F (FF) is characterized by interbedded sandstone and mudstone or siltstone in cm- to dm-scale beds with 20-40% clay and silt content (Fig. 7.7G-J). This facies locally consists of muddy sandstone (10-40% mud) or silty sandstone in units with intense bioturbation. Sharp-based

sandstone beds with low bioturbation intensities are common (Fig. 7.7I). These sandstone beds are dominated by oscillation ripples and wavy parallel lamination, with moderately abundant planar lamination, and rare low-angle lamination, hummocky cross-stratification, and aggradational wave ripples. Carbonaceous, thin, dark-coloured mudstone beds locally cap sandstone beds (Fig. 7.7J). The sharp bases of these mudstone beds indicate rapid emplacement and truncation of underlying deposits. Deformational features include rare flame structures, sediment loading structures, and convolute bedding. Accessory elements comprise rare to moderate pyrite, siderite and coal fragments, with rare synaeresis cracks, glaucony and wood fragments.

Ichnology

Unburrowed to pervasively bioturbated units (BI 0-5) typify FF; however, moderate to high intensities of bioturbation (BI 3-4) are generally observed. Trace fossils include: rare to moderate *Helminthopsis* and *Planolites*; local *Chondrites*, *Asterosoma*, *Schaubcylindrichnus*, *Phycosiphon*, *Palaeophycus*, and *Rhizocorallium*; rare *Skolithos*, *Teichichnus*, *Diplocraterion*, and *Siphonichnus*; and very rare fugichnia, *Thalassinoides*, *Arenicolites*, *Ophiomorpha*, and *Cylindrichnus*. Sandstone beds or layers may be bioturbated in a similar manner as FE, however most biogenic disruption occurs in the muddy to silty sandstone and mudstone interbeds. Carbonaceous mudstones are moderately to commonly burrowed and contain common occurrences of *Chondrites* (Fig. 7.7H) as well as locally abundant *Rhizocorallium*.

Interpretation

Facies F contains increased sand content and represents a more proximal setting as compared to FE. Sedimentary structures are dominated by wave-formed features suggestive of subaqueous deposition influenced by wave reworking. High sedimentation rates are indicated by aggradational wave ripples, flame structures, load structures, and rare convolute bedding. Fluvial input is implied by the presence of rare coal fragments, wood fragments, sideritized mudstone beds, and synaeresis cracks. Ichnologically, FF is dominated by deposit-feeding structures, lesser grazing traces, and rare dwellings of inferred suspension-feeding organisms. This suite is consistent with a diverse archetypal *Cruziana* Ichnofacies (Fig. 7.5). Many of the traces in this facies are rare or very rare,

such that only 8-10 ichnotaxa may be present within an individual unit. As well, there are significantly reduced bioturbation intensities in comparison to typical upper offshore deposits that are otherwise characterized by the archetypal *Cruziana* Ichnofacies. Accordingly, the ichnological suite of FF is consistent with a moderately stressed expression of the archetypal *Cruziana* Ichnofacies. Indications of high sedimentation rates and fluvial input, abundance of sand-sized particles, dominance of wave-formed structures, and the moderately stressed ichnofossil suite are interpreted to reflect deposition in a proximal prodelta setting.

Facies G: *Burrowed Sandstone with Muddy Laminae*

Sedimentology

Facies G (FG) is composed of sandstone with moderate to common mudstone and siltstone laminae, and cm-dm scale interbedded sandstone with <20% mudstone (Fig. 7.8A-D). This facies also includes intervals of rarely burrowed, interbedded sandstone and mudstone locally with >50% mud content (Fig. 7.8A). Carbonaceous, black mudstone laminae and beds are generally several mm to 10 cm thick. This facies contains a diverse range of sedimentary structures, dominated by oscillation ripples and wavy parallel lamination, with lesser planar parallel lamination, low-angle cross lamination, aggradational wave ripples, and HCS. Sideritized intervals are rare to moderate and are typically not as pervasive as those in Facies H. Accessory elements also include rare to moderate syneresis cracks and coal fragments, as well as rare mudstone and sideritized mudstone rip-up clasts, pyrite, and glaucony. Deformation and erosion structures include rare flame structures, gutter casts, convolute bedding and local scour surfaces.

Ichnology

Bioturbation is absent to common (BI 0 to 4) in FG. Typically, however, there are rare to moderately bioturbated units (BI 1-3) intercalated. Burrowing intensities increase in some muddier intervals or locally within mudstone laminae (Fig. 7.8A). Trace fossils include: rare to moderate numbers of *Planolites*, *Helminthopsis*, *Chondrites*, *Schaubcylindrichnus*, and *Rhizocorallium*; rare

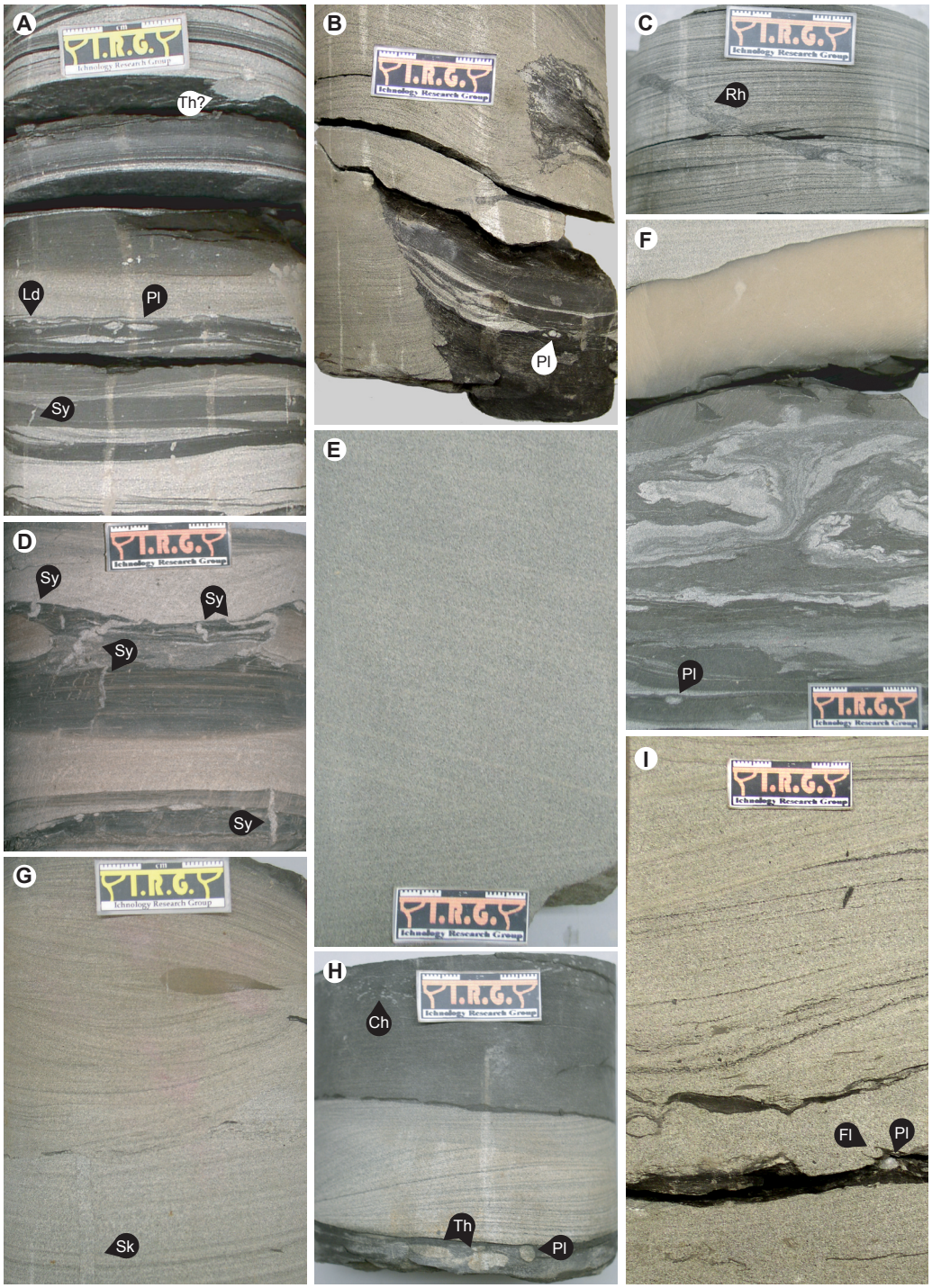

FIGURE 7.8—Wayne-Rosedale-Chain deposits. **A-D:** Facies G. **A:** Sandstone and mudstone interbeds with very little bioturbation, rare *Planolites* (Pl), possible *Thalassinoides* (Th), synaeresis cracks (Sy), and load structures (Ld), well 06-15-027-23W4 (1302.7 m). **B:** Two large mudstone gutter casts in wavy parallel laminated sandstone with *Planolites* (Pl), well 07-21-027-19W4 (1157.2 m). **C:** *Rhizocorallium* (Rh) in planar laminated sandstone, well 07-21-027-19W4 (1156.2 m). **D:** Numerous synaeresis cracks (Sy) in interbedded sandstone and mudstone, well 07-16-026-22W4 (1262.1 m). **E-I:** Facies H. **E:** Trough-cross bedding, well 10-04-030-22W4 (1246.4 m). **F:** Convolute bedding, with an overlying sideritized mudstone bed and planar laminated sandstone, well 16-11-031-24W4 (1412.8 m). **G:** Low-angle cross laminated sandstone with rare

FIGURE 7.8 (Continued)—*Skolithos* (Sk) and scoured by overlying wave rippled sandstone containing sideritized mudstone rip-up clasts, well 11-02-030-26W4 (1555.4 m). **H:** Aggradational wave ripples in sandstone with *Planolites* (Pl) and *Thalassinoides* (Th), and overlain by carbonaceous mudstone with *Chondrites* (Ch), well 10-04-030-22W29 (1251.1 m). **I:** Carbonaceous mudstone laminae with flame structures (Fl) and *Planolites* (Pl), overlain by low-angle cross laminated sandstone (HCS) with organic detritus, well 11-19-026-20W4 (1254.8 m).

Asterosoma, *Phycosiphon*, *Palaeophycus*, *Skolithos*, *Diplocraterion*, and *Thalassinoides*; and very rare *Arenicolites*, *Siphonichnus*, *Teichichnus*, *Scolicia*, *Rosselia*, and *Ophiomorpha*.

Interpretation

Units of FG contain lesser mud content, reduced bioturbation intensities and lower ichnotaxa diversity in comparison to FF, which is suggestive of deposition in a more proximal setting. Sedimentary structures indicate a dominance of wave influence and lesser current influence, with local scours in a high-energy setting. Elevated sedimentation rates are indicated by soft-sediment deformation features, carbonaceous mudstone deposits and convolute bedding. Synaeresis cracks, coal fragments and mudstone and sideritized mudstone rip-up clasts imply fresh water influx. The trace fossil suite is dominated by deposit-feeding structures with subordinate dwelling structures of inferred suspension-feeding organisms and minor grazing traces. Evidence of environmental stress includes reduced ichnofossil abundances and diversities. The suite is, therefore, consistent with a moderately stressed proximal expression of the *Cruziana* Ichnofacies (Fig. 7.5). Evidence of riverine influx coupled with a moderately stressed proximal expression of the *Cruziana* Ichnofacies are interpreted to reflect deposition in the distal delta front.

Facies H: *Weakly Burrowed Sandstone*

Sedimentology

Facies H is dominated by sandstone beds along with thinner, cm-scale interbedded, carbonaceous mudstone laminae (Fig. 7.8E-I). Interbedded carbonaceous mudstone beds with low bioturbation intensities are interspersed between some tabular sandstone units (Fig. 7.8H). Interbeds of mudstone are up to 30 cm thick, while the tabular sandstone beds typically range from centimeters to 2 m in thickness. Sandstones are dominated by physical structures, including low-

angle cross lamination and planar parallel lamination with lesser HCS, massively bedded units, oscillation ripples, and rare aggradational wave ripples and trough-cross bedding. Very rare current ripples and local scour surfaces are also present. Wave ripples commonly occur in association with mudstone laminations. Copious accessory elements in FH include rare to common sideritized mudstone rip-up clasts and coal fragments. Partially sideritized zones (in the sandstone) are rare to common, with intervals ranging from centimeters to decimeters in thickness. Other sedimentological features include rare to moderate amount of pyrite, and rare synaeresis cracks and glaucony. Flame structures, scour surfaces, convolute bedding and gutter casts are also observed.

Ichnology

Ichnologically, FH consists of units that are unbioturbated to moderately bioturbated (BI 0-2), although units are typically weakly burrowed (BI 1). A number of intervals are strictly dominated by physical structures or massive bedding without the presence of discernible traces (Fig. 7.8E). The ichnological suite consists of *Planolites* and *Helminthopsis*; rare *Chondrites*, *Skolithos*, *Rhizocorallium*, *Schaubcylindrichnus*, fugichnia, and *Asterosoma*; and very rare *Ophiomorpha*, *Thalassinoides*, *Palaeophycus*, *Diplocraterion*, and *Phycosiphon*. Commonly, *Planolites* and other deposit feeding structures (*Chondrites*), as well as grazing traces (e.g., *Helminthopsis*) are observed in carbonaceous mudstone deposits; however, some mudstones are unburrowed.

Interpretation

The predominance of low-angle cross laminations in FH is suggestive of unidirectional current activity. Massively bedded units, soft-sediment deformation features, and convolute bedding support rapid deposition during periods of high sedimentation. Accessory elements such as sideritized mudstone rip-up clasts and partially sideritized zones support interpretations of riverine influence similar to deposits of FAS1. Synaeresis cracks indicate the mixing of fluvial and marine waters, whereas gutter casts, scour surfaces and other sedimentary structures indicate high-energy conditions.

The trace fossil suite comprises a low-diversity and low-abundance of traces in a locally bioturbated facies. Ichnogenera correspond to deposit-feeding behaviors (*Planolites*) are the most profuse, whereas dwelling structures of

inferred suspension-feeders and grazing traces are rare. Significantly reduced bioturbation intensities and ichnotaxa diversity are interpreted to reflect environmental stress. The lack of structures of inferred suspension-feeding organisms and dominance of deposit-feeding traces suggests a stressed proximal expression of the *Cruziana* Ichnofacies (Fig. 7.5). FH is interpreted as proximal delta-front deposits due to the sandy nature of the rock, strong evidence of fluvial input, indications of high sedimentation rates, and the stressed proximal expression of the *Cruziana* Ichnofacies.

Facies Association 2: Summary

Profuse indications of riverine influx, high sedimentation rates and high-energy conditions are observed in facies of FAS2. These sedimentological characteristics are in contrast to those of FAS1 in which these features are rarely observed. Ichnological suites of FAS2 display characteristics (reduced ichnotaxa abundances and diversities) associated with environmental stresses, which increase from FE to FH. These observations reflect deltaic deposition, in which FE represents the distal deposits, and FH the proximal. Persistent low-angle lamination with mudstone laminae, soft-sediment deformation features, massive beds, early diagenetic siderite, a high organic-matter content and mudstone rip-up clast horizons in FAS2 are typical of river-dominated deltaic successions (Bhattacharya and Walker, 1991, 1992). Oscillation ripples and aggradational wave ripples indicate a low degree of wave reworking in the proximal delta front. Hummocky cross-stratification (HCS) is indicative of storm deposition; however, the presence of HCS is not diagnostic of wave-dominated deltaic successions, as storms affect all variations of coastlines (MacEachern et al., 2005). Thick unburrowed, carbonaceous mudstones reflect flood discharge (see discussion below). Proximal delta front deposits (FH) contain features consistent with distributary mouth-bar deposits, such as rare wave and current-rippled units (Coleman et al., 1964; Reineck and Singh, 1975; Bhattacharya and Walker, 1991), sporadic scour features, minor faunal content and some organic debris (Wright, 1985). Interbedded sandstone and mudstone with wave-formed sedimentary structures (FG) and a moderate degree of bioturbation is consistent with areas laterally adjacent to the river mouth (Pulham, 1989), such as the distal-bar setting (Reineck and Singh, 1975). Prodelta deposits are also dominated by wave-formed structures in FAS2. Accordingly, riverine and wave influence were the most

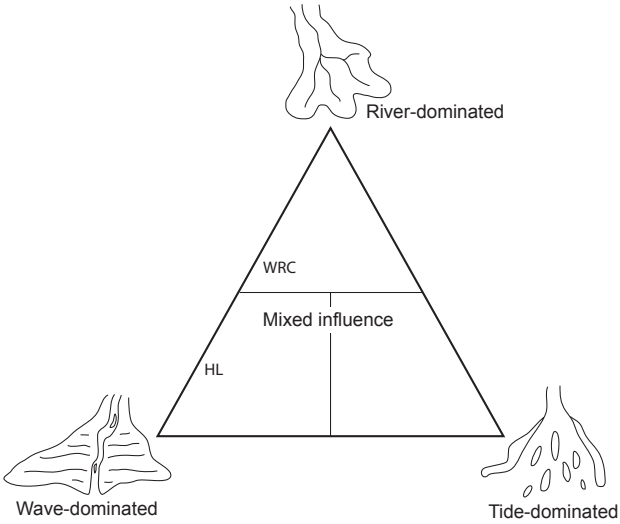

FIGURE 7.9—Tripartite classification of deltaic systems, with end-member river-, wave- and tide-dominated deltas. Deltas with mixed influence of wave, tides and/or riverine discharge plot within the triangle. The approximate plotted position of the Hamilton Lake (HL) deltaic deposits and the Wayne-Rosedale-Chain deltaic deposits (WRC) are shown. Modified from Galloway (1975).

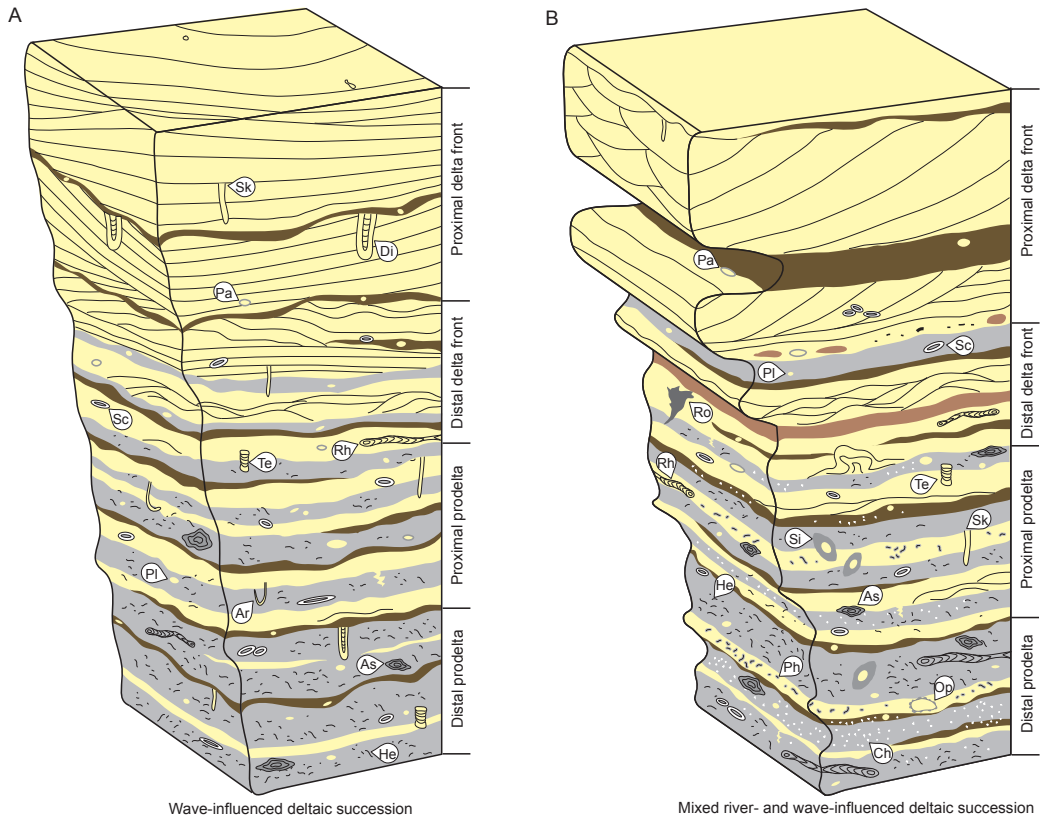

FIGURE 7.10—**A:** Wave-influenced deposits at Hamilton Lake and **B:** mixed river- and wave-influenced deposits in the Wayne-Rosedale-Chain area. Trace fossil abbreviations: *Planolites* (Pl), *Palaeophycus* (Pa), *Asterosoma* (As), *Rhizocorallium* (Rh), *Arenicolites* (Ar), *Schaubcylindrichnus* (Sc), *Diplocraterion* (Di), *Skolithos* (Sk), *Teichichnus* (Te), *Helminthopsis* (He), *Phycosiphon* (Ph), *Ophiomorpha* (Op), *Chondrites* (Ch), *Rosselia* (Ro), *Siphonichnus* (Si).

	Hamilton Lake	Wayne-Rosedale-Chain
Deltaic Environment	Wave-influenced delta	Mixed river- and wave-influenced delta
Proximal Delta Front	stressed proximal *Cruziana* Ichnofacies with stressed *Skolithos* Ichnofacies characterizing tempestite beds	stressed proximal *Cruziana* ichnofacies
Distal Delta Front	moderately stressed proximal *Cruziana* ichnofacies	moderately stressed proximal *Cruziana* ichnofacies
Proximal Prodelta	moderately stressed archetypal *Cruziana* ichnofacies	moderately stressed archetypal *Cruziana* ichnofacies
Distal Prodelta	subtly stressed archetypal *Cruziana* ichnofacies	subtly stressed archetypal *Cruziana* ichnofacies

TABLE 7.1—Comparison of ichnological assemblages from the Hamilton Lake and Wayne-Rosedale-Chain study areas.

prominent process that affected deposition, while storm activity was subordinate.

Thick, carbonaceous mudstone units in the proximal delta front (FH) are generally unburrowed (Fig. 7.8H). Similar silty convoluted mudstones have been described in river-dominated Dunvegan deposits (Bhattacharya and Walker, 1991; Gingras et al., 1998; Coates and MacEachern, 1999), Cadotte deposits (Moslow and Pemberton, 1988), Permian units of the Denison Trough (Bann and Fielding, 2004), and Scar House deposits (Martinsen, 1990). River-dominated deltas typically have high suspended-sediment loads, which can be transported via riverine discharge or in association with storm events (Gingras et al., 1998). Sediment-gravity driven, hyperpycnal discharge may follow storm or flood events as a result of abundant precipitation and increased riverine sediment load during peak flooding (Raychaudhuri and Pemberton, 1992; Wright et al., 1990; Gingras et al., 1998; Bann and Fielding, 2004 MacEachern et al., 2005). Hypopycnal plumes are deposited from suspension and the rate of sedimentation is much slower in comparison to hyperpycnal flows (MacEachern et al., 2005). A slower sedimentation rate would allow for biogenic reworking, however, the thick mudstones of FAS2 contain few traces suggestive of rapid emplacement by hyperpycnal flows that followed flood or storm events. The lack of bioturbation in these carbonaceous mudstones is likely related to the high organic content in the muds, which results in oxidation, reduced oxygen at the bed, and inhospitable conditions for infaunal organisms (Raychaudhuri and Pemberton, 1992; Gingras et al., 1998; Coates and MacEachern, 1999; Coates, 2001; Bann and Fielding, 2004; MacEachern et al., 2005). Analysis of microfossil content also revealed

an atypical lack of foraminifera suggesting a departure from normal marine conditions (cf. MacEachern et al., 1999c).

The ichnological assemblages in the proximal delta front of the WRC area are approximately comparable to the river-dominated deltaic successions in the Dunvegan Formation (Gingras et al., 1998; Coates and MacEachern, 1999) and deltaic deposits of the Cadotte (Moslow and Pemberton, 1988). The WRC proximal delta front deposits, however, contain a subtly more diverse assemblage with a slightly higher degree of bioturbation in some cases. In the distal delta front and prodelta, expressions of the *Cruziana* Ichnofacies display evidence of reduced environmental stresses in comparison to other wave-dominated deltaic successions (e.g., Cadotte and Dunvegan; cf. Moslow and Pemberton, 1988; Coates and MacEachern, 1999; Gingras et al., 1998). This reduction in stresses associated with deltaic deposition in the WRC area is interpreted to reflect subtle wave-influenced moderation of environmental stresses associated with riverine discharge.

Sedimentologically and ichnologically, the WRC proximal delta-front deposits are similar to the mouth-bar, delta front and prodelta deposits of the mixed river- and wave-influenced deltaic deposits in Permian formations of the Denison Trough (Bann and Fielding, 2004). FAS2 is also sedimentologically similar to the Belly River mixed wave- and river-influenced deltaic deposits in which tempestites and massive and deformed beds are indicative of storm and riverine processes, respectively (Coates, 2001; Hanson and MacEachern, 2007). Lithological, sedimentological, and ichnological features of FAS2 are consistent with riverine influence, but additional characteristics imply increased wave influence in comparison to typical river-dominated successions. Accordingly, deposits of FAS2 in the WRC study area are consistent with a mixed river- and wave-influenced deltaic system.

DISCUSSION

The tripartite classification of deltas is the classical approach in delineating deltaic facies models (Fig. 7.9; Galloway, 1975). The complexity of processes operating in a deltaic system does not always lead to end-member classifications, as apparent in the HL and WRC Viking deposits. Instead, there

may be complex sedimentary and ichnological relationships related to varying degrees of influence from riverine, tidal, wave, and storm processes. Comparison of lithological, sedimentological and ichnological attributes of the HL and WRC deposits illustrate the various processes that influenced deposition in each instance (Fig. 7.10, Table 7.1).

Principal sedimentological differences between FAS1 and FAS2 reside in the proximal delta-front deposits (FD and FH; Fig. 7.10). Units of FD (FAS1) contain abundant HCS, indicative of storm influence, whereas units of FH (FAS2) contain low-angle cross laminated beds and massive bedding signifying predominant riverine influence, unidirectional current activity, and high sedimentation rates. Mouth-bar deposits were significantly reworked by waves and storms in the HL area. Subtle storm and wave influences in the WRC study area resulted in partial reworking of mouth-bar deposits and preservation of thick mudstones deposited following storm or flood events. Distal delta-front and prodelta deposits of both study areas are dominated by wave-formed structures and differ in the thicknesses of sandstone (tempestite) beds.

In comparison to shoreface successions, there is a paucity of dwelling structures of inferred suspension-feeding organisms and corresponding dominance of deposit-feeding structures in deltaic deposits (Gingras et al., 1998; Coates and MacEachern, 1999; Bann and Fielding, 2004; MacEachern et al., 2005). Between the two study areas, ichnological suites show greater proportions of dwellings of inferred suspension-feeding animals in the HL wave-influenced deposits (FAS1; Table 7.1; Fig. 7.10). This is interpreted to reflect wave-energy induced stress mitigation of turbid waters, high concentrations of suspended sediment, and decreased salinity related to riverine discharge (Moslow and Pemberton, 1988; Gingras et al., 1998; Coates and MacEachern, 1999; Bann and Fielding, 2004; MacEachern et al., 2005). In the mixed river- and wave-influenced delta system (FAS2), harsh ecological conditions were more prevalent and inhibited colonization by suspension-feeding organisms.

With respect to specific trace fossils, the mixed-influenced deposits (FAS2) contain an increased proportion of *Chondrites* and *Phycosiphon*, especially in the prodelta. As a result of harsher environmental conditions, the niche typically colonized by suspension-feeding organisms was vacant and permitted colonization by opportunistic deposit-feeders and grazers. Carbonaceous mudstones in FAS2, in particular, are organic rich and thoroughly burrowed with *Chondrites*, which is interpreted as a deep-tier trace made by an

opportunistic colonizer feeding on bacteria from the degrading organic material in the mudstones (Fig. 7.7E; Raychaudhuri and Pemberton, 1992).

Tempestite beds are especially prevalent in the prodelta of FAS2, and to a lesser extent in the prodelta of FAS1. Rare opportunistic suites in the Hamilton Lake deposits (FAS1) include *Arenicolites*, *Skolithos*, *Phycosiphon*, and *Diplocraterion* traces. Grazing and deposit-feeding structures in tempestites are more common in facies E and F of FAS2, and include *Phycosiphon*, *Helminthopsis*, *Ophiomorpha*, *Skolithos*, *Rosselia*, and *Asterosoma* (Fig. 7.7D, E). Opportunistic colonization of tempestite beds in shoreface successions typically consists of vertical dwelling structures of suspension-feeding organisms of the *Skolithos* Ichnofacies (Pemberton and Frey, 1984). However, tempestites of FAS1 and especially FAS2 show an impoverishment of elements of the *Skolithos* Ichnofacies. This suppression of suspension-feeding behaviors in tempestites is common to deltaic deposits (Gingras et al., 1998; Coates and MacEachern, 1999; Bann and Fielding, 2004).

CONCLUSIONS

Facies analysis from two adjacent study areas, Hamilton Lake and Wayne-Rosedale-Chain, resulted in the identification of two facies associations. Deposits of the HL area consist of four facies comprising FAS1, interpreted to record progradation from distal prodelta (FA) to proximal delta front (FD) settings in a wave-influenced delta complex. Subtle indications of riverine input, high sedimentation rates and salinity variations, as well as a subtly stressed ichnological suite indicate wave-mitigation of riverine derived stresses.

Facies Association 2 of the WRC area comprises four facies, in which the distal prodelta (FE) gradually coarsens upward to the proximal delta front (FH) in a mixed river- and wave-influenced deltaic system. In comparison to FAS1, the indications of riverine influx, high sedimentation rates, and salinity variations are more pronounced in FAS2. The ichnological suites of FAS2 also contain very few dwellings constructed by inferred suspension-feeding animals. This ichnologic signature is consistent with turbid conditions and high concentrations of suspended sediment, which are persistent with minimal wave-reworking.

The specific environmental stresses placed on ichnological suites

of ancient deltaic deposits are difficult to ascertain. Environmental stresses can include: variations in salinity, temperature, substrate consistency and sedimentation rates, as well as hypopycnal-induced turbidity, rapid sediment influx, flood discharges, hyperpycnal-induced sediment gravity flows, fluid mud deposition, and reduced oxygenation (e.g., Moslow and Pemberton, 1988; Gingras et al., 1998; Coates and MacEachern, 1999; Coates, 2001; Bann and Fielding, 2004; MacEachern et al., 2005; Bhattacharya and MacEachern, 2009). In the HL deltaic deposits, variations in salinity and sedimentation rates, as well as fluid mud deposition and associated reduced oxygenation can be inferred. Salinity variations are evident from the presence of syneresis cracks, and evidence of variable sedimentation rates is based on the interbedding of mudstone laminae and beds with HCS sandstones. Carbonaceous, sharp-based mudstone deposits are suggestive of riverine-derived fluid mud hyperpycnite deposition (Bhattacharya and MacEachern, 2009). Correspondingly, low burrowing intensities of these mudstones are associated with reduced oxygen at the bed as a result of oxidation of organic material (cf. Raychaudhuri and Pemberton, 1992; Gingras et al., 1998; Coates and MacEachern, 1999; Coates, 2001; Bann and Fielding, 2004; MacEachern et al., 2005). Deposition of FAS2 was influenced by the similar stresses as FAS1 (e.g., salinity and sedimentation rate variations, fluid mud deposition, and reduced oxygenation), which were more pronounced due to heightened riverine influence. Hyperpycnal mudstone deposits are recognized by the thick, graded beds with a paucity of biogenic structures and gradational to sharp underlying contacts.

Understanding processes and environmental stresses that influenced deposition of Viking deltaic deposits in south-central Alberta provides a basis for understanding stratigraphic relationships and environmental distributions.

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CHAPTER 8 – WAVE-INFLUENCED DELTAIC SANDSTONE BODIES AND OFFSHORE DEPOSITS WITHIN A STRATIGRAPHIC FRAMEWORK IN THE VIKING FORMATION, HAMILTON LAKE AREA, SOUTH-CENTRAL ALBERTA, CANADA

INTRODUCTION

Historically, sandy Lower Cretaceous (Albian) Viking Formation (Fig. 8.1) reservoirs have been interpreted as offshore bars and tidal bars (Evans, 1970; Beaumont, 1984; Amajor, 1986; Cant and Hein, 1986; Hein et al., 1986; Leckie, 1986; Amajor and Lerbeckmo, 1990a, b). Explaining the transport mechanisms and processes that concentrated sediment into linear, coarsening-upward bodies was problematic in these interpretations (Downing and Walker, 1988). More contemporary interpretations of Viking sand packages encompass lowstand shorefaces (Walker and Wiseman, 1995), forced regressive deposits (Davies and Walker, 1993), transgressively incised shorefaces (Downing and Walker, 1988; Raddysh 1988; Boreen and Walker, 1991; Davies and Walker 1993; Posamentier and Chamberlain, 1993; and Walker and Wiseman, 1995), and deposition of deltaic strata (Raychaudhuri and Pemberton, 1992; Raychaudhuri, 1994; MacEachern et al., 1999b). This study provides a detailed facies analysis of Viking deposits at Hamilton Lake (HL) in order to further refine the depositional history of the area (Fig. 8.2).

Previous analysis of Viking units around HL include the study by Amajor and Lerbeckmo (1990a, b) in which sand bodies were interpreted as offshore units deposited below fair-weather wave base in a tide-dominated setting. These authors proposed that sand bodies formed at consistent or shallowing water depths, which produced a morphology similar to ridge-and-swale topography. To explain the formation of sand bodies, Amajor and Lerbeckmo (1990b), suggested mechanisms such as redistribution and reshaping of gravity flows or older deltaic deposits into sandridges by submarine currents.

Subsequently, Burton (1997) interpreted HL deposits as lower to upper

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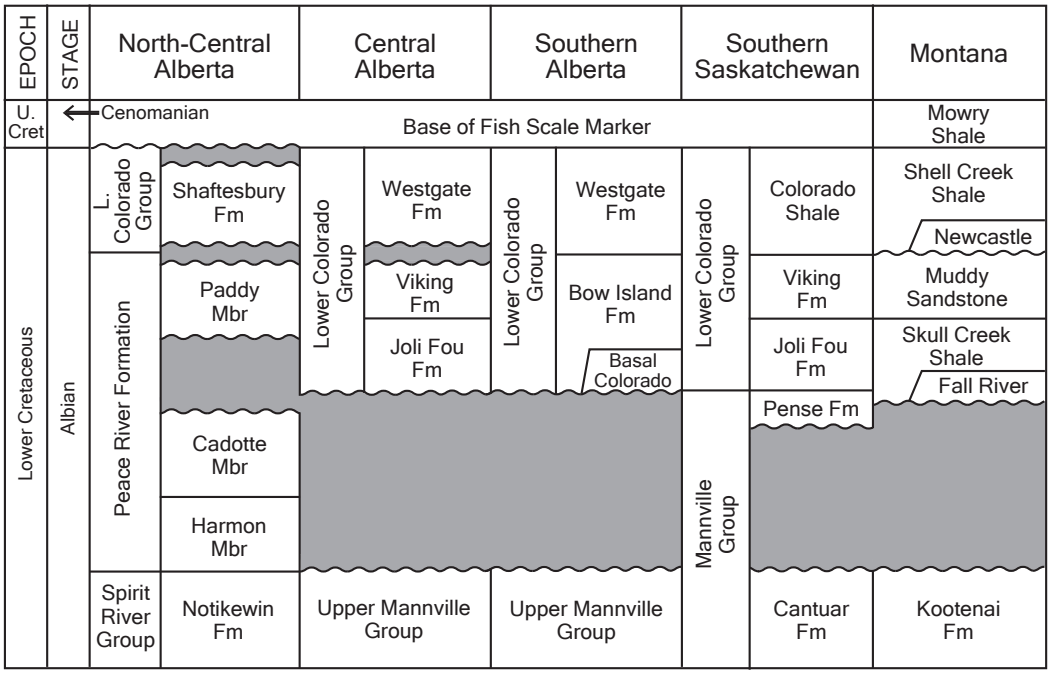


FIGURE 8.1—Stratigraphic correlation chart for the Viking Formation and equivalents (modified from MacEachern et al. 1999a).

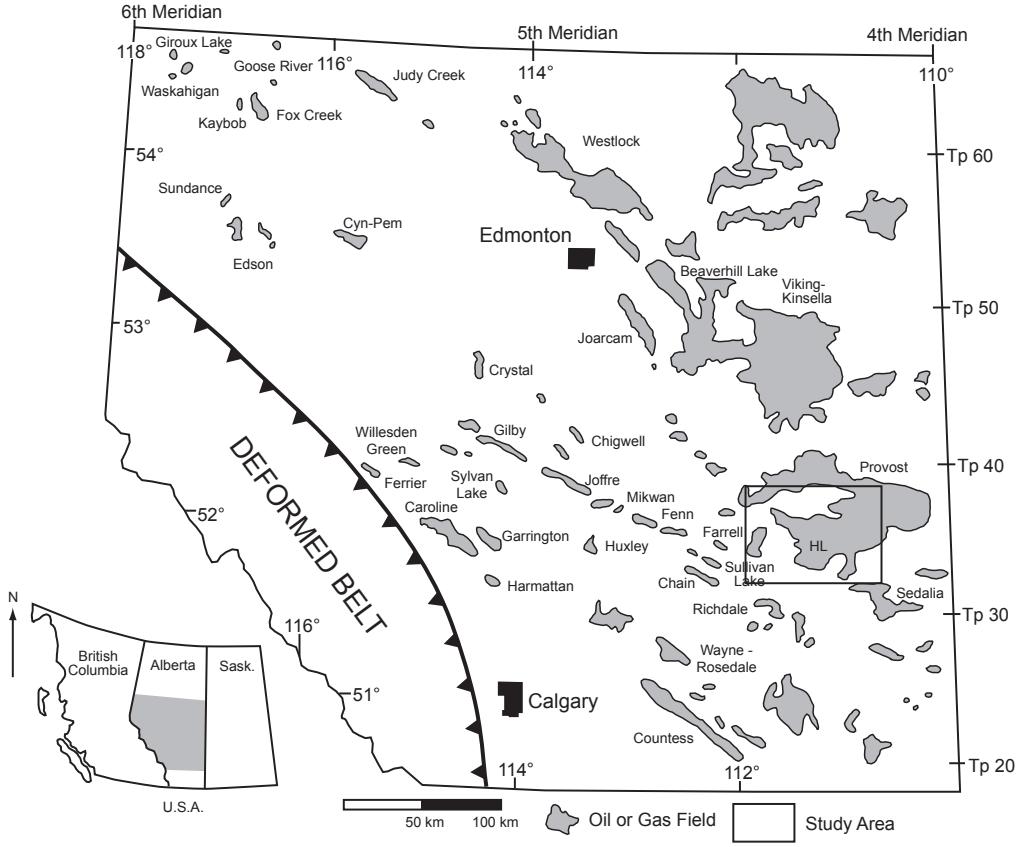


FIGURE 8.2—The Hamilton Lake (HL) study area in southeastern Alberta, Canada. Modified from MacEachern et al. (1999a).

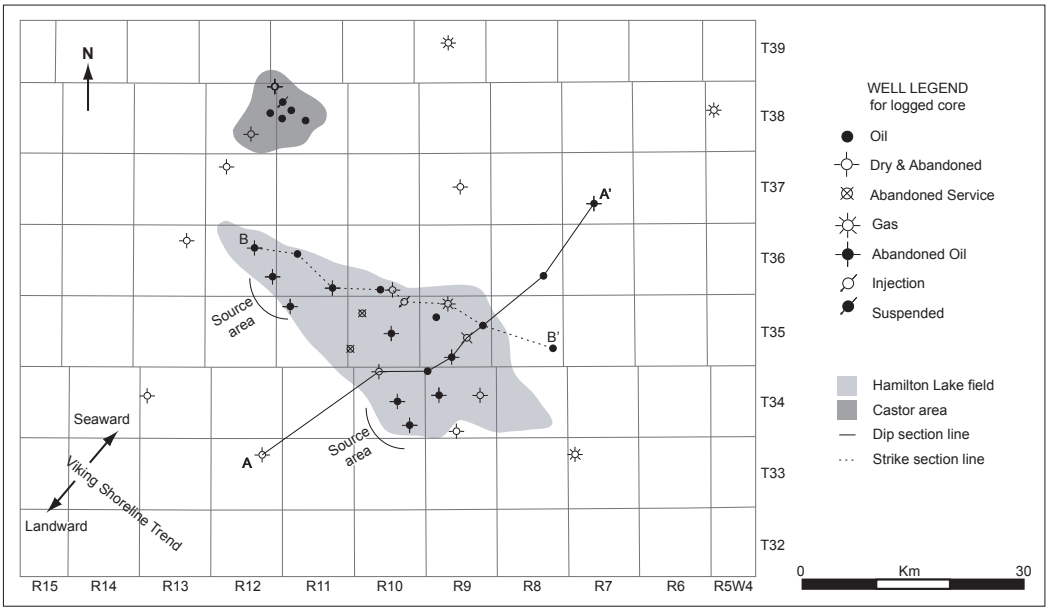


FIGURE 8.3—The study area with locations of logged core and outline of the Hamilton Lake field and Castor area. Cross sections were completed using cored intervals.

offshore strata capped by transition zone and lower shoreface deposits. These interpretations were primarily based on the dominance of hummocky cross-stratification and an ichnological suite characteristic of the *Cruziana* Ichnofacies (Burton, 1997). A more recent ichnological study addressed the uppermost Bounding Discontinuity 4 (BD4), a transgressively modified sequence boundary at the top of the Viking Formation (MacEachern and Burton, 2000). In the HL field, this discontinuity is uncharacteristically demarcated by a distal expression of the *Glossifungites* Ichnofacies. The following analysis incorporates ichnological, sedimentological and stratigraphic data, which provides a framework for deltaic and offshore deposition in the HL area.

Study Area and Methods

The study area is located in south-central Alberta, Canada (Fig. 8.2), and includes the HL field and surrounding area encompassing townships 32 to 39 and ranges 6W4 to 15W4 (Fig. 8.3). Within this study area, 41 drill cores were logged and utilized to conduct comprehensive facies analysis through integration of sedimentological and ichnological attributes. The facies outlined in this paper are interpreted based on distinguishing sedimentological and ichnological features and association to the stratal architecture.

FACIES DESCRIPTIONS

The lithological, sedimentological and ichnological characteristics of the 12 facies described from HL are summarized in Table 8.2. Bioturbation within facies is reported using a bioturbation index (BI), as well as corresponding descriptive terms. A bioturbation index of 0 is equivalent to unbioturbated, BI 1 corresponds to sparsely burrowed, BI 2 indicates a low degree of burrowing, BI 3 is equivalent to a moderate degree of burrowing, common burrowing is represented by a BI 4, abundant burrowing reflects BI 5, and pervasive burrowing corresponds to a BI 6 (cf. Reineck, 1967; Taylor and Goldring, 1993; Bann et al., 2004). Trace fossils are listed in the order of decreasing abundance and occurrence. Ichnological suites are interpreted with regards to ichnofacies, and interpretations of depositional environments are summarized in Table 8.2 and expanded upon in the following section.

FACIES ASSOCIATIONS

Based on similar attributes, facies were grouped into three facies associations (Table 8.2). Each facies association comprises a vertical succession of genetically-related facies in which the facies are gradational in nature with respect to lithology, degree of burrowing, and trace fossil suite. The facies associations include: 1) delta front and prodelta, 2) upper offshore, and 3) lower offshore and transgressive.

Facies Association 1: Delta Front and Prodelta

Facies association 1 (FAS1) encompasses the proximal shoreline deposits in the study area. Facies of this association are defined by increasing mudstone content, increasing bioturbation, and decreasing abundance of sedimentary structures from Facies A through D. The predominance of hummocky cross-stratified (HCS) sandstone in this association has been previously interpreted to reflect shoreface deposition (Burton, 1997). However, subtle sedimentological and ichnological evidence of riverine discharge in FAS1 is interpreted to reflect deltaic origin (Table 8.2).

Description	Sedimentological Characteristics	Ichnological Characteristics	Interpretation
Facies Association 1: Wave-Influenced Delta Front and Prodelta			
Facies A: *Sparsely burrowed sandstone*	• sandstone with rare to moderate occurrences of carbonaceous mudstone laminae • dominated by low-angle cross-laminations and lesser aggradational wave ripples and planar parallel laminae • rare occurrences of massive bedding and mud drapes as couplets • rare mudstone rip-ups, glaucony, sideritized mudstone laminae, wood fragments and coal fragments	• rarely bioturbated (BI 1) • ichnofossils include: rare to moderate Pl, Pa, Di, Sk, Sc; rare As, He, Th, Rh, Ch; very rare Op, Ro, Te, fu. • dwellings of inferred suspension-feeding organims observed within sandstone beds • moderately stressed proximal *Cruziana* Ichnofacies with tempestite beds characterized by stressed *Skolithos* Ichnofacies	• some mudstone laminae were produced by rapid outflows of riverine discharge • rapid sedimentation implied by aggradational wave-ripple laminations and massive bedding • mudstone rip-ups and trough-cross lamination indicate current energy • proximity to a fluvial source suggested by coal and wood fragments • proximal delta front (reworked distributary mouth-bar deposits into HCS)
Facies B: *Moderately burrowed sandstone*	• sandstone with common occurrences of carbonaceous mudstone laminae/beds or muddy sandstone with up to 20% mud content • aggradational wave-ripple laminations with rare low-angle cross-laminations, wave ripples, and double mud drapes • rare coal fragments, mudstone rip-ups, glaucony and siderite intervals	• low to moderate burrowing (BI 2-3) • bioturbation intensity is greater in the muddy sandstone • traces comprise: rare to moderate Pl, He, Sc, Di; rare As, Sk, Pa, Th; very rare Rh, Ch, Ar, Ph, Ro • subtly stressed proximal expression of the *Cruziana* Ichnofacies	• high sedimentation rates indicated by aggradational wave ripples • high-energy conditions suggested by mudstone rip-up clasts and sharply based mudstone laminae which are suggestive of hyperpycnal fluvial discharge • siderite cementation may indicate fresh water influx • interpreted as distal delta front deposits
Facies C: *Burrowed muddy sandstone*	• muddy sandstone with 20-35% mud • moderate occurrences of carbonaceous mudstone laminae • aggradational wave-ripple laminae and lesser occurrences of wave ripples • rare convoluted bedding, mudstone rip-ups, synaeresis cracks, glaucony and wood fragments	• moderate to common bioturbation (BI 3-4) • trace fossils include: rare to moderate He, Pl, Sc, As, Rh, Sk; rare Di, Pa, Ar, Te, fu, Zo; very rare Th, Ph, Op, Ro • moderately stressed expression of the archetypal *Cruziana* Ichnofacies	• rapid sedimentation indicated by aggradational wave ripples and convoluted bedding • synaeresis cracks imply salinity variations • riverine discharge suggested by wood fragments and carbonaceous mud deposits • interpreted as proximal prodelta deposits
Facies D: *Burrowed muddy sandstone to sandy mudstone*	• muddy sandstone with 30-45% mud, sandy mudstone with 15-50% sand or interbedded sand and mud • rare to moderate occurrences of aggradational wave ripples and wave ripples • intermittent mudstone laminae • rare soft-sediment deformation, synaeresis cracks, siderite, glaucony, shell fragments and pyrite	• commonly bioturbated (BI 4) • ichnological suite includes: moderate He; rare to moderate Pl, Sc, Rh, Sk, As; rare Di, Pa, Te, Zo, Ar, Th, Ro; very rare fu; Ch, Si, Ph, Cy • subtly stressed archetypal expression of the *Cruziana* Ichnofacies	• high sedimentation rates implied by soft-sediment deformation and aggradational wave ripples • synaeresis cracks signify mixing of fresh and marine waters • fine-grained nature interpreted to reflect deposition in the distal prodelta

Facies Association 2: The Distal Lower Shoreface to Upper Offshore			
Facies E: *Homogenized muddy sandstone*	• rarely observed facies • muddy sandstone with 20-30% mud • rare preservation of sedimentary structures • local occurrences of glaucony and siderite, as well as, rare pyrite and coal fragments	• moderate to pervasive burrowing (BI 3-6) • ichnofossils encompass: common He; moderate Pl, Ph; rare to moderate Sc, Rh, Sk, Ro, Si; rare Pa, Cy, Ar, Te, Th • archetypal expression of the *Cruziana* Ichnofacies	• abundance of sand and pervasive bioturbation indicates a setting between the upper offshore and proximal lower shoreface • *Rosselia* traces are typical of the lower shoreface; however, *Helminthopsis* is typically found in the offshore. • interpreted as the distal lower shoreface
Facies F: *Homogenized silty to muddy sandstone*	• silty to muddy sandstone with 20-45% silt and/or clay particles • rare occurrences of aggradational wave ripples and wave ripples • rare coal fragments	• commonly bioturbated (BI 4) • traces consist of moderate Pl, He; rare to moderate Sc, As, Sk, Rh; rare Di, Ar, Th, Ch, Si, Zo, Te, Ro, So, Pa, Ph • archetypal expression of the *Cruziana* Ichnofacies	• deposited between fair weather and storm wave base • sandy nature and diverse trace fossil assemblage are interpreted to represent the proximal upper offshore
Facies G: *Homogenized sandy siltstone to sandy mudstone*	• sandy siltstone to sandy mudstone facies contains 15-40% sand grains • rare aggradational wave ripples and wave ripples • very rare shell fragments, pyrite, glaucony, siderite, and coal fragments	• pervasively bioturbated (BI 5-6) • biogenic structures include: common He; moderate Pl, Sc, As, Ph; rare to moderate Pa, Rh, Zo; rare Sk, Di, Th, Ar, Te, Si, fu, Ch • archetypal expression of the *Cruziana* Ichnofacies	• deposited between fair weather and storm wave base • dominance of deposit feeding structures with secondary dwellings of suspension feeders • interpreted as distal upper offshore deposits
Facies Association 3: Lower Offshore and Transgressive Deposits			
Facies H: *Burrowed sandy mudstone to silty mudstone*	• sandy mudstone with 5-15% sand grains, or silty mudstone with sandstone laminae • rare to moderate wave ripples, starved current ripples, and planar laminae • very rare coal fragments, organic fragments, glaucony, pyrite and siderite	• rare to pervasive burrowing (BI 1-5), but typically moderate (BI 3) • Trace fossils comprise: moderate He, Pl, rare to moderate Sc, Ph; rare Sk, Zo, Te, As, Pa, Th, fu, Di, Rh, Si • distal expression of the *Cruziana* Ichnofacies	• presence of wave ripples indicates deposition above storm wave base, but below fair weather wave base • fine-grained nature and low to moderate diversity trace fossil suite interpreted to reflect proximal lower offshore deposition
Facies I: *Sparsely burrowed sandy mudstone*	• sandy mudstone contains less than 5% sand grains • sandstone laminae/lenses with rare to moderate occurrences of planar and wavy parallel laminae • rare siderite and shell fragments	• unbioturbated to commonly bioturbated (BI 0-4) • lack of contrast in the mudstone results in a paucity of biogenic structures • ichnogenera observed include: rare to moderate Pl; rare He, Ph; very rare Zo, Te, Sc, As, fu, Ar, Sk, Rh, Th • distal expression of the *Cruziana* Ichnofacies	• deposited between storm and fair weather wave base • scarcity of sand grains supports an offshore setting in conjunction with dominant grazing and deposit feeding structures • interpreted as deposits of the distal lower offshore

Facies J: *Massive Mudstone to Shale*	• dark mudstone with rare sandstone laminae characterized by aggradational wave ripples • rare to moderate occurrences of sideritized intervals and convolute bedded sandstone beds • rare pyrite	• very rare burrowing (BI 1) • burrowing restricted to intervals with a slight increase in silt particles or within isolated sandstone beds or laminae • trace fossils encompass: rare He, Sc, Pl, As, Ph	• deposited below storm wave base • trace fossils comprise opportunistic suites colonized during deposition of distal sandy storm beds • interpreted as shelf mudstones
Facies K: *Chaotic sandy mudstone to muddy sandstone*	• lithologically similar to Facies F and G except for reduced bioturbation and chaotic organization of the sediment • muddy sandstone with 30-40% mud content to sandy mudstone with 20-40% sand grains • very rare wave ripples • rare pyrite nodules, wood fragments and pebbles	• moderate to pervasive bioturbation (BI 3-5 and possibly over-exaggerated due to chaotic nature) • biogenic structures include: moderate to common Pl, He; rare Sk, As, Sc, Pa, Rh, Zo, Th, Ro, Di, Te, fu, Ar • distal to archetypal expressions of the *Cruziana* Ichnofacies	• transgressive lag formed at the onset of a marine flooding event • trace fossils indicate sufficient time for colonization of the lag during transgression • reworking of proximal deltaic deposits occurred in the upper to lower offshore with subsequent colonization by a low diversity and low abundance trace fossil suite
Facies J: *Convolute bedded sandy siltstone to sandy mudstone*	• finely laminated, highly convolute to interbedded sand and mud, with load and flame structures • rare pyrite nodules and moderate glaucony	• some bioturbation may be present in 10-03-036-10W4, but it is difficult to determine owing to the deformed nature of the sediment • no bioturbation in the highly convolute deposits of 10-04-036-10W4	• lack of wave-formed structures and trace fossils atypical for offshore deposition • associated with erosion of the lowermost parasequence (PSA) in Hamilton Lake • deposited through slumping due to erosion of PSA

TABLE 8.1—Facies descriptions for deposits in the Hamilton Lake area. The 11 facies are grouped into three facies associations – deltaic, upper offshore and lower offshore to transgressive associations. Trace fossil abbreviations: *Planolites* (Pl), *Palaeophycus* (Pa), *Schaubcylindrichnus* (Sc), *Rosselia* (Ro), *Teichichnus* (Te), *Helminthopsis* (He), *Phycosiphon* (Ph), *Rhizocorallium* (Rh), *Arenicolites* (Ar), *Skolithos* (Sk), *Diplocraterion* (Di), *Thalassinoides* (Th), *Siphonichnus* (Si), *Cylindrichnus* (Cy), *Asterosoma* (As), *Scolicia* (So), *Zoophycos* (Zo), fugichnia (fu), *Chondrites* (Ch), and *Ophiomorpha* (Op).

Interpretation of Facies A: Sparsely Burrowed Sandstone – Proximal Delta Front

In Facies A (FA), the presence of prominent low-angle, cross-laminated sandstones (Fig. 8.4A, D, E) interpreted as HCS, in combination with carbonaceous mudstone deposits, siderite, localized wood and coal fragments and evidence of rapid sedimentation suggests prominent wave and riverine influence. The occurrence of HCS in sparsely burrowed sandstone is generally thought to reflect shoreface deposition (Dott and Bourgeois, 1982). However, continuous and pronounced wave energy acting on the shoreface would inhibit preservation of the observed intermittently burrowed, sharp-based, carbonaceous mudstone deposits (Fig. 8.4A, C). These mudstone deposits are interpreted to reflect hyperpycnal flows associated with enhanced riverine discharge and phytodetrital pulses (MacEachern et al., 2005).

Physical structures that indicate episodes of rapid sedimentation include mudstone rip-up clasts (Fig. 8.4C), localized massive bedding, and aggradational wave-ripple laminae. In addition, possible double mud drapes (Fig. 8.4A, B, E) suggest a weak tidal influence during deposition (Visser, 1980). The presence of rare sideritized mudstone beds can indicate riverine influx. The organic nature of fluvial-sourced muds may be conducive to bacterially-facilitated precipitation of siderite (Coleman, 1993). Alternately, the consumption of organic matter by sulfate-reducing bacteria can be inhibited by high sedimentation rates. Pronounced sedimentation leads to shorter residence times in the aerobic oxidation and sulfate reduction zones, which promotes siderite precipitation (Gautier, 1982). These physical structures imply riverine influx in the presence of wave-reworking.

The ichnological suite of FA is dominated by deposit-feeding structures – *Planolites* and *Palaeophycus* – observed within or near carbonaceous mudstone deposits (Fig. 8.4C). In general, these mudstones possess low degrees of bioturbation likely due to depletion of oxygen at the sediment-water interface (Raychaudhuri and Pemberton, 1992; Gingras et al., 1998; Coates and MacEachern, 1999). Structures exhibiting inferred suspension-feeding behaviors include: *Diplocraterion* (Fig. 8.4E), *Skolithos* and *Schaubcylindrichnus* (Fig. 8.4B), which are observed within sandstone beds of FA. These ichnofossil suites are consistent with elements of the proximal *Cruziana* and *Skolithos* Ichnofacies (Fig. 4; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001).

The abundance and diversity of structures of inferred suspension feeders is

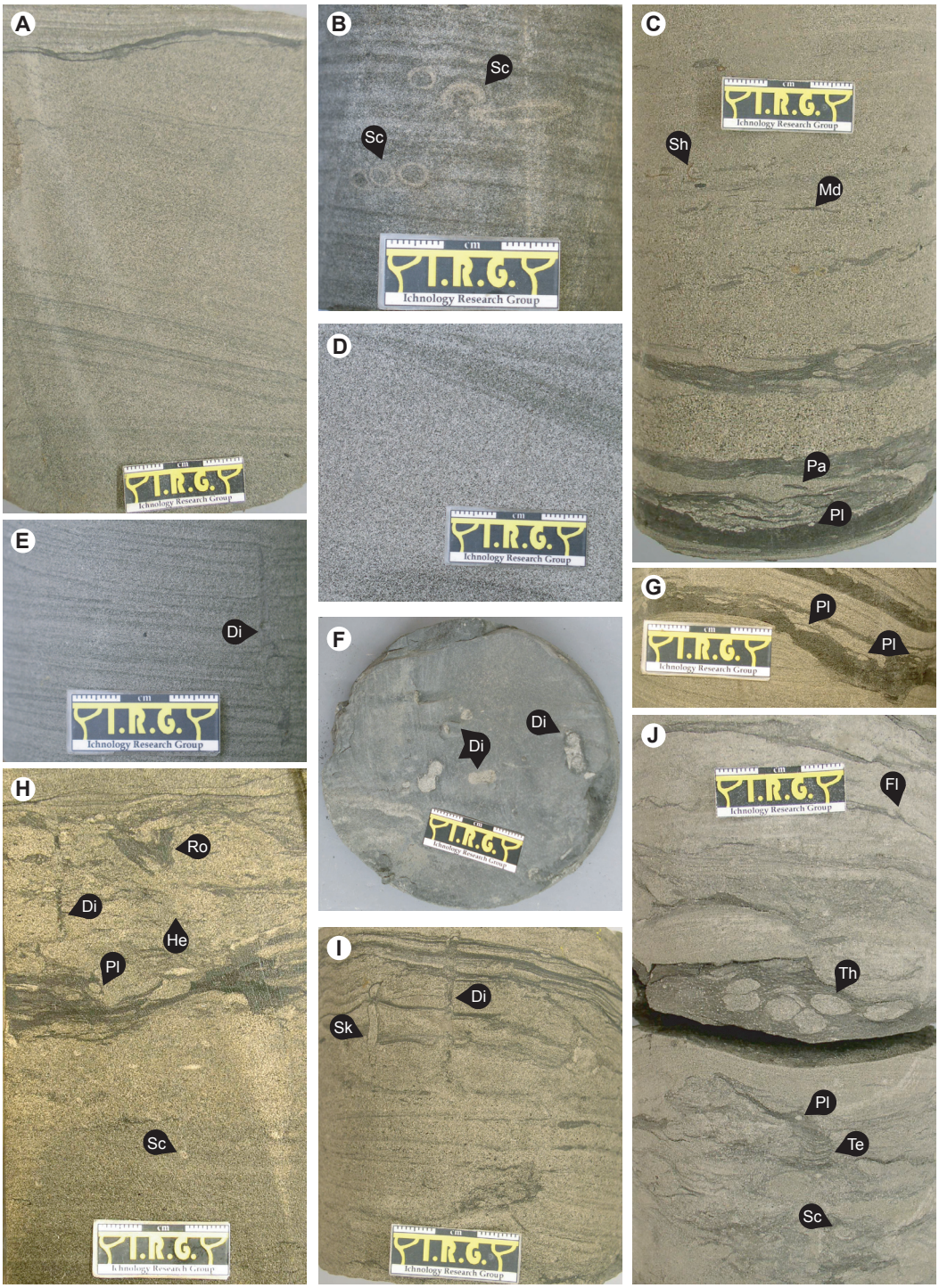


FIGURE 8.4—A-E: Facies A. **A:** Low-angle laminae (HCS) capped by a thin carbonaceous mudstone lamina overlain by wave-rippled sandstone (12-20-034-09W4). **B:** Large, robust, thick-walled *Schaubcylindrichnus* (Sc) in low-angle laminated (HCS) sandstone (10-30-033-07W4). **C:** Mudstone laminae containing small *Planolites* (Pl) and *Palaeophycus* (Pa) at the base of a sandstone containing small shell fragments (Sh) and mudstone rip-up clasts (Md; 10-35-35-10W4). **D:** Apparently massive to wave-rippled sandstone (10-04-034-09W4). **E:** *Diplocraterion* (Di) in planar to low-angle laminated (HCS) sandstone (10-04-034-09W4). **F-J:** Photos of Facies B. **F:** *Diplocraterion* (Di) traces occur on the top of a carbonaceous mudstone laminae (04-26-036-12W4). **G:** Thick mudstone laminae between sandstone beds with interface traces consisting

FIGURE 8.4 (Continued)—of *Planolites* (Pl; 02/06-33-035-09W4). **H:** Partially reworked mudstone laminae with *Rosselia* (Ro), *Schaubcylindrichnus* (Sc), *Planolites* (Pl), *Helminthopsis* (He) and *Diplocraterion* (Di; 12-31-034-09W4). **I:** *Skolithos* (Sk) and possible *Diplocraterion* (Di) traces penetrating mudstone laminae draping wave-rippled sandstone. Underlying planar laminae incorporate organic detritus (10-02-036-11W4). **J:** Wave-rippled sandstone with a thick sharp-based mudstone deposit burrowed by *Thalassinoides* (Th). Other traces include *Teichichnus* (Te), *Planolites* (Pl) and *Schaubcylindrichnus* (Sc). The top of the core exhibits reduced bioturbation, and flame structures (Fl) can be seen at the top of thin mudstone laminae (04-32-035-11W4).

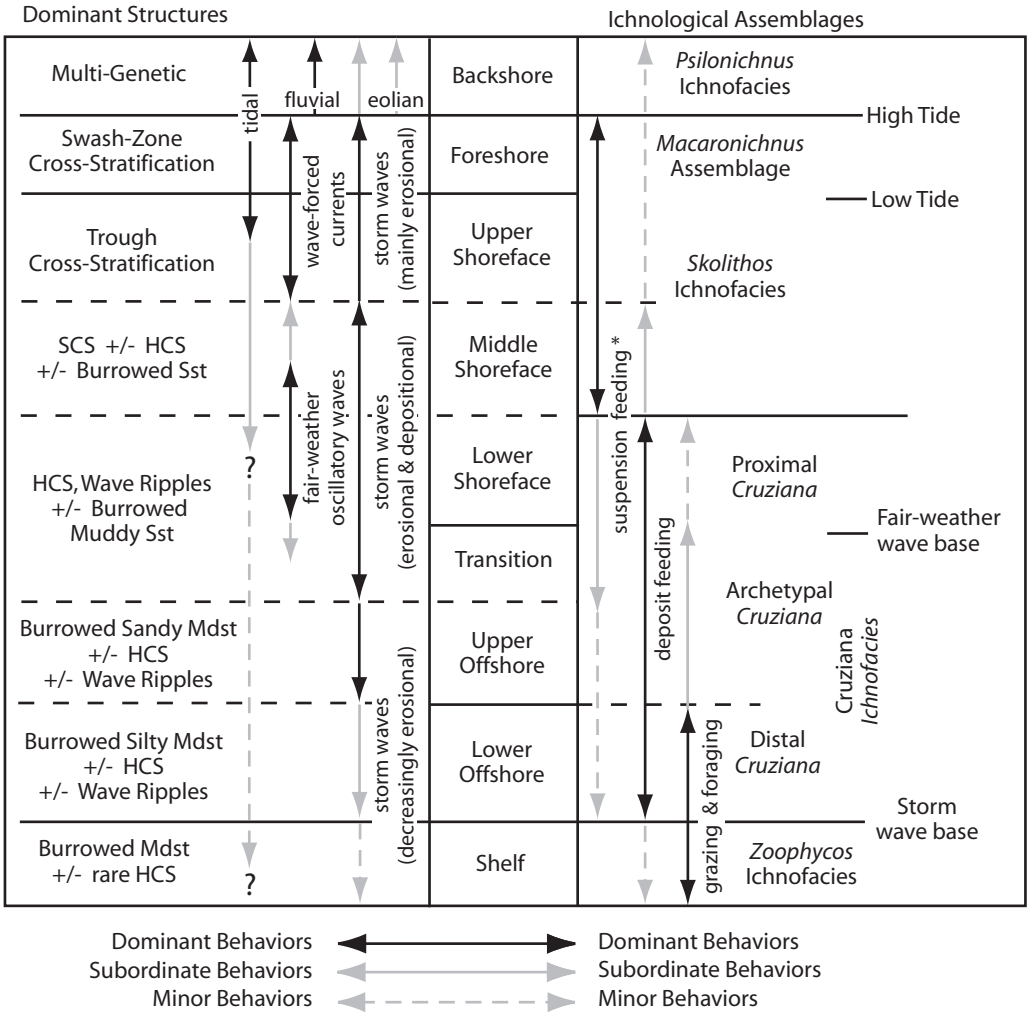


FIGURE 8.5—Ichnological assemblages characteristic of shoreface strata in the Western Canada Sedimentary Basin. Arrows indicate the dominant, subordinate and minor trace fossil behaviors observed in each ichnofacies, as well as the dominant sedimentary processes. Modified from MacEachern et al. (1999a).

significantly reduced in comparison to typical shoreface successions characterized by the *Skolithos* Ichnofacies (Moslow and Pemberton, 1988; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). Impoverishment in dwellings of inferred suspension feeders and prevalence of the *Cruziana* Ichnofacies is interpreted to reflect deltaic influence (Moslow and Pemberton, 1988; Gingras et al., 1998; Coates and MacEachern, 1999). The suppression of dwellings of inferred suspension-feeding animals was described by MacEachern et al. (2005) to be directly associated to increased water turbidity and suspended sediment concentrations. Turbidity is produced by hypopycnal riverine discharge, which results in clay flocculation and suspension settling of material that interferes with filter-feeding apparatuses to inhibit suspension-feeding activities (MacEachern et al., 2005). In addition, the deposit-feeding suite of FA is moderately diverse with a low abundance of traces that also reflects environmentally stressful conditions. Overall, high sedimentation rates reduce bioturbation intensities by altering the substrate consistency and/or food content (MacEachern et al., 2005). Furthermore, reduced salinities can lead to decreased trace-fossil diversity (MacEachern et al., 2005). Accordingly, the ichnofossil suite of FA is interpreted as a moderately-stressed proximal expression of the *Cruziana* Ichnofacies with tempestite beds characterized by stressed expressions of the *Skolithos* Ichnofacies.

Burton (1997) interpreted these deposits as transitional to lower shoreface units characterized by the *Cruziana* Ichnofacies. However, structures suggestive of riverine influence, in addition to the presence of a stressed trace suite, suggests deposition under deltaic influence. Facies A lacks the abundance of cross-stratification documented in distributary mouth-bar deposits of river-dominated deltaic lobes (Bhattacharya and Walker, 1991). In contrast, distributary mouth-bar deposits of wave-dominated delta fronts can be completely reworked by waves (into HCS) during abandonment of the distributary (Suter, 1994). The physical and biogenic structures in FA are interpreted to reflect deposition in proximal delta front settings which are neither river- nor wave-dominated, but represent an intermediate state.

Interpretation of Facies B: Moderately Burrowed Sandstone – Distal Delta Front

Physical sedimentary structures and accessory elements in this facies imply wave and riverine influence similar to that of FA (Table 8.2; Fig. 8.4F-

I). However, sharp-based, carbonaceous mudstones are more prevalent as are biogenic structures. The ichnological suite is characterized by moderate diversity with a low abundance of ichnofossils. Prevailing biogenic structures in FB include deposit-feeding (*Planolites*) and grazing (*Helminthopsis*) traces with fewer structures of inferred suspension-feeders (*Schaubcylindrichnus* and *Diplocraterion*) structures. Suppression of typical levels of dwellings of inferred suspension-feeding organisms found in sandy shoreface deposits is also observed in this facies. Accordingly, the trace fossil suite is attributed to a subtly-stressed proximal expression of the *Cruziana* Ichnofacies (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). In view of the increased preservation of mudstone deposits in comparison to FA, evidence of riverine influx, and stressed ichnofossil suite, FB represents deposition in the distal delta front.

Interpretation of Facies C: Burrowed Muddy Sandstone – Proximal Prodelta

Soft-sediment deformation features in Facies C (FC) suggest episodic rapid sedimentation (Fig. 8.6D). Additionally, wood fragments and carbonaceous, hyperpycnal-derived mudstone laminae and beds (Fig. 8.6A, C) imply riverine discharge. The presence of rare synaeresis cracks in this facies further implies proximity to a freshwater source during deposition. Synaeresis cracks form when a subaqueous, flocculated, clay-rich layer comes into contact with saline conditions and spontaneously contracts as a result of interparticle attraction (Tanner, 2003). This process results in expulsion of water forming a shrinkage crack that can be infilled during subsequent deposition.

Planolites, *Asterosoma*, *Rhizocorallium* (Fig. 8.6B) and *Helminthopsis* dominate the ichnofossil suite of FC with subordinate *Schaubcylindrichnus* and *Skolithos*. The overall suite exhibits moderate diversity and abundance of structures signifying environmental stress during deposition. This suite is interpreted as a moderately-stressed archetypal expression of the *Cruziana* Ichnofacies (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). The muddy nature of the sandstone, indications of riverine influx, and stressed trace fossil suite are interpreted to reflect deposition in a proximal prodelta setting.

Interpretation of Facies D: Burrowed Muddy Sandstone to Sandy Mudstone –

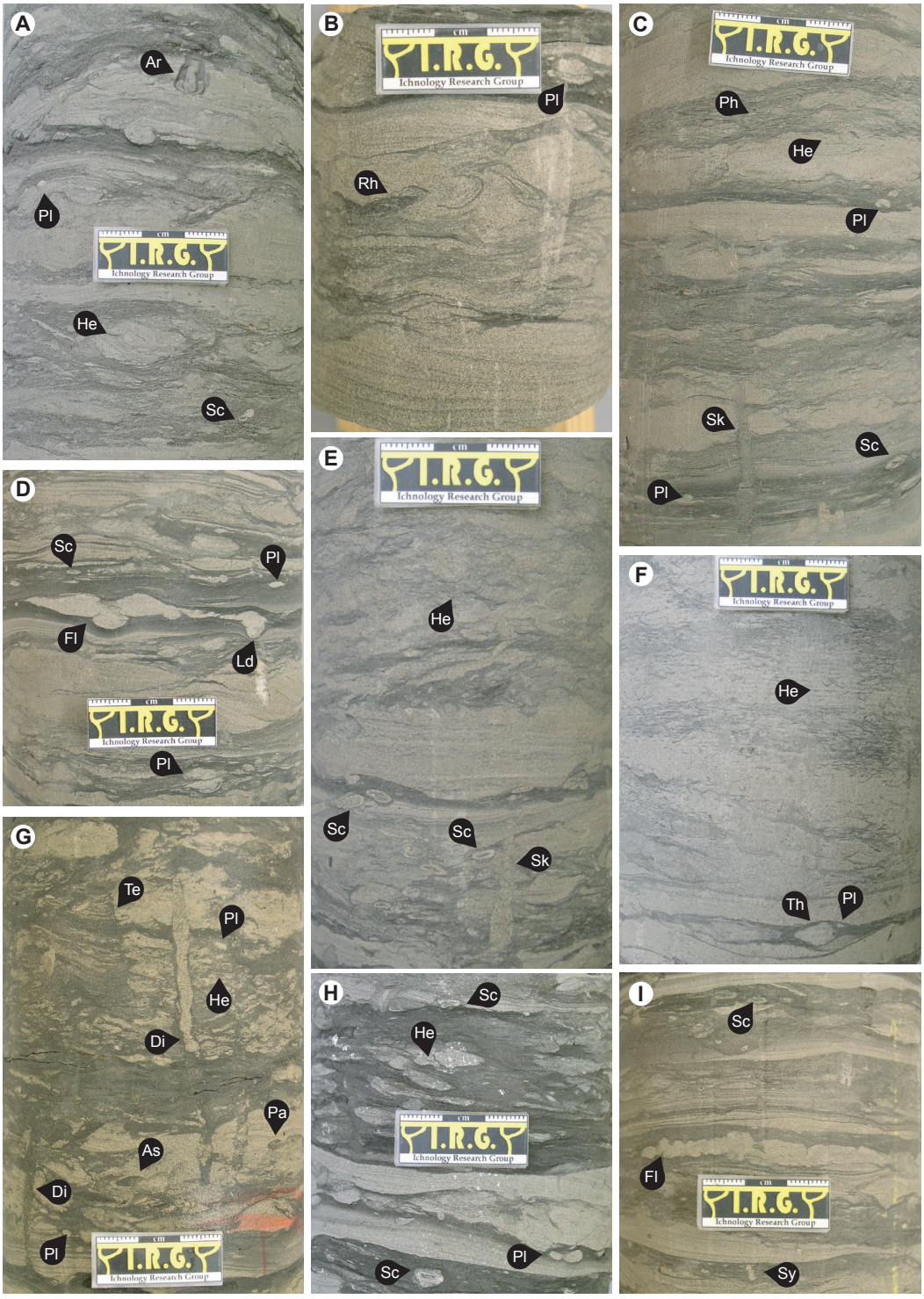


FIGURE 8.6—A-D: Facies C. **A:** Relatively thick, partially-reworked muddy sandstone with *Planolites* (Pl), *Helminthopsis* (He) and *Schaubcylindrichnus* (Sc). *Arenicolites* (Ar) represents an opportunistic trace (10-12-036-12W4). **B:** Wavy-laminated sandstone with *Rhizocorallium* (Rh) and *Planolites* (Pl; 12-29-035-10W4). **C:** Interbedded wavy-parallel laminated sandstone and carbonaceous mudstone deposits bioturbated by *Phycosiphon* (Ph), *Helminthopsis* (He), *Skolithos* (Sk) and *Planolites* (Pl; 10-02-036-11W4). **D:** Interbedded sandstone and mudstone with flame (Fl) and load (Ld) structures, as well as the ichnofossils *Planolites* (Pl) and *Schaubcylindrichnus* (Sc; 10-23-034-09W4). **E-I:** Photos of Facies D. **E:** Highly-burrowed muddy sandstone with

FIGURE 8.6 (Continued)—*Schaubcylindrichnus* (Sc), *Helminthopsis* (He) and a reburrowed *Skolithos* (Sk; 09-15-035-09W4). **F:** A preserved carbonaceous mudstone lamina reworked by *Thalassinoides* (Th) and *Planolites* (Pl) and overlain by pervasively burrowed muddy sandstone containing *Helminthopsis* (He; 10-09-037-07W4). **G:** Burrowed sandy mudstone with *Diplocraterion* (Di), *Asterosoma* (As), *Palaeophycus* (Pa), *Teichichnus* (Te), *Planolites* (Pl) and *Helminthopsis* (He; 11-11-036-08W4). **H:** Wave-rippled sandstone with *Schaubcylindrichnus* (Sc), *Helminthopsis* (He), and *Planolites* (Pl; 10-12-036-12W4). **I:** Interbedded unit with reduced bioturbation intensities, flame structures (Fl), a synaeresis crack (Sy), fining-upward thin beds and *Schaubcylindrichnus* (Sc; 02/06-33-035-09W4).

Distal Prodelta

The presence of aggradational wave ripples, sharply bounded carbonaceous mudstones (Fig. 8.6E, H, I), soft-sediment deformation structures, and synaeresis cracks suggests admixture of fresh and marine waters occurred during FD deposition. Intense biogenic reworking is suggestive of deposition in a more distal setting (Fig. 8.6E-I). The ichnofossil suite is dominated by grazing traces (*Helminthopsis*; Fig. 8.6F) and deposit-feeding structures (*Planolites*, *Rhizocorallium* and *Asterosoma*) with secondary dwellings of inferred suspension-feeders (*Schaubcylindrichnus*). Relative to FC, there is a marginal increase in the diversity and abundance of trace fossils. Nevertheless, the degree of burrowing and trace diversity is reduced in comparison to the typical archetypal expression of the *Cruziana* Ichnofacies (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). Accordingly, the ichnofossil suite is characterized by a subtly-stressed archetypal expression of the *Cruziana* Ichnofacies. This ichnological suite combined with localized indications of riverine discharge in a mudstone-dominated lithology is interpreted to reflect deposition in the distal prodelta.

Facies Association 2: The Distal Lower Shoreface and Upper Offshore

Facies comprising Facies Association 2 (FAS2) are lithologically comparable those of FAS1. Facies E through G are differentiated from those of FAS1 based on the abundance and diversity of biogenic structures and lack of sedimentological attributes suggestive of riverine input. The characteristics of Facies E through G are consistent with that of the upper offshore-lower shoreface transition zone and the proximal and distal upper offshore (Table 8.2).

Interpretation of Facies E: Homogenized Muddy Sandstone – Distal Lower Shoreface

Pervasively bioturbated muddy sandstone characterizes Facies E (FE; Fig. 8.7A, B). The trace-fossil suite is dominated by grazing traces (*Helminthopsis* and *Phycosiphon*) and deposit-feeding or dwelling structures (*Planolites*, *Rhizocorallium*, *Teichichnus*, *Cylindrichnus* and *Thalassinoides*) with fewer structures representing inferred suspension-feeding behaviors (*Rosselia*, *Schaubcylindrichnus*, *Skolithos*, *Siphonichnus*, and *Arenicolites*). This diverse suite of traces is characteristic of an archetypal expression of the *Cruziana* Ichnofacies (Fig. 4; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). The ichnofossil *Rosselia* (Fig. 8.7A), which is often prevalent in the lower shoreface (Pemberton et al., 2001), is observed in conjunction with abundant grazing traces. This concurrence of traces is similar to that of the offshore-lower shoreface transition strata described by Raychaudhuri et al. (1992), which was dominated by *Helminthopsis*. Accordingly, FE is interpreted to reflect deposition in the distal lower shoreface.

Interpretation of Facies F: Homogenized Silty to Muddy Sandstone – Proximal Upper Offshore

The proportion of sand-sized grains and rare wave-produced structures in Facies F (FF) signifies a depositional environment above storm wave base. Bioturbation is pronounced, and the trace fossil suite is diverse within the homogenized silty to muddy sandstone (Fig. 8.7C, D). Deposit-feeding structures (*Planolites*, *Asterosoma*, *Rhizocorallium*, *Thalassinoides*, *Chondrites*, *Teichichnus*, *Scolicia*, and *Palaeophycus*) dominate the facies, while grazing traces (*Helminthopsis*, *Zoophycos* and *Phycosiphon*) are secondary and dwelling structures of inferred suspension-feeders (*Rosselia, Schaubcylindrichnus*, *Skolithos*, *Diplocraterion*, *Arenicolites*, and *Siphonichnus*) are minor. The trace fossil suite resembles that of FE; however, fewer structures of inferred suspension-feeding animals are observed in conjunction with increased deposit-feeding and grazing ichnofossils. This suite is indicative of a more distal depositional setting in comparison to FE; however, the diversity and abundance of traces also reflects an archetypal expression of the *Cruziana* Ichnofacies (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). In accordance with the trace-fossil suite, lithology, and paucity of

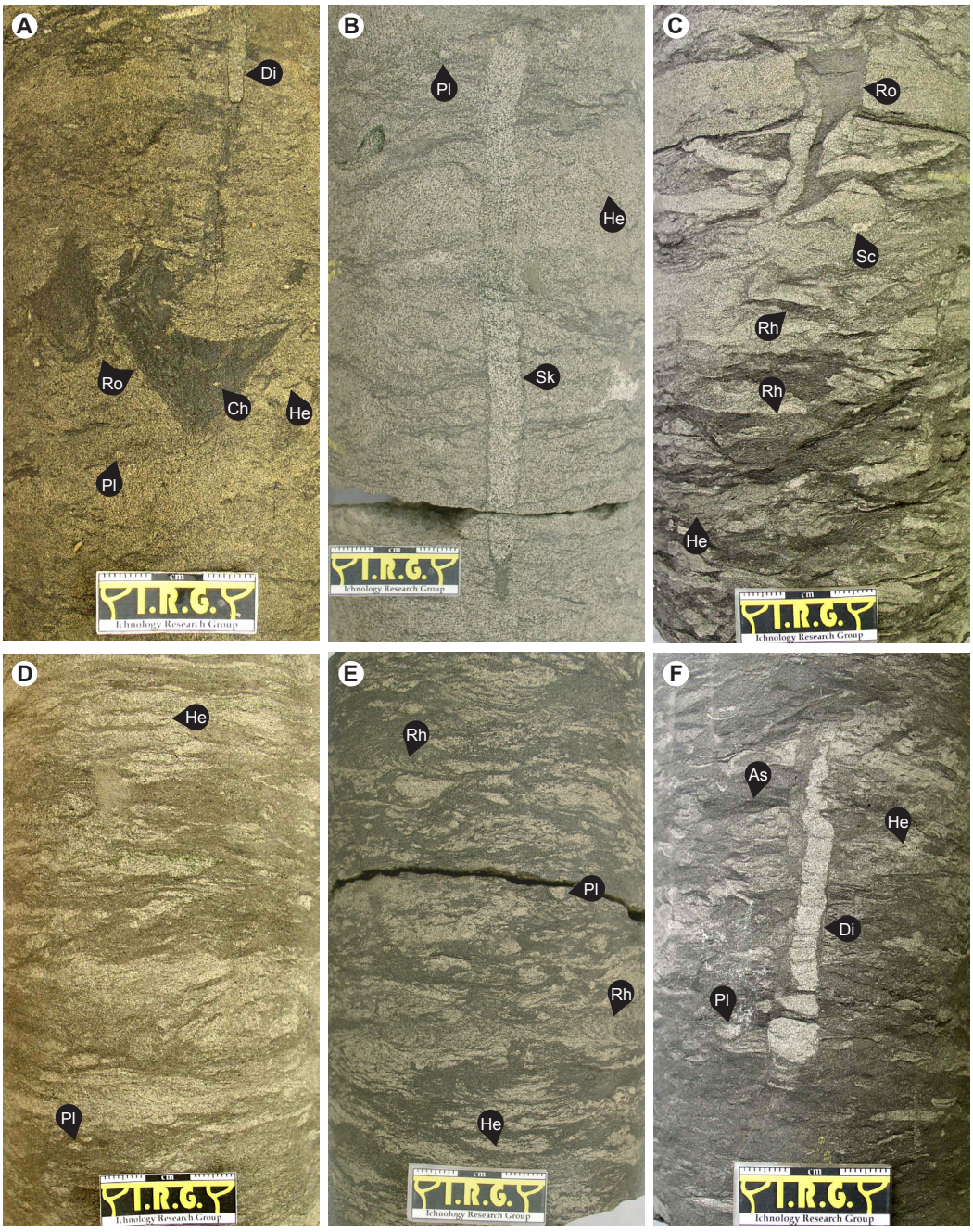


FIGURE 8.7—A-B: Facies E. **A:** Muddy sandstone with *Rosselia* (Ro) that is partially reburrowed by *Chondrites* (Ch). Other traces include *Diplocraterion* (Di), *Helminthopsis* (He) and *Planolites* (Pl; 10-02-036-11W4). **B:** Large partially lined *Skolithos* (Sk) with background burrowing including *Helminthopsis* (He) and *Planolites* (Pl; 10-35-035-10W4). **C-D:** Photos of Facies F. **C:** Muddy sandstone with abundant burrowing including *Rosselia* (Ro), *Schaubcylindrichnus* (Sc), *Rhizocorallium* (Rh) and *Helminthopsis* (He) traces (10-12-036-12W4). **D:** Muddy sandstone with few discernable traces including *Helminthopsis* (He) and *Planolites* (Pl; 15-15-035-10W4). **E-F:** Photos of Facies G. **E:** Sandy mudstone with pervasive bioturbation comprising *Rhizocorallium* (Rh), *Planolites* (Pl), and *Helminthopsis* (He) (02/06-33-035-09W4). **F:** Large *Diplocraterion* (Di) in sandy mudstone with common occurrences of *Helminthopsis* (He), as well as *Asterosoma* (As) and *Planolites* (Pl; 10-04-034-09W4).

sedimentary structures, FF represents deposition in a proximal upper offshore setting.

Interpretation of Facies G: Homogenized Sandy Siltstone to Sandy Mudstone – Distal Upper Offshore

Appreciable sand-sized grains and the presence of wave-formed structures implies that Facies G (FG) was also deposited above storm wave base (Fig. 8.7E, F). The sandy siltstone to sandy mudstone is characterized by a diverse ichnological suite dominated by deposit-feeding and dwelling structures (*Planolites*, *Asterosoma*, *Palaeophycus*, *Rhizocorallium*, *Thalassinoides*, *Teichichnus* and *Chondrites*) with significant occurrences of grazing traces (*Helminthopsis*, *Phycosiphon*, and *Zoophycos*), and rarer structures reflecting inferred suspension-feeding behaviors (*Schaubcylindrichnus*, *Skolithos*, *Diplocraterion*, *Arenicolites*, and *Siphonichnus*). This diverse suite also reflects an archetypal expression of the *Cruziana* Ichnofacies (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). In comparison to FF, there are fewer dwellings of inferred suspension-feeding organisms and increased proportions of grazing traces, which implies deposition in a more distal setting. The diverse ichnofossil suite and fine-grained nature of FG is interpreted to reflect deposition in the distal upper offshore.

Facies Association 3: Lower Offshore and Transgressive Deposits

The final facies association (FAS3) consists of 3 fine-grained facies in the HL area, as well as a facies with a disorganized internal fabric and a facies dominated by convoluted bedding (Table 8.2; Fig. 8.8). The proportion of sand-sized grains and observable bioturbation decreases from Facies H through J, which reflect deposition in proximal lower offshore to shelfal settings. Facies K and L are directly associated with transgressive erosion, where Facies K is interpreted as a transgressive lag deposit and Facies L reflects slumping associated with ravinement.

Interpretation of Facies H: Burrowed Sandy Mudstone to Silty Mudstone – Proximal Lower Offshore

The rare to moderate occurrence of wave ripples in Facies H (FH) is suggestive of a deposition under wave influence. However, the paucity of sand-sized grains implies deposition beyond the upper offshore (Fig. 8.8 A, B).

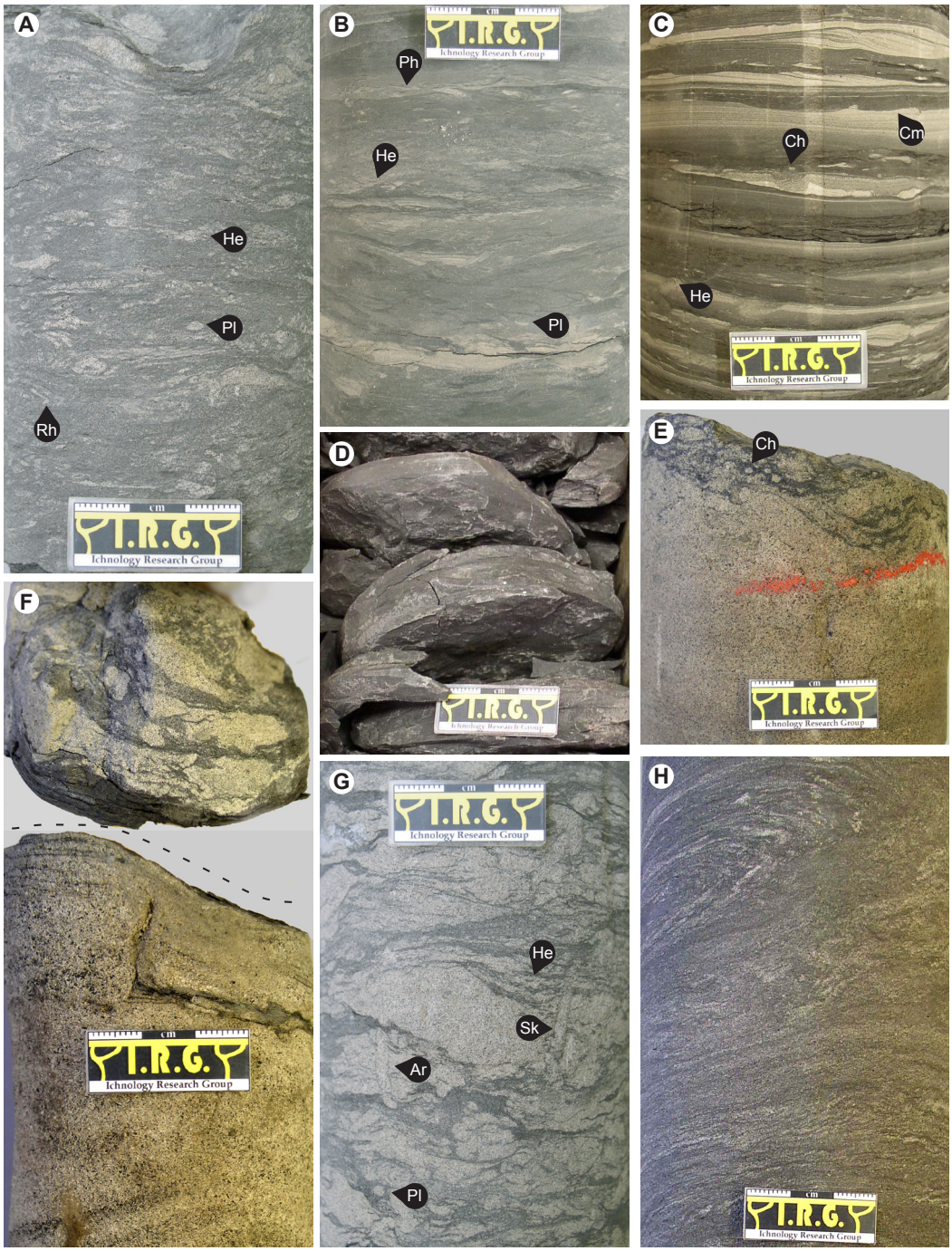


FIGURE 8.8—A-B: Facies H. **A:** Homogenized sandy mudstone with abundant *Helminthopsis* (He), as well as *Planolites* (Pl) and *Rhizocorallium* (Rh; 09-15-035-09W4). **B:** Silty mudstone with common occurrences of *Phycosiphon* (Ph), and lesser *Helminthopsis* (He) and *Planolites* (Pl; 10-23-034-09W4). **C:** Photo of Facies I with distal silty to very fine sandy tempestite beds with scattered ichnofossils including *Chondrites* (Ch) and *Helminthopsis* (He). The lack of burrowing may be related to low oxygenation associated with the sharp-based carbonaceous mudstones (Cm; 12-24-035-09W4). **D:** Facies J characterized by homogeneous mudstone with no observable traces (10-12-036-12W4). **E-G:** Photos of transgressive flooding surface 1 (FS1) overlain by Facies K. **E:** A burrowed contact at FS1 (10-20-036-11W4). **F:** A sharp, inclined contact at FS1 (dashed line), which is overlain by muddy sandstone of Facies K (06-29-035-09W4). **G:** Muddy sandstone of Facies K with no clear laminae or sedimentary structures. Traces in this unit include: *Planolites*

FIGURE 8.8 (Continued)—(Pl), *Arenicolites* (Ar), *Skolithos* (Sk), and *Helminthopsis* (He; 10-04-034-09W4). **H:** Convoluted sandy siltstone of Facies L (10-04-036-10W4).

Bioturbation intensities are typically moderate for FH; although, the high fluidity, level of compaction, and textural homogeneity of the fine-grained sediment may have resulted in a decreased preservational potential of traces (cf. Archer and Hattin, 1984). Identifiable traces are predominantly structures reflecting deposit-feeding (e.g., *Planolites*, *Teichichnus*, *Asterosoma*, *Palaeophycus*, *Thalassinoides*, and *Rhizocorallium*) and grazing behaviors (e.g., *Helminthopsis*, *Phycosiphon* and *Zoophycos*) with rare dwellings of inferred suspension-feeders (e.g., *Schaubcylindrichnus*, *Skolithos*, and *Diplocraterion*). This suite delineates a distal expression of the *Cruziana* Ichnofacies, representative of a proximal lower offshore setting (Fig. 8.5; e.g., Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001).

Interpretation of Facies I: Sparsely Burrowed Sandy Mudstone – Distal Lower Offshore

Relatively few identifiable trace fossils are recognized in Facies I (FI), which is directly a function of the muddy nature of the sediment (Fig. 8.8C). The discernible trace fossil suite is dominated by deposit-feeding or dwelling traces (*Planolites*, *Teichichnus*, *Asterosoma*, *Rhizocorallium*, *Thalassinoides, and Zoophycos*) and grazing traces (*Helminthopsis* and *Phycosiphon*), with very rare dwellings of inferred suspension-feeders (*Schaubcylindrichnus*, *Arenicolites*, and *Skolithos*). This suite of biogenic structures is also consistent with a distal expression of the *Cruziana* Ichnofacies (Fig. 8.5; cf. Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001). Indirect deltaic influence may have contributed to the overall paucity of burrowing, by lowering oxygenation near the bed through emplacement of organic-rich mud deposition. The scarcity of sand-sized grains and reduction in trace-fossil abundance in comparison to FH suggests that this facies was deposited in the distal lower offshore.

Interpretation of Facies J: Massive Mudstone/Shale – Shelf

The fine-grained nature, lack of wave-formed structures, and general paucity of observable bioturbation in this facies indicates that deposition likely

occurred below storm wave base (Fig. 8.8D). During deposition of Facies J (FJ) conditions were conducive to siderite formation, which can occur in suboxic (slightly reducing) conditions with low sedimentation rates and low organic concentrations (Mozley and Wersin, 1992), which is typical of shelfal environments. Rare ichnofossils in this facies comprise opportunistic suites that colonized distal sandy tempestites. The overall lack of bioturbation in this facies was interpreted by Burton (1997) to reflect low oxygenation, although a lack of lithological contrast may also have resulted in a low preservation potential. These aforementioned sedimentological and ichnological characteristics are interpreted to reflect sedimentation below storm wave base on the shelf (Fig. 8.5; Pemberton and MacEachern 1995; MacEachern et al. 1999a; Pemberton et al., 2001).

Interpretation of Facies K: Chaotic Sandy Mudstone to Muddy Sandstone – Transgressive Lag

Facies K (FK) is interpreted as deposits that formed during the onset of marine transgression. The disorganized nature of the sediment is exemplified in the general paucity of physical structures and presence of localized wood fragments and pebbles (Fig. 8.8F, G). Evidence of biogenic disruption, however, implies a sufficient period of time for colonization of the sediment during the transgression and formation of the lag deposit. The moderately diverse ichnological suite is dominated by deposit-feeding and grazing traces (*Planolites* and *Helminthopsis*), with rare structures of inferred suspension-feeding organisms (Table 8.2). This ichnological suite is consistent with a stressed distal to archetypal expression of the *Cruziana* Ichnofacies. Facies K is comparable to the highly-burrowed pebbly and sandy shale facies of MacEachern et al. (1992), which was interpreted to be associated with transgressive ravinement. Similarly, the formation of FK occurred at the onset of marine transgression where sandy deltaic deposits were eroded in a more proximal setting. A portion of the sandy sediment was likely transported offshore in addition to the reworking of the uppermost deltaic deposits. The lag was subsequently exposed to an upper to lower offshore setting, permitting colonization of the sediment prior to deeper marine deposition.

Interpretation of Facies J: Convolute Bedded Sandy Siltstone to Sandy Mudstone – Slump Deposit

Deposits of Facies J (FJ) occur in two well locations: 10-04-036-10W4

and 10-03-036-10W4 (Fig. 8.8H). Similar slump deposits were also reported by Burton (1997) in well 12-27-034-10W4. The highly deformed strata is devoid of discrete trace fossils. The paucity of wave-formed sedimentary structures is typical of offshore fine-grained deposits. The convolute nature of the sediment and association with erosion along the lowermost bounding discontinuity (BD1; see following section) suggests that FJ was deposited due to slumping associated with erosion. Rapid deposition of a slump deposit may have 1) precluded preservation of wave-formed structures and colonization by trace-makers, or 2) primary stratification and initial biogenic modification may have been deformed as a result of slumping.

STRATIGRAPHY

It is proposed here that the Viking Formation at Hamilton Lake is divided into a number of stratigraphic packages informally named A through I from the base to top of the Viking, respectively. These units are connected through complex stratigraphic relationships involving a number of relative sea level (RSL) changes in a shallow Cretaceous basin.

Bounding discontinuities used in the stratigraphic nomenclature generally corresponds to that of Burton (1997). In the HL area, stratigraphic surfaces are subtle, in that lag deposits are generally composed of very fine- to fine-grained sandstone with scattered dark chert granules or small pebbles. Commonly, lag deposits are burrowed, thin, or reflect a concealed surface in which only contrasting sand is preserved within the burrows. Surfaces characterized by trace fossil reflect palimpsest suites (see Chapter 9) in which the colonized sediment was either soft or stiff, in contrast to the more classical firmground traces of the *Glossifungites* Ichnofacies. The predominance of palimpsest suites reflects a unique situation at HL, which was first recognized by Burton (1997) and MacEachern and Burton (2000): a distal expression of the *Glossifungites* Ichnofacies. (Chapter 9 contains detailed descriptions of the different expressions of palimpsest suites). The subtle nature of lags and palimpsest suites is likely related to the inconsistent distribution of surfaces across the study area. Surfaces may be masked by muddy deposits, not survive preservation if burrowing did not occur locally at the site of coring, or a thin lag may be bioturbated beyond

recognition. As such, surfaces possess various characteristics that can change along strike and dip.

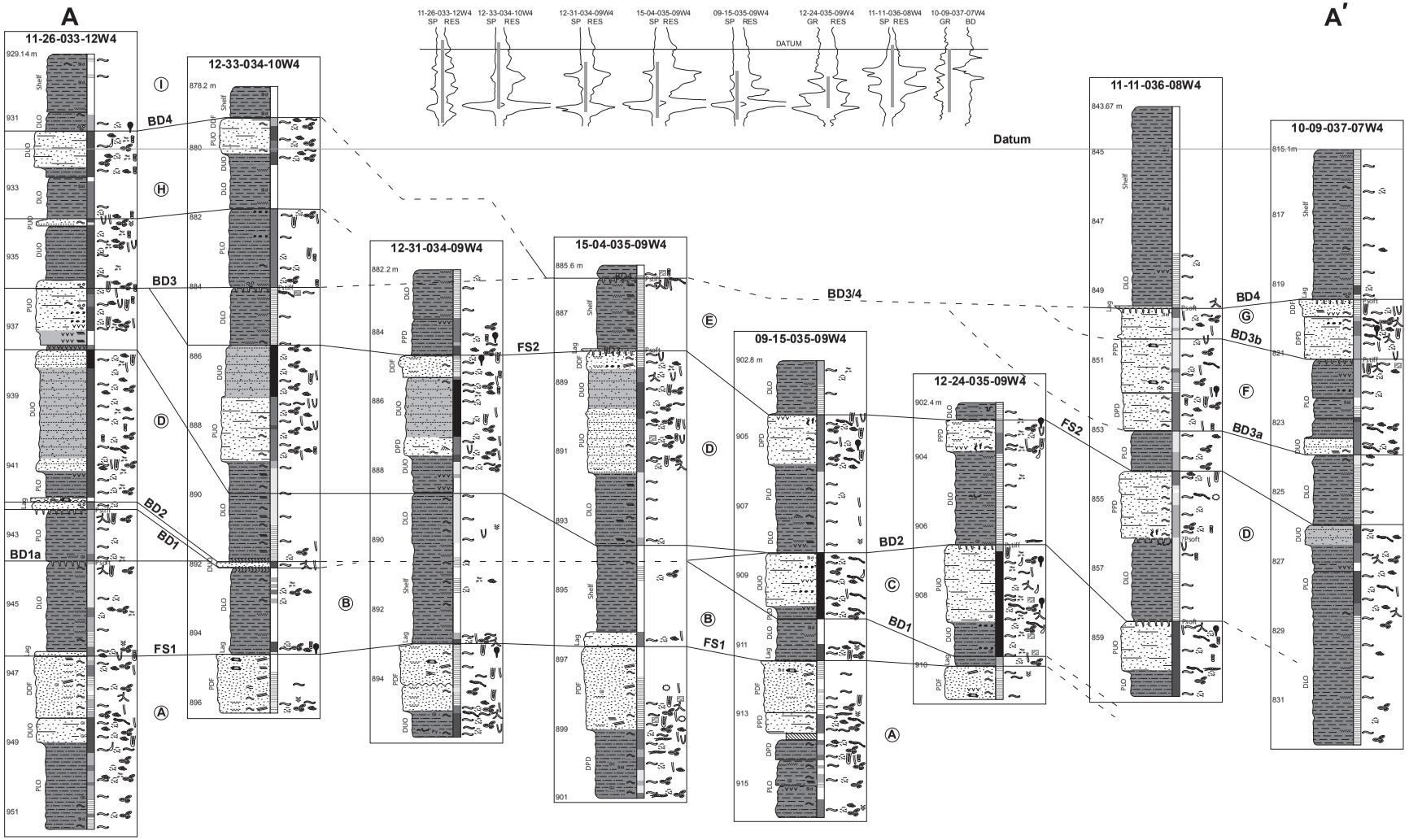
Based on correlations from cross sections A–A′ (Fig. 8.9) and B–B′ (Fig. 8.10) and characteristics of the bounding discontinuities, the following sequence of stratigraphic events is interpreted for the lower, middle and upper Viking Formation.

Lower Viking Formation

Initial Viking deposition in the HL area began with falling relative sea level (RSL) and progradation of shorelines across the study area, producing packages of strata that coarsen upward from offshore/prodelta to sandy proximal delta front deposits (Unit A). Progradation ceased when relative sea-level began to rise during transgression, which produced a laterally extensive surface overlying Unit A—transgressive flooding surface 1 (FS1). FS1 is generally sharp but is locally burrowed or gradational from the underlying sandstone to deep marine mudstones. The surface is overlain by 10-50 cm of deposits comprising FK, which reflects reworking of sandy deposits in an offshore setting. Burton (1997) also reported a bioturbated sandy to muddy deposit with rare pebbles and wood fragments characterizing this stratigraphic surface.

Following transgression, progradation resumed in a landward locality to the southwest of HL (Fig. 8.3), which resulted in deposition of equivalent distal units comprising lower offshore to shelf mudstones in the HL area (Unit B). Subsequently, a short-lived fall in RSL was succeeded by rapid transgression in which no associated shoreface deposits were preserved. This formed Bounding Discontinuity 1a (BD1a), which is present in southwestern localities: 11-26-033-12W4 (Fig. 8.9) and 10-19-034-13W4. This palimpsest softground to stiffground is characterized by *Diplocraterion*, *Thalassinoides* and *Skolithos* infilled with fine-grained, salt-and-pepper-coloured sandstone with rare glaucony (Fig. 8.11A). BD1a potentially reflects an amalgamated sequence boundary and transgressive surface of erosion (SB/TSE), which was subsequently truncated by BD1 (Fig. 8.9). However, there is no evidence of subaerial exposure along BD1a, although the palimpsest suite cross-cuts distal facies indicating a notable drop in RSL.

Transgression was succeeded by offshore deposition and another major drop in RSL, which shifted the shoreline to a point northeast of the HL field. This led to subaerial exposure to the southwest and removal of strata within


A
A′
11-26-033-12W4
12-33-034-10W4
12-31-034-09W4
15-04-035-09W4
09-15-035-09W4
12-24-035-09W4
11-11-036-08W4
10-09-037-07W4
SP RES
GR RES
GR BD
DATUM
Datum
BD4
BD3
BD3/4
BD2
BD1
BD1a
FS2
FS1
BD3b
BD3a
Ⓘ
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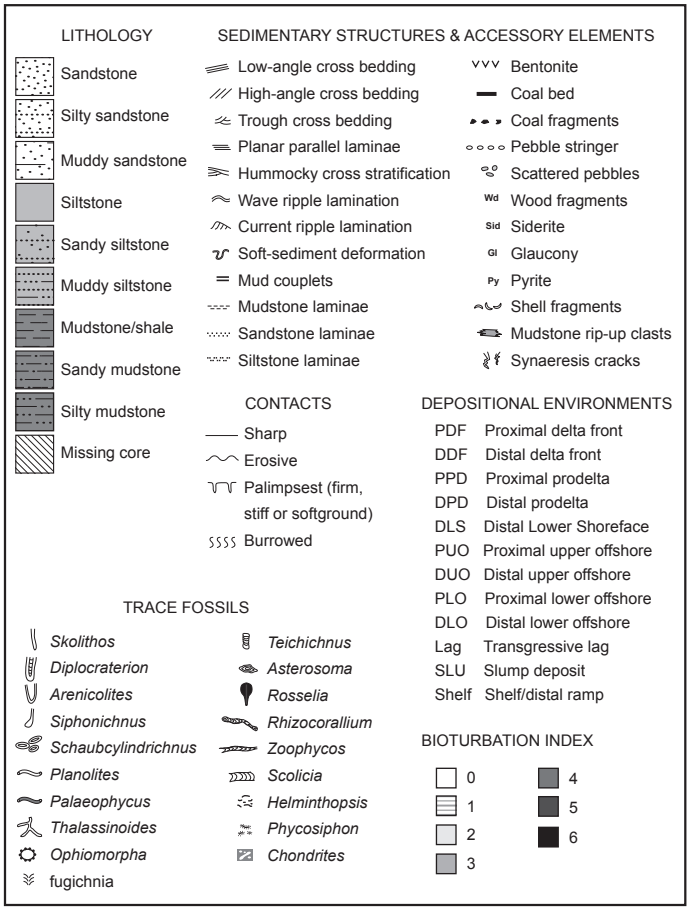
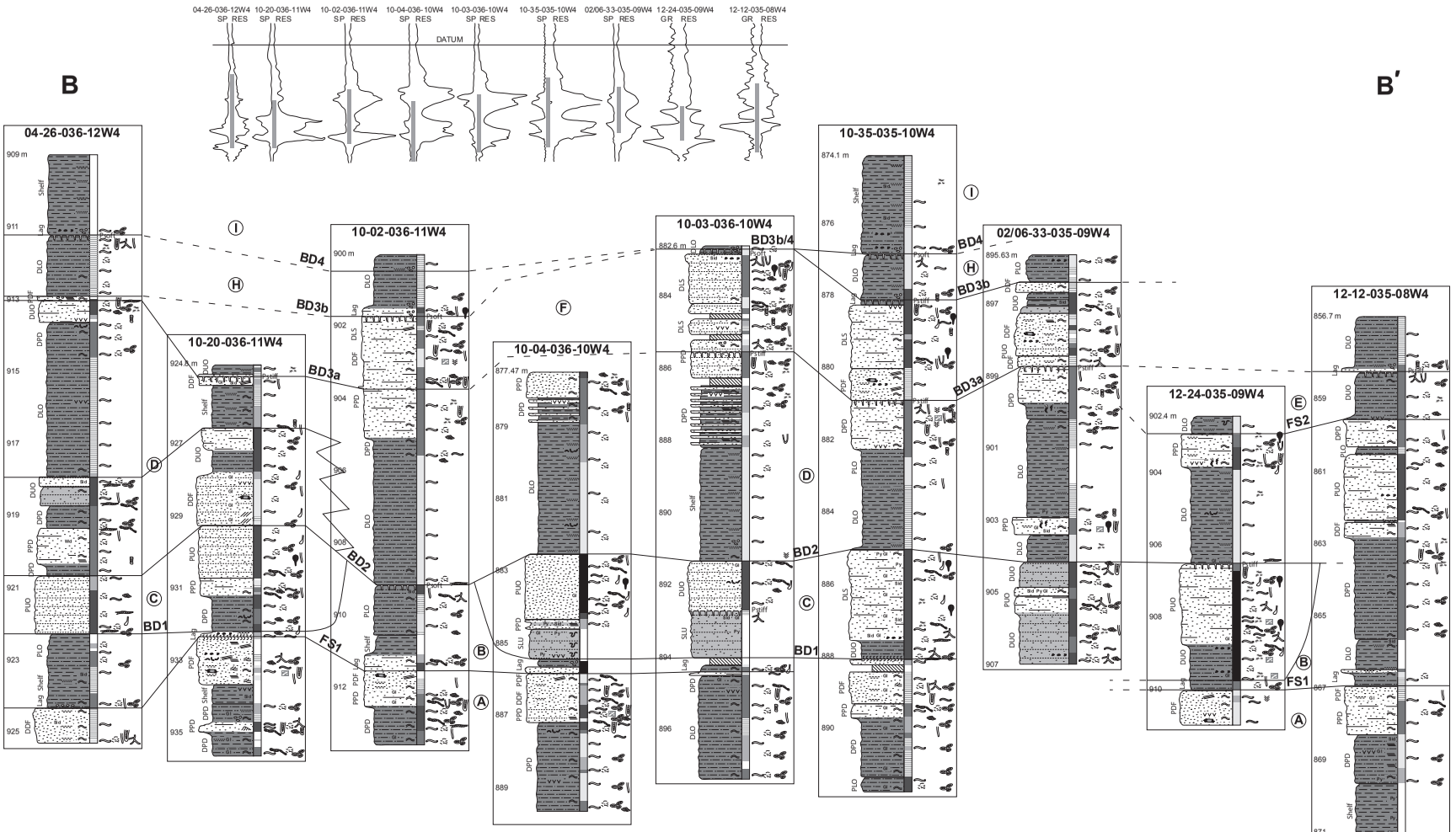


LEGEND (This page)—List of symbols and abbriviations for Figures 8.9 and 8.10.

FIGURE 8.9 (Previous page)—Cross section A–A′ along depositional dip through the Hamilton Lake area (see Fig. 8.2). The datum used is a prominent well log signature due to the lack of an appropriate datum intersecting all of the cored intervals. Letters indicate order of depositional units from the base to the top of the Viking Formation from A through I. There are two major transgressive flooding surfaces and four major bounding discontinuities.

FIGURE 8.10 (Next page)—Cross section B–B′ along depositional strike near the northeastern edge of the Hamilton Lake field. The datum used is a prominent well log signature within the overlying Westgate Formation due to the lack of an appropriate datum intersecting all of the cored intervals. Note the patchy nature of Unit C and the truncation of the upper major flooding surface by BD3.


B
B′
04-26-036-12W4 SP RES
10-20-036-11W4 SP RES
10-02-036-11W4 SP RES
10-04-036-10W4 SP RES
10-03-036-10W4 SP RES
10-35-035-10W4 SP RES
02/06-33-035-09W4 SP RES
12-24-035-09W4 GR RES
12-12-035-08W4 GR RES
DATUM
04-26-036-12W4
10-20-036-11W4
10-02-036-11W4
10-04-036-10W4
10-03-036-10W4
10-35-035-10W4
02/06-33-035-09W4
12-24-035-09W4
12-12-035-08W4
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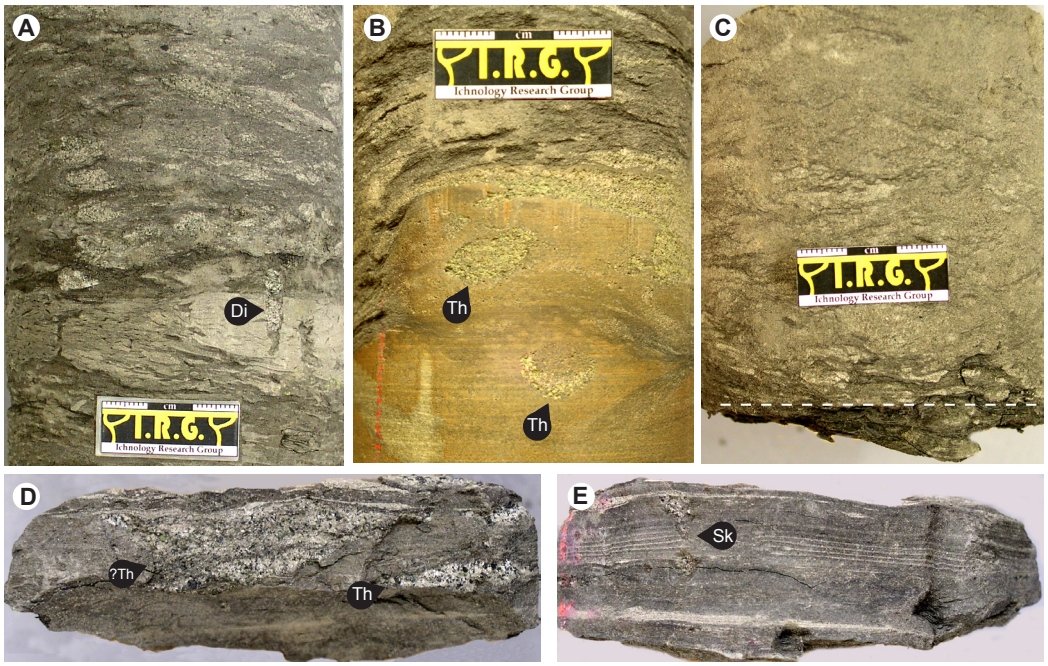

FIGURE 8.11—Aspects of Bounding Discontinuity 1. **A:** BD1a characterized by a palimpsest softground suite including *Diplocraterion* (Di) infilled with fine, salt and pepper coloured sandstone and rare glaucony (11-26-033-12W4). **B:** Overlying the slump deposits above BD1 is a palimpsest stiffground demarcated by *Thalassinoides* (Th) infilled with glaucony-rich, very fine sandstone and underlain by 13 cm of siderite (10-03-036-10W4). **C:** BD1 demarcated by a simple sharp contact (04-26-036-12W4). **D-E:** A palimpsest stiffground demarcating BD1 with *Thalassinoides* (Th), and *Skolithos* (Sk) infilled by fine-grained, salt and pepper coloured sandstone (11-26-033-12W4).

Units A and B at the base of the lower shoreface (Figs. 8.9, 8.10). This RSL fall was followed by transgression, during which the shoreline paused in the HL area and prograded during stillstand conditions to deposit Unit C. This transgressively incised shoreface is underlain by BD1, which is typically a sharp contact and weakly burrowed with evidence of only minimal erosion, despite the obvious truncation of underlying strata (Figs. 8.9, 8.10, 8.11C). There are, however, a few locations in which removal of strata is indicated along the BD1 surface. Southwest of HL, 11-26-033-12W4 displays evidence of erosion, where the surface is demarcated by a palimpsest stiffground characterized by *Thalassinoides*, *Skolithos* and *Diplocraterion* infilled by fine-grained, salt-and-pepper-coloured sandstone and overlain by 23 cm of muddy sandstone with scattered granules and small pebbles (Fig. 8.11D, E). Deposits overlying BD1 reflect deposition well below fair-weather wave base, which implies that the surface corresponds to a SB modified during subsequent transgression (SB/TSE) rather than serving solely as a regressive surface of marine erosion (cf.

MacEachern et al., 1999a).

Deposits of Unit C in section B–B′ include slump deposits (FJ) in 10-03-036-10W4 and 10-04-036-10W4. The slump deposits are capped by a palimpsest surface in 10-03 that is demarcated by stiffground *Thalassinoides* infilled with glaucony-rich sandstone and underlain by 13 cm of siderite cemented mudstone (Fig. 8.11B). Slumping was likely associated with the bevel created along BD1 during RSL fall, which led to accumulation of unstable sediment that subsequently slumped prior to deposition of the incised shoreface (before or during transgression).

Overall, the erosional edge of BD1 is irregular and is most pronounced along the northwestern margin of the HL field. The incised shoreface thins landward in the vicinity of T35 and R10W4 (Fig. 8.3). At localities where BD1 and the corresponding shoreface are not preserved, there is generally no evidence of subaerial exposure or of transgressive ravinement apparent within the muddy offshore/shelf deposits (e.g., 12-12-035-08W4; Fig. 8.10). Evidence of subaerial exposure was likely removed during transgressive ravinement, producing mud-on-mud contacts that are extremely difficult to discern. The irregular nature of BD1 is possibly explained by paleotopography of the underlying strata. During lowstand, paleotopography may have been affected by tidal ravinement. Localities in which more extensive tidal ravinement may have taken place include the areas located northwest and southeast of T35 R11W4. In the vicinity of T35 R11W4, underlying strata escaped erosion forming a topographic high such that Unit C was not deposited in this area. Seaward of HL, Unit C grades to distal offshore and shelf deposits.

Middle Viking Formation

Deposition of the lower Viking Formation ceased during resumed transgression, which removed upper shoreface deposits of Unit C during shoreface retreat. This ravinement surface constitutes Bounding Discontinuity 2 (BD2). BD2 is commonly represented by a sharp contact, but is locally demarcated by a palimpsest softground or stiffground ichnofossil suite. Palimpsest traces include *Diplocraterion*, *Planolites*, *Skolithos*, and *Thalassinoides* infilled with fine- to medium-grained, salt-and-pepper-coloured sandstone, locally containing glaucony and rare chert granules (Fig. 8.12A, C). A lag deposit without associated ichnofossils occurs in some intervals, such as in core 04-32-035-

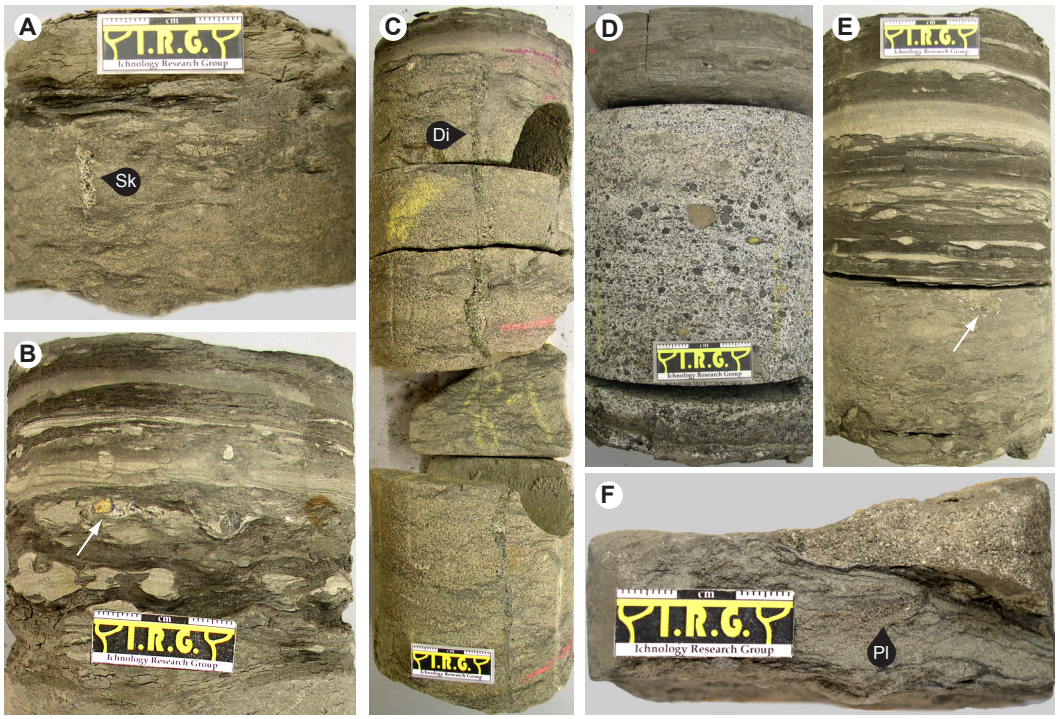

FIGURE 8.12—A-D: Bounding Discontinuity 2. **A:** A concealed palimpsest softground with *Skolithos* (Sk) infilled by a discontinuous lag of salt and pepper coloured, fine to medium sandstone (11-11-036-08W4). **B:** A discontinuous lag with small, dark to orange coloured chert pebbles (white arrow) and sand with preserved load structures at the contact (04-32-035-11W4). **C:** Long *Diplocraterion* demarcating a palimpsest stiffground infilled with glaucony-rich, fine to medium sandstone distending from a sharp contact (12-24-035-09W4). **D:** Scoured surface overlain by 12 cm of pebbly, salt and pepper coloured, fine to very coarse sandstone with calcite cement and sideritized mudstone rip-up clasts (11-26-033-12W4). **E-F:** Photos of Flooding Surface 2. **E:** A sharp contact with a small, fine sandstone lens (white arrow) containing a chert granule that is carved into underlying deposits (12-33-034-10W4). **F:** A palimpsest softground demarcated by *Planolites* overlain by an undulatory surface and 7 cm of fine to medium sandstone (15-04-035-09W4).

11W4. There, the lag is discontinuous, with chert pebbles and underlying loading structures (Fig. 8.12B). BD2 is rarely expressed as a burrowed interface, underlain by siderite, and/or demarcated by a glauconitic and pyritic bed. In the southwest of the study area, BD2 overlies BD1 with a scoured surface and 12 cm of pebbly, salt-and-pepper-coloured, fine- to very coarse-grained sandstone (11-26-033-12W4; Fig. 8.12D).

Transgression was succeeded by highstand progradation leading to accumulation of coarsening-upward offshore and deltaic deposits of Unit D (Figs. 8.9, 8.10). Due to variation in proximity to source areas and concordant shore-parallel deltaic influences, deposits reflect offshore, mixed offshore and deltaic, and (in rarer cases) strictly shelf-like conditions (12-07-035-10W4). Source areas

are thought to be located near T34 R10 and T36 R12 (Fig. 8.3). The paucity of prominent deltaic deposition in comparison to Unit A suggests a general decrease in riverine influx and/or migration of the point source. This package reflects progradation of two deltaic shingles (parasequences) separated by a minor flooding surface (Figs. 8.9, 8.10).

Highstand progradation was followed by a rise in RSL and transgressive flooding. In cross section A–A′, sandy deltaic deposits present in core 12-31-034-09W4 were likely removed in landward settings (e.g., 12-33-034-10W4 and 11-26-033-12W4) during this episode of flooding. The transgressive flooding surface (FS2) overlying Unit D is typically sharp where preserved; however, the surface has commonly been removed by Bounding Discontinuity 3 (BD3; Fig. 8.10). The flooding surface is also expressed as a scoured-to-burrowed contact in 10-23-034-09W4, burrowed contact in 02-22-034-10W4, a small, scoured lens with a chert granule in 12-33-034-10W4 (Fig. 8.12E), and a softground palimpsest suite in 15-04-035-09W4 (Fig. 8.12F). This palimpsest suite is typified by *Planolites* and *Arenicolites* infilled with fine- to medium-grained sandstone. Following transgressive flooding, offshore strata were deposited as distal equivalents of a landward-positioned shoreline system (Unit E).

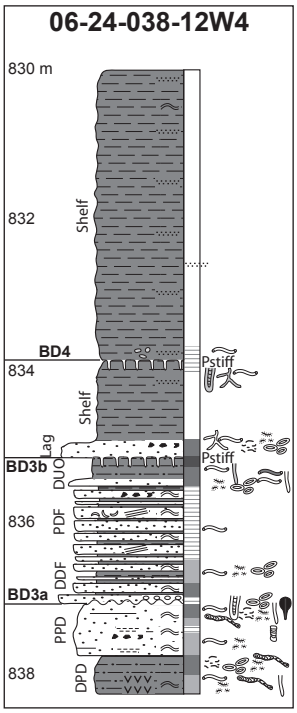

FIGURE 8.13—Type core log from the Castor area showing multiple erosional and palimpsest suites in the upper Viking.

Upper Viking Formation

The upper Viking Formation at HL consists of a number of units preserved within a relatively thin interval. Correlation of Bounding Discontinuity 3 (BD3) differs from that of Burton (1997), in that the surface is subdivided into "BD3a" and "BD3b" where multiple shorefaces have been incised into underlying strata in the northern portion of the study area (Figs. 8.9, 8.10). This includes the Castor area to the northwest (Fig. 8.3) in which multiple upper surfaces are present in the core (Fig. 8.13). Along the landward side of HL, BD3 is typically represented by a single surface that is locally amalgamated with BD4. In some places, BD3b may also be amalgamated with BD4 (Figs. 8.9, 8.10).

Upper Viking Formation events began with the cessation of Unit E deposition following major RSL fall and concordant migration of the shoreline to a position northeast of HL. During this sea-level fall, another bevel was created at the base of the lower shoreface in the northern portion of the study area forming BD3a. Subsequently, RSL rose slightly, and during stillstand, a deltaic-influenced shoreline prograded and deposited Unit F in the bevel carved during RSL fall. Surface BD3a thus reflects a transgressively modified sequence boundary (SB/TSE). This surface resembles BD1, in that it is locally sharp with no indications of erosional truncation of underlying strata. However, BD3a is also expressed as a palimpsest stiffground or softground demarcated by traces that include: *Skolithos*, *Diplocraterion*, *Arenicolites*, ?*Planolites*, ?*Thalassinoides* (Fig. 8.14A, B). These traces are infilled with very fine-grained sandstone with rare chert granules. The surface can also be characterized by a very fine- to coarse-grained sandstone lens with rare chert granules.

Following deposition of Unit F, a minor drop in RSL resulted in migration of the lower shoreface slightly to the northeast. This led to the down-cutting of Unit F forming surface BD3b (Fig. 8.9, 8.10). Progradation resumed during stillstand conditions, depositing a deltaic-influenced package (Unit G). This minor RSL drop was unlikely to have resulted in subaerial exposure; accordingly, surface BD3b reflects a TSE carved by wave ravinement. This surface is locally demarcated by a sharp contact or a palimpsest stiffground or softground suite of *Diplocraterion*, *Planolites*, *Skolithos*, and *Thalassinoides* (Fig. 8.14C, D). The unit containing this suite is overlain by very fine- to fine-grained sandy mudstone with scattered granules and small pebbles. In the absence of a palimpsest suite, the surface is demarcated by an anomalous fine-grained sandstone bed.

Where BD3a and b are represented by a single surface (in the

southwestern landward direction), BD3 is typified by a palimpsest stiffground. The stiffground contains *Thalassinoides*, *Planolites*, *Chondrites*, *Rhizocorallium*, *Diplocraterion*, *Skolithos*, and *Arenicolites* overlain by very fine- to very coarse-grained sandstone or muddy sandstone (Fig. 8.14F). In addition, the lag generally contains granules, rare chert pebbles and very rare glaucony. In a few instances, the surface is underlain by siderite cemented mudstone. Other expressions of BD3 include reworked surfaces represented by scattered chert granules or burrowed sandy mudstone with chert pebbles and an absence of an ichnofossil-demarcated surface (Fig. 8.14E). This surface was reported by Burton (1997) to have been removed in a number of wells; however, in this study, it was observed only in some localities to be amalgamated with BD4 (e.g., 15-04-035-09W4 in A–A′).

Following deposition of the transgressively incised shoreface of Unit G, transgression resumed with the flooding of the HL area. Highstand deposition of two parasequences of distal shoreline equivalents (Unit H) separated by a minor flooding surface succeeded transgression (Fig. 8.9). Viking deposition was ensued by a final major RSL drop that was likely associated with subaerial exposure, and is potentially related to forced regressive or lowstand packages to the northeast. Subsequently, there was rapid transgression with wave ravinement that modified the exposed surface to form an amalgamated SB/TSE referred to as Bounding Discontinuity 4 (BD4).

This uppermost bounding discontinuity (BD4) is generally characterized by a palimpsest softground, stiffground or firmground suite with ichnofossils including: *Thalassinoides*, *Skolithos*, *Teichichnus*, *Rhizocorallium*, *Chondrites*, *Planolites*, *Diplocraterion*, ?*Arenicolites*, and *Zoophycos* (Fig. 8.14G, H). The surface is overlain by burrowed very fine- to coarse-grained sandy mudstone to muddy sandstone with scattered chert granules and rare small pebbles, shell fragments, coal fragments and calcite cement. The underlying sediment is only rarely siderite cemented beneath the ichnofossils. In a few instances, BD4 is characterized by a lag without any associated colonization of the substrate. In such localities, it is demarcated by very fine- to fine-grained sandy mudstone containing rare chert pebbles and scattered granules. This uppermost discontinuity was overlain by shelf mudstones of the Westgate Formation (Colorado Shales; Unit I).

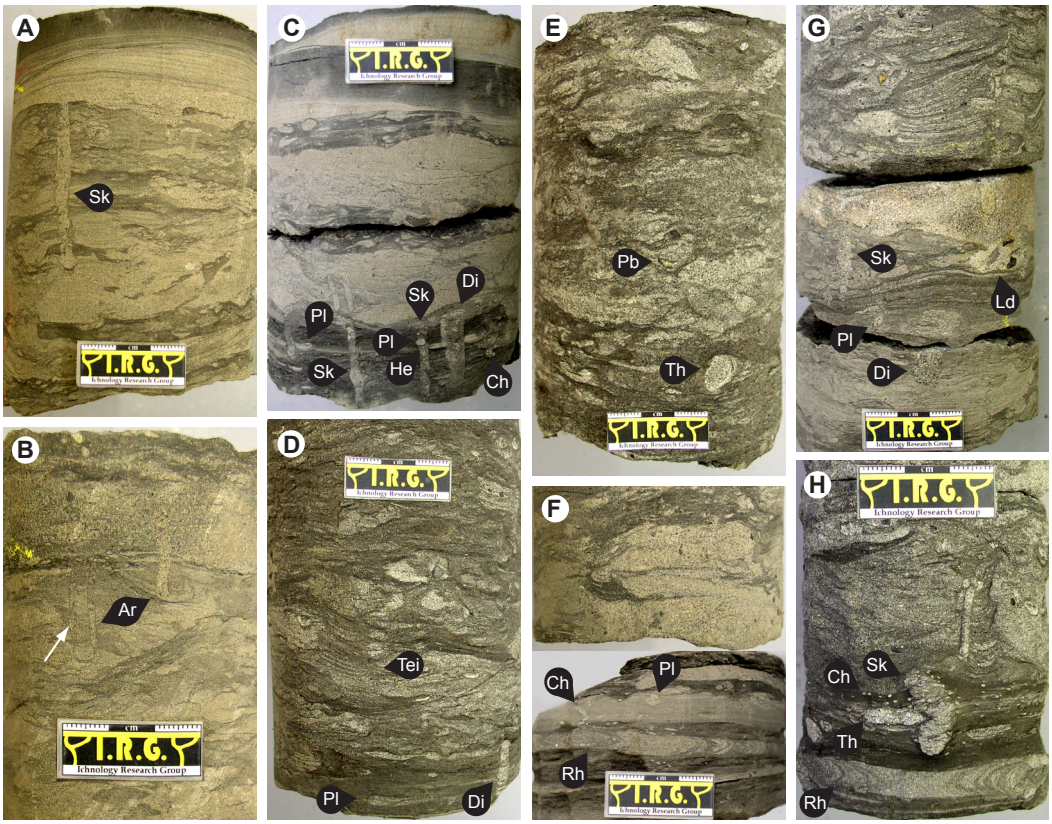

FIGURE 8.14— A-F: Bounding Discontinuity 3. **A:** BD3a demarcated by a palimpsest stiffground with *Skolithos* (Sk) infilled with very fine-grained sandstone containing carbonaceous debris and overlain by 2-3 cm of wave rippled sandstone (02/06-33-035-09W4). **B:** A palimpsest softground characterizing BD3a with *Arenicolites* (Ar) overlain by 2-3 cm of very fine sandstone (12-29-035-10W4). **C:** BD3b typified by palimpsest stiffground ichnofossils including: *Diplocraterion* (Di), *Planolites* (Pl) and *Skolithos* (Sk) that are reburrowed with *Helminthopsis* (He), *Chondrites* (Ch) and *Planolites* (Pl) and overlain by muddy, very fine-grained sandstone (10-09-037-07W4). **D:** *Diplocraterion* (Di) and *Planolites* (Pl) demarcating a palimpsest stiffground along BD3b overlain by 13 cm of sandy mudstone with a prominent *Teichichnus* (Tei) and scattered granules and small pebbles (10-35-035-10W4). **E:** In this example of BD3 there is no particular surface, however, the boundary is indicated by a burrowed, fine-grained, sandy mudstone with one yellow chert pebble (Pb) and *Thalassinoides* (Th) (02-22-034-10W4). **F:** A palimpsest stiffground demarcating BD3 with *Rhizocorallium* (Rh), *Chondrites* (Ch), and *Planolites* (Pl), which are overlain by 10 cm of muddy sandstone with scattered coarse-grained sand to small chert pebbles (12-33-034-10W4). **G-H:** Photos of Bounding Discontinuity 4. **G:** *Diplocraterion* (Di), *Skolithos* (Sk) and *Planolites* (Pl) characterizing a palimpsest stiffground infilled with fine-grained sandstone and overlain by 10 cm of muddy sandstone. The surface also has loading structures (Ld) and the infill also contains coal fragments, calcite cement, scattered chert granules to pebbles, and shell fragments. (10-12-036-12W4). **H:** BD4 demarcated by palimpsest softground *Rhizocorallium* (Rh), *Chondrites* (Ch), *Thalassinoides* (Th), and *Skolithos* (Sk) overlain by very fine- to fine-grained sandy mudstone with rare granules (02-36-034-10W4).

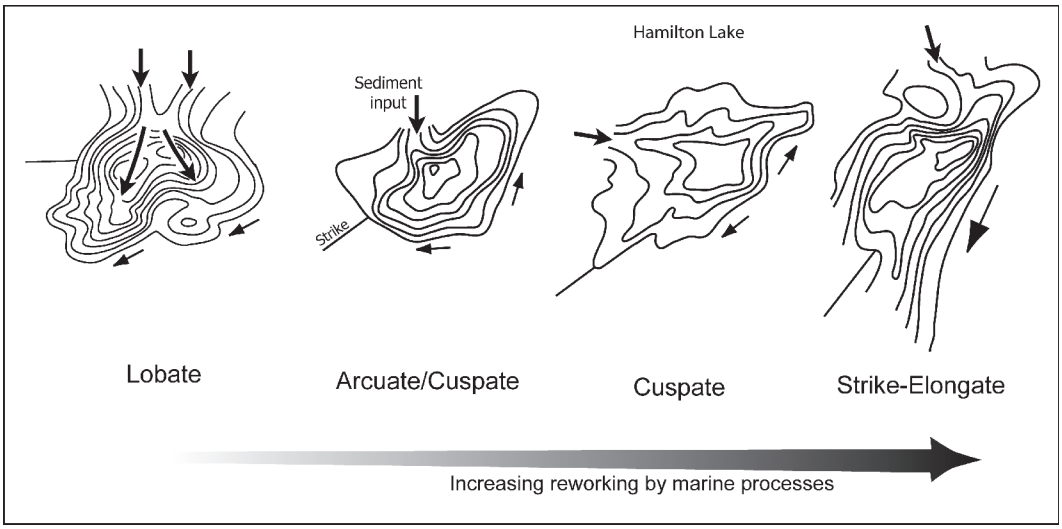

FIGURE 8.15—Delta morphologies produced as a result of increasing wave influence. The lobate delta is river-dominated, and the strike-elongate delta reflects conditions of wave-dominance. Arrows indicate sediment input and directions of sand transport. Modified from Weise (1979).

FAS1: WAVE-INFLUENCED DELTAIC DEPOSITS

Deltaic facies models are typically classified using the tripartite division of Galloway (1975). These models are used to categorize the morphology and facies architecture of delta fronts based on the dominance of a particular process. Wave-dominated deltas are well documented and have been described by a number of authors (e.g., Weise, 1979; Tankard and Barwis, 1982; Bhattacharya, 1988; Bhattacharya and Walker, 1992; Seidler and Steel, 2001; Nouidar and Chellai, 2002). The degree of wave-dominance in a delta depends upon the ability of waves to rework the river-supplied sediment, which influences the geometry, distribution and orientation of the resulting sand bodies (Fig. 8.15; Coleman, 1981). Interactions between marine (wave and tide) and fluvial processes can produce complex facies relationships in which no single process dominates during deposition of the succession.

Recently, wave-influenced deltas were described by Bhattacharya and Walker (1991) from the Dunvegan Formation. Bhattacharya and Giosan (2003) also discussed general characteristics of asymmetrical wave-influenced deltas, which consist of prograding beach ridges resembling a progradational strandplain passing along strike into more river-influenced lobes. Wave-influenced deltas can be differentiated from modern strandplains based on the arcuate to cuspate morphology of the beach ridges, a decrease in the proportion of filter-feeding

Publication	Delta classification	Proximal delta front	Distal delta front	Proximal prodelta	Distal prodelta
This publication: Viking Fm, Hamilton Lake	wave-influenced	moderately-stressed expression of the *Cruziana* Ichnofacies with lesser occurrences of the *Skolithos* Ichnofacies	subtly-stressed proximal expression of the *Cruziana* Ichnofacies	moderately stressed archetypal expression of the *Cruziana* Ichnofacies	subtly stressed archetypal expression of the *Cruziana* Ichnofacies
Gingras et al., 1998: Dunvegan Fm, Alberta, Canada	wave-dominated	"healthy" though incompletely preserved, *Skolithos* Ichnofacies	proximal *Cruziana* Ichnofacies	robust and diverse *Cruziana* Ichnofacies	
Coates and MacEachern, 1999: Dunvegan Fm	wave- and storm-dominated	mixed *Skolithos-Cruziana* assemblage		"stressed" *Cruziana* assemblage	
Bann and Fielding, 2004: Permian Denison Trough, Queensland, Australia	mixed river- and wave-influenced	sporadically distributed, stressed proximal expression of the *Cruziana* Ichnofacies	sporadically distrib-uted, stressed *Cruziana* Ichnofacies and very rare *Skolithos* ichnofacies	sporadically distributed, stressed expression of the distal *Cruziana* Ichnofacies	

TABLE 8.2—Comparison of ichnological assemblages interpreted from deltaic deposits described from this study; the Dunvegan Formation of Alberta, Canada (Gingras et al., 1998; Coates and MacEachern, 1999); and the Permian Denison Trough of Queensland, Australia (Bann and Fielding, 2004).

organisms, a decrease in diversity and abundance of trace fossils, and indications of high sediment influx (Gingras et al., 1998; Coates and MacEachern, 1999; Bhattacharya and Giosan, 2003; Bann and Fielding, 2004). In general, wave-influenced deltas possess characteristics of both end-member river- and wave-dominated deltas (Bhattacharya and Walker, 1991).

The deltaic Viking deposits in this study comprise coarsening-upward packages with abundant wave-formed structures including hummocky cross-stratification. However, FAS1 also contains subtle evidence of rapid sedimentation and freshwater input that includes localized carbonaceous mudstones, synaeresis cracks, and soft-sediment deformation structures, as well as stressed ichnofossil suites. In comparison to reported wave-dominated ichnological suites from particular units of the Dunvegan Formation (Gingras et al., 1998; Coates and MacEachern, 1999), there are heightened environmental stresses associated with FAS1 (Table 8.3). The “stress” associated with ichnofossil suites within HL is highlighted by reduced diversities and abundances of trace fossils (especially dwellings of inferred suspension-feeding organisms). In conjunction with a stressed trace fossil suite, mudstone units of FAS1 lack foraminiferal assemblages typical of marine Viking deposits (cf. MacEachern et al. 1999c).

Conversely, the ichnological suites of FAS1 exhibit reduced environmental stress as compared to those described by Bann and Fielding (2004) from Permian deltaic deposits in Australia (Table 8.3). These Permian deposits are described as

mixed river- and wave-influenced delta lobes with a low-diversity ichnological suite. The trace diversity and abundance of dwellings of inferred suspension-feeders is diminished in comparison to HL strata. This suggests that the influence of river-sediment influx is more pronounced in the Permian strata. As wave influence increases, the impact of riverine discharge and associated environmental stresses (turbidity, high concentration of suspended sediment, and decreased marine salinity) are progressively minimized (cf. MacEachern et al., 2005, 2007).

Accordingly, deposits of FAS1 can be interpreted as the products of wave-influenced deltas based on: 1) subtle physical structures and lithological elements indicative of river-sediment influx; and 2) subtly to moderately stressed trace fossil suites with an overall reduction in abundance of structures attributed to suspension-feeding animals. Morphology of the deltas could not be ascertained despite the laterally extensive deltaic deposits within Unit A, owing to truncation and modification along FS1 and BD1. The delta systems were most likely cuspate and formed under moderate wave influence (Fig. 8.15).

CONCLUSIONS

The Viking Formation in the HL area consists of a diverse assemblage of facies that are grouped based on lithological, sedimentological and ichnological criteria into three facies associations. Facies of FAS1 are interpreted as proximal and distal components of the delta front and prodelta, based on evidence of carbonaceous mudstone deposition, high sedimentation rates, salinity fluctuations, and the presence of stressed ichnological suites. Environmental stresses associated with riverine influx including: heightened water turbidity, high concentrations of suspended sediment, fluid mud deposition, high sedimentation rates, reduced salinity, and reduced oxygenation. Conversely, deposits of FAS2 reflect deposition under more normal marine conditions, as biogenic reworking was pervasive leading to homogenized muddy sandstones to sandy mudstones of the distal lower shoreface and upper offshore. The lower offshore and shelf deposits of FAS3 reflect more distal deposition, whereas the transgressive lag and slump deposits are associated with erosion along BD1.

Initially, Hamilton Lake sand bodies were interpreted as offshore bars (Amajor and Lerbeckmo, 1990a, b), and later reinterpreted as coarsening-upward

shelf to shoreface successions (Burton, 1997). The detailed facies analysis of this study, however, reveals subtle sedimentological and ichnological indicators pointing to wave-influenced deltaic deposition. Deltaic deposition was prominent within Unit A, which was succeeded by a transgressive shoreface incisement and resumed mixed deltaic and offshore deposition. The upper Viking also contains two additional transgressively incised shorefaces, capped by the uppermost SB/TSE (BD4).

Implications of this study for petroleum exploration and development include enhanced recognition of wave-influenced deltaic deposits in ancient successions. The model provides a better understanding of the nature of potential reservoirs with respect to lithology and morphology. Unlike wave-dominated deltas or shoreface strata, sandy deposits in these wave-influenced complexes would be expected to contain greater proportions of mud, especially mudstone laminae that reduce overall permeability between sandstone beds. Furthermore, sandstone geometries would reflect cuspate, shoreline-parallel bodies rather than lobate or linear features. The subtle nature of wave-influence suggests a potential for reinterpretation of other ancient strata.

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CHAPTER 9 – DEFINING THE NATURE OF PALIMPSEST SOFTGROUND, STIFFGROUND, AND FIRMGROUND TRACE FOSSIL SUITES USING MODERN AND ANCIENT EXAMPLES

INTRODUCTION

Ichnology has proven to be exceedingly useful in the interpretation of stratigraphic surfaces in two important ways: (1) through identification of substrate-controlled ichnofacies; and (2) ichnological analysis of vertical successions (MacEachern et al., 1992). Stratigraphically significant surfaces tend to be associated with a period of hiatus and/or erosion, during which time infauna may colonize the surface, producing a suite of traces that cross-cut precursor trace fossil assemblages. These substrate-controlled ichnofacies reflect time-averaging of successive communities, and are referred to as palimpsest trace fossil suites (Bromley and Asgaard, 1991; Bromley, 1996). Palimpsest suites reflect substrate colonization, wherein conditions have typically changed between successive communities; the specific character of the palimpsest ichnofossil suite will depend upon the consistency of the underlying substrate at the time of colonization (MacEachern and Hobbs, 2004). Established substrate-controlled ichnofacies include the *Glossifungites* (Fig. 9.1), *Trypanites* (Fig. 9.2A), and *Teredolites* (Fig. 9.2B) ichnofacies reflecting palimpsest firmground, hardground and woodground substrates, respectively (Bromley, 1975; Bromley et al., 1984; Pemberton and Frey 1985). Owing to their affinity with erosional discontinuities, such suites are also referred to as "omission suites."

More recently, researchers have recognized palimpsest softground ichnofossil suites (e.g., Hobbs, 2003; Sadeque and Bhattacharya, 2004; Buotois et al., 2005; Gingras and Bann, 2006; Dafoe et al., 2007; MacEachern et al., 2007a) and palimpsest stiffground ichnofossil suites (e.g., Martino, 1989; Gingras et al., 2000; Hladil et al., 2004; Lettley et al., 2007). The focus of this work is to establish criteria to differentiates these more recently recognized palimpsest suites from the more familiar firmground *Glossifungites* Ichnofacies. This chapter also investigates environmental and stratigraphic influences on palimpsest suites,

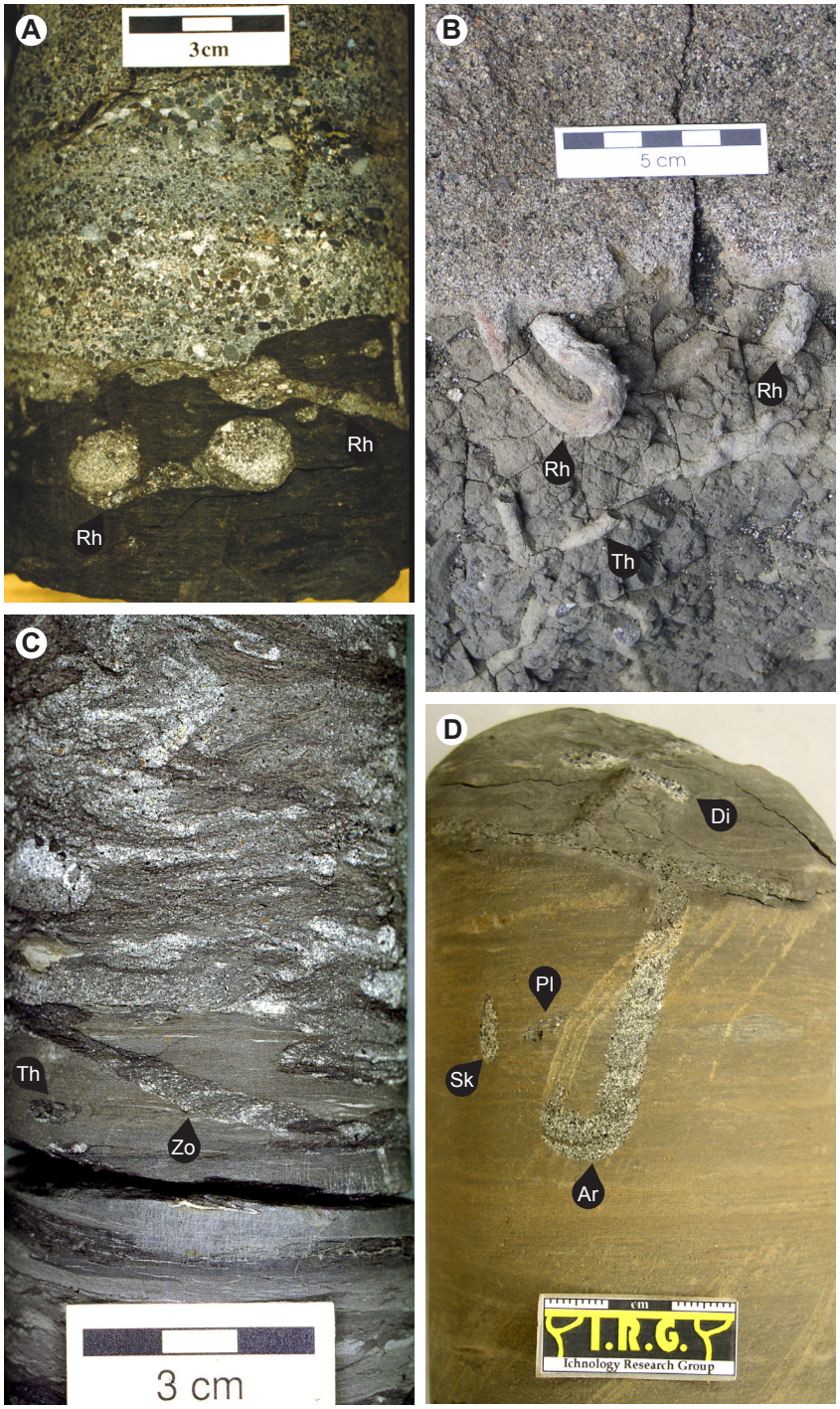


FIGURE 9.1—The firmground *Glossifungites* Ichnofacies (see Table 5 for additional details). **A:** Sharp-walled firmground *Rhizocorallium saxicava* (Rh) subtending from a scoured contact at the base of an incised valley in the Viking Formation of the Willesden Green Field. **B:** The margin of a submarine canyon between the Nihotupu and Tirikohua Formations of New Zealand. The contact is demarcated by scratch-marked *Rhizocorallium* (Rh) and *Thalassinoides* (Th). **C:** In the Hamilton Lake area, the Viking Formation is characterized by a distal firmground suite consisting of *Zoophycos* (Zo) and *Thalassinoides* (Th) along a SB/TSE. **D:** A firmground suite from the Viking Formation at Hamilton Lake in which sharp-walled *Arenicolites* (Ar), *Skolithos* (Sk), *Diplocraterion* (Di) and *Planolites* (Pl) colonized initially incipiently siderite cemented mudstone.

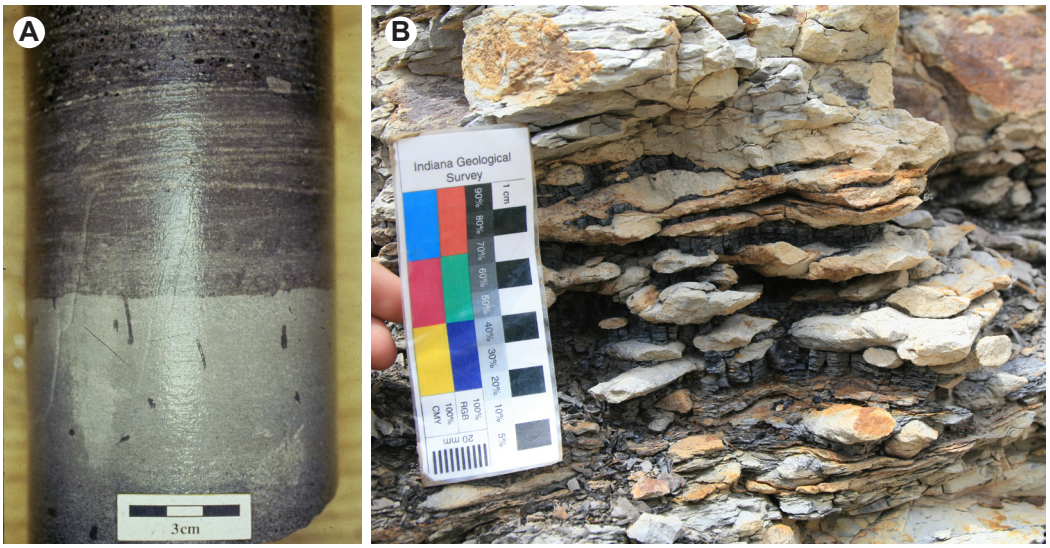


FIGURE 9.2—The **A:** *Trypanites* Ichnofacies, and **B:** *Teredolites* Ichnofacies. **A:** Palimpsest hardground from the Triassic Halfway Formation of Alberta. **B:** Thalassinid borings within a coal bed from the Ferron Sandstone near Emery, Utah (photo courtesy of Ryan King).

conditions in which these suites develop, their preservation potential, and the broader applications of these suites in facies analysis.

Overprinting, Tiering and Palimpsest Suites

A palimpsest suite (especially softground) may resemble ichnofossil tiering; however, these forms of overprinting are distinctly different. Overprinting may occur in the form of: 1) tiering of organisms within a community, and 2) time-averaging of successive communities or palimpsest ichnofossil suites. Ichnological tiering was described by Wetzel and Aigner (1986) as the vertical zonation of traces within the substrate, which is a function of vertical gradients in physical, chemical and biological characteristics (Fig. 9.3A; Bromley and Ekdale, 1986; Bromley, 1996). Such gradients can include: degree of compaction, substrate consistency, organic matter concentrations, oxygenation, pH, physical factors, distribution of food particles, early diagenesis, penecontemporaneous erosion, sedimentation rates, the organisms present, and the position of the redox zone (Goldring et al., 1991; Bromley, 1996). Based on cross-cutting relationships, one can determine the nature of infaunal tiering (Bromley and Ekdale, 1986) because an individual tier reflects mutually intersecting traces produced at a similar depth (Wetzel and Aigner, 1986). During burial, sediment becomes compacted, which alters the texture and consistency leading to it becoming firmer

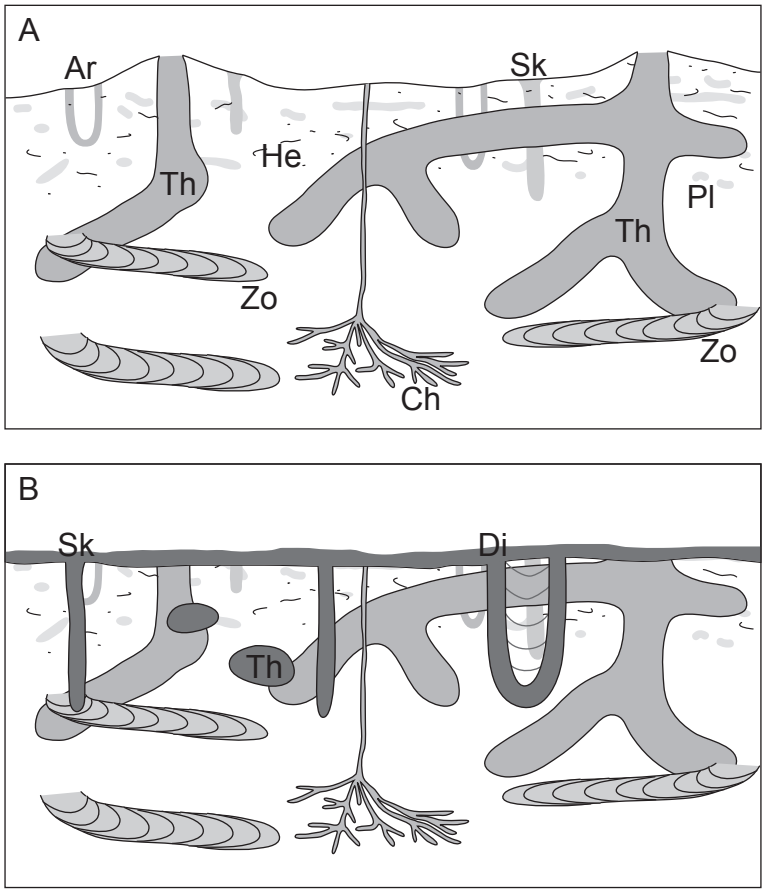


FIGURE 9.3—Various forms of overprinting. **A:** Tiering of an ichnofossil suite in which deep-tier structures (*Zoophycos* (Zo) and *Chondrites* (Ch)) have overprinted mid-tier traces (*Thalassinoides* (Th) and *Helminthopsis* (He)) that initially overprinted shallow tiers (*Arenicolites* (Ar) and *Skolithos* (Sk)). **B:** Time averaging of successive ichnofossil communities whereby the softground suite of (A) is truncated and cross-cut by the unrelated suite containing *Skolithos* (Sk), *Thalassinoides* (Th) and *Diplocraterion* (Di).

with depth (Bromley and Ekdale, 1986). Accordingly, shallow tiers become compacted and display ill-defined trace boundaries, whereas occupants of successively deeper tiers intersect stiffer sediment and their biogenic structures exhibit well-defined boundaries (Bromley and Ekdale, 1986). Deeper tiers typically possess an enhanced preservation potential, but tend to be less abundant (Wetzel and Aigner, 1986), which preserves an ecologically incomplete and biased paleocommunity (Bromley and Ekdale, 1986).

Time-averaging, on the other hand, addresses the overlapping of time-lines, such that several successive communities are found in a single assemblage of traces (Fig. 9.3B; Bromley, 1996). Time-averaging of trace fossil suites is indicative of a palimpsest suite wherein conditions have changed between the periods of initial and subsequent colonization. A palimpsest surface often has

been considered to simply reflect two superimposed ichnofossil suites within the same rock unit (e.g., Bromley and Asgaard, 1991; Brekke, 1995). However, the palimpsest suite may not always cross-cut an underlying trace fossil suite due to a paucity in bioturbation or recognizable traces within the underlying substrate (especially in deep marine mudstones). As such, it is proposed here that a palimpsest suite must be recognized by: 1) the cross-cutting of an underlying precursor suite of trace fossils, and/or 2) a change in paleodepositional conditions across the surface.

In some instances, especially where palimpsest suites demarcate autogenically generated surfaces, the distinction between tiering and palimpsesting may be unclear, as deep tiers inherently involve colonization of stiffer substrate (Bromley and Ekdale, 1986). Tiering can be distinguished from palimpsest suites through identification of two key attributes. 1) Tiering generally reflects colonization during continuous deposition, such that there is no discrete surface; as such, without a change in conditions, infilling sediment is unlikely to contrast with the host media. Palimpsest suites, on the other hand, reflect some degree of discontinuous deposition and concomitant changes in environmental conditions. A change in depositional conditions produces a discrete surface that is subsequently colonized with burrows that are infilled with typically contrasting superjacent sediment. 2) Traces of a palimpsest suite tend to reflect colonization of a surface during a comparatively shorter time frame, such that their constituent ichnofossils generally do not cross-cut one another. However, tiered ichnofossils reflect continuous deposition during which deeper tiers may cross-cut one another (especially those constructed by differing trace-makers).

Discriminating Between Soft-, Stiff- and Firmgrounds

One of the most important factors controlling colonization and trace fossil distribution is the substrate character (Goldring and Kazmierczak, 1974; Bromley and Ekdale, 1986; MacEachern et al., 2007a). In modern sediments, there is a clear distinction between soft-, stiff- and firmground substrates mad apparent by organism-sediment interactions observed in each substrate. Softground substrates have undergone some degree of dewatering and burrows are maintained with mucous linings (e.g., Pearson and Gingras, 2006; Lettley et al., 2007; MacEachern et al., 2007a). Stiffground substrates, on the other hand, reflect stabilized sediment yielding open, unlined burrows and tunnels that are at least semi-permanent (e.g.,

Thalassinoides; Wetzel and Uchmann, 1998; Lettley et al., 2007; MacEachern et al., 2007a). In contrast, firmgrounds are considered to be firm, dewatered, and compacted sediment with burrows showing little compactional deformation, sharp burrow outlines and distinct bioglyphs (Goldring, 1995; Wetzel and Uchmann, 1998; Mikuláš et al., 2003; MacEachern et al., 2007a). These unique organism-sediment interactions observed in the modern realm translate to discrete and predictable characteristics for palimpsest soft-, stiff- and firm- substrate suites in ancient successions.

Previous literature, however, has rarely discriminated between these suites, and palimpsest soft- and stiffground suites have been mistakenly attributed to the *Glossifungites* Ichnofacies (e.g., Brekke, 1995). For example, Ruffel and Wach (1998) proposed a hierarchy of firmgrounds that ranges from very mature, mature, immature and loose or soft. The immature firmgrounds most likely reflect stiffground conditions, whereas the loose or soft firmgrounds are, in fact, palimpsest softgrounds. Modern "firmgrounds" observed in Willapa Bay by Gingras et al. (2000) were deemed temporally insignificant, and are now recognized as "stiffground". In other instances, the uniqueness of stiffground substrates was recognized, but suites were still attributed to the *Glossifungites* Ichnofacies (e.g., Mikuláš et al., 2003).

Soft-, stiff- and firmground palimpsest ichnofossil suites can be discriminated from one another through identification of trace fossil attributes that reflect non-cohesive, semi-cohesive, and cohesive substrate conditions during endobenthic colonization in ancient sediments (e.g., Lettley et al., 2007), and by the degree of substrate firmness in modern sediments (e.g., Gingras and Pemberton, 2000; Gingras et al., 2000).

Challenges in Defining Palimpsest Suites

There are two main challenges with defining palimpsest soft-, stiff-and firmground suites: 1) the gradational character of substrate firmness; and 2) the variable expression of palimpsest suites. Experiments in modern environments have shown compactional differences between these substrates, based on a modified Brinell hardness test (Gingras and Pemberton, 2000). The Brinell hardness test consists of a sphere dropped from a fixed height onto the substrate. The diameter of the indent is inversely proportional to the firmness of the substrate (Fig. 9.4; Gingras and Pemberton, 2000). Softgrounds generally exert

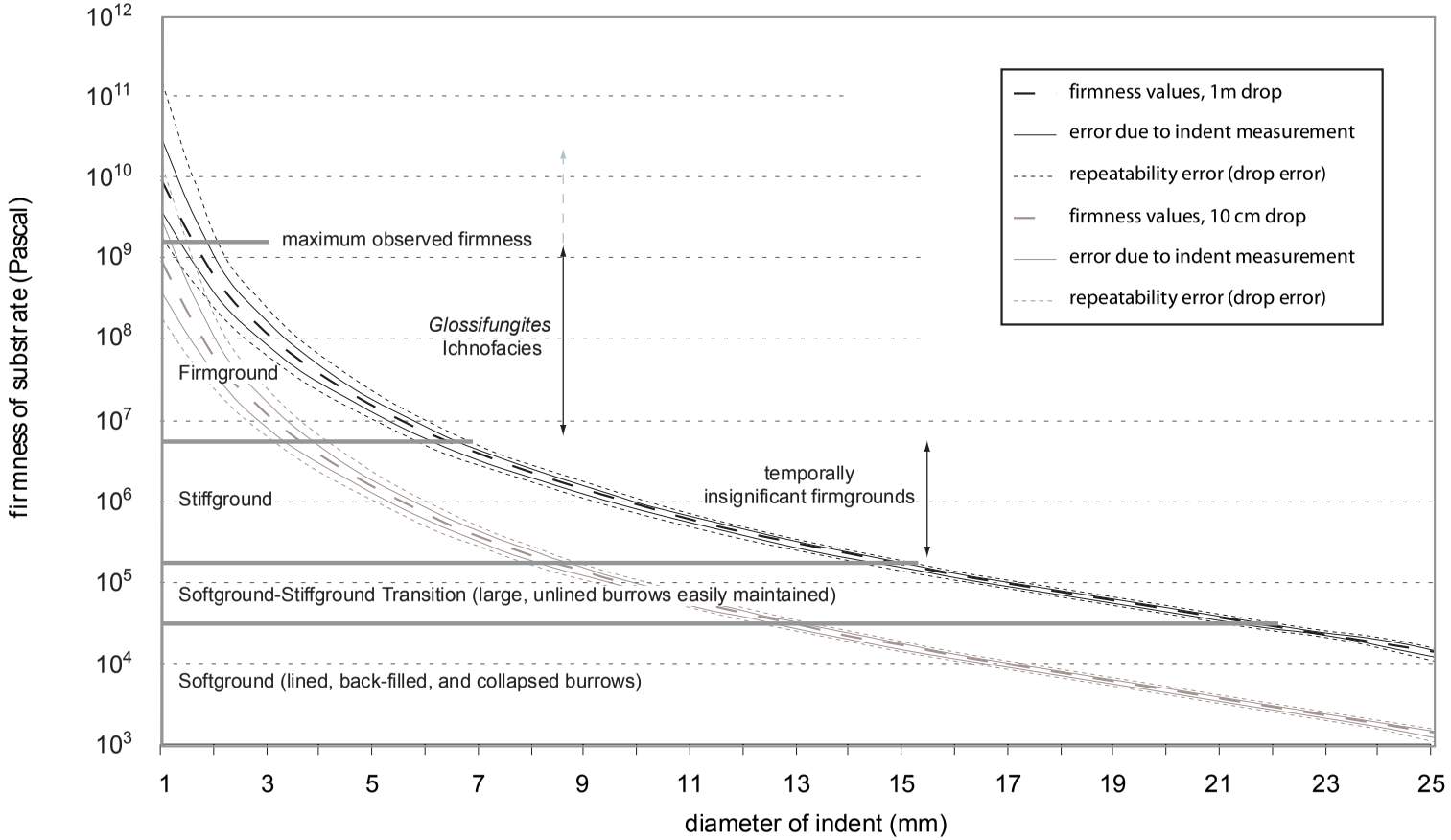


FIGURE 9.4—The diameter of the indentation in the substrate as a function of the pressure exerted by the substrate. The upper curve corresponds to the values created during a 1 m free fall firmness test, and the lower curve is representative of a 10 cm fall. Softground substrates are characterized by lined, back-filled and collapsed burrows, whereas the softground to stiffground transition contains large, unlined burrows that are easily maintained. The stiffground substrate corresponds to the temporally insignificant firmgrounds, whereas the firmground substrate occurs where the pressure exerted by the substrate lies above 10^7 Pa. At this point, trace fossil suites yield features characteristic of the *Glossifungites* Ichnofacies. Modified from Gingras et al. (2000).

a pressure less than 3.2 x 10^4 Pa, stiffgrounds range from 3.2 x 10^4 to 10^7 Pa, and firmground record yield strength in excess of this (Fig. 9.4; Gingras et al., 2000). The gradational nature of substrate firmness results in transitional realms between soft and stiff, and between stiff and firm. Colonization of a substrate possessing firmness within a transitional zone may yield palimpsest ichnofossils exhibiting characteristics of more than one type of suite (see section on localized variability at the ichnofossil scale).

Palimpsest suites can be differentiated from one another, but also may be characterized by a variety of attributes. Variable expressions between palimpsest soft-, stiff-, and firmgrounds is primarily a function of the character of the underlying substrate. The development and expression of these ichnofossil suites is further modified as a result of associated environmental and stratigraphic influences, in addition to the processes that led to the formation of the palimpsest suite.

Differentiation between suites of the firmground *Glossifungites* Ichnofacies and palimpsest soft- and stiffground ichnofossil suites enhances our understanding and ability to interpret successions and their associated stratigraphic discontinuities in modern and ancient examples. The aim of this paper is to: 1) define the characteristics of palimpsest soft-, stiff- and firmground trace fossil suites; 2) discuss the environmental influence(s) on palimpsest suites; 3) evaluate stratigraphic influences on the generation of palimpsest suites; 4) propose mechanisms by which the suites form; and 5) determine the application of palimpsest suites in modern and ancient successions.

METHODS

In this study, modern and ancient examples of palimpsest soft-, stiff- and firmground ichnofossil suites were employed. Observations from outcrop and core were compiled, to highlight characteristics that define these suites (Table 9.1). Their attributes tend to fall into hierarchical categories, in that all variations of palimpsest suites: (1) cross-cut the underlying ichnofossil suite; and/or (2) indicate a change in depositional conditions across the surface. Additional characteristics fall into primary (distinguishing) and secondary (commonly associated) attributes. The characteristics of these suites are described below

Attribute	Palimpsest Softground	Palimpsest Stiffground	Firmground Glossifungites (Pemberton et al., 2001)	Hardground Trypanites (Bromley, 1975; Pemberton et al., 2001)	Woodground Teredolites (Bromley et al., 1984; Pemberton et al., 2001)
Principal	Traces cross-cut elements of an underlying ichnofossil suite and/or indicate a significant change in depositional conditions across the surface	Traces cross-cut elements of an underlying ichnofossil suite and/or indicate a significant change in depositional conditions across the surface	Traces cross-cut elements of an underlying ichnofossil suite and/or indicate a significant change in depositional conditions across the surface	Boring cross-cut elements of an underlying ichnofossil suite	Borings are cut into a woodground or xylic substrate
Primary	• Indistinct or irregular trace boundaries • Mixing of superjacent sediment and host softground media • Surrounding halo of disturbance within host sediment • Traces are lined • Significant warping of laminae adjacent to ichnofossils • Surface displays pronounced loading	• Traces are relatively sharp-walled in mudstone (Lettley et al., 2007) or display irregular, but unlined boundaries in sandy sediment • Laminae are distorted (upwards or downwards) adjacent to traces (Lettley et al., 2007) • Plastic deformation of the uppermost stiffground to form flame and loading structures • Traces are generally unlined (Lettley et al., 2007), but may possess minor partial lining	• Traces are unlined and sharp-walled • Surface displays evidence of significant scouring • Traces possess bioglyphs (ornamented), particularly scratch marks • Traces occur within incipiently cemented substrate (e.g. siderite)	• Borings are sharp-walled • Boring boundaries display evidence of mineral grain/clast truncation • Borings are perpendicular to the substrate • Boring display avoidance of resistant grains	• Borings are sharp-walled • Walls are ornamented with the texture of the host substrate
Secondary	• Traces are actively or passively infilled • Traces are significantly compacted • Traces or host sediment is sheared or deformed • Traces are reburrowed • Traces are diminutive • Traces occur in low population densities or dense monospecific assemblages • Traces may display evidence of truncation due to erosion • Traces display progressive palimpsesting	• Traces are actively or passively infilled • Traces are compacted (Lettley et al., 2007) • Traces are sheared or deformed • Traces are reburrowed • Traces are diminutive (Lettley et al., 2007) • Traces occur in low population densities or dense monospecific assemblages • Traces may display evidence of truncation due to erosion • Traces display progressive palimpsesting • The palimpsest surface possess an undulatory topography (Gingras et al., 2000)	• Traces are actively or passively infilled • Traces are robust • Traces occur in low diversity • Traces occur in low population densities or dense monospecific assemblages	• Borings may be cylindrical to vase-, tear- or U-shaped domiciles of inferred suspension feeders or passive carnivores • Borings occur in moderately low population densities • Includes raspings and gnawings of algal grazers • Individual borings may be abundant • Borings can be superimposed	• Borings are stumpy to elongate subcylindrical or clavate subparallel excavations • Borings occur in low diversity, commonly monospecific suites • Boring possess size-class variation

TABLE 9.1 (Previous page)—Comparison of characteristics of trace fossil suites reflecting palimpsest softground conditions and palimpsest stiffgrounds, as well as the *Glossifungites*, *Trypanites* and *Teredolites* ichnofacies. Characteristics are subdivided into the principal attribute, which is necessary in recognition of the trace fossil suite, the primary attributes that distinguish the suite, and secondary attributes that are commonly, but not necessarily associated with a suite.

Location and Figure	Modern Palimpsest Suite	Stratigraphic Importance
Niawiakum Estuary, WS, USA Figure 9.14A	• soft to stiff transition within fine-grained organic sediment • *Arenicolites*- and *Skolithos*-like burrows pass through upper (beige) softground into underlying oxygen-poor stiffground sediment • burrows are sharp walled in the stiffground, but poorly defined in softground	• autogenic • upper point bar surface underwent autocompaction through dewatering
Shepody River, New Brunswick, Canada Figure 9.14B	• soft to stiff transition within accretionary bank deposits • *Corophium volutator* and *Macoma balthica* burrows reflecting *Arenicolites*-, *Diplocraterion*-, and *Siphonichnus*-like structures that are sharp-walled in the lower stiffground and poorly defined in the upper softground	• seasonal fluctuations in sedimentation, freeze/thaw, compaction and dewatering (Lettley et al., 2007) • autogenic related most likely to synaeresis forcing the expulsion of pore water (Lettley et al., 2007)
North Cove, WS, USA Figure 9.14C	• compacted and exhumed stiffground sandy tidal flat mud • incipient *Thalassinoides* formed by shrimp approximately 200 ybp.	• exhumation on a transgressive beach due to bay margin migration
Goose Point, Willapa Bay, WS, USA Figures 9.14D	• firmground *Diplocraterion*- and *Skolithos*-like burrows easily maintained without lining or mucous • cross-cuts earlier suite • oxidation next to burrows suggests reduced sediment conditions	• c.a. 100,000 yrs. predominantly wave ravinement and lesser tidal ravinement on surface.
Modern sediment X-ray Figure 9.7A	• non-palimpsest typical softground assemblage containing prominent bivalves	• none
Modern sediment X-ray Figure 9.7B	• palimpsest softground *Cylindrichnus*-like burrow extends from surface and cross-cuts underlying softground assemblage (threadworm and *Saccoglossus* structures) • faint burrow lining at top of burrow and general sediment disruption in adjacent sediment • soupground at top with sediment more cohesive (but still soft) at base	• likely insignificant stratigraphically
Modern sediment X-ray Figure 9.7B	• palimpsest stiff- to firmground rhythmically laminated saltmarsh sediment extensively rooted • *Arenicolites*-like structures cross cut the rhizoliths	• autocompaction of sediment likely aided by abundant rhizoliths
Modern sediment X-ray Figure 9.7C	• palimpsest firmground with bivalves cross-cutting burrowed sediment • uneven surface topography	• autogenic • subaqueous tidal channel eroded into salt marsh deposits

TABLE 9.2—Modern examples of palimpsest suites from sedimentary surfaces and X-ray.

Formation, Location (Age, Figure)	Underlying Unit	Softground Palimpsest Suite	Overlying Unit	Stratigraphic Importance
Heather Formation, Norwegian Shelf (Middle Jurassic) Figure 9.6A	• homogenized muddy sandstone (BI 5)	• *Diplocraterion* and *Thalassinoides* • poorly defined to irregular boundaries • mixing of lag and host sediment • reburrowed	• fine- to medium-grained sandy mudstone with scattered pebbles less than 3 cm in diameter	• amalgamated sequence boundary and flooding surface • fault blocks suggest surface related to tectonic activity
Viking Formation 06-11-039-14W4 (Lower Cretaceous) Figure 9.6B	• mudstone • shelf	• *Rhizocorallium* • indistinct boundaries • mixing of lag and host sediment • trace fossil is poorly distinguished	• burrowed sandy mudstone lag succeeded by Colorado Shales	• uppermost amalgamated SB/TSE of the Viking • BD4 in Hamilton Lake area
Viking Formation 10-30-033-07W4 (Lower Cretaceous) Figure 9.6C	• silty mudstone • lower offshore	• *Rhizocorallium* • halo of disturbance • progressive palimpsesting	• burrowed muddy sandstone lag succeeded by Colorado Shales	• uppermost amalgamated SB/TSE of the Viking • BD4 in Hamilton Lake area
Viking Formation, 06-29-038-18W4 (Lower Cretaceous) Figure 9.6D, E	• a) muddy fine sandstone; stressed archetypal *Cruziana* Ichnofacies; prodelta to distal delta front • b) carbonaceous mudstone (possibly hypopycnal river-sourced)	• 2 successive suites: a) *Arenicolites* and *Skolithos* ◦ indistinct boundaries ◦ lined traces b) *Planolites* and *Thalassinoides* ◦ indistinct boundaries ◦ mixing of host and superjacent sediment ◦ loading along surface	• a) 1-2 cm fine- to medium-grained sandstone capped by carbonaceous mudstone • b) resumed deposition consists of the same facies as underlying surface (a)	• autogenic • a) likely related to slight increase in energy of the setting resulting in coarser clastic deposition • b) possibly related to dewatering of fluid mud
Bluesky Formation, 06-32-074-12W6 (Lower Cretaceous) Figure 9.6F	• laminated looseground sandy sediment • shoreface	• *Conichnus* • pronounced disruption of the host sediment material • surrounding halos of sediment disturbance • indistinct trace fossil boundaries • mixing of host and lag material	• muddy fine- to medium-grained sandstone with scattered granules	• transgressive surface of erosion separating parasequences (Brekke, 1995)
Viking Formation 10-23-034-09W4 (Lower Cretaceous) Figure 9.6G	• mudstone with interlaminated very fine-grained sand and silt • lower offshore	• *Skolithos*, *Planolites*, *Thalassinoides*, ?*Rhizocorallium* • underlying sediment convolute bedded and deformed • indistinct boundaries • compaction	• burrowed muddy sandstone lag succeeded by Colorado Shales	• uppermost amalgamated SB/TSE of the Viking • BD4 in Hamilton Lake area

TABLE 9.3—Ancient examples of palimpsest softground suites.

Formation, Location (Age, Figure)	Underlying Unit	Transitional Palimpsest Suite	Overlying Unit	Stratigraphic Importance
Viking Formation, 12-24-035-09W4 (Lower Cretaceous) Figure 9.6H	• muddy sandstone • upper offshore	• long *Diplocraterion* containing fine to medium-grained sandstone and dark green glaucony • intermittent lining with indistinct boundary walls	• no preserved lag deposit other than within ichnofossils • sharp contact overlain by interlaminated mudstone, siltstone and fine-grained sandstone • weakly burrowed strata suggestive of reduced oxygenation	• wave ravinement surface • overlies a transgressively incised shoreface
Pebbley Beach Formation, Clear Point, New South Wales, Australia (Permian) Figure 9.6I	• heterolithic sandstone and mudstone • estuarine basin deposits (Bann et al., 2004; Gingras and Bann, 2006)	• *Diplocraterion habichi* • infilled with coarser grained sand mixed with muddy sandstone • sheared and deformed traces	• heterolithic sandstone and mudstone • channel-fill deposit (Bann et al., 2004; Gingras and Bann, 2006)	• tidal ravinement surface
Snapper Point Formation, Snapper Point South, New South Wales, Australia (Permian) Figure 9.6J	• low-angle laminated sandstone • sparse bioturbation (BI 1)	• *Rosselia socialis* • variation in lag incorporation • varying degree of lining • warping of laminae adjacent to traces	• undulatory sharp contact • medium- to coarse-grained sandstone; pebbles (< 2 cm in diameter) • planar lamination to high-angle cross-bedding	• autogenic fluctuations in sediment supply

TABLE 9.3 (Continued)

TABLE 9.4 (Next page)—Ancient examples of palimpsest stiffground suites.

Formation, Location (Age, Figure)	Underlying Unit	Stiffground Palimpsest Suite	Overlying Unit	Stratigraphic Importance
McMurray Formation, Alberta (Lower Cretaceous) Figures 9.10A, 9.13A	• sandstone IHS bed • point bar deposition in estuarine channel	• *Gyrolithes* are compacted and indiscernible in the upper portion of the mud bed with decreasing abundance of sand • apparent bed junction • Figure 13A displays deformation of the traces	• mudstone IHS bed • point bar deposition in estuarine channel	• autogenic • deformation and compaction in upper soft mud and well defined structures at base due to stiffground conditions
Viking Formation, 10-09-037-07W4 (Lower Cretaceous) Figure 9.13B	• mudstone (BI 1) • poorly oxygenated lower offshore	• sharp walled *Skolithos*, *Diplocraterion*, *Planolites* and *Thalassinoides* • reburrowed with *Helminthopsis* and *Chondrites* • loading along surface	• heterolithic sandstone and mudstone (BI 2-5) • prodelta to delta front succession	• wave ravinement surface separating transgressively incised shorefaces • BD3b Hamilton Lake
Viking Formation, 02-36-034-10W4 (Lower Cretaceous) Figure 9.13C	• mudstone (BI 0-1) • shelf (low oxygen)	• *Rhizocorallium* (sharp walled), *Skolithos* (deformed), *Thalassinoides* (compacted), *Planolites* • reburrowed with *Chondrites*, *Helminthopsis*	• muddy sandstone lag followed by mudstone (BI 0-1) • shelf	• uppermost amalgamated sequence boundary and transgressive surface of erosion
Pebas Formation, Amazonia (Miocene) Figure 9.13D	• pedogenically altered mud containing rhizoliths	• *Thalassinoides* • compaction • complete reworking of the palimpsest surface	• shell hash and sandy mud • low-energy, dysoxic, distal bay	• transgressive surface of erosion (Hovikoski et al., 2007)
Snapper Point Formation, Snapper Point South, New South Wales, Australia (Permian) Figure 9.13E	• planar laminated sandstone with *Diplocraterion* (BI 0-1) and overlain by a fluid mudstone bed	• *Thalassinoides* • sharp walled • marked compaction	• HCS sandstone and coarse clastic beds. • *Diplocraterion*, *Rosselia*, *Palaeophycus*	• autogenic change in sediment supply • river sourced fluid mud dewatered and compacted under hypoxic conditions prior to burrowing
West Ahken Field, Nile Delta (Miocene) Figure 9.13F, G	• interlaminated sandstone and mudstone that may be inclined (BI 1-2)	• lined *Skolithos* • compacted *Thalassinoides* • deflection of adjacent laminae	• fine- to medium-grained sandstone • angular pebbles up to 1.5 cm in diameter	• submarine canyon incision that forms part of a sequence boundary
McMurray Formation, Alberta (Lower Cretaceous) Figure 9.10B	• mudstone IHS bed • point bar deposition in estuarine channel	• *Planolites* and *Thalassinoides* infilled with sandstone • passively or actively infilled with sandstone • sharp ichnofossil boundaries	• unpreserved or remnant sandstone laminae	• autocyclic seasonal variations in water circulation and sediment texture (Lettley et al., 2007)
Viking Formation, (Lower Cretaceous) 02-04-037-19W4 Figure 9.10C	• interbedded sandstone and mudstone (BI 1-3); delta front	• *Diplocraterion*: discontinuous lining, deformation of adjacent laminae, sharp walled • loading along surface	• thin discontinuous sandstone lag with small pebbles • overlain by shelf mudstones	• uppermost amalgamated sequence boundary and transgressive surface of erosion

Formation, Location (Age, Figure)	Underlying Unit	Firmground Glossifungites Ichnofacies	Overlying Unit	Stratigraphic Importance
Viking Formation, Willesden Green Field Figure 9.1A	• dense shelf mudstone with *Phycosiphon*, *Chondrites* and *Zoophycos*	• *Rhizocorallium saxicava* • sharp boundaries • robust • scoured surface	• burrowed pebbly sandstone containing *Teichichnus*, *Ophiomorpha*, *Palaeophycus* and *Planolites* • tidal inlet fill	• migration of tidal channel • amalgamation with the initial transgressive surface and sequence boundary (MacEachern and Pemberton, 1994)
Nihotupu and Tirikohua Formations, New Zealand Figure 9.1B	• mudstone of the Nihotupu Formation	• *Rhizocorallium* and *Thalassinoides* • *Rhizocorallium* display distinctive scratch marks • robust	• gritty sandstone of the Tirikohua Formation	• submarine canyon incision (Hayward, 1976).
Viking Formation, 06-13-035-09W4 Figures 9.1C	• mudstone with rare sandstone and siltstone laminae	• *Zoophycos* and *Thalassinoides* • sharp walled • no disruption to adjacent laminae	• bioturbated sandy mudstone with scattered pebbles	• uppermost amalgamated sequence boundary and transgressive surface (MacEachern and Burton, 2000)
Viking Formation, 14-18-44-07W4 Figure 9.1D	• siderite cemented mudstone containing intermittent sand/silt laminae (BI 0-1)	• *Arenicolites*, *Skolithos*, *Planolites* and *Diplocraterion* • sharp walled • associated to incipient siderite cementation	• mudstone containing intermittent sand/silt laminae (BI 0-1) • poorly oxygenated	• amalgamated sequence boundary and transgressive surface
Viking Formation, Gilby A Field 08-17-040-01W5 Figure 9.10D	• siderite cemented • offshore silty shales	• *Skolithos* • sharp-walled, unlined • passively infilled • associated to incipient siderite cementation	• pebbly sand • lag deposit	• transgressive surface of erosion (MacEachern et al., 1992)

TABLE 9.5—Ancient examples of palimpsest firmground suites.

Formation, Location (Age, Figure)	Underlying Unit	Transitional Palimpsest Suite	Overlying Unit	Stratigraphic Importance
Bluesky Formation (Lower Cretaceous) Figure 9.11A	• bioturbated sandy mudstone • upper offshore	• transitional palimpsest soft- to stiffground with *Skolithos* • boundaries well defined at the base, but poorly defined to diffuse at the top of the *Skolithos*	• coarse clastic sand and overlain by a pebbly lag material	• wave ravinement surface
Viking Formation, 16-34-038-25W4 (Lower Cretaceous) Figure 9.11B	• bioturbated silty to muddy sandstone • offshore strata	• transitional palimpsest soft- to stiffground demarcated by *Diplocraterion* and *Skolithos* • upper portion - indistinct boundaries, mixing of host and lag sediment and partial to extensive burrow linings (softground) • lower portion - sharp boundaries and deformation in sandy sediment (stiffground)	• medium- to coarse-grained sand with scattered granule lag deposit	• amalgamated sequence boundary and transgressive surface
Viking Formation, 10-03-036-10W4 (Lower Cretaceous) Figure 9.11C	• siderite cemented muddy sandstone (BI 4-5) that transitions to mudstone • upper offshore	• transitional palimpsest soft- to stiffground • *Skolithos* - sharp boundary walls with slight deflection of adjacent laminae (stiffground) • *Thalassinoides* and *Arenicolites* - indistinct boundaries, mixing of host and lag sediment (softground)	• mudstone with interspersed sand and silt (BI 3-5) • lower offshore	• uppermost sequence boundary and transgressive surface in Hamilton Lake area (see Chapter 8)
Pebbley Beach Formation, Clear Point, New South Wales, Australia (Permian) Figure 9.11D	• interbedded sandstone and mudstone of fluid mud origin (BI 1-3) • delta front	• transitional palimpsest soft- to stiffground characterized by *Diplocraterion* • stiffground colonization in upper mudstone with deflection of laminae adjacent to the traces and load and flame structures • in underlying muddy sandstone, traces are lined and display indistinct trace boundaries with mixing of host and lag sediment suggestive of palimpsest softground colonization	• mudstone with thin interlaminated sandstone beds (BI 1-3) • distal prodeltaic deposition	• wave ravinement surface • high energy conditions during colonization
Moosomin B, Red Jacket Formation, Saskatchewan, 04-18-015-02W2 (Jurassic) Figure 9.11E	• calcareous sandy mudstone with minor, poorly preserved pelecypod molds • brackish water deposition	• transitional palimpsest soft- to stiffground demarcated by *Diplocraterion parallelum* • random sharp to diffuse boundaries • localized mixing of host and lag sediment • patchy incipient calcareous cementation likely resulted in transitional nature	• silty and sandy lenses interbedded with mudstone • extensively bioturbated • grades upward into marine mudstones (Kreis 1991)	• marine ravinement (pers. commun. Kreis, 2007)

TABLE 9.6—Ancient examples of transitional palimpsest suites.

Formation, Location (Age, Figure)	Underlying Unit	Transitional Palimpsest Suite	Overlying Unit	Stratigraphic Importance
Viking Formation, 02/07-22-038-20W4 (Lower Cretaceous) Figure 9.11F	• low-angle parallel laminated sandstone with mudstone laminae (BI 1-3) • deltaic • siderite cemented	• transitional palimpsest soft- to firmground • cross-sectional representations of *Thalassinoides*: indistinct boundaries, mixing of sandy infill and sideritized mudstone (softground) • vertical *Thalassinoides*: sharp walled with sideritized mudstone clasts in infill (firmground)	• low-angle parallel laminated sandstone with mudstone laminae (BI 1-3) • deltaic	• autogenic • deposition of a thick fluvial sourced mudstone, opportunistic colonization and incipient siderite cementation
Panther Tongue, Star Point Formation, Utah, USA Figure 9.11G, H	• laminated sandstone • deltaic strata	• transitional palimpsest soft- to stiffground • overall character of traces reflects the nature of both soft- and stiffground overprinted substrates • *Rosselia* and *Skolithos* - boundaries are sharp to diffuse with localized halos of disturbance • unlined character also suggests passive fill in stiffground	• mudstones • fully marine	• transgressive surface of erosion at the top of the Panther Tongue (Bhattacharya et al., 2007)
Viking Formation, 12-35-036-25W4 (Lower Cretaceous) Figure 9.12	• interbedded sandstone and mudstone (BI 3-5) • prodelta	• transitional palimpsest stiff- to firmground with *Diplocraterion* • within upper siderite: sharp-walled (firmground) • underlying interlaminated sediment: relatively sharp-walled, rare partial linings, deflection of laminae and fabric adjacent to the traces, and compaction deformation (stiffground)	• pebbly and medium- to coarse-grained, sand-sized material • overlain by interbedded interlaminated sandstone and mudstone • prodelta	• wave ravinement surface with major change in depositional conditions

TABLE 9.6 (Continued)

using examples presented in Tables 9.2-9.6. Through analysis of the underlying ichnofossil suite, the palimpsest suite, and the overlying ichnofossil suite, each surface can be identified as allogenic or autogenic in origin (cf. MacEachern et al., 1992; MacEachern et al., 2007c). Using these studied examples, the influences of environment and stratigraphy on the palimpsest suites were evaluated. Processes resulting in the formation of palimpsest suites are described, and the applications of palimpsest suites are discussed.

SUBSTRATE INFLUENCE ON PALIMPSEST SUITES

Substrate Properties

The various forms of substrate include: soupground, softground, looseground, stiffground firmground, hardground and woodground. The most important factor controlling colonization is the degree of cohesion or consistency of the substrate (Goldring and Kazmierczak, 1974). For example, the same mud deposit can be firm, soupy, soft or hard at the time of colonization. Sediment firmness is dependent upon a number of factors including: grain size and shape; pore-water content; compaction; early diagenetic cementation; mineralogy; drainage (on sloped sediment surfaces); as well as sedimentary fabric, temperature, turbulence, sedimentation rate, and salinity (Goldring and Kazmierczak, 1974; Wetzel, 1990; Ruffel and Wach, 1998; Wetzel and Uchmann, 1998; Gingras and Pemberton, 2000; Gingras et al., 2001).

Muddier substrates are particularly susceptible to forming palimpsest suites, because the sediment typically possesses increased water content and coherence, which tends to produce stiff- and firmgrounds upon burial, compaction, dewatering and subsequent exhumation. Heterolithic sandstone and mudstone, sandy mudstone, and muddy sandstone possess overall larger sediment calibres, reduced water contents, and reduced compatibility. As such, they are susceptible to palimpsest soft- and stiffground colonization. Sandy sediment can also be colonized by firmground trace-makers, leading to suites attributable to the *Glossifungites* Ichnofacies, especially where incipient cementation has occurred.

Based on the data gathered from ancient strata and modern settings, there are exist specific identifying characteristics of trace fossil suites that demarcate soft- to firmground substrate. The principal, primary, and secondary

characteristics are described below using particular modern and ancient examples.

Palimpsest Softground Suites

Palimpsest softground suites are associated with non-cohesive substrate conditions during subsequent endobenthic colonization. In previous studies, palimpsest softgrounds were only related to the overprinting of trace fossils in sandy substrates (e.g., Brekke, 1995; Hobbs, 2003; MacEachern and Hobbs, 2004). In these studies, traces demarcating palimpsest softground suites were attributed to the *Skolithos* Ichnofacies (e.g. MacEachern and Hobbs, 2004; Buatois et al., 2005). Conversely, Bromley and Asgaard (1991) attributed muddy and sandy palimpsest softgrounds separating pre- and post-turbidite deposits to the *Nereites* Ichnofacies. Accordingly, palimpsest softground suites clearly form in a range of substrates including: compacted sand, heterolithic sand and mud, sandy mud, and dewatered mud. Regardless of the underlying substrate lithologies and their consistencies, palimpsest softground suites can be differentiated from other palimpsest scenarios (Table 9.1).

Principal Attributes

As with any palimpsest suite, the principal characteristic includes that: 1) traces cross-cut elements of an underlying ichnofossil suite; and/or 2) the suite indicates a change in depositional conditions across the surface. In some instances, however, it may be difficult to differentiate palimpsest softground suites from deep-tier ichnofossils that cross-cut shallow tiers of the softground. In Figure 9.5A, deep-tier *Arenicolites* cross-cuts the shallow-tier, horizontal, mud-lined trace (*Palaeophycus*?) and appears to be related to the overlying surface. However, the *Arenicolites* is infilled with sandstone consistent with the surrounding host sediment, rather than the overlying coarse deposit, which indicates that infill of the trace occurred prior to formation of the surface. If the *Arenicolites* reflected colonization of the erosional surface and was open during subsequent deposition, it would be infilled with coarser sand and small pebbles concordant with the overlying lag. Conversely, Figure 9.5B depicts a scenario wherein *Arenicolites* appears to display a similar relationship, except the burrows infill consists of coarse-grained sand sourced from the overlying lag deposit. This indicates that this trace is part of the palimpsest softground suite. In

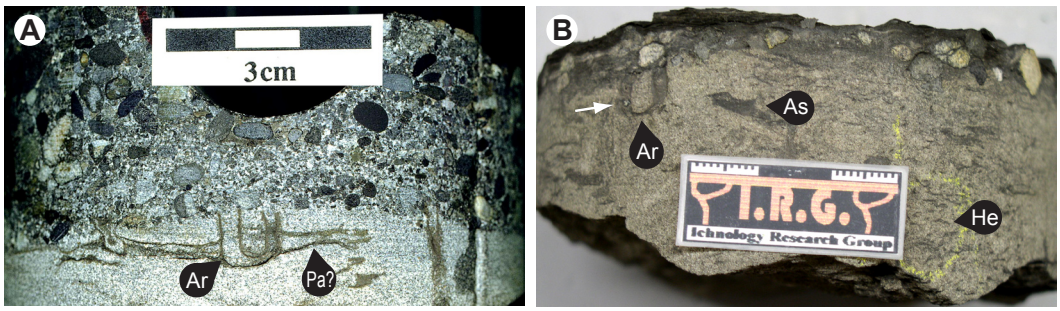


FIGURE 9.5—Softground trace fossil suite versus palimpsest softground trace fossil suite. **A:** A softground trace fossil suite is truncated by an erosional event, and superficially resembles a palimpsest softground suite. However, the *Arenicolites* (Ar) is infilled with sandstone consistent with the lower unit, indicating that infill occurred prior to erosion. If the *Arenicolites* was associated with the erosional event as part of a palimpsest suite, then coarser sand and small pebbles similar to that of the lag should be present in the trace fossils. **B:** *Arenicolites* (Ar) contains a coarse-grained sand and mud consistent with the overlying lag deposit indicating that this structure was open along the interface allowing coarse material to be piped into the burrow. This suggests that the trace characterizes a palimpsest trace suite. The poorly defined trace fossil boundaries suggest that the *Arenicolites* comprises a palimpsest softground ichnofossil suite that overprinted the *Asterosoma* (As) and *Helminthopsis* (He) dominated unit (02-33-034-20W4, 1189.03 m depth).

addition, the dwelling of an inferred suspension-feeding organism reflects a shift in environmental conditions that contrasts with the horizontal, deposit-feeding structures predominating the underlying upper offshore strata. This surface is ultimately overlain by shelf mudstones, and reflects an amalgamated SB/TSE at the top of the Viking Formation of Alberta, Canada.

Primary Attributes

There are diagnostic primary attributes of suites that indicate that palimpsesting occurred within softground sediment. The identification of a single primary attribute is sufficient for classifying the type of palimpsest suite observed. The identification of multiple primary attributes enhances this interpretation (Tables 9.1-9.3). Softground primary characteristics include: 1) indistinct or irregular trace fossil boundaries; 2) mixing of host and superjacent sediment; 3) surrounding halo of disturbance within the host substrate; 4) traces are lined; 5) laminae are significantly warped next to palimpsest traces; and 6) surfaces displaying pronounced loading.

Palimpsest ichnofossils displaying indistinct or irregular boundaries suggest that sediment grains were easily manipulated by the trace-maker during colonization of softground sediment. In the Jurassic Heather Formation,

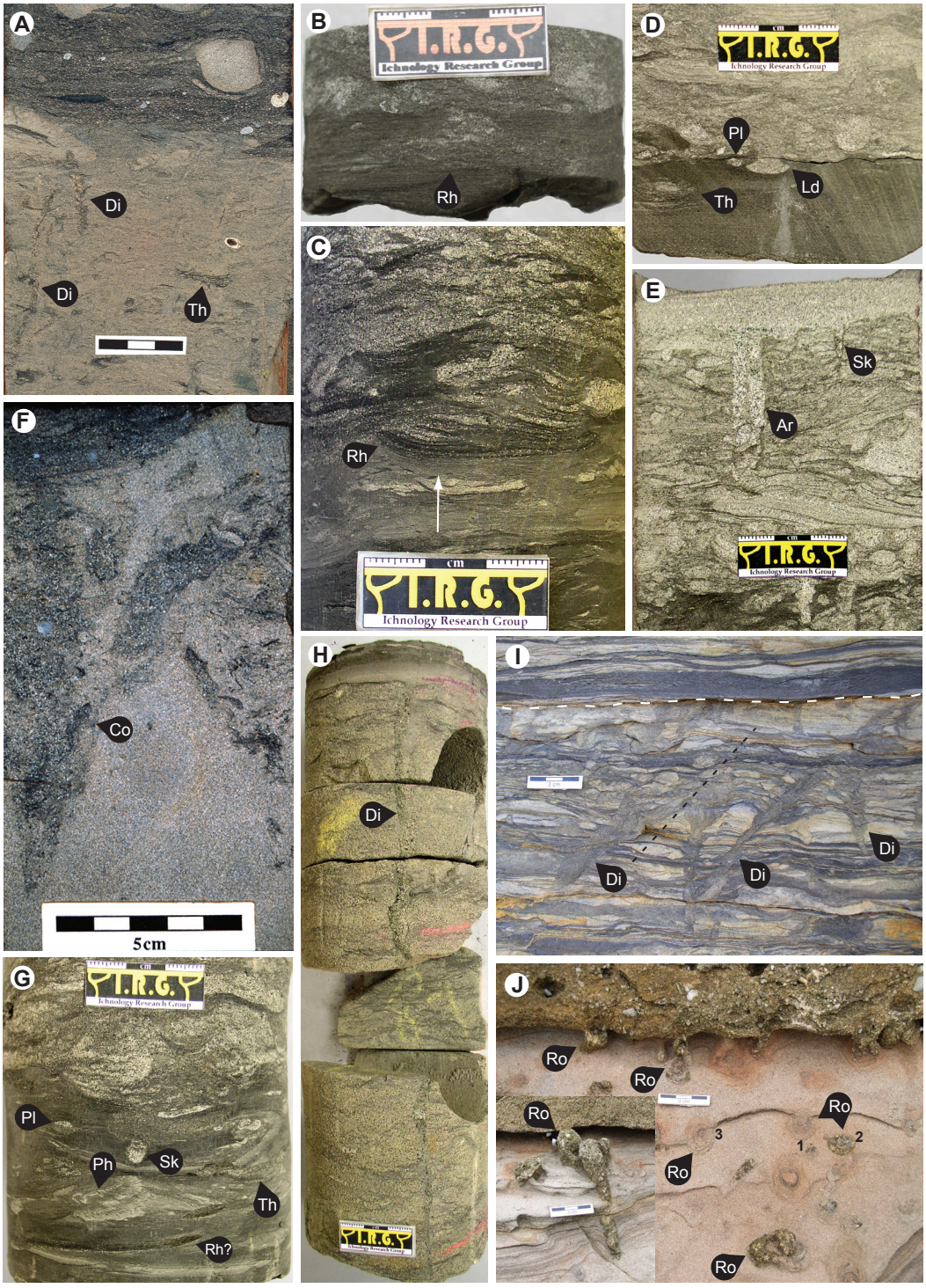


FIGURE 9.6—Examples of palimpsest softground trace fossil suites (see Table 9.3 for additional details). **A:** The Heather Formation (Middle Jurassic) off the Norwegian Shelf contains a palimpsest ichnofossil suite comprising *Diplocraterion* (Di) and *Thalassinoides* (Th) with poorly defined boundaries. The fill mixes the lag and host sediment, and shows minor reburrowing. **B:** *Rhizocorallium* (Rh) with indistinct ichnofossil boundaries demarcating a palimpsest suite in the Viking Formation (06-11-039-14W4). **C:** A palimpsest *Rhizocorallium* (Rh) with a surrounding halo of disturbance in the Viking Formation (10-30-033-07W4). **D-E:** Two successive palimpsest softgrounds from the Viking Formation (06-29-038-18W4). The lower suite (E) is demarcated

FIGURE 9.6 (Continued)—by *Arenicolites* (Ar) and *Skolithos* (Sk) with indistinct to lined boundaries, overlain by *Thalassinoides* (Th) and *Planolites* (Pl) displaying indistinct walls and the mixing of host and lag sediment within carbonaceous mudstone (D). **F:** Palimpsest *Conichnus* (Co) in the Bluesky Formation displaying pronounced disruption of the host sediment and indistinct boundaries (06-32-074-12W6). **G:** *Skolithos* (Sk), *Planolites* (Pl), *Thalassinoides* (Th) and ?*Rhizocorallium* (Rh) cross-cutting convoluted and deformed soft sediment with sheared *Phycosiphon* (Ph) in the Viking (10-23-034-09W4). **H:** An intermittently lined, elongate *Diplocraterion* (Di) defining a wave ravinement surface in the Viking Formation (12-24-035-09W4). **I:** Sheared and deformed *Diplocraterion habichi* (Di) from the Pebbley Beach Formation. Sediment creep leading to the deformation of the traces along a tidal ravinement surface. **J:** *Rosselia socialis* (Ro) from the Snapper Point Formation displaying variation in the incorporation of lag material and warping of laminae (inset).

a palimpsest suite typically consists of *Diplocraterion* and *Thalassinoides* displaying poorly defined to irregular boundaries (Fig. 9.6A). This suite demarcates an amalgamated sequence boundary and flooding surface related to tectonic activity, based on the presence of fault blocks in the area. The Lower Cretaceous Viking Formation also contains erosional surfaces demarcated by lag deposits commonly in association with trace fossil suites. The uppermost bounding discontinuity (BD4; see Chapter 8) of the Viking in the Hamilton Lake area is a SB/TSE that is typically demarcated as a palimpsest softground suite. One expression of this surface shows *Rhizocorallium* with indistinct boundaries, in which the mixing of lag and host sediment is so extensive that the ichnogenus itself is difficult to identify (Fig. 9.6B).

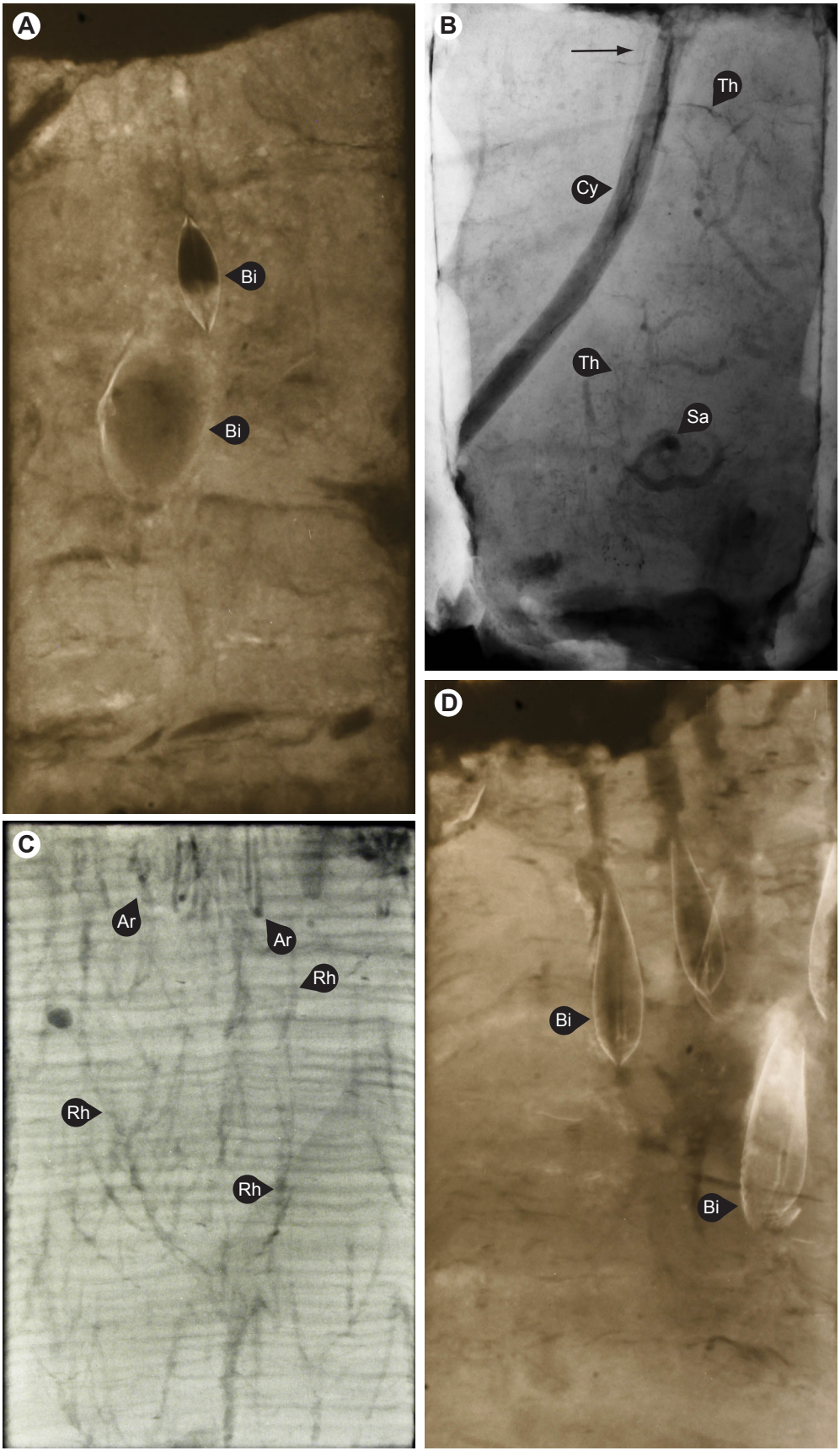
The mixing of superjacent (typically lag) and host softground sediment is also diagnostic to palimpsest softground colonization as this also suggests an ease of grain manipulation. Mixing of host and superjacent sediment may occur in various ways described below. The Lower Cretaceous Bluesky Formation reflects a transitional setting between the coastal plain of the Gething Formation and the open marine conditions of the Wilrich Member (Male, 1992). Within this setting, a discontinuity is demarcated by palimpsest *Conichnus* exhibiting pronounced disruption of the host sediment material as a result of extensive mixing of lag and host media (Fig. 9.6F). Colonization of looseground sandy sediment is the most plausible explanation for the chaotic nature of this palimpsest suite. This surface separates two parasequences as a transgressive surface of erosion. Another expression of "lag and host" mixing occurs within Permian strata that crops out along the coastline of New South Wales (NSW) of Australia. A palimpsest softground in the Snapper Point Formation consists of *Rosselia socialis* displaying variations in the incorporation of lags, owing to active infilling at the time of

lag deposition (Fig. 9.6J). Variation includes: gritty lag strictly within the stalk, the bulb, both the bulb and stalk, and sparse incorporation of coarse material interpreted to reflect timing of burrowing relative to deposition of the coarse-grained material. The surface likely reflects autocyclic fluctuations in sediment supply (possibly related to glacial processes; cf. Veevers and Powell, 1987) because over- and underlying strata are broadly comparable and the surface appears genetically conformable with underlying hummocky cross-stratification.

At Hamilton Lake, the Viking Formation along Bounding Discontinuity 4 (BD4) exhibits an additional primary feature—a surrounding halo of disturbance within the host sediment. In Figure 9.6C, the base of the *Rhizocorallium* exhibits an approximately 2 mm wide halo within the host sediment in which the primary fabric has been destroyed, possibly due to compaction or grain shifting adjacent to the burrow structure. Modern sediments can also exhibit characteristics diagnostic to softground palimpsesting (Table 9.2). A modern X-ray image in Figure 9.7B depicts a *Cylindrichnus*-like burrow that subtends from the sediment surface and cross-cuts the underlying softground suite. Along the length of the structure, there is disruption of the surrounding host sediment (lighter coloured halo) suggesting it reflects a palimpsest softground condition. The surface is, however, stratigraphically insignificant though it depicts a minor shift in the burrowing community.

The *Cylindrichnus*-like structure in Figure 9.7B also exhibits a faint burrow lining near the surface, although not at depth. The sediment likely possessed a soupground-like character near the sediment surface, but was more cohesive at depth so that a lining was no longer required. Burrow linings of ichnofossils within a palimpsest suite indicates that the trace-maker needed to stabilize its burrow walls, in order to maintain the structure (prevalent with semi-permanent domiciles). Such linings may be robust and thick (Fig. 9.8A) or thin (Fig. 9.9A). One particular example of a lined trace occurs in the Viking

FIGURE 9.7 (Next page)—X-ray images of modern deposits in which the sediment surface is towards the top of each photo (see Table 2 for detailed descriptions). **A:** A typical softground assemblage of modern organisms and burrow structures including bivalves (Bi). The upper sandier portion of the sediment is admixed, and not significantly dewatered, so that burrows were not open nor infilled. **B:** Palimpsest softground *Cylindrichnus*-like (Cy) burrow cross-cutting threadworm (Th) and *Saccoglossus* (Sa) structures. The *Cylindrichnus*-like structure is lined near the top and displays general sediment disruption along the length of the burrow. **C:** Transitional palimpsest stiff- to firmground, in which *Arenicolites*-like burrows cross-cut rhizoliths (Rh) within salt marsh deposits. **D:** Firmground colonized by bivalves (Bi) from the base of a subaqueous tidal channel.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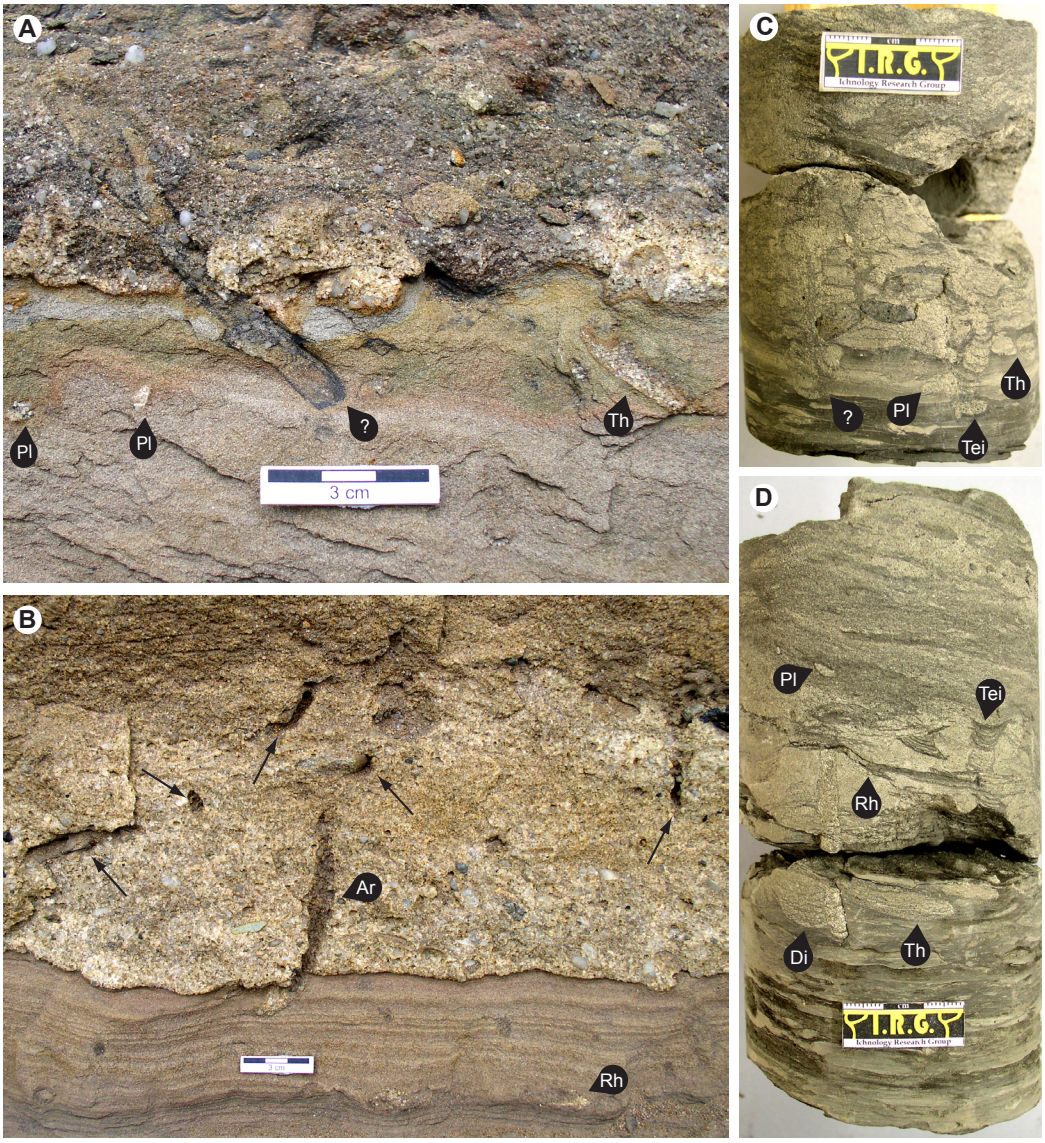

FIGURE 9.8—Progressive palimpsesting from **A-B:** The Snapper Point Formation, Snapper Point South, New South Wales, Australia and **C-D:** The Viking Formation, Alberta, Canada. **A:** Softground palimpsest suite of unlined *Planolites* (Pl) and *Thalassinoides* (Th) with a lined (?) trace that extends below the palimpsest surface and up into the overlying coarse clastic deposit. **B:** Palimpsest softground suite consisting of weakly lined *Arenicolites* (Ar) that extends up into the overlying coarse clastic material with a poorly defined *Rhizocorallium* (Rh) that has depressed the underlying laminae. Identification of traces within the lag deposit is difficult due to preferential weathering. **C:** Palimpsest softground to stiffground suite in well 14-18-044-07W4 demarcated by an unknown trace (?), *Teichichnus* (Tei), *Planolites* (Pl) and *Thalassinoides* (Th) with sharp to diffuse boundaries and local partial linings. The *Teichichnus* extends upwards into the overlying muddy sandstone lag. **D:** Palimpsest stiffground from well 15-04-035-09W4 which is characterized by *Diplocraterion* and *Thalassinoides* and overlain by muddy sandstone containing *Planolites* (Pl), *Teichichnus* (Tei) and *Rhizocorallium* (Rh). The *Diplocraterion* extends upwards into the overlying lag unit.

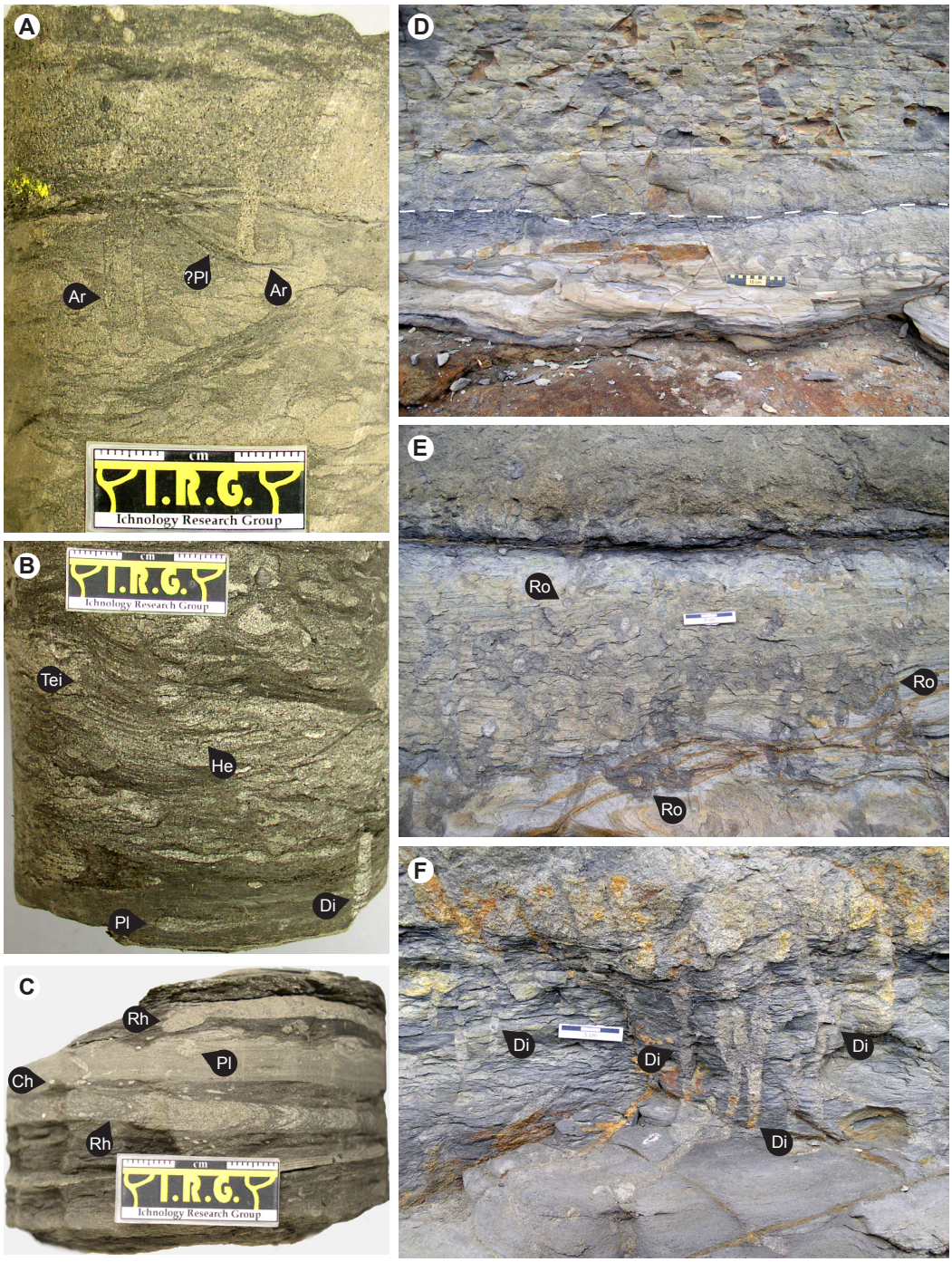

FIGURE 9.9—Palimpsest surfaces displaying spatial and/or temporal variation. **A-C:** Palimpsest suites from the Viking Formation that reflect spatial and temporal variation along surfaces that have become amalgamated. **A:** The BD3a SB/TSE at Hamilton Lake (see Chapter 8) is demarcated by a palimpsest softground with lined *Arenicolites* (Ar) and a probable *Planolites* (?Pl; 12-29-035-10W4). **B:** The overlying BD3b wave ravinement surface demarcated by transitional palimpsest softground to stiffground, sharp-walled *Diplocraterion* (Di) and indistinctly walled *Planolites* (Pl). The overlying lag deposit contains notable *Teichichnus* (Tei) and *Helminthopsis* (He). **C:** The BD3 surface reflecting an amalgamation of the BD3a and BD3b surfaces in a landward direction. The stiffground is characterized by sharp-walled *Rhizocorallium* (Rh) and *Planolites* (Pl) with a post-palimpsest suite of *Chondrites* (Ch). **D-F:** Localized spatial variation

FIGURE 9.9 (Continued)— along a palimpsest suite in the Pebbley Beach Formation at Clear Point, NSW, Australia. **D:** A view of the outcrop illustrating the transition of substrates beneath the surface (dashed line). To the left of the photo, the surface is underlain by mudstone, whereas to the right of the photo, the surface is underlain by laminated sandstone. **E:** Close-up view of the palimpsest softground suite containing *Rosselia* (Ro) that are heavily lined. **F:** Close-up view of the stiffground palimpsest suite containing *Diplocraterion* (Di) that are sharp walled.

Formation in which two palimpsest softground suites occur in succession (Fig. 9.6D, E). Deposits under- and overlying the suites are characterized by an environmentally stressed ichnofossil suite reflecting deposition in a prodelta to distal delta-front setting based on the lack of structures of inferred suspension feeders, sharp-based carbonaceous mudstones and presence of unbioturbated strata (cf. MacEachern et al., 2005). The lower palimpsest suite is demarcated by unlined *Arenicolites* and lined *Skolithos* reflecting a slight change in energy that resulted in colonization by inferred suspension-feeding organisms and slightly coarser-grained sediment deposition. This surface and the overlying surface separate genetically related deposits.

The final primary characteristics of palimpsest softgrounds include significant warping of laminae adjacent to the ichnofossils, and surfaces displaying pronounced loading due to superjacent sediment deposition. Warping of laminae can be observed in the inset photo of Figure 9.6J where sandy laminae have been deformed next to the *Rosselia,* suggesting that laminae were indirectly disturbed during colonization. Possible loading along a palimpsest surface is depicted in Figure 9.6D. This surface overlies the suite containing *Arenicolites* and *Skolithos* in Figure 9.6E. High-energy sandstone deposition was likely followed by extensive fluid mud deposition, which may have depleted oxygen at the bed due to the organic nature of the mud (Raychaudhuri et al., 1992; Gingras et al., 1998; Coates and MacEachern, 1999). This resulted in a period of bioturbation reduction, possibly permitting dewatering of the mudstone and subsequent palimpsesting. Extensive loading was also observed in the Snapper Point Formation (Fig. 9.8A) in which coarse clastic material was emplaced leading to pronounced loading structures.

Secondary Attributes

Features that fall under secondary attributes are commonly (but not necessarily) associated with palimpsest softground suites. As such their presence is not diagnostic in identifying this form of overprinting. For example, the active

and/or passive infilling of traces occurs within soft-, stiff- and firmground suites. As such, this is not a diagnostic characteristic, although it does provide useful information regarding trace-maker behaviors. Palimpsest softground suites exhibiting *active* infilling include those in Figure 9.6A-D, G, I, J, and passive infilling of overprinted softground ichnofossils is prevalent with dwelling structures of inferred suspension feeders shown in Figure 9.6E, H, and passive carnivores (Fig. 9.6F).

Due to the lack of significant burial and compaction that typically occurs in softground successions, ichnofossils of palimpsest suites may display post-depositional compaction. Such compaction is observed in *Thalassinoides* along an autocyclic surface of the Viking (Fig. 9.6D) and with a number of ichnofossils from the uppermost Viking SB/TSE in well 10-23-034-09W4 (Fig. 9.6G). In the latter example, the *Skolithos* appears shortened and cross-sections of the other traces are ovate indicating that the host substrate underwent compaction.

Also apparent within well 10-23-034-09W4, is the convolute nature of the host sediment directly underlying the palimpsest surface (Fig. 9.6G). The overprinted ichnofossil suite, however, displays no evidence of shearing and cross-cuts the contorted underlying fabric. Within the deformed sediment, *Phycosiphon* have been sheared, and laminae are strongly deformed. The cause of this localized deformation (not observed with any other expressions of the BD4 surface) is unknown. In addition to deformation of the host softground, ichnofossils of the palimpsest suite may also be deformed. Within the Permian Pebbley Beach Formation of NSW, Australia, a palimpsest softground is demarcated by inclined *Diplocraterion habichi* that have been deformed due to down-slope sediment creep (Gingras and Bann, 2006). The surface is interpreted to reflect a tidal ravinement surface separating estuarine basin from channel fill deposits.

Traces demarcating palimpsest suites may also be reburrowed by successive, post-palimpsest traces. Reburrowing may explain the stubby nature of *Skolithos* in Figure 9.6G. Alternatively, palimpsest softgrounds are often typified by diminutive traces such as the *Skolithos* mentioned above, as well as traces from the Heather Formation (Fig. 9.6A) and from other Viking examples (Fig. 9.6B, D, E). Although, there are exceptions in which large, robust structures characterize palimpsest softground suites (Fig. 9.6F, I, J). One striking example is from a wave ravinement surface that overlies the lowermost incised shoreface at Hamilton Lake (Fig. 9.6H; see Chapter 8). The presence of elongate *Diplocraterion*

demarcating the surface contrasts with the underlying upper offshore strata predominated by horizontal deposit-feeding structures and the overlying unbioturbated deep marine strata suggestive of low oxygenation (cf. Burton, 1997). This example illustrates the presence of a high-energy environment that existed only during colonization of the palimpsest substrate, which further implies that wave ravinement occurred. As the only record of lag deposition is found within the traces, this example shows the importance of ichnofossils in identifying the stratigraphic significance of surfaces.

Other characteristics commonly associated with palimpsest softgrounds include low population densities such as in Figure 9.6A-F, and H. However, other factors may influence the density of traces such that some surfaces are densely populated by monospecific suites (Fig. 9.6J, I). Traces of palimpsest softgrounds may also display evidence of truncation due to erosion. Finally, traces can display progressive palimpsesting in which ichnofossils subtend below the surface and extend up into the overlying substrate (Fig. 9.6C; see Environmental Influence section).

Palimpsest Stiffground Suites

Principal Attribute

Unlike palimpsest softground suites, the cross-cutting of an underlying suite along a palimpsest stiffground surface is easily recognizable due to sharp ichnofossil boundaries and a general lack of trace linings. However, not all stiffgrounds will reflect a significant shift in depositional conditions across the surface. For instance, muddy tidal flats can become compacted and dewatered without significant burial such that colonization and overlying deposition occurs within the same tidal flat setting.

Primary Attributes

Palimpsest stiffground suites can be differentiated from other substrate-controlled ichnofacies by evidence of semi-cohesive sediment conditions during endobenthic colonization (Tables 9.1, 9.2, 9.4). The four primary attributes of stiffground suites include: 1) traces are relatively sharp-walled (Goldring and Kazmierczak, 1974; Gingras et al., 2000; Lettley et al., 2007) or display irregular (but unlined) boundaries in sandy sediment; 2) laminae are distorted (upwards or

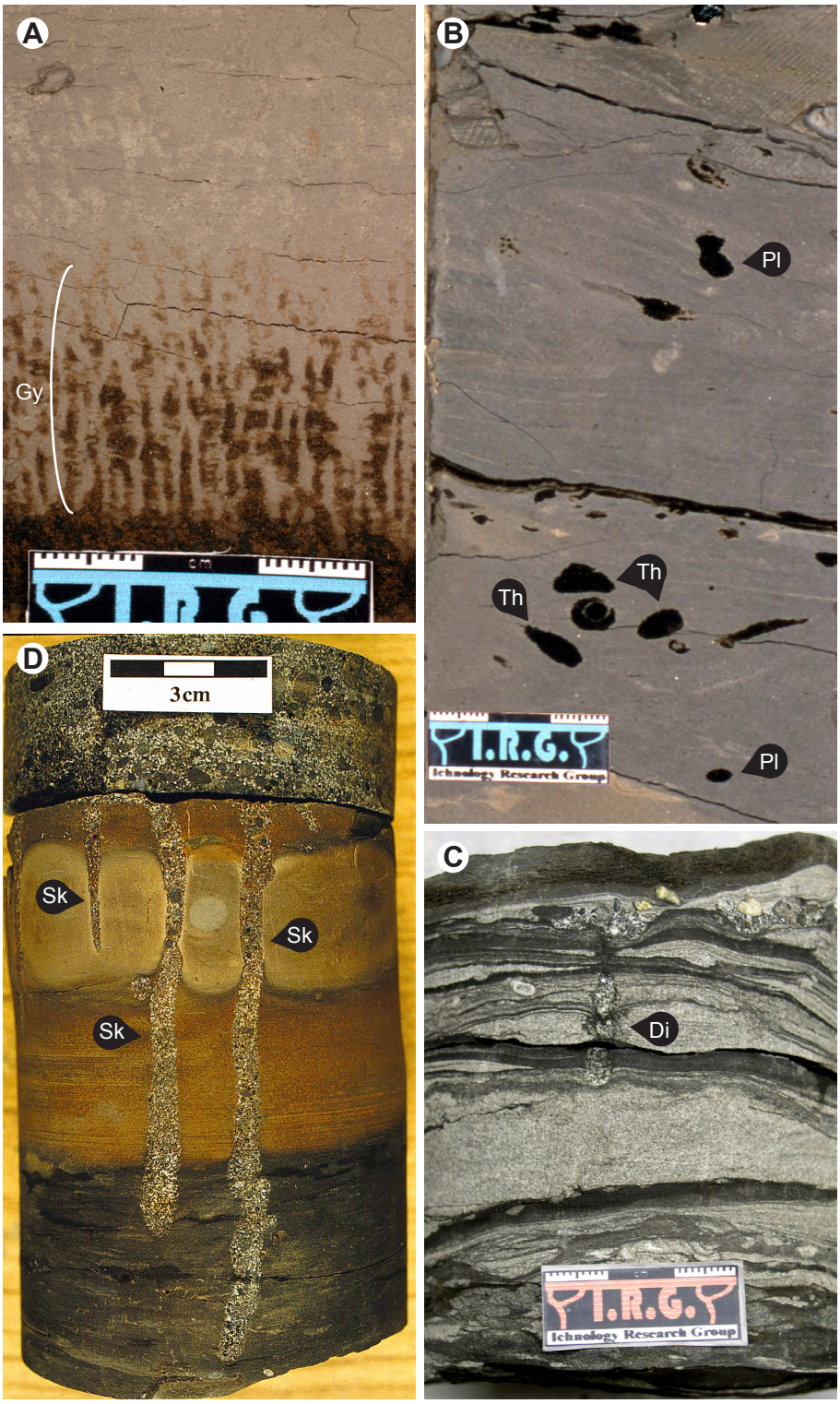

FIGURE 9.10—Representative examples of the models depicted in Figure 9.18 (see Tables 9.4 and 9.5 for detailed descriptions). **A:** *Gyrolithes* as part of an apparent bed junction in the McMurray Formation. **B:** Oil-stained *Planolites* and *Thalassinoides* as part of an autocyclic palimpsest stiffground suite in the McMurray Formation. **C:** *Skolithos* from the Viking Formation as part of an allocyclic palimpsest stiffground (02-04-037-19W4). **D:** *Skolithos* from the Viking Formation as part of a firmground *Glossifungites* Ichnofacies (08-17-040-01W5, 1721.5m depth).

downwards) adjacent to traces (Lettley et al., 2007); 3) the stiffground displays plastic deformation with flame and load structures; and 4) traces are generally unlined (Lettley et al., 2007), but may display minor partial linings within sandy substrates.

A prime example of sharp-walled stiffground ichnofossils occurs in the Lower Cretaceous McMurray Formation. This formation is dominated by the alteration of sandstone and mudstone in inclined heterolithic stratification (IHS) formed through point-bar deposition in estuarine channels (Lettley et al., 2007). In Figure 9.10B, sand-infilled *Thalassinoides* and *Planolites* are observed within mudstone beds in which the overlying sandstone bed is preserved as a remnant. This relationship suggests that the burrows were passively (or perhaps actively) infilled with sand prior to removal of the overlying sandstone bed. The lack of burrowing within the mudstone and obvious juxtaposition of the sand-filled traces in combination with their sharp-walled nature suggests palimpsest stiffground colonization. Lettley et al. (2007) suggested that seasonal variations in water circulation and sediment texture resulted in the formation and exposure of stiffground sediment. These autocyclically formed surfaces, however, are highly localized (Lettley et al., 2007). In contrast to muddy host sediment, stiffground traces that occur within sandy substrate, exhibit irregular boundaries and are unlined. This is seen within the lowermost portion of *Diplocraterion* in Figure 9.11B and Figure 9.12.

Similar to palimpsest softground surfaces, laminae may be distorted (albeit to a lesser degree) upwards or downwards adjacent to stiffground trace fossils. This attribute is exhibited in the uppermost SB/TSE of the Viking Formation (Fig. 9.10C). The surface overprints a heterolithic sandstone and mudstone unit in which laminae are primarily down-warped next to the *Diplocraterion*. The presence of structures of inferred suspension feeders along the surface suggests a change in depositional energy and conditions during palimpsesting that contrast the restricted underlying brackish suite and deep marine, seemingly unbioturbated, overlying stratum.

Deposition of superjacent sediment overlying palimpsest stiffgrounds may also result in loading along the surface as a result of plastic deformation. This form of deformation is observed in Figure 9.10C in which medium to coarse sand and small, cherty pebbles forms a discontinuous lag overlying the surface. Alternatively, burrowing of the palimpsest surface may be so extensive that the surface and any initial features have been removed. This is the case with

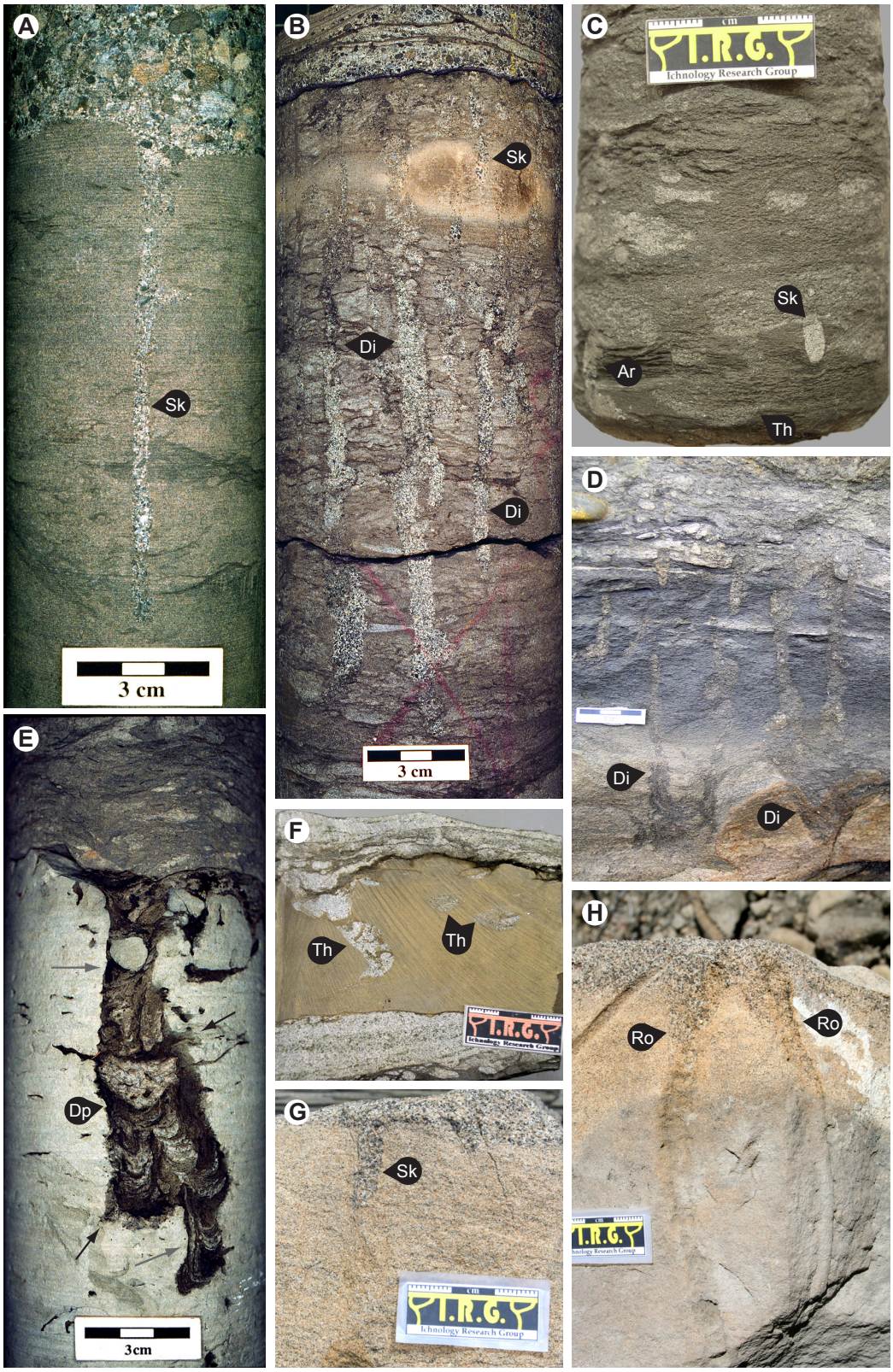

FIGURE 9.11—Transitional palimpsest softground to stiffground suites (see Table 9.6 for additional details). **A:** *Skolithos* (Sk) with boundaries that appear to be fairly well defined at the base (stiffground expression), however, the upper few centimeters are more poorly defined (softground expression). This variation in trace boundary configuration is likely related

FIGURE 9.11 (Continued)—to compaction of the sand at depth within the Bluesky Formation. **B:** Vertical transition between the upper softground with lined to indistinctly walled *Diplocraterion* (Di) and *Skolithos* (Sk) and the lower sharp-walled, but compacted stiffground components. From the Viking Formation (16-34-038-25W4). **C:** Sharp-walled *Skolithos* (Sk) and poorly defined *Thalassinoides* (Th) and *Arenicolites* (Ar) from the Viking (10-03-036-10W4, 882.75 m depth). **D:** *Diplocraterion* (Di) from the Pebbley Beach Formation at Clear Point in which the traces display sharp-walled stiffground colonization within the upper mudstone and are lined within the underlying sandstone (softground expression). **E:** Large *Diplocraterion parallelum* (Di) from the Moosomin B unit of the Red Jacket Formation (04-18-015-02W2, 723.9m depth). This trace displays well-defined boundaries to mixing of host and lag sediment of both palimpsest soft- and stiffground suites. Early diagenetic cementation likely played a role in the patchy nature of the substrate. **F:** Softground (diffuse boundaries) to firmground (sharp-walled with mudstone clasts) expressions within siderite cemented substrate containing *Thalassinoides* (Th) within the Viking Formation (02/07-22-038-20W4). **G-H:** Photos of the surface at the top of the Panther Tongue, Star Point Formation. **G:** *Skolithos* (Sk) with irregular, but well-defined trace boundaries suggesting stiffground colonization. **G:** *Rosselia* (Ro) displaying indistinct boundaries with a mixing of the lag and host sediment suggesting more of a palimpsest softground nature.



FIGURE 9.12—A transitional stiffground (at depth) to firmground (near the surface) palimpsest suite from the Viking Formation (12-35-036-25W4). The presence of incipient siderite cementation near the surface resulted in firmground *Diplocraterion* (Di) that pass to stiffground within the lower heterolithic sediment (see Table 6 for more details).

the base of the Miocene, Pebas Formation which is demarcated by stiffground *Thalassinoides* that have completely reworked the initial palimpsest surface (9.13D). The degree of sediment compaction and shear destruction of the palimpsest surface suggests that the sediment was stiff during colonization. This contact was interpreted by Hovikoski et al. (2007) as a transgressive surface of erosion.

Ichnofossils demarcating palimpsest stiffgrounds are generally unlined (Lettley et al., 2007); however, traces may possess minor partial linings especially within sandy sediment. Representative examples of unlined structures occur in the Viking Formation at Hamilton Lake. In well 10-09-037-07W4, the BD3b surface is characterized by unlined *Diplocraterion* and *Skolithos*—traces that are typically lined within softground sediment (Fig. 9.13B). This surface reflects a wave ravinement surface separating transgressively incised shorefaces (see Chapter 8). Conversely, in the West Ahken Field, a stiffground was colonized by partially lined *Skolithos* exhibiting sharp boundaries (Fig. 9.13G). Lining occurs within the sandier laminae suggesting that some burrow wall stabilization was required in the looser material. This suite reflects a submarine canyon incision that forms part of a sequence boundary. Partial lining is also observed along the *Diplocraterion* in Figure 9.10C where the trace intersects sandier sediment.

Secondary Attributes

Stiffground palimpsest suites may be characterized by actively and passively infilled burrows. Examples of potentially actively infilled structures include: *Gyrolithes* (Fig. 9.13A), *Rhizocorallium* (Fig. 9.13C), and *Planolites* (Fig. 9.13B, C). Passively infilled traces can include: *Skolithos* (Fig. 9.13B, C, G), *Diplocraterion* (Fig. 9.13B), and *Thalassinoides* (Fig. 9.13B-F). Despite the nature of infilling, palimpsest stiffground traces often display evidence of compaction (Lettley et al., 2007). Compaction is easily identified with ovate *Thalassinoides* cross-sections, such as those in the West Ahken Field (Fig. 9.13F) and in the Pebas Formation (Fig. 9.13D). In the Snapper Point Formation of NSW, Australia, compacted *Thalassinoides* are also prevalent within a stiffground suite. This suite reflects an autocyclic palimpsest surface in which an initially fluid mudstone was dewatered and compacted possibly under hypoxic conditions prior to burrowing. This autocyclic surface reflects changes in sediment supply and burrowing activities within genetically related strata.

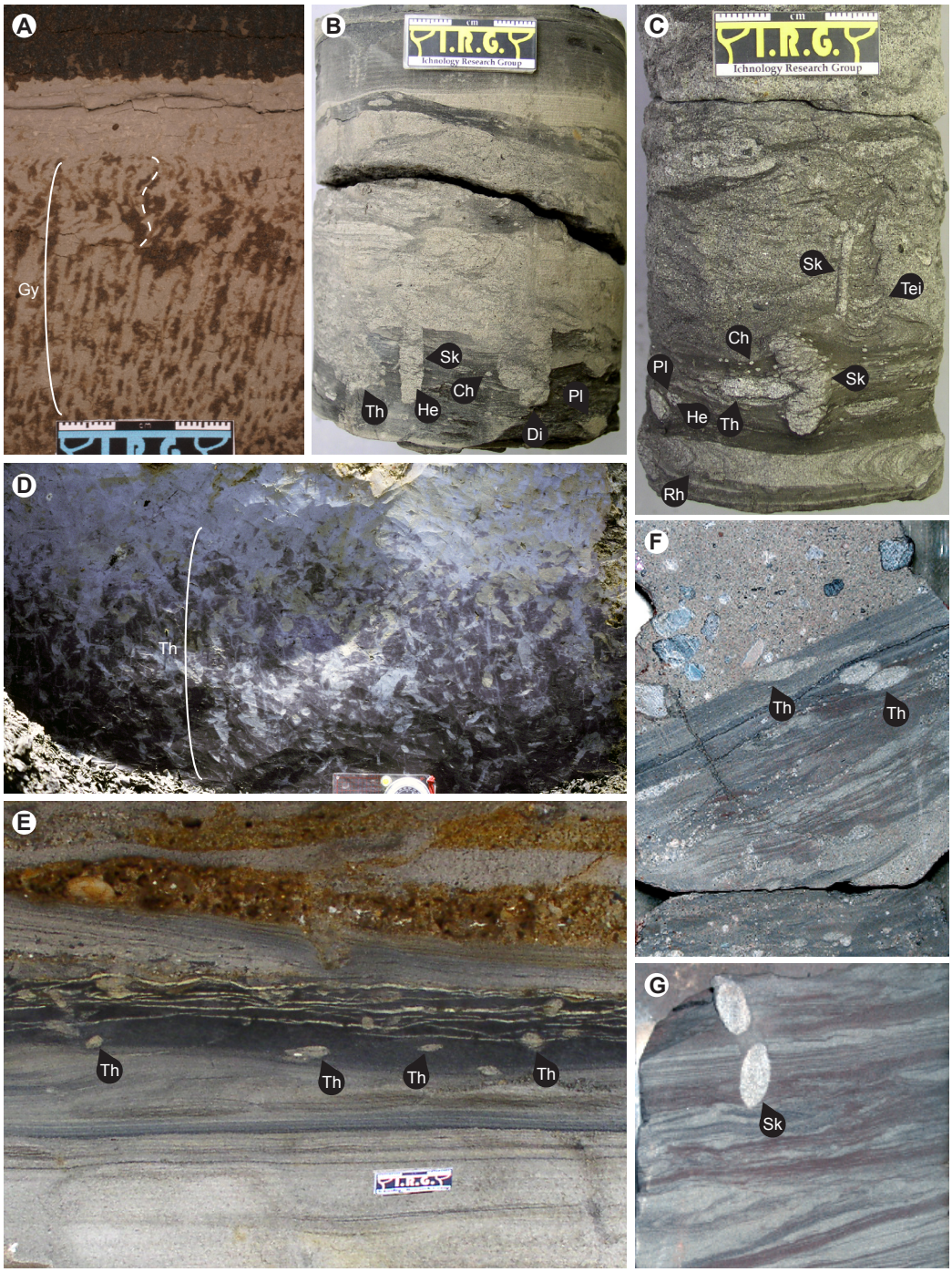

FIGURE 9.13—Palimpsest stiffground suites (see Table 9.4 for additional information). **A:** Stiffground *Gyrolithes* (Gy) within a mudstone IHS bed of the McMurray Formation. Compaction of the upper portion of the burrows has occurred within the uppermost stiffground. **B:** A palimpsest stiffground in the Viking Formation demarcated by sharp-walled *Skolithos* (Sk), *Thalassinoides* (Th), *Diplocraterion* (Di) and *Planolites* (Pl). Slight loading is present along the surface in addition to reburrowing by *Helminthopsis* (He) and *Chondrites* (Ch; 10-09-037-07W4). **C:** Sharp-walled *Rhizocorallium* (Rh), deformed *Skolithos* (Sk) and compacted *Thalassinoides* (Th) in addition to *Planolites* (Pl) in the Viking Formation. *Teichichnus* (Tei) within the lag deposit appears to have avoided the underlying stiffground substrate and reburrowing by *Chondrites* (Ch) and *Helminthopsis* (He) is present (02-36-034-10W4). **D:** Pebas Formation palimpsest

FIGURE 9.13 (Continued)—*Thalassinoides* (Th) that display compaction and complete reworking of the surface. **E:** Sharp-walled *Thalassinoides* (Th) in the Snapper Point Formation in which compaction of the stiffground autocyclic surface is evident. **F-G:** Palimpsest suite in the West Ahken Field which consists of compacted, sharp-walled *Thalassinoides* (Th) and mud-lined *Skolithos* (Sk) with deflection of adjacent laminae (West Ahken-1 core, 4375.3 ft and 4379.8 ft).

The cohesive, yet pliable nature of stiffground sediment can also result in shearing or deformation of stiffground burrows (Lettley et al., 2007). A prime example of deformed palimpsest stiffground *Skolithos* occurs in the Viking Formation (Fig. 9.13C). The *Skolithos* is deformed around a *Thalassinoides* possibly as a result of timing of burrowing; i.e. *Thalassinoides* was constructed following excavation by the *Skolithos* trace-maker. Further evidence suggesting stiffground colonization is the evidence of a *Teichichnus* (possibly *Rhizocorallium*?) trace-maker that burrowed only above the palimpsest interface. This surface defines the uppermost SB/TSE in the Hamilton Lake area. Pronounced deformation of *Gyrolithes* also occurs within the McMurray Formation (Fig. 9.13A). Where sandy IHS beds are overlain by relatively thick muddy beds, *Gyrolithes* are highly visible in the lower part of the mud unit (due to the presence of sand-sized grains), but become compacted and indiscernible in the upper portion of the mud bed with decreasing abundance of sand (Fig. 9.10A). Biogenic mottling is, however, prevalent within the upper portion of the mudstone bed, but traces are poorly defined due to deformation and compactional alteration. The condition of the *Gyrolithes* within the upper portion of the mudstone bed likely reflects the compaction and distortion of the ichnofossils within softground sediment. At depth, however, the softground was underlain by stiffground mudstone that allowed for enhanced preservation of the ichnofossils as a result of reduced compaction. In Figure 9.13A, the uppermost stiffground containing *Gyrolithes* has been deformed possibly due to compaction and down-slope sediment creep. These sand and mud couplets reflect autocyclic changes in deposition within the estuary due to tidal cyclicity, seasonal fluctuations, storms and floods (Thomas et al., 1987).

Ichnofossils within palimpsest stiffground suites may also be reburrowed by post-palimpsest suites. In Figure 9.13B, *Skolithos*, *Thalassinoides*, *Planolites* and *Diplocraterion* are reburrowed by *Helminthopsis* and *Chondrites*. Similarly, *Skolithos*, *Thalassinoides*, *Rhizocorallium* and *Planolites* are reburrowed by *Chondrites* and *Helminthopsis* in Figure 9.13C. Stiffground traces also tend to be diminutive (Fig. 9.13A-C, E-G; Lettley et al., 2007), although some examples

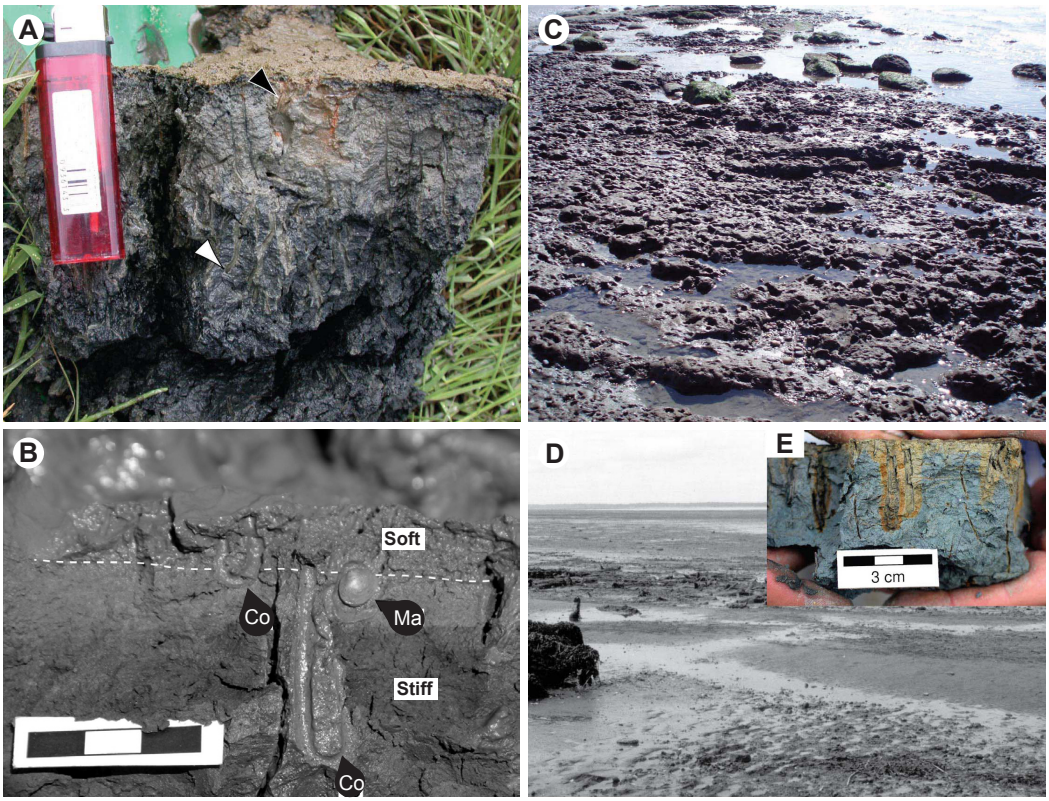

FIGURE 9.14—Modern examples of different substrate consistencies (see Table 2 for additional details). **A:** Softground (black arrow) to stiffground (white arrow) transition in fine-grained organic sediments of the Niawiakum Estuary, WS. **B:** Soft- to stiffground transition within accretionary bank deposits in the Shepody River area, New Brunswick. *Corophium volutator* (Co) and *Macoma balthica* (Ma) produced burrows resembling *Arenicolites*-, *Diplocraterion*-, and *Siphonichnus*-like traces that are sharp-walled in the lower stiffground and poorly defined in the upper softground. **C:** Stiffground comprised of compacted and exhumed tidal flat sandy mud. Exhumation is occurring in the foreshore of a transgressive beach of North Cove, WS. The dominant burrow type is incipient *Thalassinoides* that were produced by shrimp approximately 200 ybp (field of view is 2 m). **D:** Firmground at Goose Point, Willapa Bay, WS. In this example, the sediment is very firm, and burrows (inset photo **E**) are easily maintained open without the aid of lining or even mucus (field of view is 10 m).

reflect robust trace-maker colonization (Figs. 9.9F, 9.13D). Population densities within palimpsest stiffgrounds can be low (Fig. 9.13B, E-G), or, similar to softground suites, dense monospecific suites may colonize the substrate (Fig. 9.13D). In Washington State, North Cove contains a highly burrowed stiffground comprised of compacted and exhumed sandy tidal flat mud (Fig. 9.14C). The dominant burrow type is incipient *Thalassinoides* that were produced by shrimp approximately 200 ybp. This recent stiffground formed due to exhumation on the foreshore of a transgressive beach in which migration of the bay margins has exposed a newly exhumed substrate in the bay.

It is possible that some stiffground suites may be truncated due to

subsequent erosion. For instance, in the McMurray Formation, overlying sandstone beds were truncated (although the ichnofossils were unaffected; Fig. 9.10B). Analogous to palimpsest softground surfaces, stiffground traces can also display progressive palimpsesting in which ichnofossils extend up into the overlying unit (Fig. 9.8D). Stiffground surfaces may also display an undulatory nature, especially in modern settings (Fig. 9.14C; Gingras et al., 2000b). Finally, Lettley et al. (2007) reported that depth of the trace penetration could be less than 10 times that of the diameter of the burrow. This relationship may not always be true, and the colonization depth is likely a function of a number of other factors including: trace-maker behaviors, time permitted for colonization, sedimentation rate, population density, degree of stiffness, and food value of the sediment (especially for deposit feeders).

Firmground *Glossifungites* Ichnofacies

Characteristics of the *Glossifungites* Ichnofacies have been well established in previous literature (e.g., Pemberton and Frey 1985; MacEachern et al. 1991, 1992; Pemberton and MacEachern, 1995; Gingras et al., 2000; Pemberton et al., 2004; MacEachern et al., 2007a, c) and are reviewed here in conjunction with a few examples.

Principal Attribute

In the same manner as palimpsest stiffground suites, the firmground *Glossifungites* Ichnofacies is easily recognizable as cross-cutting elements of previous ichnological suites and most often indicates a significant shift in depositional conditions across the surface. Whether the surface is demarcated by robust *Skolithos* or actively infilled *Zoophycos*, the firmground ichnofossil suite often contrasts that of previous and overlying suites (if present). However, in some instances, firmground suites can form autocyclically such that under- and overlying strata are genetically related.

Primary Attributes

Similar to stiffground colonization, the *Glossifungites* Ichnofacies is characterized by unlined and sharp-walled traces (Pemberton et al., 2001); however, there is no partial lining of structures. Palimpsest firmground traces

reflect limited burrowing capabilities of trace-makers, which are not permitted free movement, but are rather constricted to excavation of semi-permanent burrows (MacEachern and Burton, 2000). The sharp-walled, unlined nature of the *Glossifungites* Ichnofacies is exhibited in the Viking Formation along a transgressive surface of erosion in the Gilby A Field (Fig. 9.10D; MacEachern et al., 1992). In this example, *Skolithos* trace-makers cut into initially incipiently siderite-cemented offshore silty shales, and the traces were subsequently passively infilled. In modern settings, the sharp-walled and unlined nature of firmground burrows can be confirmed. At Goose Point, Willapa Bay, a sedimentary surface was identified as exceedingly firm with burrows that were easily maintained open without the aid of lining or even mucus (Fig. 9.14D, E). Burrows include sharp-walled *Diplocraterion*-like and *Skolithos*-like structures that cross-cut the previous biogenic suite. Oxidation of sediment adjacent to burrow structures indicates the reduced nature of the firmground substrate. This surface reflects c.a. 100,000 yrs. of predominantly wave ravinement influence, and possibly to a lesser extent tidal ravinement.

The development of firmground substrate typically requires extensive burial, compaction and erosion to expose firm substrate to marine or marginal marine colonization (Pemberton et al., 2001). As such, palimpsest firmground surfaces may display evidence of significant scouring (Pemberton et al., 2001). In the Willesden Green Field, the Viking Formation consists of a lowstand incised valley system (MacEachern and Pemberton, 1994). Within these lowstand incised valleys, migration of tidal inlets and channels can produce tidal ravinement surfaces (TRS). Such a surface is presented in Figure 9.1A in which *Rhizocorallium saxicava* delineates a *Glossifungites* Ichnofacies overlain by pebbly sandstone of a tidal inlet fill. The surface is inclined and undulatory and amalgamates with the initial transgressive surface and sequence boundary (MacEachern and Pemberton, 1994). The amalgamated nature of this surface is likely the reason that this TRS exposed firmground substrate that generally requires extensive exhumation. Similarly, the modern X-ray in Figure 9.7D depicts bivalves that have colonized an incipient firmground within a subaqueous tidal channel. The channel eroded into salt marsh deposits, and the bivalves cross-cut a homogenously burrowed sediment in which the topography is uneven as a result of scouring within the channel.

Another diagnostic attribute of palimpsest firmground suites is the ornamentation of traces or presence of bioglyphs or scratch marks (Pemberton

et al., 2001). Between the Nihotupu and Tirikohua Formations, New Zealand, a well preserved *Glossifungites* Ichnofacies exists along a submarine canyon incision (Fig. 9.1B; Hayward, 1976). During lowstand, there is sediment bypass on the continental shelf and deposition at the shelf edge. If the shelf edge is over-steepened, slumping may occur along with erosion by sediment gravity flows, which produces a submarine canyon. This lowstand incised surface has a high potential for colonization by trace-makers as the surface is formed within the marine realm (Pemberton et al., 2001). In this particular outcrop, the surface is colonized by *Rhizocorallium* and *Thalassinoides* in which *Rhizocorallium* display distinctive scratch marks typical of firmground colonization (Fig. 9.1B).

The degree of erosion required to expose firm, dewatered and compacted mudstone is likely extensive (2 m or more was estimated by Gingras et al., 2000). Firmground can also be formed through incipient growth of cements especially of siderite in marine and marginal marine settings. In the Viking Formation, sharp-walled *Arenicolites*, *Skolithos*, *Planolites* and *Diplocraterion* occur within siderite-cemented, deep marine mudstone (Fig. 9.1D). These ichnofossils are not borings, but reflect colonization of the sediment during which time siderite cementation was taking place to form a firm substrate. In the deep marine, suboxic conditions combined with low sedimentation and low organic concentrations can facilitate siderite precipitation (Mozley and Wersin, 1992). The high-energy *Glossifungites* suite of predominately inferred suspension-feeding structures suggests a major change in depositional conditions at the time of palimpsesting. This surface is interpreted to reflect a SB/TSE that occurs above the uppermost Viking deposits within the Colorado Shale.

Secondary Attributes

Unlike the palimpsest soft- and stiffground suites, the *Glossifungites* Ichnofacies is not characterized by: measurable compaction; shearing or deformation of traces; or progressive palimpsesting due to the firmness of the substrate. On the other hand, like that of soft- and stiffground ichnofossils, firmground burrows may be passively (more commonly) or actively infilled (Pemberton et al., 2001). Firmground traces reflect the cohesive nature of the sediment at the time of colonization and passive infilling indicates that the burrows were stable following vacation of the trace-maker (MacEachern et al., 2007a). Examples of passively infilled *Glossifungites* Ichnofacies are typically

those of inferred suspension feeders or passive carnivores, which includes *Skolithos* (Figs. 9.1D, 9.10D), *Arenicolites* (Fig. 9.1D) and *Diplocraterion* (Fig. 9.1D) and some dwelling structures such as *Thalassinoides* (Fig. 9.1B, C). Actively infilled traces are typically those of deposit-feeding or foraging animals including *Rhizocorallium* (Fig. 9.1A, B) and *Zoophycos* (Fig. 9.1C). *Zoophycos* and *Thalassinoides* in Figure 9.1C demarcate a palimpsest surface in which the traces are sharp walled and there is no disruption to laminae in the host substrate. This firmground suite reflects the uppermost amalgamated SB/TSE in the Viking Formation from the Hamilton Lake area (MacEachern and Burton, 2000).

Additional secondary features that may or may not be associated with firmground suites include robust ichnofossils (Figs. 9.1A, B, 9.10D) and a general low diversity of traces (Figs. 9.1A-C, 9.10D, 9.14D-E; Pemberton et al., 2001). In some instances, populations densities may be low (Fig. 9.1C, D), but monospecific suites tend to be densely populated (Figs. 9.1A, B, 9.14D-E; Pemberton et al., 2001).

Localized Variability at the Ichnofossil Scale

Local variations in substrate coherence can result in changes in burrow structure. For example, Frey (1978) suggested that thick-walled burrows near the surface can become thinner walled and more ornamented at depth where the sediment is more compacted. This form of localized variation at the scale of individual ichnofossils can be exhibited in a number of ways (Figs. 9.11, 9.12, Table 9.6) including:

1) adjacent traces display varying palimpsest characteristics;
2) vertical variation of ichnofossils in a homogeneous lithology;
3) vertical variation of ichnofossils in a heterolithic lithology;
4) variation due to incipient cementation; and
5) overall character can reflect different interpretations of palimpsesting.

Adjacent Ichnofossils Displaying Varied Characteristics

In the Viking Formation at Hamilton Lake, an example of the uppermost SB/TSE is demarcated by a palimpsest surface characterized by adjacent individual traces that reflect soft- and stiffground colonization (Fig. 9.11C). In this example, a short *Skolithos* displays sharp boundary walls with slight deflection

of adjacent laminae suggesting stiffground colonization. Other traces along the surface consist of *Thalassinoides* and *Arenicolites* with indistinct boundaries and mixing of host and lag sediment suggestive of softground palimpsesting. Potentially, the stiffground *Skolithos* is lined, which would be indistinguishable from the host substrate, and may explain the concentration of sandy material that passively infilled a vacated burrow. Alternatively, the softground expressions may be related to timing of colonization or activities of the burrowers that produced a more softground expression. Most likely, the overall sediment character reflected a degree of compaction transitional between soft and stiff sediment (Fig. 9.4) in which traces reflect characteristics of both suites depending on method of construction or burrowing activities.

Vertical Variation in Homogeneous Sediment

Within the Lower Cretaceous Bluesky Formation, a palimpsest wave ravinement surface is demarcated by *Skolithos* in which the ichnofossil boundaries are well defined at the base of the burrow, but poorly defined in the upper few centimeters (Fig. 9.11A). This variation in boundary configuration is likely related to compaction of the sand, which was more prevalent at depth. This example exhibits the ability of sandy substrates to retain stiffground properties especially at depth within the substratum.

Another example of vertical variation within a consistent lithology occurs along a SB/TSE in the Viking Formation in which *Diplocraterion* and *Skolithos* extend at depth into bioturbated silty to muddy sandstone (Fig. 9.11B). Upper portions of the traces are characterized by indistinct boundaries, mixing of host and lag sediment and partial to more extensive ichnofossil linings indicative of palimpsest softground colonization. In contrast, the lower portion of traces exhibit sharp boundaries with evidence of slight deformation of the traces where they intersect sandier laminae (stiffground expression). In the upper portion of the palimpsest substrate, siderite cementation is also present; however, in contrast to other examples (Fig. 9.11F, 9.12), cementation was likely in a very incipient stage or occurred post-palimpsesting.

Vertical variation of substrate properties is common within modern settings. In the Niawiakum Estuary, a modern soft- to stiffground transitional suite is present within fine-grained organic sediments (Fig. 9.14A). Softground conditions persist in the uppermost centimeters, while stiffground conditions

persist at depth in dark grey, reduced sediment. *Arenicolites*- and *Skolithos*-like burrows are sharp-walled and easily maintained within the stiffground, but are more poorly defined within the upper softground. This surface reflects an autocyclically formed surface at the top of a point bar in which autocompaction has occurred within dewatered muds. A similar scenario takes place in the Shepody River area where soft mud overlies stiffground mud on accretionary banks (Fig. 9.14A). *Arenicolites*-, *Diplocraterion*- and *Siphonichnus*-like burrows are sharp-walled and easily maintained in the lower stiff mud, but poorly defined in the upper soft sediment (Lettley et al., 2007). The formation of the transitional sediment package was suggested by Lettley et al. (2007) to be related to stiffening during winter months.

Vertical Variation in Heterolithic Sediment

Near the top of the Pebbley Beach Formation at Clear Point, a palimpsest suite is found to extend at depths into two different lithologies (Fig. 9.11D). *Diplocraterion* reflect stiffground colonization within the upper mudstone deposit due to the presence of sharp trace boundaries, slight deflection of laminae adjacent to the traces, and loading and flame structures along the surface. Within the underlying muddy sandstone, the same traces are lined, display indistinct trace boundaries, and mixing of host and lag sediment suggestive of palimpsest softground colonization. The juxtaposition of palimpsest stiffground mud over softground sand is an atypical scenario and is further explained in a subsequent section (see Stratigraphic Influence). The surface is interpreted as a wave ravinement surface at which high energy conditions persisted during colonization.

Variation as a Function of Incipient Cementation

Incipient cementation can produce varied palimpsest expressions including: 1) random variation within an individual ichnofossil; 2) varied expression between different traces; and 3) vertical variation within the same trace due to a limited depth of cementation.

In the Red Jacket Formation of southeastern Saskatchewan, Kreis (1991) defined the Jurassic Moosomin Member. Within this unit, a surface is characterized by transitional palimpsest soft- to stiffground *Diplocraterion parallelum* (Fig. 9.11E). The boundaries of this trace vary from sharp (stiffground

expression) to diffuse (softground expression) with a non-systematic distribution. Incipient calcareous cementation likely played a role in the variable substrate properties such that cementation was patchy rather than uniform. The Moosomin B is interpreted by Kreis (1991) to reflect brackish water deposition of a tidal flat setting reflecting overall shallowing, and the surface likely reflects marine ravinement (pers. commun. Kreis, 2007).

Within the Viking Formation, a siderite cemented bed contains *Thalassinoides* that reflect soft- to firmground conditions (Fig. 9.11F). Cross-sectional representations of *Thalassinoides* display indistinct ichnofossil boundaries with a mixed sandy and sideritized mudstone infill. The vertical *Thalassinoides*, however, is sharp walled and contains sandstone with sideritized mudstone clasts reflecting firmground colonization. Mudstone clasts within the ichnofossil further imply firmground conditions at the time of colonization as the clasts must have been durable enough to remain intact. This surface is interpreted as autocyclic in nature based on the presence of low-angle laminated deltaic sandstone below and above the surface. Within deltaic strata, siderite can form due to the organic nature of fluvial-sourced muds that may result in bacterially-facilitated precipitation of siderite (Coleman, 1993). Variation in the palimpsest expression is likely due to the timing of burrowing relative to the degree of incipient cementation. Cross-sectional *Thalassinoides* were likely formed during the early stages of incipient siderite cementation when the substrate acted as softground. Conversely, the sharp-walled *Thalassinoides* likely formed during late stage incipient cementation at which time the mudstone was firm. Bromley (1975) discussed a similar scenario in which lithification of carbonaceous sediments may occur during burrowing activities.

In the Viking Formation at well location 12-35-036-25W4, there is an unusual occurrence in which *Diplocraterion* and *Skolithos* subtend from a surface through sideritized mudstone and into underlying interlaminated sandstone and mudstone (Fig. 9.12). Within the siderite unit, ichnofossils indicate firmground colonization based on the sharp-walled nature of the traces. However, within the underlying interlaminated unit, the traces were emplaced within stiffground sediment indicated by the relatively sharp-walled nature of the traces, rare partial lining, deflection of laminae adjacent to the trace fossil boundaries, and deformation found in the pinching and swelling of the traces (i.e. compaction). The transition from stiffground at depth to firmground near the colonized surface is atypical. In general, one would expect firmground substrate to be found at

greater depths due to more prolonged compaction and dewatering, while stiffer sediment would be found closer to the sediment surface. In this instance, siderite cementation was likely incipient at the time of colonization such that the substrate was not fully lithified, but possessed a greater degree of cohesion as compared to underlying heterolithic sediment. Strata below and above the surface reflects deltaic deposition based on ichnological and sedimentological attributes. The presence of siderite in conjunction with a pebbly lag and robust structures of inferred suspension feeders (which are absent from the host and overlying sediment) suggests that a major shift in depositional conditions occurred. Perhaps the surface reflects a minor drop in relative sea level, subsequent relative sea-level rise and wave ravinement. In this example, the presence of a palimpsest ichnofossil suite is the only evidence of a major depositional shift.

Overall Character Reflects Different Interpretations

The Late Cretaceous Panther Sandstone of the Star Point Formation outcrops on the eastern side of the Wasatch Plateau and the western side of the Book Cliffs in Utah, USA. At the top of this unit, a surface reflects a transitional palimpsest softground to stiffground in which the overall character of the traces reflects the nature of both soft and stiff overprinted substrates (Fig. 9.11G, H). The traces include *Rosselia* and *Skolithos* in which trace boundaries possess a sharp to diffuse character with localized halos of disturbance (softground expression). The unlined nature of burrows within sandy substrate suggests passive infilling within stiffground sediment wherein burrows were stable and did not require wall stabilization. These characteristics appear to reflect palimpsest softground colonization while the nature of the burrow within sandy substratum suggests that the sediment was compacted enough to retain some stiffground properties. Local diffuse boundaries and disturbance of the surrounding sediment suggests that the incohesive nature of the sandy sediment made it easy to manipulate grains along burrow boundaries. Likely the degree of compaction was transitional between typical softground and stiffground sediment (Fig. 9.4). This palimpsest suite characterizes a transgressive surface of erosion separating underlying deltaic strata from overlying fully marine mudstones (Bhattacharya et al., 2007).

In the modern, the degree of sediment cohesion is more readily apparent; however, it is more difficult to define characteristics of individual traces that have not passed into the historical record. In the modern X-ray in Figure 9.7C,

rhythmically laminated saltmarsh sediment was extensively rooted based on the presence of rhizoliths. *Arenicolites*-like burrows cross-cut the rooted sediment that is transitional between stiffground and firmground. The transitional nature of this palimpsest surface is based on the cohesion of the modern strata (cf. Gingras et al., 2000). This surface was formed through autocompaction that was likely aided by the presence of extensive rhizoliths.

ENVIRONMENTAL INFLUENCE

Aside from the substrate, the expression of a palimpsest suite is highly dependent upon key environmental factors. Ichnofossils of the *Glossifungites* Ichnofacies have been predominantly described as vertical to subvertical U-shaped, cylindrical, or tear-shaped domiciles of suspension feeders (e.g., *Diplocraterion*, *Skolithos*, *Psilonichnus*, *Arenicolites*, *Conichnus*, *Bergaueria*) and to a lesser extent deposit-feeding organism (e.g., *Thalassinoides*; MacEachern et al., 2007a). However, in studying the Viking Formation in the Hamilton Lake area, MacEachern and Burton (2000) recognized atypical expressions of the *Glossifungites* Ichnofacies characterized by foraging, probing and deposit-feeding structures including: *Thalassinoides*, *Rhizocorallium* and *Zoophycos*. These trace fossil suites characterize the uppermost bounding discontinuity in the Viking Formation (BD4), which reflects an amalgamated SB/TSE (MacEachern and Burton, 2000; see Chapter 8). This surface would have been cut under high-energy conditions; however, ichnofossils reflect colonization in a proximal offshore, low-energy setting (MacEachern and Burton, 2000). These suites were referred to as distal *Glossifungites* Ichnofacies by MacEachern and Burton (2000).

Based on the examples described above (Tables 9.2-9.6), the same distal versus proximal trends can be seen with palimpsest soft- and stiffground suites. Environmental influence plays an important role in the type of infaunal colonization, behavior of trace-makers, size of trace fossils and relationship of organisms to resumed sedimentation. Accordingly, aside from substrate, the three most important environmental factors that determine the attributes of the palimpsest ichnofossil suite include: 1) the depositional setting; 2) energy regime; and 3) sedimentation rate at the time of palimpsest colonization (Fig. 9.15), in addition to the trace-maker morphology and exhibited behavior.

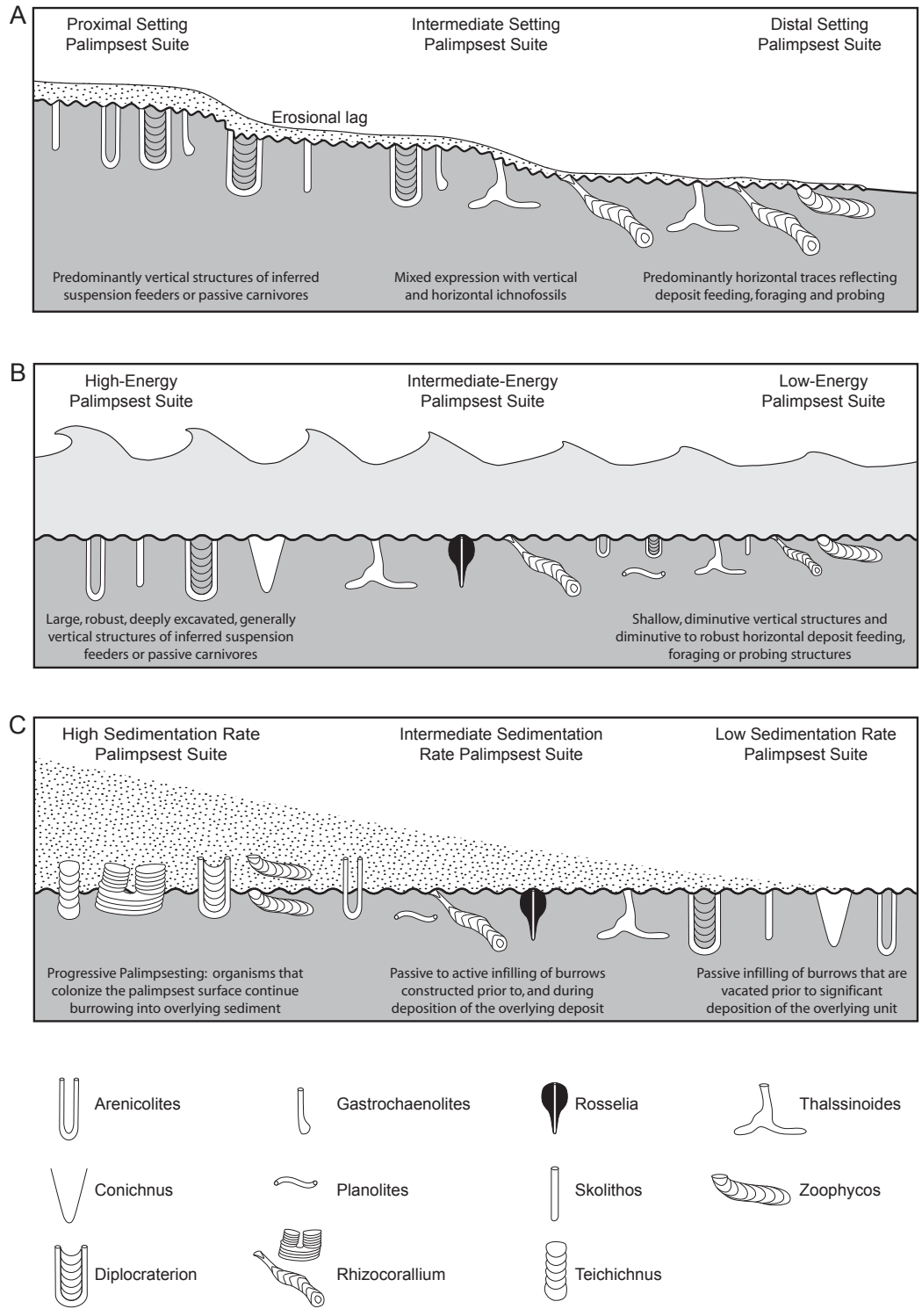

FIGURE 9.15—The environmental influence on palimpsest suites. **A:** Proximal to distal trends in trace fossil suites (modified from MacEachern and Burton, 2000). **B:** The influence of energy on ichnofossil suites. **C:** The influence of sedimentation rate on the expression of a palimpsest suite.

Depositional Environment

The depositional environment that persists during palimpsesting influences the suite, diversity, and abundance of ichnofossils (MacEachern et al., 2007a). In general, vertical structures of inferred suspension feeders or passive carnivores will colonize proximal settings while horizontal deposit-feeding structures predominant distal settings (Fig. 9.15A; MacEachern et al., 2007a). Proximal palimpsest suites will tend to include: *Diplocraterion* (Fig. 9.12), *Skolithos* (Fig. 9.11A) *Arenicolites* (Fig. 9.1D), *Psilonichnus*, *Conichnus* (Fig. 9.6F), *Bergaueria* and to a lesser degree *Thalassinoides* (Fig. 9.13D; MacEachern et al., 2007a), *Rosselia* (Fig. 9.6J) and *Gyrolithes* (Fig. 9.13A). Distal expression of palimpsesting includes *Thalassinoides* (Fig. 9.1B), *Spongeliomorpha*, *Rhizocorallium* (Fig. 9.13C), and *Zoophycos* (Fig. 1C; MacEachern and Burton, 2000) in addition to *Planolites* (Fig. 9.6G) and *Teichichnus* (Fig. 9.8C). *Chondrites* may cross-cut the palimpsest suite; however, these traces tend to contain a contrasting infill that reflects post-omission burrowing. For example, the palimpsest *Chondrites* described by Schieber (2003) likely reflect a deeper tier ichnofossil that colonized the substrate at a later time. Distal settings may also be colonized by diminutive vertical structures of inferred suspension feeders such as *Skolithos* (Fig. 9.11C). While intermediate depositional settings will be colonized by a mixed expression of the proximal and distal suites (Fig. 9.13B).

The diversity and abundance of palimpsest ichnofossils can also depend upon the depositional setting. For instance, within a modern *Glossifungites* assemblage at Willapa Bay, Gingras et al. (2001) found that intertidal zonation led to colonization by different organisms. Subtidal and lower to middle intertidal firmground exposures were colonized by crustaceans and rarer bivalves forming *Thalassinoides*- and *Gastrochaenolites*-like traces. In contrast, the upper intertidal was burrowed by *Polydora* forming small *Diplocraterion*- and *Arenicolites*-like traces. In this case, the presence of low-diversity suites was dependent on intertidal zonation that was a function of lithology, degree of cohesion and overlying lag deposition (Gingras et al., 2001). The abundance of ichnofossils will likely be dependent upon the suitability of the setting to the trace-makers, the degree of opportunistic colonization of sediment, and the time permitted for colonization. In the Pebas Formation, a suitable setting and likely ample time led to the complete destruction of the stiffground surface (Fig. 9.13D). Conversely, a lack of opportunistic colonization and potentially rapid shift in the environment led to a sparsely burrowed contact in the Viking Formation in Figure 9.10C.

Energy Regime

Energy regime also influences the nature of trace-maker colonization during palimpsesting (MacEachern and Burton, 2000; MacEachern et al., 2007a). High-energy settings tend to be colonized by large, robust, deep, vertical structures of inferred suspension feeders or passive carnivores (Fig. 9.15B). Low-energy conditions, however, tend to result in colonization by diminutive, shallow, vertical structures and robust to diminutive horizontal deposit-feeding, probing or foraging structures (Fig. 9.15B).

Depositional setting and energy regime are closely associated in that large, vertical structures tend to be associated with high energy, proximal settings. For example, wave ravinement surfaces in the Viking (Fig. 9.6H) and Bluesky (Fig. 9.11A) formations were colonized by robust, vertical ichnofossils within proximal upper offshore muddy sandstone. Similarly, a tidal ravinement surface in the Pebbley Beach Formation cuts into estuarine basin deposits and is characterized by deep, robust *Diplocraterion* (Fig. 9.6I). In the same fashion, low-energy palimpsesting tends be associated within distal settings. For example, distal colonization of the Viking uppermost SB/TSE produced suites containing *Zoophycos* (Fig. 9.1C) and *Rhizocorallium* (Fig. 9.6C). There are, however, exceptions to these generalized relationships. For instance, in proximal deposits of the Heather Formation (Fig. 9.6A) and Viking Formation (Fig. 9.6D, E), the palimpsest softground ichnofossils are diminutive and shallow suggesting relatively low-energy conditions during colonization. Intermediate energy during palimpsesting within proximal settings will tend to be demarcated by a mix of vertical and horizontal structures. In the Panther Tongue of the Star Point Formation, diminutive *Skolithos* and robust *Rosselia* suggest an intermediate energy regime (Fig. 9.11G, H). Another example of intermediate energy within a proximal setting is suggested by *Thalassinoides* in the Snapper Point Formation in which the palimpsest suite replaces vertical *Diplocraterion* within the underlying sandstone (Fig. 9.13E). Intermediate energy conditions can also persist in more distal settings, which is expressed by a mixed palimpsest ichnofossil suite containing vertical and horizontal traces such as those from the Viking along wave ravinement (Fig. 9.13B) and SB/TSE (Fig. 9.13C) surfaces.

One would expect that stiffground and firmground suites are typically associated with high-energy conditions as these substrates tend to require some degree of erosion and removal of overlying strata. However, it is the energy regime at the time of colonization that influences the ichnofossil suite regardless

of the energy of the system that may have led to erosion along a surface. Interrelationships between numerous environmental, substrate and stratigraphic factors also play a role in the development and expression of the palimpsest suite such that generalized trends between energy and the type of palimpsest suite cannot be necessarily made.

Sedimentation Rate

The nature of a palimpsest ichnofossil suite will also depend, to a lesser extent, on the sedimentation rate (Fig. 9.15C). When sedimentation rates are low, deposition of lag or superjacent sediment tends to occur following construction of palimpsest ichnofossils. In this case, traces are passively infilled following vacation by trace-makers. These ichnofossils are typically vertical structures of inferred suspension feeders or passive carnivores such as *Skolithos* (Fig. 9.10D) and *Diplocraterion* (Fig. 9.10C). Although, structures of inferred suspension feeders may not always be passively infilled, such as *Diplocraterion* in the Pebbley Beach Formation (Figs. 9.6I, 9.11D) and the Moosomin B (Fig. 9.11E). In addition, horizontal dwelling structures like *Thalassinoides* may be passively infilled such as those in the Pebas Formation (Fig. 9.13D) and the West Ahken Field (Fig. 9.13F).

With intermediate sedimentation rates, lag deposition typically occurs during or shortly after initial colonization such that ichnofossils may be passively or actively infilled with the overlying deposit. Ichnofossils that may be influenced by intermediate sedimentation could include foraging or deposit feeding structures such as *Rhizocorallium*, *Zoophycos*, *Thalassinoides*, *Planolites* and *Rosselia*. Such a mix of passively and actively infilled traces is found in the Viking along the uppermost SB/TSE (Fig. 9.11C, 9.13C). Where sedimentation rates are comparatively high, organisms that formed burrows subtending from the surface may continue burrowing up into the overlying deposit (e.g., Fig. 9.6C). The occurrence of traces spanning across the palimpsest surface reflects a unique form of palimpsesting referred to herein as progressive palimpsesting. Ichnofossils found in this setting may incorporate a variety of structures including *Diplocraterion*, *Arenicolites*, *Teichichnus* and *Rhizocorallium* that adjust upwards with sedimentation.

Progressive Palimpsesting

In studying modern firmground assemblages at Willapa Bay, Gingras et al. (2001) observed portions of firmground burrows existing within the sediment veneer as well as in the firmground. Based on these modern biogenic structures, Gingras et al. (2001) hypothesized that only the burrow component within the firmground would likely pass into the historical record. This may be the case in some scenarios; however, within the Snapper Point Formation of Australia and the Viking Formation of Alberta, palimpsest traces have been observed extending into the overlying unit (Fig. 9.8). These examples are defined by palimpsest softground and stiffground suites rather than the firmground *Glossifungites* Ichnofacies. Perhaps the active burrowing (as opposed to passive infilling typical of firmground suites) associated with palimpsest softground and stiffground suites is more conducive to progressive palimpsesting in which trace-makers continue burrowing to keep pace with sedimentation. Although, rapid sedimentation in a distal setting in which deposit-feeding or foraging organism colonize the surface could produce progressive palimpsesting in firmground substrate.

In the examples presented below, evidence suggests that rapid deposition of the overlying unit took place such that trace-makers were required to keep pace with sedimentation. This progressive palimpsesting reflects colonization of an autocyclic surface in the Snapper Point Formation and an amalgamated SB/TSE in the Viking Formation.

Snapper Point Formation—At the Snapper Point South locality of NSW, the Snapper Point Formation is characterized by numerous palimpsest trace fossil suites, two of which display progressive palimpsesting. The lowermost palimpsest softground suite is characterized by *Planolites* and *Thalassinoides* with indistinct boundaries, mixing of host and lag deposits and partial trace linings, and an unknown lined, inclined trace (Fig. 9.8A). The latter trace is heavily lined suggesting that palimpsesting of looseground sediment occurred, and the ichnofossil contains an infill consistent with the under- and overlying units. The palimpsest surface also displays prominent load casts suggestive of soft or looseground overprinting followed by rapid deposition of the overlying coarse clastic unit. The heavily lined trace reflects active infilling such that the trace-maker either penetrated down through an initial lag deposit, or adjusted upwards through the sediment as lag deposition occurred. Most likely, as the coarse material was being rapidly deposited, the trace-maker would not have burrowed

downward as the sediment-water interface progressed upwards.

The second overlying surface is demarcated by palimpsest ?*Arenicolites* the bulk of which occurs within the overlying lag deposit (Fig. 9.8B). The trace appears lined at the base, while additional *Rhizocorallium* exhibits diffuse boundaries and disruption to underlying laminae suggesting softground colonization. Loading is also present along this surface, but is less pronounced as compared to the underlying surface. Within the overlying coarse clastic material, burrowing is common; however, traces are unidentifiable due to preferential weathering of the ichnofossils.

Burrowing across these surfaces suggests that there was a slight shift in the community: the pre-omission suites include sparse *Rosselia*, *Diplocraterion*, and *Palaeophycus* overprinted by *Planolites*, *Thalassinoides*, *Arenicolites* and *Rhizocorallium*. The continuation of burrowing by the palimpsest suite into overlying strata suggests that conditions remained optimal enough for trace-makers to continue thriving. In this case, burrows are likely actively infilled rather than passively as burrows remain occupied by animals as they kept pace with sedimentation. Traces that are part of the palimpsest suites, but do not exhibit progressive palimpsesting (*Thalassinoides*, *Planolites* and *Rhizocorallium*) likely colonized the sediment at an early stage and were passively infilled prior to significant deposition. Traces extending across the surface may indicate that burrowing began prior to lag deposition or following some deposition of coarse clastics.

The lower palimpsest surface separates underlying swaley cross-stratified sandstone (storm deposition) from overlying lag deposits and sandy mudstones that reflect a highly bioturbated, fair-weather suite. In contrast, the upper palimpsest suite separates hummocky cross-stratified sandstone from overlying trough-cross bedded sandstone. Both surfaces are interpreted to reflect autocyclic fluctuations in sediment supply possibly related to ice-rafting (cf. Veevers and Powell, 1987) within an overall conformable succession.

Viking Formation—Traces as part of palimpsest stiffgrounds and softgrounds that extend into the overlying deposit are also present within the Viking Formation. In the first example (Fig. 9.8C), transitional palimpsest softground to stiffground is demarcated by *Teichichnus*, *Planolites*, *Thalassinoides* and an unknown structure, which are partially lined with sharp to diffuse boundaries. The ichnofossil of interest is the *Teichichnus* that subtends from the surface and extends up into

the overlying lag deposit. This surface represents the uppermost SB/TSE of the Viking Formation underlain by weakly bioturbated deltaic deposits and overlain by lower offshore to shelf mudstones.

The example presented in Figure 9.8D consists of *Thalassinoides* and *Diplocraterion* that constitute a palimpsest stiffground with sharp ichnofossil boundaries and no discernible disruption to underlying laminae. The *Diplocraterion* subtends below the surface into lower offshore strata and extends up into the overlying Colorado Shales. This surface reflects an obvious shift in depositional conditions at the time of palimpsesting in which structures suggestive of a more proximal setting are found in otherwise weakly burrowed mudstones reflecting the uppermost SB/TSE of the Viking Formation.

The presence of progressive palimpsesting along this Viking surface is likely associated to rapidly changing conditions during palimpsesting. Within the overlying lag deposit of the BD4 surface in the Hamilton Lake area, *Teichichnus* is a relatively common trace, the upwards adjustment of this burrow suggests the need for trace-makers to keep pace with sedimentation during resumed deposition. Transgression was likely rapid such that the window for colonization during palimpsesting was short prior to any lag deposition and subsequent deep marine conditions. This progressive palimpsesting contrasts with that of the Snapper Point Formation in that traces display continual readjustment along allocyclically generated surfaces. Accordingly, the presence of progressive palimpsesting can be an important indicator of the depositional conditions at the time of colonization.

Trace-maker Colonization

The type of ichnofauna that colonize the substrate, the burrow density and depth of burrows depends primarily on substrate attributes and environmental and physio-chemical conditions that persisted during the hiatal break (Gingras and Pemberton, 2000; Gingras et al., 2001; Pemberton et al., 2004). While firmground substrates may inhibit formation of *Rosselia* and *Planolites* by deposit-feeders, suspension feeders and passive carnivores may thrive, especially in the absence of other burrowers. Conversely, palimpsest soft- and stiffgrounds likely attract more deposit feeders and a broader range of organisms, but may also be colonized by inferred suspension-feeding organisms as well. The construction of semi-permanent dwellings in firmground substrates requires an initial expenditure of energy; however, no long-term energy is required to stabilize burrow walls. On

the other hand, burrowing within soft- and stiffground requires less of an initial energy expenditure; however, more long-term energy is required to maintain burrow walls, especially in softground sandy sediment. In studying modern palimpsest suites, Gingras et al. (2001) noted a strong correlation between the firmness of the sediment and the observed burrowing behaviors. At Willapa Bay, sediment firmness is heterogeneous where different burrowers colonize varying substrate firmnesses: *Polydora* populated substrate displaying a firmness of about 1×10^7 Pa, whereas very firm substrates ($>1 \times 10^9$ Pa) were typically devoid of burrowing (Gingras et al., 2001).

Ultimately, the colonizing organisms determine the type of trace fossil constructed, size, and inferred ethology. Inherently, organisms-sediment interactions with the substrate can change between firmgrounds and softgrounds, and potentially different trace fossils may be constructed. However, the nature of palimpsest suites will reflect the morphology and behavior of the trace-making organisms. The size of palimpsest ichnofossils will likely be a function of the permanency of burrows. Burrows reflecting dwelling and inferred suspension-feeding activities tend to be semi-permanent and likely become enlarged as the individual trace-maker grows (Fig. 9.10D, 9.12). Whereas deposit-feeding structures typically reflect temporary burrow activity in which sediment is mined and the burrow is actively infilled as the trace-maker moves through the sediment (Fig. 9.13C). The temporal significance of deposit-feeding structures is shorter, and as such these structures may be diminutive, although that may not always be the case (Fig. 9.1A, B).

STRATIGRAPHIC INFLUENCE ON PALIMPSESTING

Degree of Burial, Erosion, and Hiatus

Ruffel and Wach (1998) suggested that the maturity of a firmground is related erosional events or to the magnitude of the associated hiatus. With increasing depth of erosion, the probability of exposing a firmground that may be colonized to produce a *Glossifungites* Ichnofacies increases. The depth of erosion will depend on: 1) the energy and duration of the erosional event; 2) characteristics of the substrate; and 3) slope of the depositional surface. With increasing energy and duration of an erosional event, the depth of erosion potentially increases. For instance, wave ravinement surfaces form in the

shoreface during transgression and typically reflect continual high-energy conditions. A storm scour or shallow tidal ravinement surface, on the other hand, may represent brief scouring conditions that may not expose deeper firmground substrate, and instead favor softground colonization. The characteristics of the substrate can also influence the degree of erosion as firm mud will be more durable than loose sand, and incipient cementation can inhibit extensive erosion. The slope of the depositional surface will also influence the degree of erosion and probability of exposing firmer sediment. Ravinement across a relatively flat surface will likely be rapid with minimal erosion; however, ravinement of a sloped surface such as a preexisting forced regressive shoreface will likely be slow and extensive (Fig. 9.16).

With burial of sediment, compaction and dewatering occurs which enhances the cohesion of the substrate. Although, the formation of firm- and stiffgrounds may not require extensive burial, as muds exposed on tidal flats can undergo autocompaction in which sediment dewaters and compacts despite prolonged burial (Fig. 9.7C, 9.13A, 9.14A, B). In modern settings, the firmness of the substrate is generally a function of age (burial time) and exposure time to modern processes (Gingras et al., 2001). In these settings, the firmness tends to be more heterogeneous with "patches" that are firmer producing an overall undulatory firmness profile (decimeter scale; Gingras et al., 2000). In general, the burial depth required to form a firmground will depend upon the sediment texture, initial pore-water content, sedimentation rate and amount of burial time (Dewhurst and Aplin, 1998; Gingras et al., 2000). Gingras et al. (2000) suggested that exposed durable firmgrounds likely involve removal of 2 m or more of sediment. Where the sediment has good drainage, the sediment also tends to exhibit firmer profiles (Gingras et al., 2000).

Hiatuses may occur in the marine realm along a condensed section in which semi-lithified or lithified sediment may form without erosion (Pemberton et al., 2004). In the Falher A cycle, Hobbs (2003) also identified palimpsest trace fossil suites characterizing maximum flooding surfaces. Amalgamation of erosional and/or hiatal events will also result in an increased potential for palimpsesting due to prolonged erosion or dewatering. During subaerial exposure, sediment dewaters and compacts. The amalgamation of a subaerially exposed sequence boundary and transgressive surface of erosion will often expose firm substrate. The tidal ravinement surface amalgamated with the initial transgressive surface and sequence boundary in the Viking Formation at Willesden Green

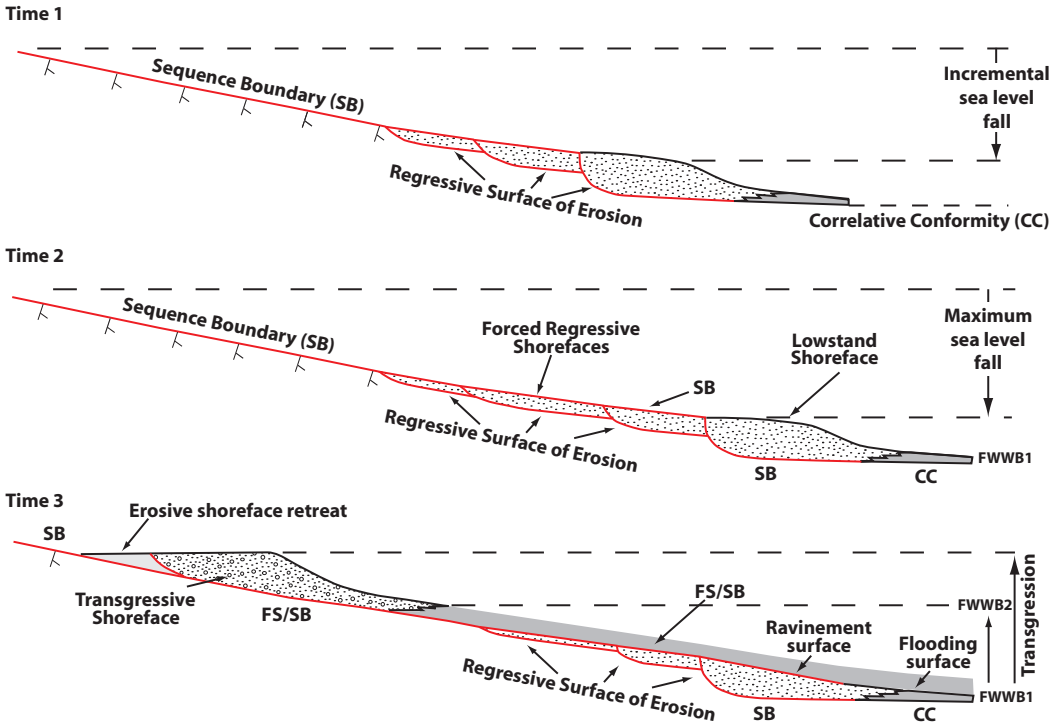

FIGURE 9.16—The formation of incised shorefaces. **Time 1:** As sea level falls in increments, forced regressive shorefaces are carved. The sequence boundary is formed due to subaerial exposure and grades into regressive surfaces of erosion and the correlative conformity in the offshore. **Time 2:** Maximum sea level fall carves the lowstand shoreface, which is underlain by a continuation of the sequence boundary. **Time 3:** Transgression ensues and the former sequence boundary is amalgamated with the ravinement surface to form a FS/SB as the shoreface retreats. During stillstand a transgressively incised shoreface may be preserved overlying the FS/SB. Modified from MacEachern et al. (1999b).

resulted in firmground colonization by robust *Rhizocorallium* (Fig. 9.1A).

Rates of Transgression or Erosion

The development of a palimpsest suite may also be a function of the rate of erosion (Gingras et al., 2001). Depending on fluctuations in relative sea level, the rate of transgression may slow, remain constant or increase over time. A slower rate of transgression tends to result in increased erosional truncation of underlying deposits, which may potentially expose firmer substrates. Whereas rapid transgression tends to flood an area resulting in minor erosion during shoreface retreat favoring palimpsest soft- or stiffground colonization. Examples presented from the uppermost SB/TSE of the Viking Formation at Hamilton Lake record distal expressions of palimpsest suites (Fig. 9.1C, 9.6B, C, G,

9.11C, 9.13C). Rapid transgression at Hamilton Lake is suggested by progressive palimpsesting, a low abundance and diversity of traces within the lag deposit and traces suggestive of keeping pace with sedimentation (e.g., *Teichichnus*). Most likely, in this distal Viking setting, erosion was limited during a rapid transgression along BD4 (see Chapter 8).

During transgression, periods of stillstand reflect a pause in the overall relative sea level rise. This pause results in the formation of a bevel carved in the underlying deposits as the shoreface preserves its concave upward profile (Fig. 9.16). Stillstand conditions therefore generate increased localized erosion to expose firmgrounds to marine trace-makers. The bevel created along BD1 in the Viking Formation at Hamilton Lake is typically demarcated by a sharp contact with little evidence of erosion except the obvious truncation of underlying strata. In this case, the BD1 surface was first carved during relative sea level fall and subsequently modified during transgression, which may have been rapid such that conditions were not ideal to palimpsesting (Fig. 9.16; see Chapter 8).

Lag Deposition

The deposition of a lag deposit or contrasting superjacent sediment is key in preserving traces associated with palimpsest suites, as the traces may otherwise appear as part of the underlying suite if the infilling material is similar. A change in grain size within palimpsest softground traces, especially, differentiates these ichnofossils from the underlying trace fossil suite. Colonization of a palimpsest substrate by trace-makers, may, in some instances require deposition of overlying sediment. In a modern study at Willapa Bay, Gingras et al. (2001) observed heterogeneity in the *Glossifungites* Ichnofacies, which was associated to the presence or absence of a sediment veneer. A sediment veneer of >1 cm in thickness precluded the *Polydora* Association, and 3-5 cm of sediment veneer precluded the *Petricola* Association while *Upogebia* was unaffected by a sediment veneer (Gingras et al., 2001).

Spatial and Temporal Surface Variability

A single discontinuity can be characterized by palimpsest softground, firmground, woodground and hardground suites (MacEachern et al., 2007a) as substrate consistency can change both laterally and vertically (Bromley, 1996).

There may be gradation between softground, stiffground and firmground suites in siliciclastic sediments, while carbonates may transition to hardgrounds as well. MacEachern et al. (2007a) suggested that allocyclic discontinuities can vary in nature spatially as a result of the underlying substrate, substrate cohesion, energy regime during subsequent colonization and depositional conditions at the time of colonization. Based on the examples presented below (Fig. 9.9), this variation may occur over significant distances or within meters of outcrop.

Viking Formation – Spatial-Temporal Transition

In the upper Viking strata in the Hamilton Lake area, two transgressively incised shorefaces persist along the northern edge and to the north of the field (see Chapter 8; Figs. 8.2, 8.8). Towards the southwest of Hamilton Lake, the bases of these shorefaces are amalgamated into one surface—BD3 (Fig. 9.9C). However, where the shorefaces exist separately, the surfaces are denoted as BD3a (Fig. 9.9A) and BD3b (Fig. 9.9B). These surfaces, where demarcated by ichnofossil suites can be characterized by either a palimpsest softground or stiffground suite. However, the amalgamated surface, where demarcated by trace fossils, is consistently a stiffground suite.

The BD3a surface in Figure 9.9A consists of a palimpsest softground overlain by 2-3 cm of fine to medium sandstone infilling lined *Arenicolites* and a possible *Planolites*. The surface separates stressed *Rhizocorallium* and *Asterosoma* dominated prodeltaic deposits (BI 3-5) from weakly deltaically influenced distal upper offshore strata. The palimpsest surface reflects a SB/TSE (see Chapter 8), which exhibits an obvious shift in depositional conditions between the under- and overlying strata.

The wave ravinement surface of BD3b is demarcated by a transitional palimpsest soft- to stiffground with sharp-walled *Diplocraterion* displaying well defined spreite and *Planolites* displaying indistinct boundaries. The overlying deposit contains *Teichichnus* suggestive of rapid deposition of the sandy mudstone lag. Underlying strata comprises homogenized (BI 5-6) upper offshore strata predominated by *Helminthopsis*, *Rosselia* and *Planolites*. While overlying strata consists of moderately to weakly burrowed (BI 1-3) sandy mudstone to mudstone with interlaminated fine sandstone suggestive of deeper marine conditions. In this locality, the second transgressively incised shoreface was not deposited, but strata reflect lower offshore deposition during progressive deepening.

The BD3 surfaces become amalgamated in the landward direction and are expressed as a single stiffground assemblage in Figure 9C. In this example, the stiffground is demarcated by *Rhizocorallium* and *Planolites*. All of the trace display sharp boundaries with minor disruption to preexisting laminae suggestive of stiffground colonization. The *Chondrites* are infilled with distinctly lighter coloured sand suggesting that these traces are related to post-palimpsest burrowing. Amalgamation of the BD3 surfaces implies two things: 1) increased erosion and/or exposure along the same surface, and 2) increased time reflected by the single, amalgamated surface. Overprinting of successive surfaces tends to expose stiffer substrate due to an increased depth of erosion. The amalgamated surface reflects both a spatial (landward versus basinward) and temporal (one amalgamated surface versus two temporally less significant surfaces) transition.

Pebbley Beach Formation – Lateral Lithological Variation

In the Pebbley Beach Formation at Clear Point, a palimpsest surface displays lateral lithological variation such that different lithologies are characterized by different palimpsest ichnofossil suites (Fig. 9.9D-F). Along the outcrop, the surface is underlain by either a burrowed muddy sandstone or weakly burrowed silty mudstone (Fig. 9.9D). The burrowed sandstone is characterized by trough-cross beds, while the mudstone deposit appears to have infilled topographic highs between sandy bedforms. These deposits comprise the upper portion of an interbedded sandstone and fluid mudstone unit that is weakly to moderately burrowed with combined flow ripples and current ripple lamination. The thick sharp-based mudstones and general paucity of bioturbation suggests deltaic deposition (cf. MacEachern et al., 2005). Variation in lithology below the surface is a function of the muddy unit pinching out against the sandier unit in either direction (at the scale of meters). This variation is likely a function of the initial sedimentary topography whereby depressions between sandy dunes were infilled with muddy deposits possibly as hyper- or hypopycnal riverine discharge.

Directly overlying the palimpsest surface is a gritty mudstone which infills the burrows. The gritty sediment consists of fine to very coarse sand grains in conjunction with glendonite crystals. The lag material tends to pinch and swell and there is localized loading along the surface. Traces defining the palimpsest suite include *Diplocraterion* and *Rosselia*. *Rosselia* occur within the muddy sandstone, are infilled with gritty sediment, and are heavily mud lined

suggesting palimpsest softground conditions (Fig. 9.9E). Where the surface is primarily underlain by mudstone deposits, sharp-walled *Diplocraterion* dominate the palimpsest stiffground ichnofossil suite (Fig. 9.9F). Where the underlying lithology transitions, there tends to be a transitional suite consisting of both *Diplocraterion* and *Rosselia*.

Overlying the lag deposit is mudstone with thin interlaminated sandstone beds that is overall moderately to commonly bioturbated (BI 1-3). This facies is interpreted to reflect distal prodeltaic deposition based on the fine-grained nature of the deposit, paucity in trace fossil abundance suggestive of environmentally stressful conditions, and overall coarsening upward nature of the stratal unit. The palimpsest suites likely reflect a minor rise in relative sea level possibly associated with wave ravinement.

Stratigraphic Surfaces

Substrate-controlled ichnofacies are important in delineating potentially significant stratigraphic surfaces in the rock record and have been discussed extensively by previous authors (e.g., MacEachern et al., 1991; MacEachern et al., 1992; MacEachern and Pemberton, 1994; Pemberton et al., 1994; Pemberton and MacEachern, 1995; MacEachern et al., 1999; Pemberton et al., 2001; MacEachern et al., 2007a, c). The presence of palimpsest soft-, stiff- and firmground suites along stratigraphic surfaces is briefly reviewed here.

Based on the examples presented above, palimpsest soft-, stiff- and firmground ichnological suites characterize both allocyclically and autocyclically formed surfaces in modern and ancient settings. The newly established soft- and stiffground suites can be as stratigraphically significant as suites attributable to the *Glossifungites* Ichnofacies. There is equal potential for soft-, stiff- and firmground colonization of stratigraphically significant allocyclic surfaces such as: 1) sequence boundaries and regressive surfaces of erosion associated with submarine canyon incision, forced regressive and lowstand shorefaces and incised valleys; 2) transgressive surfaces of erosion (TSE) associated with wave ravinement surfaces (WRS) and tidal ravinement surfaces (TRS); and 3) amalgamated sequence boundaries and flooding surfaces (FS/SB) which involve initial transgression across the sequence boundary, transgressive erosion across valley interfluves, and wave ravinement across sequence boundaries (SB/TSE).

However, the erosion (and possibly hiatus) associated with palimpsest

softground and stiffground suites may be less extensive in comparison to the *Glossifungites* Ichnofacies. Accordingly, the probability of palimpsest soft- and stiffgrounds reflecting stratigraphically significant discontinuities is likely lower in comparison to firmground suites, and higher for autocyclically generated surfaces. Although, it is evident from the presented examples that various conditions can also produce important palimpsest soft- and stiffground ichnofossil suites (Figs. 9.6, 9.11, 9.13).

DEVELOPMENT AND PRESERVATION OF PALIMPSEST SUITES

The development of palimpsest soft- and stiffground trace fossil suites may resemble that of the firmground *Glossifungites* Ichnofacies, wherein colonization of the surface succeeds varying degrees of erosion and/or depositional hiatus (Figs. 9.17, 9.18). Due to the gradational nature of softground to firmground substrates, there are numerous methods in which palimpsest substrates can form, which likely results in the especially varied nature of palimpsest soft- and stiffground suites (Table 9.1). The development of stiff- to firmground substrates can be remarkably similar due to their common association with dewatered and incipiently compacted mudstones. Understanding the various processes responsible for the development of palimpsest suites is further complicated by the range in the degree of substrate "firmness" (Fig. 9.4; Gingras et al., 2000).

Palimpsest Softground

The formation of palimpsest softground involves little or no burial, compaction or erosion, such that soft substrate remains exposed (Fig. 9.17). Brekke (1995) and Hobbs (2003) initially suggested that palimpsest softgrounds characterized sandy substrates in which there is minimal or extensive erosion of sandy deposits. However, based on the examples in Figure 9.6, palimpsest softgrounds tend to develop under two different scenarios: 1) low- to high-energy conditions in sandy proximal sediment (Fig. 9.6A, E, F, H-J), and 2) low-energy conditions in (typically) distal settings within muddy sediment (Fig. 9.6B-D, G). Within proximal sandy sediment, even pronounced erosion

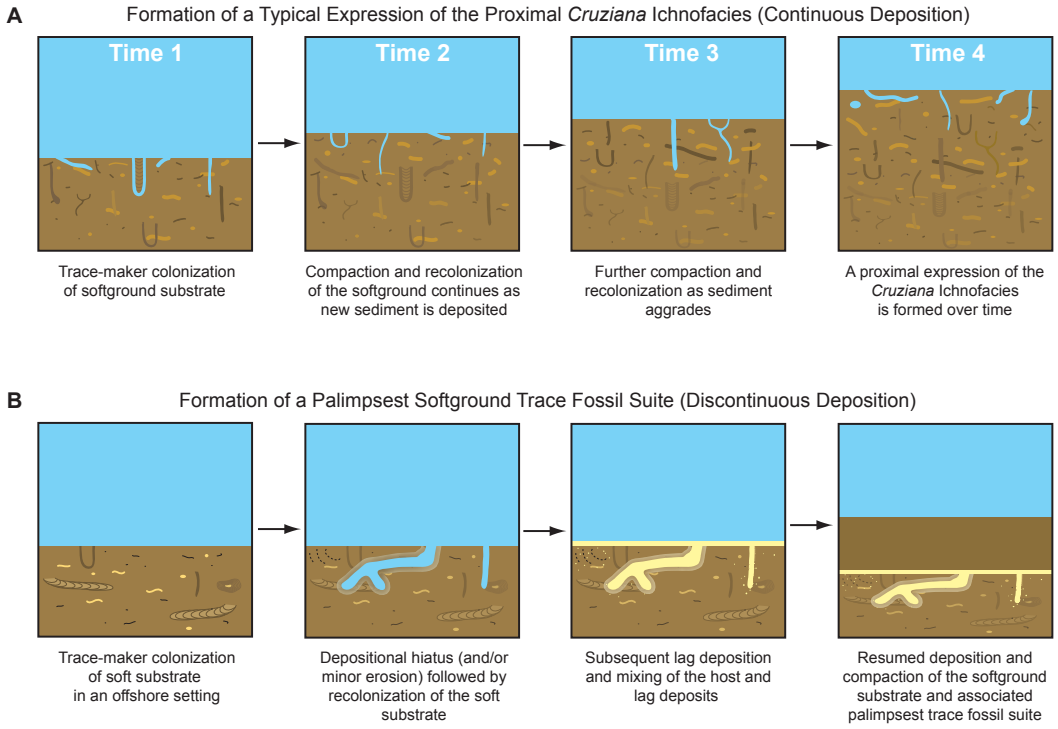

FIGURE 9.17—Models depicting the formation of softground trace fossil suites formed during continuous and discontinuous deposition. **A:** Formation of a typical proximal expression of the *Cruziana* Ichnofacies wherein colonization and deposition are continuous. **B:** Formation of a palimpsest softground trace fossil suite during discontinuous deposition. In this example, palimpsest trace-maker colonization succeeds softground colonization and potentially some degree of depositional hiatus and/or minimal erosion.

may produce a palimpsest softground due to the incohesive nature of sandy sediment. Conversely, in order for muddy substrate to escape extensive erosion, recolonization of the surface may take place in a low-energy (generally distal) environment. Development of a palimpsest softground ichnofossil suite contrasts that of tiering (Fig. 9.17A) in which there is no discrete surface or change in depositional conditions.

Palimpsest Stiffground

On a localized scale, salinity changes and water expulsion may produce stiffground substrates (cf. Lettley et al., 2007). In other cases, the formation of palimpsest stiffground sandstones may be related to sediment compaction (e.g., via surf-pounding; Gingras et al., 2000) or incipient cementation (especially with carbonates). Understanding the various processes responsible for the development of palimpsest stiffgrounds is further complicated, however, by the

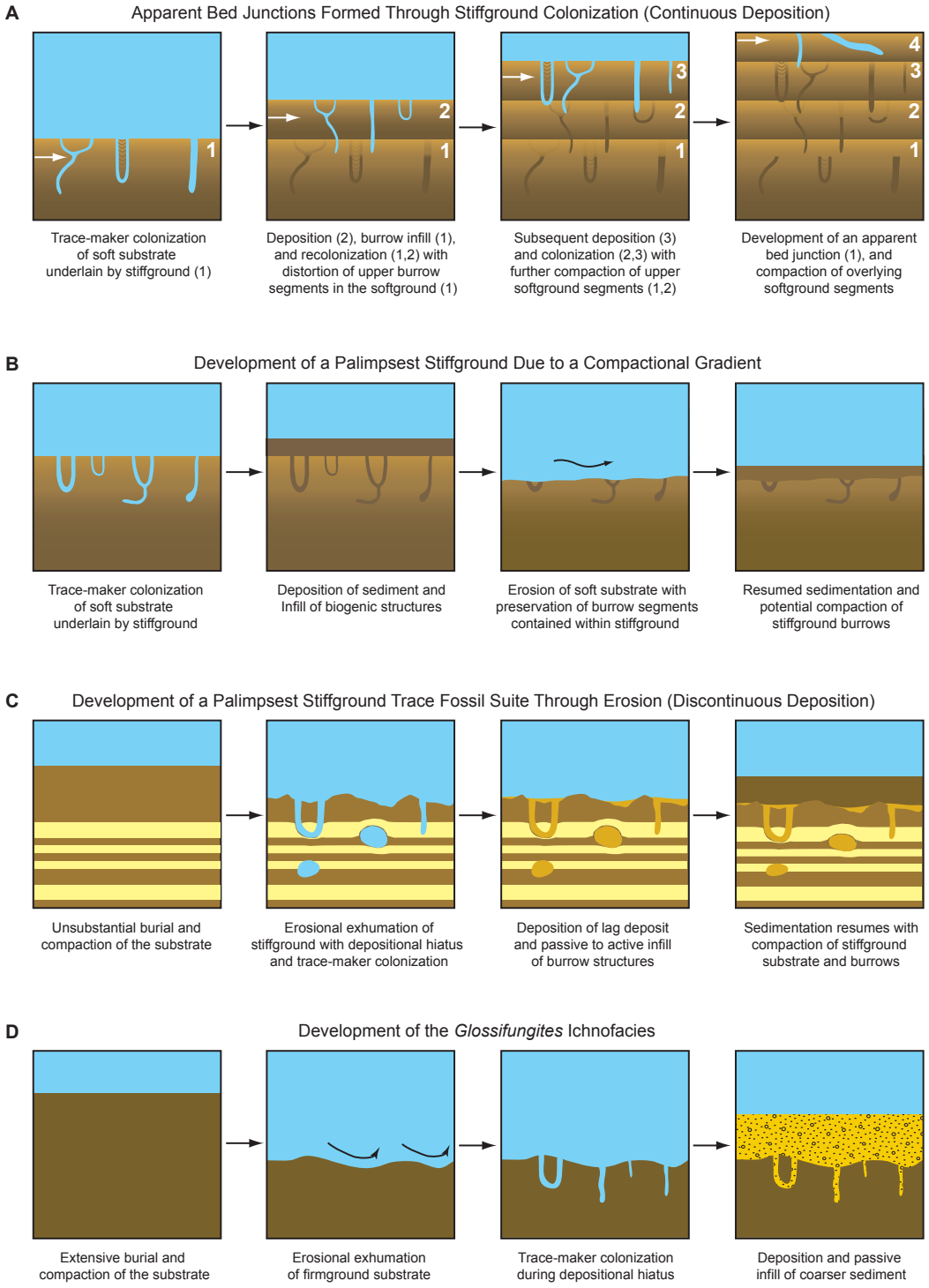

FIGURE 9.18—Models depicting the development of trace fossil suites in stiffground and firmground. **A:** Development of apparent bed junctions formed through stiffground colonization during continuous deposition. Initial colonization of the substrate consisting of stiffground overlain by a veneer of soft sediment (1). White arrow indicates the transition depth between softground and stiffground. Subsequently, there is deposition of a new sediment package (2), which infills the burrows in bed 1. The new sediment layer (2) is colonized by trace-makers, and the softground layer is now present at the top of this bed (2). The previous softground veneer in bed 1 is compacted as a result of deposition of overlying sediment, distorting the upper burrow

FIGURE 9.18 (Continued)—segments contained in the softground. Burrow segments originally constructed within the stiffground, however, remain identifiable. With deposition of a new bed (3), softground sediments of bed 1 are further compacted and corresponding trace segments are barely visible. Upper softground segments of burrows in bed 2 are also distorted through compaction. Bed 3 is subsequently colonized by trace-makers, and burrows are subsequently infilled during deposition of bed 4. Following deposition of bed 4, softground burrow segments in bed 1 are no longer visible, and traces infilled with contrasting sediment appear to have no connection to the overlying bed. Since deposition is continuous, these traces actually reflect an apparent bed junction. **B:** Development of a palimpsest stiffground ichnofossil suite due to a compactional gradient. Muddy substrates commonly comprise stiffgrounds overlain by a veneer of softer sediment. When organisms colonize the substrate, the burrows subtend through this into the underlying stiffground. Deposition of new sediment infills the burrows. Subsequent erosion can erode down into the stiffground; accordingly, lower segments of biogenic structures may be preserved but commonly display compaction due to resumed sedimentation. **C:** Development of a palimpsest stiffground ichnofossil suite through significant erosion. The softground substrate undergoes minor burial and compaction (i.e., a firmground is not formed). The overlying softer substrate is eroded to exhume the stiffground, which may possess a locally undulatory surface expression. This stiffground is colonized during a depositional hiatus. In sandier substrates burrows may be partially lined to maintain stability. Subsequent deposition of a lag may lead to passive or active burrow infill. Resumed sedimentation leads to compaction of the stiffground and concomitant burrow compaction. **D:** Development of the *Glossifungites* Ichnofacies. Initially, there is extensive burial and compaction of a softground substrate. Deposition is succeeded by extensive erosional exhumation of firmground substrate. During the ensuing depositional hiatus, organisms colonize this firmground. The burrows are then passively or actively infilled by a typically coarse lag deposit to form elements of the *Glossifungites* Ichnofacies.

range in the degree of substrate "firmness" (Fig. 9.4; cf. Gingras and Pemberton, 2000; Gingras et al., 2000). Accordingly, some possible scenarios of stiffground formation are described below and schematically depicted in Figure 9.18A-C with analogous examples presented in Figure 9.10A-C.

Stiffgrounds Constructed During Continuous Deposition

Bromley (1996) recognized the importance of lateral and vertical changes in substrate such that softground may overlie firmground sediments. In this case, the firmground is said to be "concealed" as it is not in direct contact with the water column (Ekdale et al., 1984). This vertical substrate change may produce thick-walled burrows near the surface that become thinner-walled, more ornamented burrows at depth due to compactional variation (Frey, 1978). A similar scenario has been observed in modern settings where stiffground sediment is typically overlain by a veneer of 1-20 cm of softer mud (Figs. 9.14A, B, 9.18A). Burrows within the stiffer substrate are more stable and more likely to be preserved in the rock record, which could form a "concealed" stiffground or an

apparent bed junction (Fig. 9.18A).

In order to form an apparent bed junction, the substrate must consist of stiffground overlain by a veneer of soft sediment in which the soft sediment is compacted during continuous deposition. The "concealed" stiffgrounds observed in modern settings (e.g., Pearson and Gingras, 2006; Lettley et al., 2007) are generally colonized contemporaneously with the overlying softground sediment (Fig. 9.14A, B). Organisms that colonize the substrate subtend through both the softground and stiffground such that burrow segments may possess linings within the softground, but remain unlined within the stiffground. Subsequent deposition infills these burrows and produces overburden pressure that compacts the softground veneer into a stiff sediment to distort upper burrow segments (Fig. 9.18A). The burrow segments that were originally constructed within stiffground, however, remain identifiable. As new sediment layers are deposited, the original softground veneer is further compacted such that the burrow segments that were initially within the softground are no longer discernable (Fig. 9.18A). Accordingly, the initial stiffground traces appear to be infilled with contrasting sediment with no apparent connection to the overlying bed. Since deposition is continuous, these traces actually reflect an apparent bed junction. This pattern could repeat in a succession such that multiple apparent bed junctions overly one another.

The scenario of repeating apparent bed junctions has been documented in the McMurray Formation (Fig. 9.19; e.g., Lettley et al., 2007). The McMurray Formation is predominated by inclined heterolithic stratification (IHS) formed through point bar deposition in estuarine channels (Lettley et al., 2007). Apparent bed junctions are formed where sandy IHS beds are overlain by relatively thick mud beds (Fig. 9.10A). In this instance, the *Gyrolithes* traces are highly visible in the lower part of the mud unit (due to the presence of sand-sized grains and stiffground colonization), but become compacted and indiscernible in the upper portion of the mud bed. The sand and mud couplets are interpreted to reflect autocyclic fluctuations in depositional conditions (Thomas et al., 1987) during rather continuous deposition. Lettley et al. (2007) suggested that the background bioturbation is overwhelmed by IHS stiffground colonization.

The presence of an apparent bed junction does not signify the presence of a stratigraphically significant surface. This form of autocyclic stiffground formation during relatively continuous deposition reflects a stiffground suite that is theoretically equivalent to any of the softground suites such as the *Skolithos*

or *Cruziana* Ichnofacies. Despite the relatively continuous deposition, there is a slight change in conditions during which *Gyrolithes* trace-makers colonize the sediment. The slight depositional change and repeated nature of these beds (Fig. 9.19) suggests a highly autocyclic nature, such that these surfaces should be segregated from allocyclically formed stiffground suites.

Palimpsest Stiffgrounds Formed Due to a Compactional Gradient

The idea of the "concealed" stiffground can also be applied to instances



FIGURE 9.19—Repeating sand and mud couplets in the McMurray Formation characterized by *Gyrolithes* within stiffground mud.

in which there is a small degree of erosion of the substrate (Fig. 9.18B). The "concealed" stiffground requires a muddy stiffground overlain by a veneer of softer sediment. During colonization of the substrate, the burrows pass through the softer sediment into the underlying stiffground. Renewed sedimentation infills these burrow structures and may lead to slight compaction of the initial softground (Fig. 9.18B). During a minor or localized erosive event, the new sedimentary layer and overlying softer substrate are removed due to the lack in cohesive resistance. However, the more resistant stiffground remains intact, and the lower segments of biogenic structures are preserved. This form of stiffground reflects a minor degree of erosion combined with possible depositional hiatus. The stiffground suite reflects an autocyclically formed surface that can also repeat throughout a facies.

The McMurray Formation is again used to exemplify the formation of this type of stiffground substrate (Fig. 9.10B). Oil stained sands tend to infill stiffground burrows such as *Planolites* and *Thalassinoides*. In Figure 9.10B, the upper *Planolites* are far removed from any significant sandstone beds suggesting that the infilling sand bed and potentially overlying softer muddy sediment were removed during erosion. With the underlying *Planolites* and *Thalassinoides*, there is a thin sandstone lamina above the traces that potentially suggests that the entire mud bed was stiff and resistant to erosion while the overlying non-cohesive sand bed was removed.

Using the modern Shepody River as an analogue to the McMurray Formation, Lettley et al. (2007) suggested that seasonal variations in water circulation within the estuary combined with sediment texture could produce the common occurrences of stiff substrate. During the winter months at Shepody River, the substrate undergoes stiffening due to: (1) reduced sedimentation, (2) freezing, which draws water from underlying the sediment surface, (3) compaction due to ice sitting atop the mud at low tide, and (4) the influx of freshwater from the melting of snow and ice. Lettley et al. (2007) further suggested that synaeresis is likely the most important factor resulting in the dewatering of substrate through changes in electrostatic configuration of clays. Within the McMurray, the presence of an underlying permeable silt/sand bed may have acted as a secondary pathway for water expulsion.

Palimpsest Stiffground Formed Through Erosion

In modern sediments, the degree of sediment firmness varies widely (cf. Gingras et al., 2000) such that stiff substrates can be exposed due to varying degrees of erosion to form palimpsest stiffground trace fossil suites such as in Figures 9.10C. In Figure 9.18C, the substrate is depicted as heterolithic sandstone and mudstone; however, the substrate could also be exclusively mudstone or sandstone. The softground substrate undergoes moderate burial and compaction (i.e. a firmground is not formed). The overlying softer substrate is eroded to exhume a stiffground, which may possess a locally undulatory surface expression. Subsequently, the stiffground is colonized by trace-makers during a depositional hiatus. In sandier substrates or interbedded sandstones and mudstones, burrows may be partially lined in order to maintain burrow stability. Subsequently, there is accumulation of a lag deposit and passive to active infilling of the burrows. Resumed sedimentation leads to compaction of the stiffground substrate and concordant compaction of burrow structures. Palimpsest stiffgrounds may form in a range of substrates including sandy sediment, heterolithic sandstone and mudstone, and most frequently within mudstone. In the case of sandy substrates, more extensive erosion is likely required to form stiffgrounds (Hobbs, 2003).

Development of the *Glossifungites* Ichnofacies

The *Glossifungites* Ichnofacies is generally produced following burial and compaction of sediment (typically muds) that forms dewatered and firm substrate at depth (Fig. 18D). This is succeeded by erosional truncation of the overlying deposits to expose the firm substrate, which is then colonized (Pemberton et al., 2001). Following the erosive activity, there is generally deposition of a lag deposit which can passively or actively infill trace fossils of the palimpsest suite. The development of palimpsest firmground suites within sandy sediment is uncommon due to the lack of cohesion of the sediment. In the modern, Gingras et al. (2001) noted that sandy firmground deposits tend to be infrequently colonized as more energy must be expended to burrow into these types of substrates. Furthermore, incipient cementation can also result in firmground colonization despite the lithology of the underlying stratum.

Taphonomy of Palimpsest Suites

Preservation potential of palimpsest suites can vary between the different forms. For the *Glossifungites* Ichnofacies, the firmness of the substrate inhibits compaction such that preservation potential is typically the greatest for these overprinted suites. Preservation is especially high if there is incipient cementation during colonization after which complete cementation of the horizon can enhance preservation. Although, firmgrounds in which the superjacent sediment does not contrast the host sediment can possess a low preservation potential (especially with mud-on-mud contacts).

The presence of a contrasting sediment infill (especially coarser grained) enhances the overall taphonomic preservation of palimpsest soft-, stiff- and firmground suites. In more proximal settings, palimpsest suites tend to be overlain by thicker and/or more coarse-grained lag deposits. In the Viking Formation, the Wayne-Rosedale area is located in a more shoreline proximal setting as compared



FIGURE 9.20—A coarse, thick lag deposit. In contrast to the muddy sandstone to sandy mudstone lag found in the Viking Formation at Hamilton Lake, in more proximal settings (Wayne-Rosedale area) lags tend to be thicker and coarser grained when located closer to the sediment source (11-19-026-20W4).

to the Hamilton Lake area (Chapter 7, Fig. 7.2). Lags in the Wayne-Rosedale area tend to be thicker and coarser grained (Fig. 9.20) as compared to the thin sandy mudstone lags at Hamilton Lake (e.g., Fig. 9.13C).

Soft- and stiffground palimpsest suites usually have a reduced preservational potential in comparison to the *Glossifungites* Ichnofacies, and represent overprinting with a moderate to high preservation potential. With softground and even stiffground palimpsest suites, deep-tier post-palimpsest traces can reburrow the palimpsest suite further reducing preservation potential (Fig. 9.13B, C). Also within these substrates shearing and other forms of deformation may occur (Fig. 9.6G, I, 9.13A). Gingras and Bann (2006) suggested that if the magnitude of strain exceeded a 2 to 1 ratio, burrows would most likely be deformed beyond recognition upon preservation in the rock record. Compaction of soft- and stiffground suites is also prevalent, which can distort or deform traces (Fig. 9.13C, F). The nature of some palimpsest softground ichnofossils also results in low preservation potential. When boundaries are indistinct, the presence of a contrasting infill may be the only evidence of burrowing along a particular horizon (Fig. 9.6B).

Additional factors that may enhance or detract from preservation includes differential erosion in outcrops. In some instances, traces may be highlighted by erosion of the host substrate (Fig. 9.6J) while others may be preferentially eroded (Fig. 9.8D). In some instances, diagenetic enhancement may also occur to highlight ichnofossils (Fig. 9.8A, 9.14E). Despite the type of palimpsest suite, Ruffel and Wach (1998) suggested that the amount of seafloor exposure time is the most important condition that influences firmground preservation. If ample time is given, organisms can modify the substrate to such a degree that the indications of even firmground conditions can no longer be surmised.

APPLICATION OF PALIMPSEST SUITES

Palimpsest suites may: 1) cross-cut an underlying suite; and/or 2) indicate a change in depositional conditions across the surface. The shift in depositional conditions can occur within a system or may be related to events external to the depositional systems. Stratigraphically significant surfaces, are allocyclic in nature and formed as a result of events that are associated to accumulation of sediments

external to the sedimentary system. These surfaces have a regional, mappable extent that separate genetically unrelated successions (MacEachern et al., 2007a). Conversely, autocyclic events are associated to accumulation of sediments that are part of the sedimentary system itself and are more common with palimpsest soft- and stiffgrounds. These suites have limited spatial distribution and are over- and underlain by genetically related strata (MacEachern et al., 2007a). Determining the auto- or allocyclic significance of a particular surface involves: 1) identification of the palimpsest suite, 2) determination of the pre-omission suite, 3) determination of the post-omission suite, and 4) an understanding of the stratigraphy.

A prime example of an allocyclically generated surface occurs in well 02-02-037-19W4 along the uppermost SB/TSE in the Viking. This surface is underlain by heterolithic delta front deposits and subsequently overlain by a discontinuous lag and shelfal mudstones (Fig. 9.10C). In some cases, however, the colonized surface is the only evidence of a drastic shift in environmental conditions. For example, the transitional firmground to stiffground in the Viking depicted in Figure 9.12 is under- and overlain by prodeltaic deposits; however the presence of robust *Diplocraterion* contrasts the predominantly diminutive, horizontal deposit-feeding structures within the under- and overlying facies.

On the other hand, examples of autocyclic depositional shifts includes the two palimpsest softgrounds within the Viking depicted in Figure 9.6D and E that are under- and overlain by distal delta front deposits. The lower surface reflects a slight increase in energy and colonization by dwellings of inferred suspension-feeding animals typically absent from the facies, while the upper surface possibly reflects dewatering of a riverine sourced mudstone. In the examples from the McMurray Formation, alternation of IHS sandstone and mudstone beds simply reflects autocyclic (and geologically insignificant) shifts in depositional conditions related to tidal cyclicity, seasonal fluctuations, storms and floods (cf. Thomas et al., 1987).

It is within these types of brackish settings that there appears to be a tendency towards the formation of palimpsest suites whether softground or stiffground and potentially firmground. Palimpsest stiffgrounds tend to form despite the general lack of burial and compaction possibly as a result of synaeresis and associated water expulsion (Lettley et al., 2007). In deltaic systems, incipient siderite cementation may produce palimpsest soft-, stiff- or firmgrounds. There is no stratigraphic importance to these types of surfaces, and the formation of these

palimpsest suites are associated to dynamics of the environment. In the sense of reflecting a shift in conditions, autocyclic stiffgrounds do reflect a change in deposition (albeit slight). However, these "surfaces" form more of an assemblage rather than a substrate-controlled ichnofacies. As Lettley et al. (2007) suggested, the complexity of assigning stiffgrounds to the Ichnofacies concept is that the burrowed stiffground can overwhelm the background bioturbation such that the colonized surfaces take on a volume of the rock unit.

Apparently, the distinction between allocyclic and autocyclic palimpsest suites needs to be made in order to avoid confusion and enhance our understanding of palimpsest suite occurrences. It has been well established that the *Glossifungites* Ichnofacies must demarcate a mappable (i.e. allocyclic) surface in order to conform to Walther's Law (cf. MacEachern et al., 2007b). Despite the lack of ichnofacies designation, it is proposed here that a similar terminology be applicable to the soft- and stiffground palimpsest suites. Where a palimpsest surface is allocyclic and mappable in nature, ichnofossils demarcating the surface should be referred to as a "mappable palimpsest suite" (whether it is softground, stiffground, or transitional in nature). Conversely, where a surface is only locally expressed and autocyclic in origin, the ichnofossils demarcating these surfaces should be referred to as a "localized palimpsest suite" (softground, stiffground, firmground, or otherwise transitional between forms). In the case of reoccurring localized palimpsest suites, such as those in the McMurray Formation, the strata should instead be referred to as containing a "localized palimpsest assemblage." In addition to this classification, suites can be modified through identification of proximal versus distal and high versus low energy expressions of a suite whether it is mappable or localized. Suite found to extend up into the superjacent sediment can be further classified as exhibiting progressive palimpsesting, which suggests rapid sedimentation rates. Determining and defining the nature of palimpsest suites can enhance our understanding of events and processes that lead to the formation of a particular suite.

SUMMARY

1. A palimpsest suite cross-cuts the underlying ichnofossil suite and/or indicates that there was a change in depositional conditions across the surface. Tiering, on

the other hand, reflects a vertical zonation of traces within the substrate due to vertical gradients in physical, chemical and biological characteristics.

2. Challenges inherent in defining and distinguishing palimpsest suites include: 1) the transitional nature between soft-, stiff- and firmgrounds; and 2) the variable nature of palimpsest suites.

3. The fundamental factor that controls the development and expression of palimpsest suites is the consistency and coherence of the substrate.

4. Palimpsest softground ichnofossil suites can be recognized by the following primary characteristics: 1) indistinct or irregular ichnofossil boundaries; 2) mixing of superjacent sediment and host softground; 3) a surrounding halo of sediment disturbance within the host sediment; 4) lined traces; 5) laminae are significantly warped adjacent to palimpsest traces; and 6) the surface displays pronounced load structures.

5. Stiffground suites are characterized by the following primary attributes: 1) relatively sharp-walled traces in mudstone and irregular (but unlined) traces in sandy sediment; 2) laminae are deflected adjacent to traces; 3) there is plastic deformation of the surface in the form of flame and load structures; and 4) traces are generally unlined, but may possess minor partial linings.

6. Firmground suites can be identified based on: 1) traces that are unlined and sharp-walled; 2) surfaces that display evidence of significant scouring; 3) traces are ornamented; and 4) traces are found within incipiently cemented substrate.

7. Due to the gradational nature in coherence of sediment, surfaces can exhibit localized variation in substrate conditions that include: 1) variation of palimpsest expression between ichnofossils; 2) vertical variation in homogeneous sediment; 3) vertical variation in heterolithic sediment; 4) variation as a function of incipient cementation; and 5) the overall character reflects different interpretations.

8. Environmental influence plays an important role in the type of infaunal colonization, behavior of trace-makers, size of trace fossils and relationship of organisms to resumed sedimentation. The depositional setting and energy

regime are closely associated such that high-energy, proximal settings tend to be colonized by vertical structures of inferred suspension feeders or passive carnivores. While distal settings tend to be lower energy and colonized by deposit feeding, foraging and probing traces. However, there are exceptions to these generalized trends.

9. Sedimentation rate plays an important role in the nature of burrow infilling and subsequent deposition. Where sedimentation rates are low, traces tend to be passively infilled. Where sedimentation rates are high, ichnofossils tend to be actively infilled such that burrows continue from below the palimpsest surface up into the superjacent sediment, which is termed progressive palimpsesting.

10. Stratigraphy also influences the development and expression of palimpsest suites. The degree of burial, erosion and hiatus will determine whether the colonized substrate is soft, stiff or firm in nature. The rate of erosion, especially during transgression, can also determine the degree of substrate removal. Rapid transgression tends to flood an area and results in minimal erosion, while slow transgression and stillstand conditions tend to enhance erosion of underlying substrate. Lag or superjacent sediment deposition is key in preserving the palimpsest suite and may influence the development or expression of ichnofossils.

11. Palimpsest surfaces can vary spatially and temporally. Where surfaces become amalgamated, a surface becomes more temporally significant, but may diverge into less temporally significant surfaces. Spatially, surfaces can be regionally or locally variable with regards to the underlying substrate and concordant palimpsest suite.

12. The development of palimpsest softground suites involves little or no burial, compaction or erosion, and simply requires a change in the depositional conditions. Whereas stiffgrounds may form through a number of processes during continuous and discontinuous deposition. Based on modern observations, stiffgrounds can form in brackish settings due to synaeresis and expulsion of pore waters without significant compaction or burial. Firmgrounds typically form through extensive burial, compaction and dewatering of fine-grained sediment.

13. The preservation potential of palimpsest suites is generally high for

firmground suites and moderate to high for soft- and stiffground suites. Soft- and stiffground suites may undergo compaction, deformation, and reburrowing that reduce preservation potential. The contrasting infill of palimpsest suites is key in preserving these traces as mud-on-mud contacts are very difficult, if not impossible to recognize.

14. A refined terminology for palimpsest suites is proposed in that mappable, allocyclic surfaces are termed mappable palimpsest suites for soft- and stiffgrounds and the *Glossifungites* Ichnofacies for firmgrounds. Where surfaces are localized and autocyclic in origin, the suite should be referred to as localized palimpsest suites for softground, stiffground, firmground, or otherwise transitional forms. Where localized palimpsest suites are reoccurring, the strata should instead be referred to as characterized by a localized palimpsest assemblage.

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CHAPTER 10 - CONCLUSIONS

The application of ichnology furthers our understanding of ancient environments and ancient animal behaviors. This thesis utilizes various ichnological subdisciplines to build upon the underlying ichnological principles. The aspects of ichnology investigated include: neoichnology, ichnotaxonomy, ichnofacies analysis, and the study of palimpsest trace fossil suites. By studying modern animals, this can aid in identifying and explaining the occurrences of ancient ichnofossils and potential trace-makers. Ichnotaxonomy involves the classification of trace fossils which is vital in the communication between ichnologists. By identifying suites of trace fossils, we can begin to interpret the depositional conditions at the time of colonization using ichnofacies analysis. Special ichnofossil suites demarcating stratigraphic discontinuities are important in interpreting allocyclic and autocyclic events. Based on these studies, key conclusions can be drawn:

1) By studying a single organism that tends to occur in monospecific assemblages, the rate at which burrowing activities occur can be assessed and applied to the rock record. Documenting these activities can also help us explain ancient occurrences of similar biogenic structures or stratification. The bioturbation rate for a mixed population of closely related tubificids (*Limnodrilus* and *Tubifex)* was calculated at 0.050 cm/d/100,000 individuals/m^2 at 21°C. This relatively rapid reworking rate, in conjunction with selective ingestion of silt and clay particles, lead to the formation of biogenic graded bedding. This form of biogenic stratification can provide information on the biological impact, initial sediment properties, sedimentation rate, current velocities and environmental conditions in ancient settings. In addition, the burrowing rate calculated for 5 *Euzonus* (0.089 cm^3/hr) was extrapolated to populations (approximately 1400-5000 worms/ m^2) estimated from Pachena Beach, which require 70-300 days to completely rework 0.1 m^3 of sediment. Using this data, it is inferred that the producers of *Macaronichnus segregatis* in the Appaloosa Sandstone persisted in dense populations and reworked sediment at a rate that exceeded deposition during overall foreshore aggradation. Grain counting of ingested and excreted mineral grains from *Euzonus mucronata* revealed preferential ingestion of felsic grains over mafic and general avoidance of shell fragments. The preferential ingestion of felsic grains is attributed to en masse feeding in felsic-rich locales identified

through sediment probing interpreted to reflect one possible mechanism used in the construction of *Macaronichnus segregatis*.

2) Preserved activities of organisms reflect a natural system in which a standardized approach to ichnotaxonomy (i.e. separating ichnofossils based on morphology) may not be the ideal method to enhance this important aspect of ichnology. New ichnotaxobases were proposed in order to classify *Macaronichnus* ichnospecies and the *Harenaparietis* ichnogenus, which includes: grain sorting and the recognition of systematized group interactions reflected in a collective morphology. In the case of these ichnofossils, ethology is not easily separated from the diagnosis as collective morphology implies a group behavior. On the other hand, in some instances, morphology can be used to distinguish traces such as the new form of *Piscichnus* from the Snapper Point Formation.
Based on the morphology and width-to-depth ratios of these traces, coupled with the inferred substrate properties at the time of generation, *P. gregorii* were interpreted to have been constructed via hydraulic jetting. In the case of these traces, the orientation of asymmetrical traces relative to outcrop exposure may have produced the varied nature of the structures, which are thought to have been formed by actinopterygian fish, holocephalan fish or possibly a coleoid cephalopod, searching for infaunal food sources.

3) Detailed analysis of trace fossil assemblages can provide valuable information about the depositional conditions that persisted during colonization of the sediment, which may deviate from normal marine conditions. At Hamilton Lake subtle evidence of riverine input is indicated by the presence of local synaeresis cracks, soft-sediment deformation features, carbonaceous (hyperpycnal) mudstone deposits, and moderately to subtly stressed expressions of the archetypal *Cruziana* Ichnofacies and stressed expressions of the mixed *Skolithos*-*Cruziana* Ichnofacies. In this area, wave-induced processes mitigated the effects of riverine influx, and the strata is described as wave-influenced deltaic. Conversely, in the Wayne-Rosedale-Chain area, significant river-derived influx is indicated by common synaeresis cracks, sideritized intervals, convolute bedding, carbonaceous mudstone deposits, and coal fragments with subtly to strongly stressed expressions in the archetypal *Cruziana* Ichnofacies. These deposits are especially impoverished of inferred suspension-feeding structures indicating harsh environmental stresses (heightened water turbidity, rapid sediment influx, and

high concentrations of suspended sediment) suggestive of deposition in a mixed river- and wave-influenced deltaic system.

4) Palimpsest trace fossil suites can reflect stratigraphically significant surfaces, as well as demarcate autocyclically generated suites and assemblages. Palimpsest softground and stiffground ichnofossil suites can be as stratigraphically significant as suites attributable to the *Glossifungites* Ichnofacies. However, the autocyclic generation of such suites should be distinguished from the allocyclically important surfaces, which is accomplished through a revised terminology. The proposed terminology includes allocyclic surfaces demarcated by mappable palimpsest suites, and autocyclic surfaces demarcated by localized palimpsest suites that can form localized palimpsest assemblages where they repeat within a facies. The differentiation of palimpsest suites enhances our understanding and ability to interpret successions and associated stratigraphic discontinuities in both modern settings and ancient strata.

APPENDIX

In 2007, the International Code of Zoological Nomenclature (ICZN) ruled that the family Tubificidae (Order Haplotaxida) be renamed to Naididae, which is subdivided into seven subfamilies including Tubificinae (Erséus et al., 2008). Prior to this ruling, the term tubificid encompassed a wide range of oligochaetes, and previous works refer to worms of this family (and not necessarily of the new subfamily Tubificinae). It should be kept in mind that the term tubificid may not reflect worms as closely related as once thought, and are used in this study as analogs or examples to the studied organisms. In this chapter, the use of the term tubificid refers to worms within the new Naididae family especially those of the genus *Tubifex* and *Limnodrilus*.