Ichnology of a Pennsylvanian Equatorial Tidal Flat—

The Stull Shale Member at Waverly, Eastern Kansas

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COVER—Specimens of *Cruziana problematica* displaying self-overcrossing in a *Gordia*-like fashion. Presence of the *Cruziana* ichnofacies in intertidal environments represents an occurrence in water shallower than expected according to standard ichnofacies models and suggests modifications to the classic onshore-offshore ichnofacies pattern.

Contents

Figures

The group of facts now noticed gives us partial glimpses into a far distant era . . . we hear the waves breaking on the shore; we perceive currents rolling along masses of sand; the tide recedes, and ripple-marks, long ridges and furrows, sharp and distinct, appear; there too, are seen worms, some of large size, crawling over the surface or burrowing in the sand. Marks left by the sea are often fugitive,—the impressions made by one tide are obliterated by another; but here they are preserved; the sand and mud are hardened, it may be, by a warm sun breaking forth and baking the surface before the return of the tide; other deposits have covered over the markings, and buried up and preserved the organic forms; and now, when these rocks are laid bare and examined, they reveal to us that the same physical laws operated during the Carboniferous Era as at the present time, and that, though the aspects of vegetation were wonderfully different, and organic life specifically distinct, yet the animals of the period were formed according to the same types, and were subject to like conditions as those now existing.

—Tate (1859)

Abstract

Integrated stratigraphic, sedimentologic, and ichnologic analyses indicate that the Stull Shale Member (Kanwaka Shale, Shawnee Group) at Waverly (Coffey County, eastern Kansas) was deposited along a microtidal shoreline directly connected with the open sea and outside of a northeast-southwest-oriented embayment. Six major subenvironments have been identified in the lower interval of the Waverly section: sand flat, mixed flat, mud flat, supratidal paleosols, intertidal runoff channels, and fluvial channel. Paleogeographic information indicates that the position of the Waverly tidal flat was equatorial.

Trace fossils are extremely abundant and diverse in the tidal-flat deposits, where 41 ichnotaxa have been recognized. This tidal-flat ichnofauna includes *Arenicolites* isp., *Asteriacites lumbricalis*, *Chondrites*? isp., *Conichnus conicus*, *Cruziana problematica*, *Cruziana* isp., *Curvolithus simplex*, *Curvolithus multiplex*, *Diplocraterion* isp. A, *Diplocraterion* isp. B, *Halopoa* isp., *Lockeia ornata*, *Lockeia siliquaria*, *Nereites cambrensis*, *Nereites imbricata*, *Nereites jacksoni*, *Nereites missouriensis*, *Palaeophycus tubularis*, *Parahaentzschelinia ardelia*, *Pentichnus pratti*, *Phycodes palmatus*, *Phycodes* isp., *Phycosiphon incertum*, *Planolites beverleyensis*, *Protovirgularia bidirectionalis* nov. isp., *Protovirgularia rugosa*, *Psammichnites grumula*, *Psammichnites implexus*, *Psammichnites plummeri*, *Psammichnites*? isp., *Rhizocorallium irregulare*, *Rosselia socialis*, *Rusophycus* isp., *Skolithos* isp., *Teichichnus rectus*, *Trichophycus* isp., chip-shaped burrows, pelletoidal chains, small horizontal cylindrical burrows, small vertical burrows, and undetermined trackways. In addition, a monospecific suite of the myriapod trackway *Diplichnites cuithensis* is present in the fluvial deposits toward the upper part of the lower interval. Vertical changes in diversity and abundance of trace fossils in the lower interval of the Waverly section reflect an overall shallowing-upward trend.

The Waverly tidal flat is characterized by the heterogeneous distribution of biogenic structures. At a large scale, zonational distribution is shown by different associations of trace fossils in sand-, mixed- (sand and mud), and mud-flat areas of the tidal flat. High abundance and diversity of ichnofossils in sand-flat deposits record the activity of a rich benthic community. In contrast, mixed- to mud-flat deposits contain a lower diversity of biogenic structures, reflecting more stressful conditions and, to a lesser extent, low preservation potential. At a smaller scale, heterogeneity occurs within each particular zone of the tidal flat, reflecting partitioning of energy resources.

The tidal-flat ecosystem is subject to extreme changes in environmental conditions, with temperature, salinity, time of subaerial exposure, energy, and substrate representing limiting factors. Changes in salinity and temperature, together with time of subaerial exposure, are extreme in the upper-intertidal zone and diminish toward the lower-intertidal zone, leading to an increase in ichnodiversity from the mud- and mixed-flat facies to the sand-flat deposits at Waverly. Overall features of the Waverly ichnofauna suggest a moderate- to low-energy coastal setting, punctuated by high-energy erosional events. Substrate consistency was also highly variable, playing a significant role in trace-fossil morphologic variability.

Analysis of the Waverly tidal-flat deposits also provides information on stratigraphic completeness. A complex sequence of colonization events separated by erosional scouring and renewed deposition is recorded by amalgamated sandstones with preferential preservation of *Lockeia siliquaria*. These bedding planes represent time-averaged surfaces recording the work of successive bivalve communities.

Careful examination of crosscutting relationships, burrowing depth, burrow-wall sharpness, trophic types, and bauplan allows recognition of a tiering structure and ichnoguild model for the Waverly tidal-flat ichnofauna. This tidal-flat community essentially occupied shallow tiers, with traces of bivalves (*Lockeia siliquaria, Protovirgularia bidirectionalis*) and sea anemones (*Conichnus conicus*) being the deepest forms in the association.

The sedimentary units of the lower interval of the Waverly succession include four fining-upward parasequences of tidal-flat progradation, separated by successive flooding surfaces. These four parasequences make up a progradational parasequence set. A major transgressive surface separates the fluvial facies at the top of the lower parasequence set from the subtidal orthomyalinid packstones and wackestones, which form a retrogradational parasequence set. Paleosols developed at the top of the Waverly tidal-flat parasequences during regressive maxima; consequently, they do not represent sequence boundaries. The *Glossifungites* ichnofacies occurs locally as part of some high-energy transgressive surfaces.

The Waverly softground assemblage represents an example of the *Cruziana* ichnofacies in intertidal environments, which reflects shallower water than expected based on standard ichnofacies models. We suggest that the classic onshore-offshore ichnofacies replacement model should be applied only to wave-dominated systems because the opposite gradient is commonly observed in ancient and modern tide-dominated systems.

Heterogeneity, unrefined interactions, predictability, and high selective pressures may have promoted evolutionary innovations in tidal-flat ecosystems. Comparative analysis of tidal-flat ichnofaunas through time supports the view of tidal flats as sites of evolutionary innovations and subsequent offshore migration. In the Waverly tidal flats, the presence of the bivalve *Wilkingia* and relatively deep bivalve burrows suggests incipient exploitation of the deep infaunal ecospace by bivalves, long before the Mesozoic revolution. This tidal-flat, bivalve-dominated ichnofauna differs from early Paleozoic trilobite-dominated trace-fossil assemblages and from post-Paleozoic crustacean- and polychaete-dominated intertidal ichnofaunas.

Introduction

Tidal flats are complex depositional environments that are highly sensitive to physical processes of sedimentation, sea-level changes, biogenic activity, climate, and tectonism. Late Paleozoic eustatic sea-level rises caused the development of extensive epicontinental seas over the cratonic USA midcontinent (Moore, 1964; Heckel, 1977; Ross and Ross, 1987; Watney et al., 1989). Extensive Carboniferous–Permian coastlines were influenced by tides, allowing the formation of tidal-flat areas that are preserved within carbonate/siliciclastic cyclothems in the midcontinent. Paleogeographic reconstructions (Scotese and McKerrow, 1990) indicate that these cyclothems accumulated in an equatorial position.

At the Waverly trace-fossil locality, in eastern Kansas (fig. 1), tidal-flat deposits occur within the Stull Shale Member of the Kanwaka Shale, Shawnee Group (Virgilian, Upper Pennsylvanian) (fig. 2). These deposits display a suite of associated physical and biogenic sedimentary structures that provide valuable insights into the paleoecological and depositional dynamics of this ancient equatorial tidal flat. Trace fossils are exceptionally diverse, abundant, and well preserved in this facies, comprising 41 different ichnotaxa. Sandstones exposed in the lower part of the succession display bedding planes densely covered with trace fossils. Associated physical sedimentary structures (e.g., wave ripples, wrinkle marks, flat-top ripples, flaser and wavy bedding) indicate deposition in a very shallow, tidal flat. Higher in the exposure, biogenic structures are represented only by large arthropod trackways preserved at the top of a channel-fill sandstone body.

Numerous studies have focused on the animal-sediment interactions in modern tidal flats (e.g., Schäfer, 1952; Van Straaten, 1952; Reineck, 1967; Howard and Dörjes, 1972; Howard and Frey, 1973, 1975; Swinbanks and Murray, 1981; Ghare and Badve, 1984; Swinbanks and Luternauer, 1987; Frey, Hong, et al., 1987; Frey, Howard, and Hong, 1987; Frey et al., 1989; Raffaelli and Hawkins, 1996; Hild and Günther, 1999; Dittman, 1999; Dittmann et al., 1999; Bertness, 1999; Little, 2000).

★ Waverly trace-fossil locality   [▨] Shawnee Group
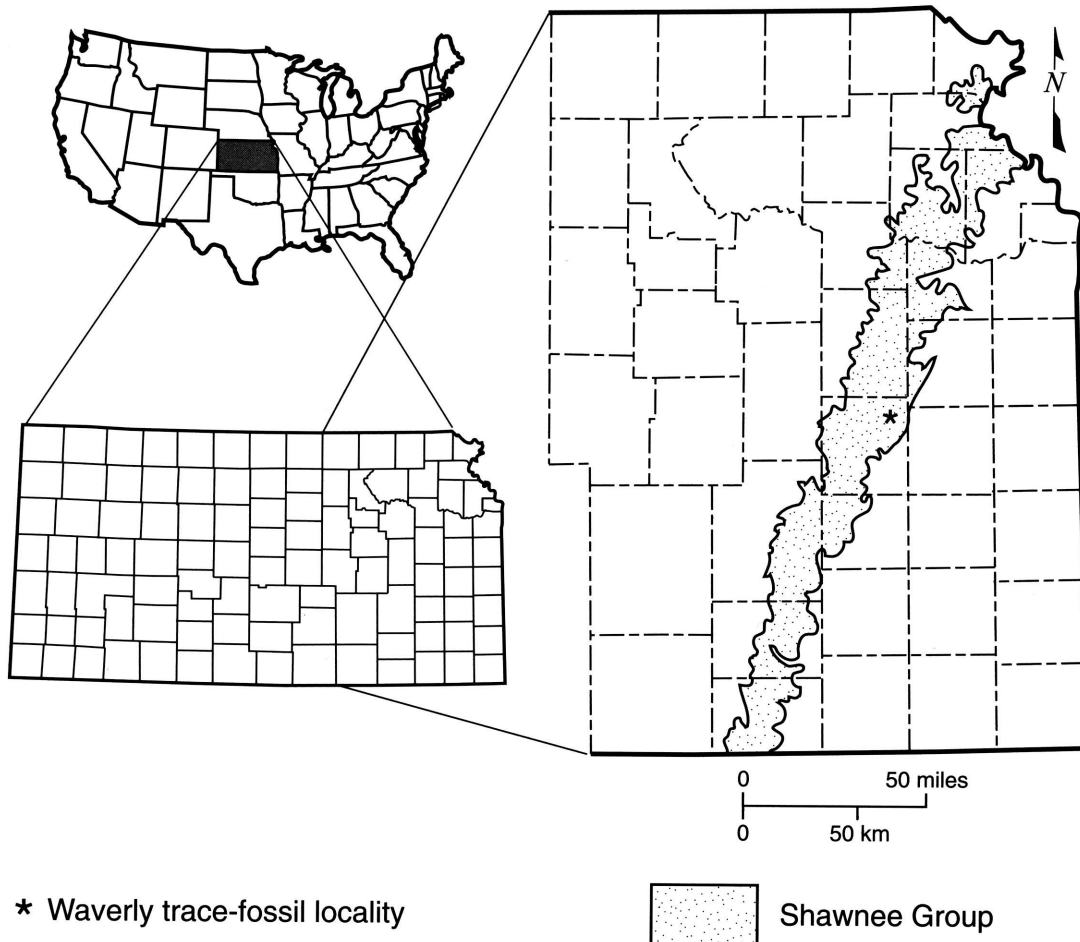
FIGURE 1—Distribution of outcrops of the Shawnee Group, showing location of the Waverly trace-fossil site.

FORMATION	MEMBER
Topeka	
Calhoun	
Deer Creek	
Tecumseh	
Lecompton	
Kanwaka	Spring Branch Limestone
	Stull Shale
	Clay Creek Limestone
	Jackson Park Shale
Oread	

(Left column: PENNSYLVANIAN | VIRGILIAN STAGE | SHAWNEE GROUP)
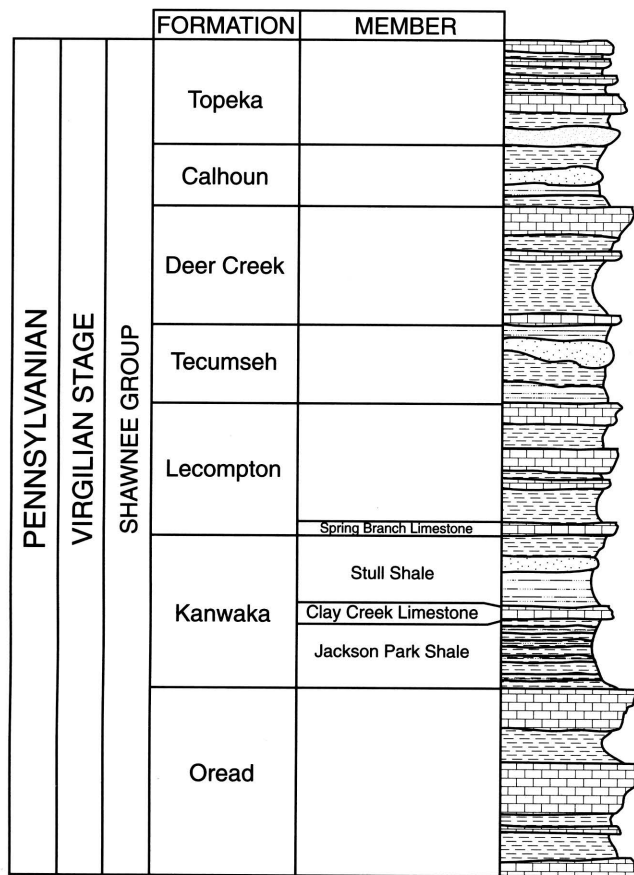
FIGURE 2—Stratigraphy of the Shawnee Group.

However, relatively few authors have attempted to apply actualistic observations and models of animal-sediment interactions to the study of ancient tidal flats (e.g., Goodwin and Anderson, 1974; Miller and Knox, 1985; Wescott and Utgaard, 1987; Simpson, 1991). The presence of trace fossils and body fossils associated with physical sedimentary structures in the Waverly succession provides an ideal opportunity to analyze the ethology of the benthic biota, to reconstruct the paleoecology of an ancient equatorial tidal-flat ecosystem, and to integrate both biogenic and sedimentologic evidence to obtain a more realistic picture of this ancient tidal shoreline. Although high-resolution data on community structure and biotic interactions are limited in the fossil record, the potential of an integrated approach in exceptionally preserved trace fossil faunas has not yet been fully explored.

Therefore, the aims of this paper are to: (1) describe and interpret the tidal-flat facies and associated deposits from the Waverly section; (2) describe the Waverly trace fossils; (3) analyze the paleoecologic and ethologic significance of this ichnofauna; (4) discuss the depositional dynamics, sea-level controls, paleotidal range, and climatic framework of this Pennsylvanian tidal coastline; (5) provide a case study of an integrated biogenic, sedimentologic, and stratigraphic approach to the analysis of coastal siliciclastic depositional systems; (6) analyze the environmental significance of the Waverly ichnofauna in the regional context of the Stull Shale Member; (7) discuss the implications of this tidal-flat assemblage for ichnofacies models of shallow-marine siliciclastic successions; and (8) analyze the importance of tidal-flat ichnofaunas from an evolutionary paleoecology perspective.

Previous Work on Pennsylvanian Ichnology in Kansas

The trace-fossil content of some Pennsylvanian units in Kansas has received considerable attention during the last three decades. One of the first series of studies was performed by Bandel (1967a,b). Bandel (1967a) analyzed the ichnofauna from two different Upper Pennsylvanian (Missourian and Virgilian) sandstones in northeast Kansas: the Rock Lake Shale Member (Stanton Limestone, Lansing Group) and the Vinland Shale Member (Stranger Formation, Douglas Group). He emphasized the different taxonomic composition of both shallow-marine assemblages and related this discrepancy to local paleoenvironmental conditions. Bandel (1967b) described and interpreted, in detail, arthropod locomotion traces from the Upper Pennsylvanian (Virgilian) Tonganoxie Sandstone Member (Stranger Formation, Douglas Group) at the Buildex quarry. He concluded that isopods and limulids made the traces, and suggested their presence close to the mouth of a fluvial valley, pioneering the idea of estuarine valley systems, subsequently developed by sedimentologists and sequence stratigraphers in the last decade.

Maerz et al. (1976) described and interpreted traces attributed to the activity of bivalves and ophiuroids from the Upper Pennsylvanian Rock Bluff Limestone Member (Deer Creek Limestone, Shawnee Group). This is one of the few publications on Pennsylvanian trace fossils from a carbonate unit in Kansas.

Hakes (1976) monographed the ichnology of four Upper Pennsylvanian (Missourian and Virgilian) units of eastern Kansas: Rock Lake Shale Member, South Bend Limestone (Stanton Limestone, Lansing Group), Stull Shale Member (Kanwaka Shale Formation, Shawnee Group), and Tecumseh Shale (Shawnee Group). He described and illustrated 41 ichnospecies and provided comments on their distribution and environmental significance. Subsequently, Hakes (1977) analyzed the trace-fossil content of the Upper Pennsylvanian (Virgilian) Lawrence Shale (Douglas Group) of eastern Kansas. Based on ichnologic evidence, he demonstrated that strata previously considered continental were actually marginal marine. His observations on marginal-marine ichnofaunas

were later summarized in a paper dealing with the diagnostic features of brackish-water assemblages (Hakes, 1985). In this paper, he also added new information on the Timberhill Siltstone Member (Stanton Limestone, Lansing Group).

More recently, Mángano et al. (1997) and Buatois, Mángano, et al. (1997, 1998a,b,c) analyzed the trace fossils of the Tonganoxie Sandstone Member at Buildex quarry. Buatois, Mángano, et al. (1997) suggested that the Buildex ichnofauna represents the activity of a freshwater biota that inhabited a tidal-influenced, fluvio-estuarine transitional environment, emphasizing the importance of ichnologic evidence in reconstructing paleosalinities in estuarine valleys. Buatois et al. (1998a) provided a systematic treatment of the Buildex traces and reanalyzed the ichnofossils originally described by Bandel (1967b), reinterpreting the supposed isopod trails as myriapod trackways. Buatois et al. (1998b) emphasized the sequence-stratigraphic significance of the Buildex ichnofauna, and Mángano et al. (1997) described superbly preserved resting and feeding traces of monuran insects and formally defined the new ichnogenus *Tonganoxichnus* for these structures. Based on ichnologic evidence, these authors reconstructed the ethology and paleobiology of these ancient wingless insects. Buatois et al. (1998c) described myriapod trackways and trails and reviewed the taxonomic status of some arthropod ichnotaxa.

Mángano and Buatois (1997) briefly discussed the variability of tidal-flat ichnofaunas formed along salinity gradients, using examples from different Upper Pennsylvanian units, including the Stull Shale Member and the Tonganoxie Sandstone Member. Selected ichnotaxa from the Stull Shale Member at Waverly also have been analyzed recently by Mángano et al. (1998), who discussed the ethologic implications of contrasting feeding strategies based on bivalve traces. These authors emphasized the importance of detailed analysis of bivalve traces as a tool to reconstruct substrate conditions and depositional history of tidal-flat strata. Mángano et al. (1999) analyzed the paleoecologic significance of the trace fossil *Asteriacites* in the Pennsylvanian of eastern Kansas and western Missouri, on the basis of specimens collected in several units, including the Stull Shale Member at Waverly.

In recent years, ichnologic studies in Kansas have expanded to include subsurface data. Buatois and Mángano (1997) and Buatois et al. (1999) analyzed trace fossils from cores of the Lower Pennsylvanian Morrow Sandstone in the subsurface of southwest Kansas. These authors emphasized the importance of detailed ichnologic analysis as a tool in refining the characterization of petroleum reservoirs. More recently, Buatois et al. (in press) discussed the importance of Morrow ichnofaunas in sequence-stratigraphic analysis.

Geologic Setting

Regional and Stratigraphic Framework

During the the mid-Pennsylvanian (late Morrowan–Desmoinesian), the collision of Laurasia and Gondwana lead to the formation of the Ouachita Mountains and the Arkoma basin as part of the tectonic events of the Wichita Orogeny (Rascoe and Adler, 1983). The Ouachita Mountains were the thrust belt, and the Arkoma basin represents the related foreland basin (Rascoe and Adler, 1983; Lillie et al., 1983; Watney et al., 1991). The Arkoma basin initially experienced high rates of subsidence and subsequently was filled with siliciclastics from the Ouachitas during the Late Pennsylvanian (Watney et al., 1991). Deposition was dominated by mass flows in a slope environment (Shanmugan and Moiola, 1995). Further north, in the cratonic areas, mixed siliciclastic-carbonate platforms occurred as a series of less-subsiding depressions, namely the Anadarko, Cherokee, Sedgwick, Salina, and Forest City basins, each separated by topographic highs (Jewett, 1951; Watney et al., 1991). In particular, the marginal-marine succession analyzed in this paper accumulated in the southern part of the Forest City basin (fig. 3), which occupied part of Missouri, Nebraska, Iowa, and northeastern Kansas (Lee, 1943; Jewett, 1951).

The Stull Shale Member is the uppermost unit of the Kanwaka Shale of Late Pennsylvanian (Virgilian) age,

which in turn is included in the Shawnee Group (Moore, 1932, 1936, 1949) (fig. 2). In southeastern Kansas, the Stull Shale Member commonly has been confused with the Doniphan Shale Member of the Lecompton Limestone (West et al., 1989). However, detailed mapping by Maples (1991) showed that many sandy shales with orthomyalinid shell beds were part of the Stull Shale Member, because they directly underlie the fusulinid-rich Spring Branch Limestone Member of the Lecompton Limestone. The Stull Shale Member consists of trace fossil-rich sandstones overlain by fossil-poor, green-to-gray shales and sandstones, and is capped by local thin coal seams in the north (Condra and Reed, 1937) or orthmyalinid-rich and chonetid-rich shell beds in the south (Baker, 1995). The Stull Shale Member is underlain by the Clay Creek Limestone Member (Kanwaka Shale) and is overlain by the Spring Branch Limestone Member (Lecompton Limestone) (Moore, 1936, 1949).

In terms of cyclothem stratigraphy, the Stull Shale Member is an "outside shale" (nearshore/terrestrial) and is part of the Oread megacyclothem (Troell, 1969; Heckel, 1977, 1985, 1986, 1994). The well-known cyclic succession of limestones and shales cropping out in Kansas represents the deposits of an epeiric sea that covered the American midcontinent during the late Paleozoic. These deposits historically have been interpreted in terms of
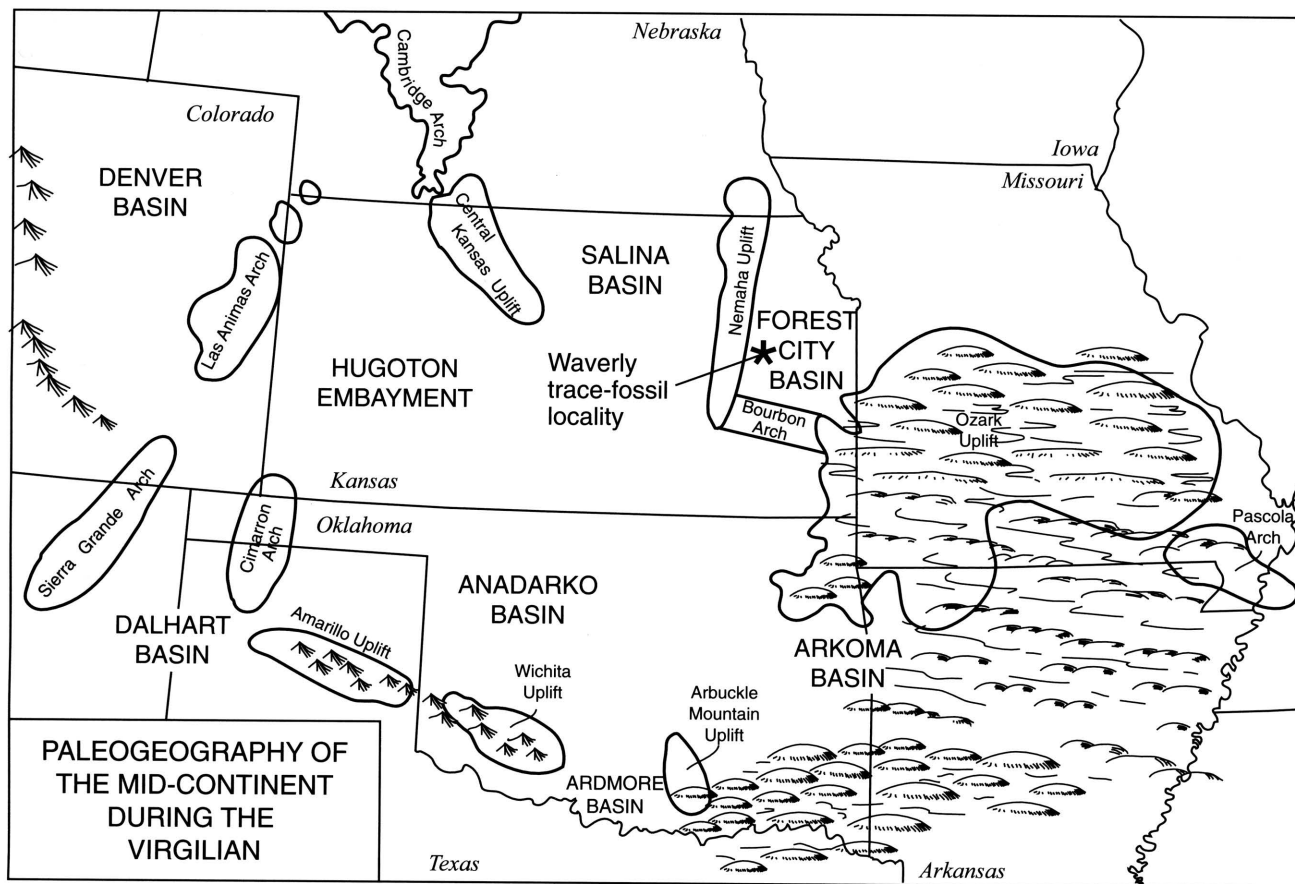
FIGURE 3—Paleogeographic map of the midcontinent during the Virgilian (modified from Rascoe and Adler, 1983).

megacyclothems and cyclothems. A cyclothem records a transgressive-regressive event. A megacyclothem can be considered as several transgressive-regressive cycles with an overall regressive trend. According to Moore's (1936) original definition, a megacyclothem is a bundle of limestones separated by shales, each having distinctive lithologies and faunal and floral assemblages. Within this framework, limestones record open-marine stages, and shales may be either fully marine (inside shale), or restricted- to nonmarine (outside shale).

Outside shales usually have been interpreted as coastal, deltaic to nonmarine deposits, recording maximum regression (Heckel, 1985; Watney et al., 1989). Common features of outside shales are abundant plant fragments, coal seams, a sparse, low-diversity marine assemblage, thin limestones, paleosols, blocky mudstones, and channel sandstones. Although considered an outside shale, the Stull Shale Member is only partially regressive and documents a more complex history.

Outcrop Locality

This study focuses on a succession of the Stull Shale Member near the town of Waverly, Coffey County, Kansas (SW NW sec. 19, T. 19 S., R. 16 E.) (West et al., 1989). The base of the member is covered and the succession capped by the Spring Branch Limestone Member (fig. 4). At this locality, the Stull Shale Member is 5.80 m thick. Detailed facies analysis is restricted to the lower 2.75 m of the exposure, where trace fossils are preserved in tidal-flat and related facies. The upper interval of the Stull Shale Member at Waverly consists of 3.05 m of shales and orthomyalinid (bivalve) packstones and wackestones of subtidal origin, which record the onset of a transgressive event that culminated with the deposition of the overlying Spring Branch Limestone Member. Orthomyalinid bivalve shells in this unit have been extensively affected by bioerosion, displaying borings by acrothoracican barnacles, polydorid worms (ichnogenus *Caulostrepsis*), and ctenostomatid bryozoans (Baker, 1995). The orthomyalinid valves also provided a substrate for an encrusting biota,
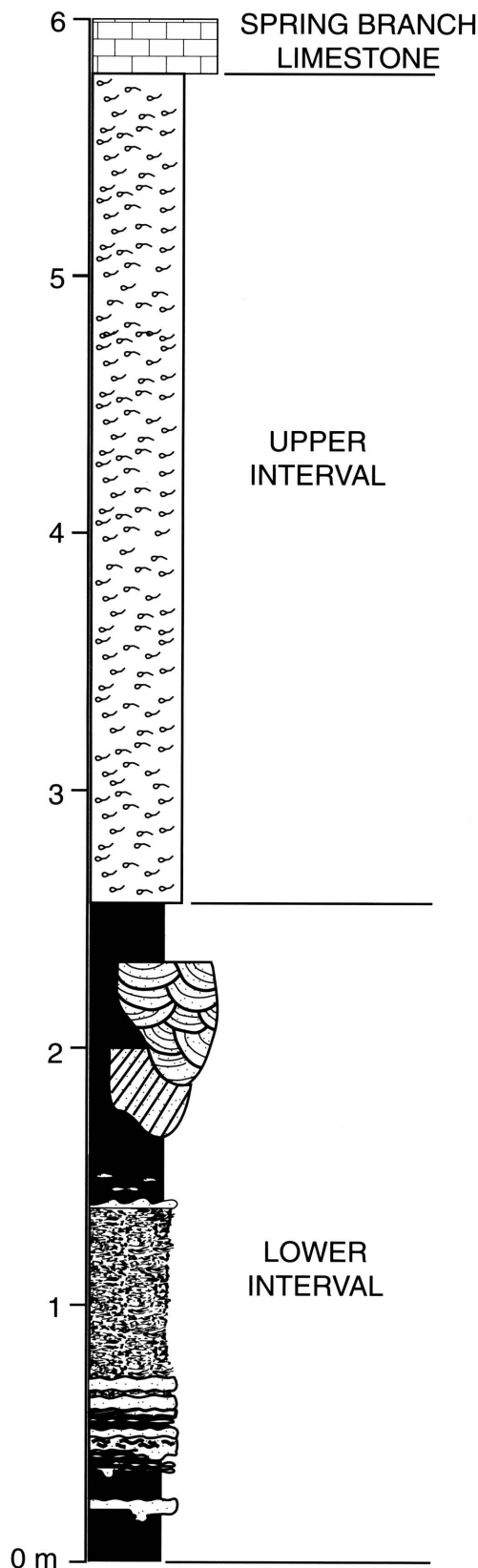
FIGURE 4—General stratigraphic column of the Stull Shale Member, Kanwaka Shale, at the Waverly trace-fossil site. See fig. 5 for legend.

including algae, the fistuliporid bryozoans, *Osagia*, and the brachiopods *Leptalosia* and *Derbyia* (Baker, 1995). This upper part of the Stull Shale Member at Waverly has been analyzed in detail by Baker (1995) and West et al. (1996).

Sedimentology

The lower interval of the Stull Shale Member at Waverly is subdivided into four vertically stacked parasequences (PA to PD), separated by transgressive surfaces (TS1 to TS4) (fig. 5). These parasequences are described below, from base to top. Each parasequence has been divided into facies units. In facies descriptions, we use the terminology of Allen (1968) for crest ripple patterns, Reineck and Wunderlich (1968) for heterolithic bedding, Dzulynski and Walton (1965) for sole marks, Myrow (1992) for gutter and pot casts, and Retallack (1990) for fossil soils. Density of trace fossils in bedding planes is expressed using the index of Miller and Smail (1997). Representative slabs with sedimentary structures have been reposited at the Kansas Geological Survey in Lawrence, Kansas.

Parasequence A

The base of this parasequence is not exposed and only the top of the package is observed. A mud-dominated heterolithic facies is the only unit recognized.

Unit A1—Mud-dominated Heterolithic Facies

DESCRIPTION—The lower part of the Waverly sequence consists of a 40-cm-thick mudstone-dominated heterolithic unit that can be observed only when the stream bed is dry (fig. 6). The base of this unit is not exposed. Unit A1 consists of gray, structureless mudstones intercalated with heterolithic intervals displaying lenticular bedding with single flat lenses of sandstone, and wavy bedding in the upper part. Small, short (less than 1.5-cm-long) groove marks are present on the soles of wavy sandstone beds. A thin (2–4-cm), laterally persistent (at the scale of about 20 m), sharp-based, very fine grained sandstone unit with flat-top ripples (fig. 7A) and sinuous wrinkle marks (also known as runzelmarken or Kinneya) (fig. 7B–D), forming honeycomb-like structures that are patchily distributed between relict and discontinuous ripple troughs, occurs in the upper part of the interval. Although locally amalgamated to form a single bed, this sandstone unit actually consists of a basal bed with wrinkle marks and an upper bed with relict ripple troughs.

Gutter and pot casts are the most striking features of the mud-dominated heterolithic facies, and they are particularly abundant in the upper levels of this unit (figs. 8A–B, 9A–D, 10A–D, 11A–D, and 12). Although preserved in situ, they more commonly are found as float.
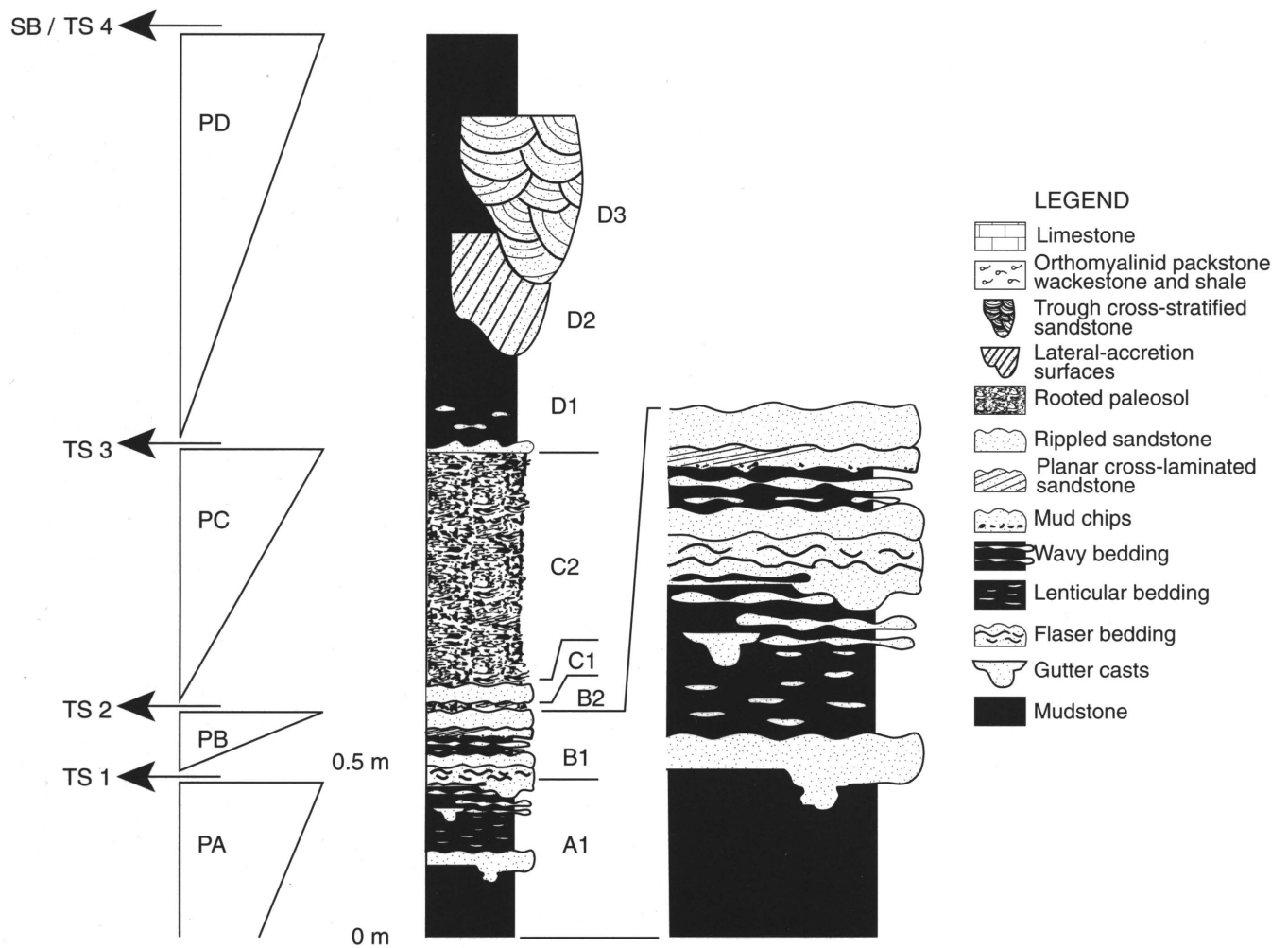
FIGURE 5—Detailed sedimentologic log of the lower interval of the Stull Shale Member at the Waverly trace-fossil locality, showing parasequences, transgressive surfaces, and depositional units discussed in the text. PA to PD = parasequences A to D. TS1 to TS4 = transgressive surfaces 1 to 4. TS4 also is a sequence boundary.
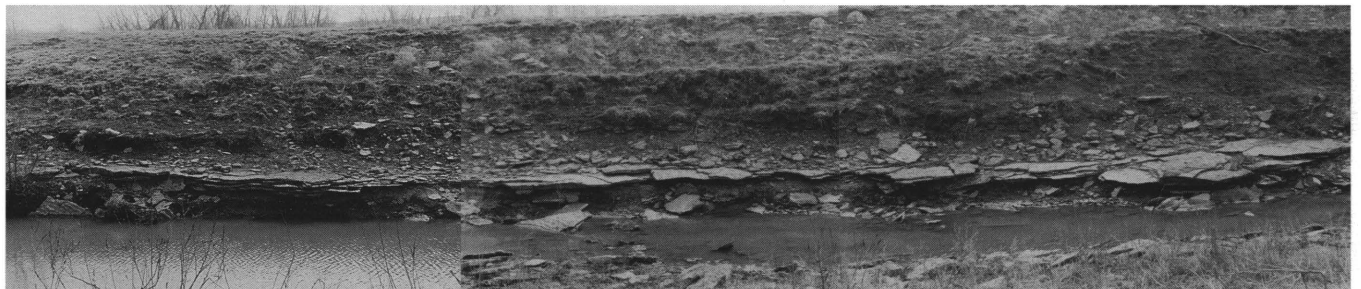
FIGURE 6—General view of tidal-flat deposits at Waverly. Note laterally persistent sand-flat facies (unit B1) overlying mud- to mixed-flat facies (unit A1).
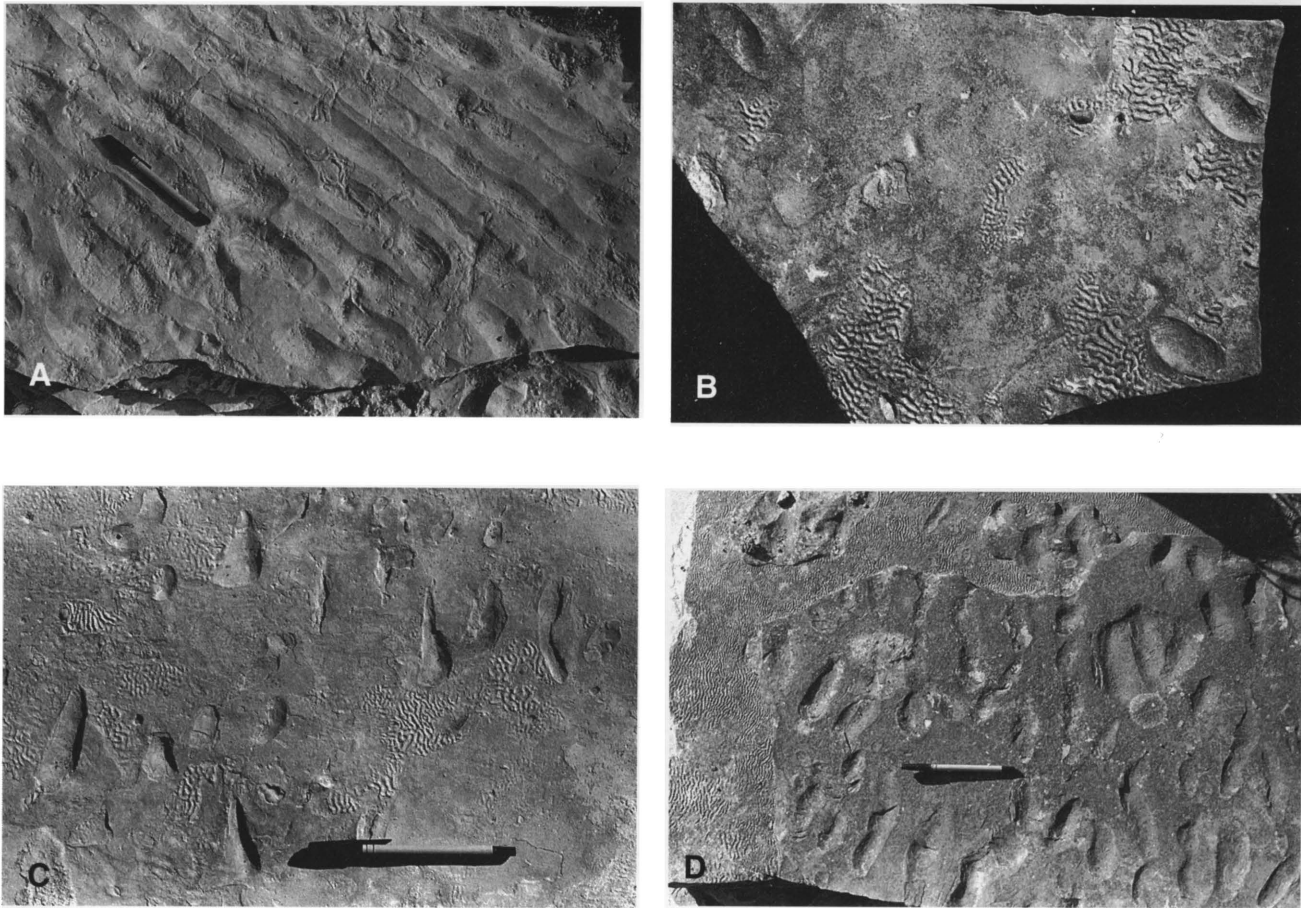
FIGURE 7—Bedding-plane physical sedimentary structures in unit A1. **A.** Flat-top ripples. **B.** Parallel oriented relict troughs and patchily distributed wrinkle marks. × 0.27. **C.** Relict troughs and associated, patchily distributed wrinkle marks. Note subparallel orientation of relict troughs. **D.** Relict troughs and more extended wrinkle marks. Pen length is 150 mm.

These erosive structures are diverse in morphology and size. Most of the gutter and pot casts are sand filled, but a few show a distinctive coarse-grained shell lag. Gutter casts commonly are connected to the overlying sandstone unit (fig. 8A–B) or to thin sandstone beds in unit A1. However, some isolated gutter casts (i.e., unconnected to overlying sandstone layers) also are present. Some of these isolated gutter casts are very wide and relatively shallow, resembling small sand lenses, but are distinguished by erosional sole marks at the base. Ripple cross lamination is by far the dominant internal sedimentary structure, but low-angle cross lamination and parallel lamination also have been observed (fig. 9A–D). Both asymmetrical and symmetrical ripples are present. Oscillatory climbing ripples with a high angle of climbing are very common (fig. 9D). Some gutter casts exhibit low-angle truncation surfaces (fig. 9B–C). Although the fill is predominantly a fine-grained sand, ripples are commonly mud-draped. The upper bedding surface commonly is covered with oscilla-tion ripples that may display flat ripple tops or wrinkle marks (fig. 10B, D). In a few cases the top has been almost

completely flattened with development of relict troughs (fig. 10D). Of 23 gutter casts observed, 18 (78%) display ripple crests perpendicular or forming an angle of 65∞–80∞ with the orientation of the gutter axis (fig. 10A–D). In the other five cases (22%), however, the gutter axes are almost parallel to the uppermost ripple crests. Cross sectional shapes range from symmetrical to strongly asymmetrical, from shallow to very deep (fig. 9A–D). Along its course, the cross sectional shape of a gutter may vary substantially (fig. 12A–C). The most common morphologies are U-shaped, V-shaped, square-shaped (i.e., flat-based), and semicircular. Steep, almost vertical and overhanging walls are common. Gutter depth ranges from 8.5 to 86.8 mm, but typically it is around 50 mm. Width is 9.3 to 60.5 mm. Plan-view geometry varies from straight to highly sinuous (fig. 11A–B). In general, smaller, shallower structures are more sinuous. Many gutters display angular turns in the axial direction (fig. 11B). Second-order gutters may join a main course or two gutters may converge forming a deeper structure (fig. 12C). Second-order gutters are, in many cases, smaller and
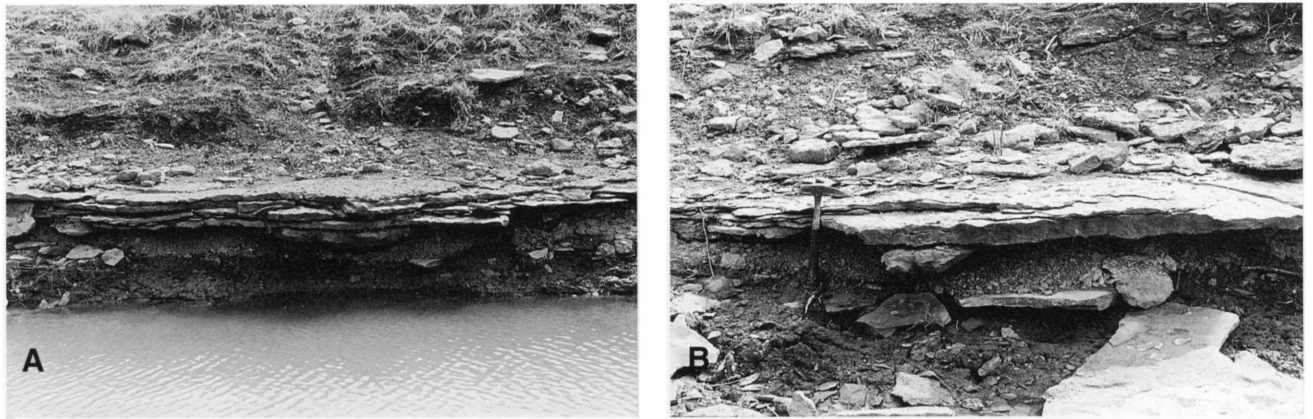
FIGURE 8—Close-up of mud- to mixed-flat facies (unit A1) overlain by sand-flat facies (unit B1). **A**. Large gutter cast incised into the fine-grained facies and connected to the overlying sandstone bed. **B**. Small gutter cast connected to a sandstone bed. Note thin, lenticular sandstone layer interbedded with the fine-grained deposits. Length of hammer is 33.5 cm.
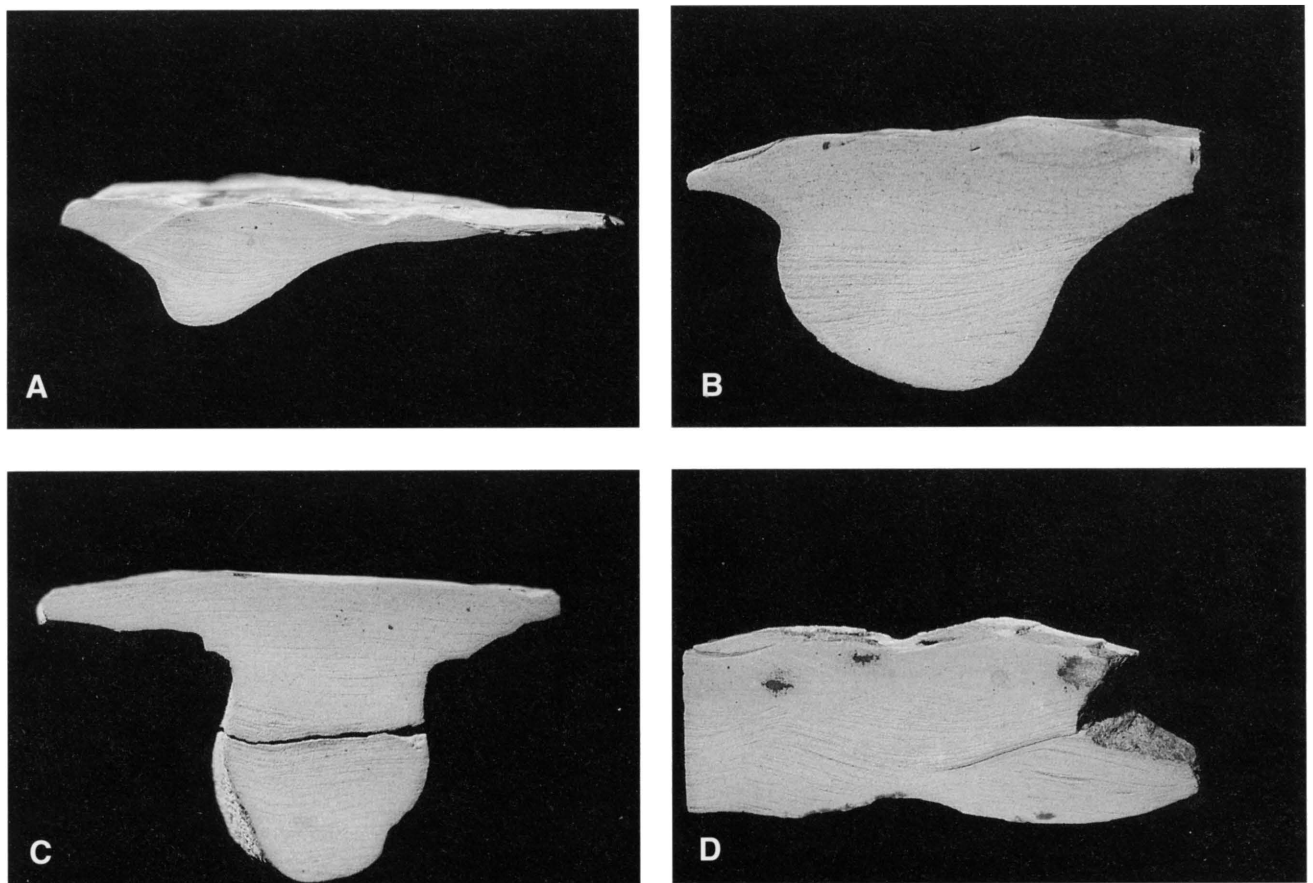
FIGURE 9—Cross sectional views of gutter casts. All photos × 0.28. **A**. Shallow, slightly asymmetrical gutter cast. Note rippled top with crest axes almost parallel to gutter axis. **B**. U-shaped, slightly asymmetrical gutter cast. Note truncation surface close to the base of the gutter and mud drapes. **C**. Deep, U-shaped, symmetrical gutter cast. Note vertical walls and mud parting (where the sample is broken) in the middle of the gutter. **D**. Longitudinal cut of a gutter cast showing oscillatory climbing cross-lamination with high angle of climbing.
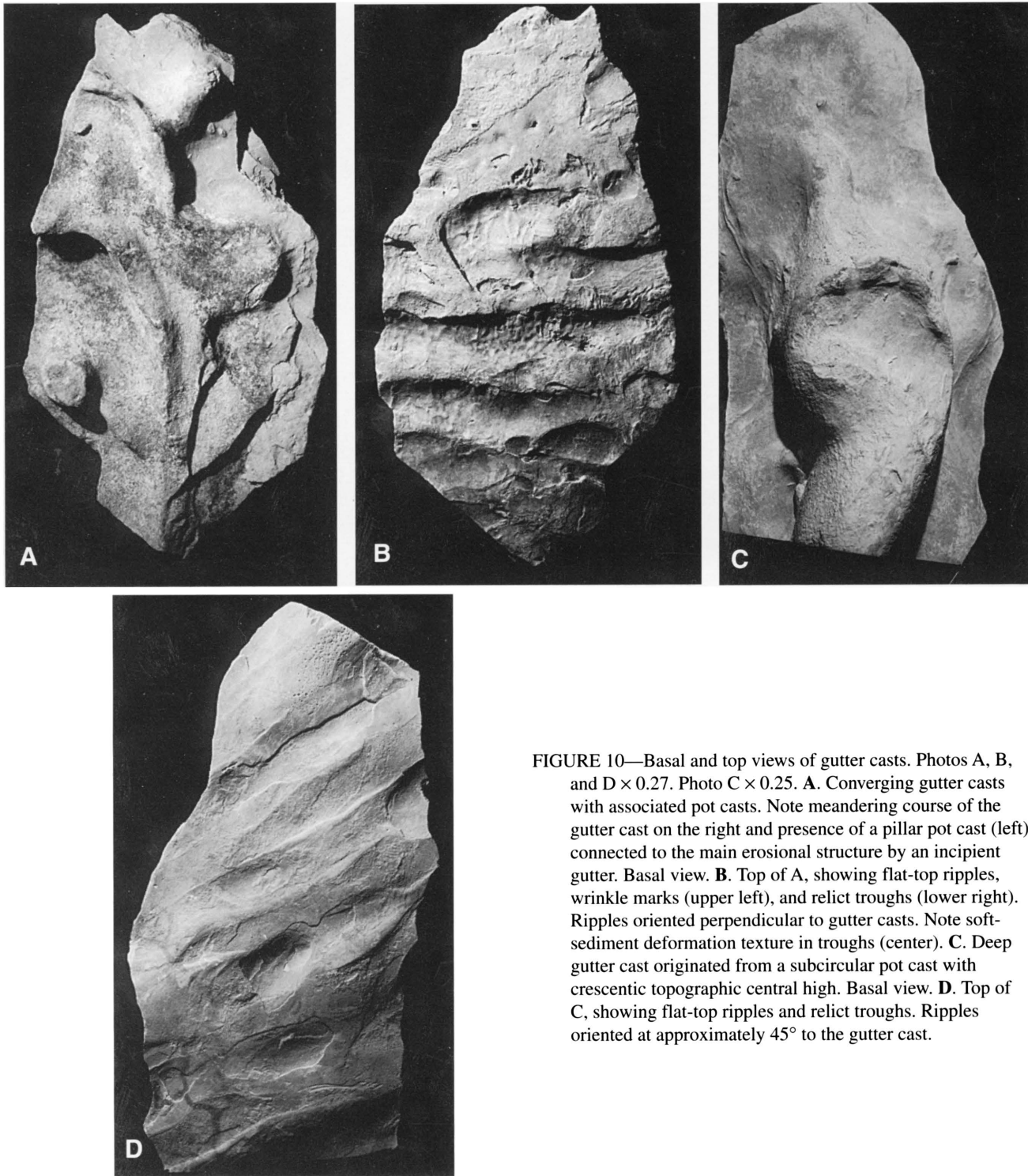
FIGURE 10—Basal and top views of gutter casts. Photos A, B, and D × 0.27. Photo C × 0.25. **A.** Converging gutter casts with associated pot casts. Note meandering course of the gutter cast on the right and presence of a pillar pot cast (left) connected to the main erosional structure by an incipient gutter. Basal view. **B.** Top of A, showing flat-top ripples, wrinkle marks (upper left), and relict troughs (lower right). Ripples oriented perpendicular to gutter casts. Note soft-sediment deformation texture in troughs (center). **C.** Deep gutter cast originated from a subcircular pot cast with crescentic topographic central high. Basal view. **D.** Top of C, showing flat-top ripples and relict troughs. Ripples oriented at approximately 45° to the gutter cast.

shallower than the gutter to which they join. Several gutters may coalesce, forming an irregular sandstone lense. Pot casts are found in close association to gutters (fig. 11A–B). In most cases, gutter casts originate from pot casts. In other cases, pot casts are connected to the main gutter by an incipient, short, shallow secondary gutter (fig. 12C). Pot casts commonly are circular to crescentic in shape. Some pot casts are deep and pillar-shaped, but most are relatively shallow structures adjacent to gutters. Most gutters exhibit sole marks along the sides and bases. Tool marks, subparallel or oblique to the main axis, are very common. Flutes and grooves are less common. Some gutters display flute marks diagonal to the gutter axis (fig. 11D). *Cruziana problematica*, which occasionally is present on the sides and bases of gutter casts (fig. 11C), have been found as much as 33.5 mm below the uppermost ripple top.

A moderate density (degree 3 to 4) of locomotion (*Cruziana problematica*, *Protovirgularia rugosa*) and grazing trace fossils (*Psammichnites grumula*) are pre-
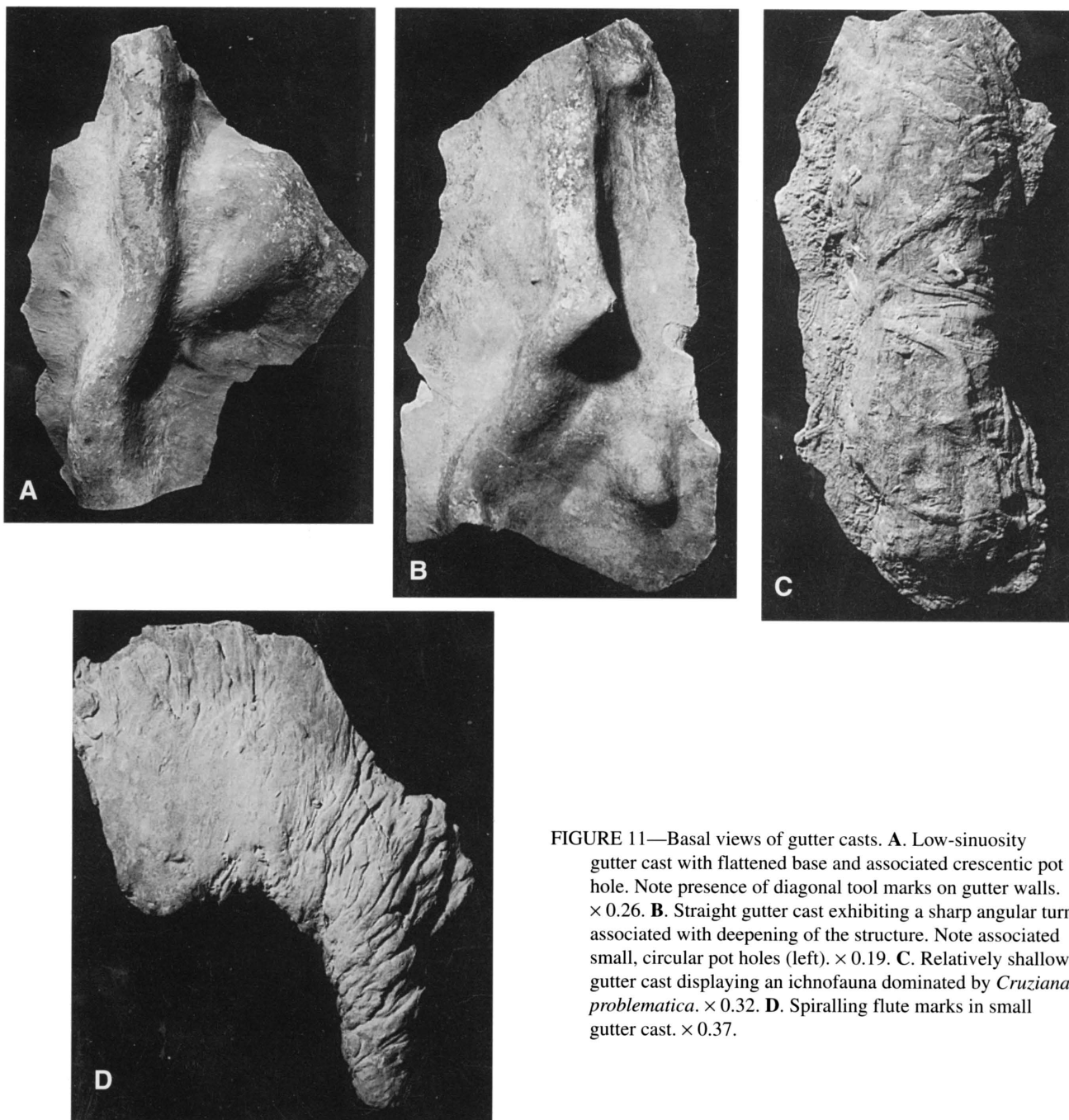
FIGURE 11—Basal views of gutter casts. **A**. Low-sinuosity gutter cast with flattened base and associated crescentic pot hole. Note presence of diagonal tool marks on gutter walls. × 0.26. **B**. Straight gutter cast exhibiting a sharp angular turn associated with deepening of the structure. Note associated small, circular pot holes (left). × 0.19. **C**. Relatively shallow gutter cast displaying an ichnofauna dominated by *Cruziana problematica*. × 0.32. **D**. Spiralling flute marks in small gutter cast. × 0.37.

served on the soles of the sandstone intercalations. Trace fossils are rare within the mudstones; only some specimens of thinly lined *Palaeophycus tubularis* filled with sand piped down from the overlying facies were observed.

INTERPRETATION—Unit A1 records, for the most part, fallout deposition of mud in a low-energy setting. Vertical accretion of fine-grained sediment was, however, punctuated by tractive sand deposition. Alternation of mud fallout and sand traction is best recorded in the upper part of unit A, where mudstones alternate with lenticular- and wavy-bedded intervals. Tool marks on the soles of the wavy-bedded sandstones indicate erosion by objects dragged through the muddy substrate by a current. Local increases

in energy also are reflected by the presence of a distinctive suite of physical sedimentary structures in the thin sandstone unit that occurs in the upper part of the facies A interval. The sharp base of the sandstone bed suggests episodes of relatively strong and erosive currents. Erosion was followed by bedload-flood transport leading to deposition of a rippled sandstone bed, whose crests subsequently were flattened during shallow-water ebb outflow, allowing only the preservation of the structure herein referred to as "relict troughs" (fig. 13A–C). Parts of the troughs were filled by sand flowing from the adjacent ripple crests during emergence, as evinced by substrate deformation in ripple troughs (cf. Reineck and Singh,
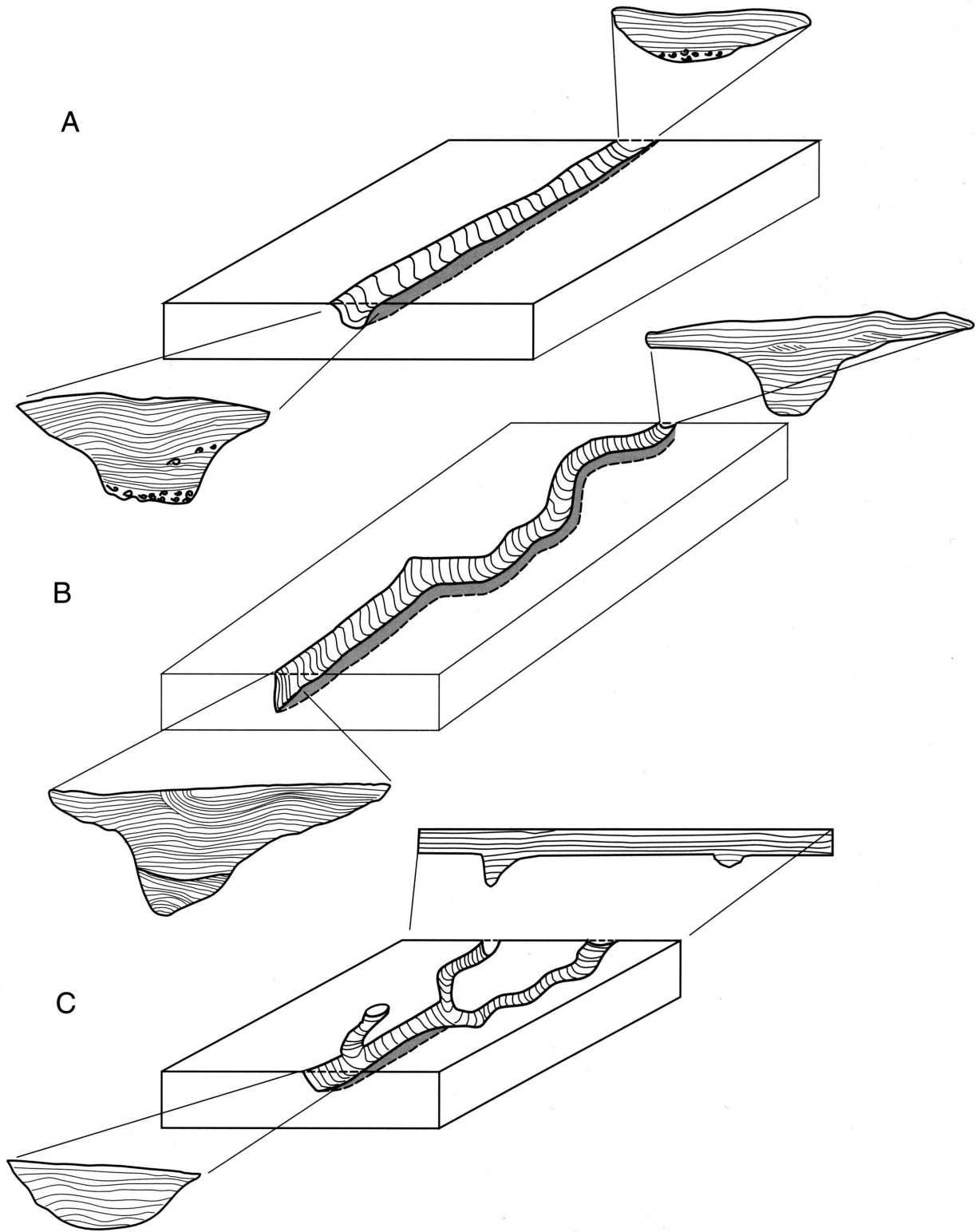
FIGURE 12—Three-dimensional reconstruction of gutter and pot casts showing plan views and changes in cross sectional morphology along the axes. **A**. Straight, flat-based gutter cast with a basal shell lag. **B**. Low-sinuous gutter cast showing changes from symmetrical to asymmetrical profiles and internal truncation surfaces. **C**. Bifurcated gutter cast with associated pot cast. Note deepening of the structure in the direction of flow.

1980). The origin of wrinkle marks has been a matter of debate. Reineck (1969) interpreted these structures as produced by wind during stormy weather. Seilacher (1982a) suggested that similar structures referred to as "Kinneya" are related to differential dewatering and settling during storm deposition. A detailed study by Allen (1985) supports an origin related to soft-sediment loading, although not necessarily associated with storms, but with subaerial emergence in intertidal areas. More recently, formation of wrinkle marks was linked to microbial mats (Schieber, 1989, 1990, 1999; Gehling, 1991; Pflüger, 1999; Hagadorn and Bottjer, 1999). These authors concluded that wrinkle marks result from microbial binding that increases the cohesiveness of sediment grains, precluding removal by erosion. The presence of wrinkle marks in these deposits suggests development of microbial mats and, therefore, stabilization by microbial binding may have played a significant role in the generation of the associated "relict troughs." It has been suggested that microbial structures, though ubiquitous in Proterozoic strata, became later restricted to hostile environments, such as upper intertidal and supratidal zones, as a consequence of increased bioturbation in shallow, normal-marine biotopes (Seilacher and Pflüger, 1994; Seilacher, 1999).

In any case, the association of flat-top ripples, relict troughs, and wrinkle marks clearly indicates extremely shallow water conditions and intermittent subaerial exposure, and rules out deposition below wave base (Häntzschel and Reineck, 1968; Reineck, 1969; Allen, 1985). Available evidence suggests that unit A1 is an intertidal, mud- to mixed-flat deposit. This interpretation also is supported by the scarcity of megafauna, which would be expected in subtidal deposits. The upward transition of mudstones to lenticular- and wavy-bedded sandstones indicates an increase in hydrodynamic energy. The presence of wrinkle marks in deposits that contain very few trace fossils is consistent with the notion that bioturbation inhibited development of microbial mats.

Absence of lateral-accretion bedding (inclined-heterolithic stratification; Thomas et al., 1987) indicates the existence of stable tidal gullies. In these cases, muddy-intertidal deposits are essentially horizontally bedded and channel-fill sequences are not important volumetrically (cf. Alexander et al., 1991). The abundance of gutter and pot casts suggests that these cut-and-fill structures probably played a major role in intertidal runoff. Two events can be recognized in the formation of a gutter: the initial erosive cut and the subsequent fill (Myrow, 1992). The time between cut and fill is difficult to assess. The wide variety of morphologies and the structure of fills at Waverly suggest that more than one mode of generation was probably involved. Except for a few gutters with shell lags, sediment fill indicates deposition under a lower-flow regime. Internal sedimentary structures record the presence of oscillatory and combined flows. Gutters or potholes with steep or overhanging walls are commonly interpreted as early-filled structures (Goldring and Aigner, 1982) that

most likely were carved by a storm event and filled during the waning phase. Spiraling patterns recorded by diagonal and oblique tool and flute marks on gutter walls indicate the development of helical flows. Although most gutters seem to record a single event of deposition, some fills exhibit internal truncation surfaces or significant mud partings, suggestive of cessation of sedimentation and re-activation (i.e., multiple-event gutters) (fig. 9B–C). Trace fossils are relatively rare on gutter walls and bases. Most gutters are over 30 mm deep and sedimentary structures (e.g., high-angle climbing ripples) indicate rapid accumulation under thick sediment-laden flows. During the depositional phase, high sedimentation rates may have inhibited colonization. Once the erosive structures were overfilled, they were probably beyond the range of bioturbation of most of the animals (cf. Myrow, 1992). When trace fossils are present, gutters are shallower than 3.5 cm and the structures are clearly not fluted, suggesting an origin subsequent to gutter erosion.

The presence of thinly lined, open burrows filled with sand from the overlying unit suggests a relatively cohesive muddy substrate. Low trace-fossil diversity is related to both taphonomic and paleoecologic controls. Absence of well-exposed bedding planes and the scarcity of sandstone interbeds (particularly in the lower part of the interval) make preservation and/or recognition of trace fossils difficult. However, even where sandstone soles are available for careful examination, trace-fossil density is remarkably lower than in unit B1 and ichnodiversity is very low. These features indicate a stressful environmental setting, perhaps from periodic desiccation, high temperature, rapid salinity fluctuations, or some combination of these factors.

Parasequence B

Parasequence B is up to 35 cm thick and consists of two units: a sand-dominated heterolithic facies (unit B1) and a mottled mudstone facies (unit B2).

Unit B1—Sand-dominated Heterolithic Facies

DESCRIPTION—This facies is a 20-cm-thick sandstone-dominated unit overlying the mudstone-dominated unit A1. Unit B1 is represented by light-green, laterally interfingering, very fine grained sandstones separated by thin mudstone partings (fig. 6). Although the sandstone unit can be traced laterally throughout the entire exposure (approximately 150 m), individual beds (1–5 cm thick) pinch out laterally and cannot be followed for more than a few meters. Bed amalgamation is a distinctive feature of this unit. Mud chips and thin (up to 2-cm-thick, but commonly less than 1-cm) shell layers of bivalves, gastropods, and crinoid ossicles are fairly common near the base of the sandstone beds. Dominant physical sedimentary structures include both symmetrical and asymmetrical ripples, interference ripples, and flat-topped
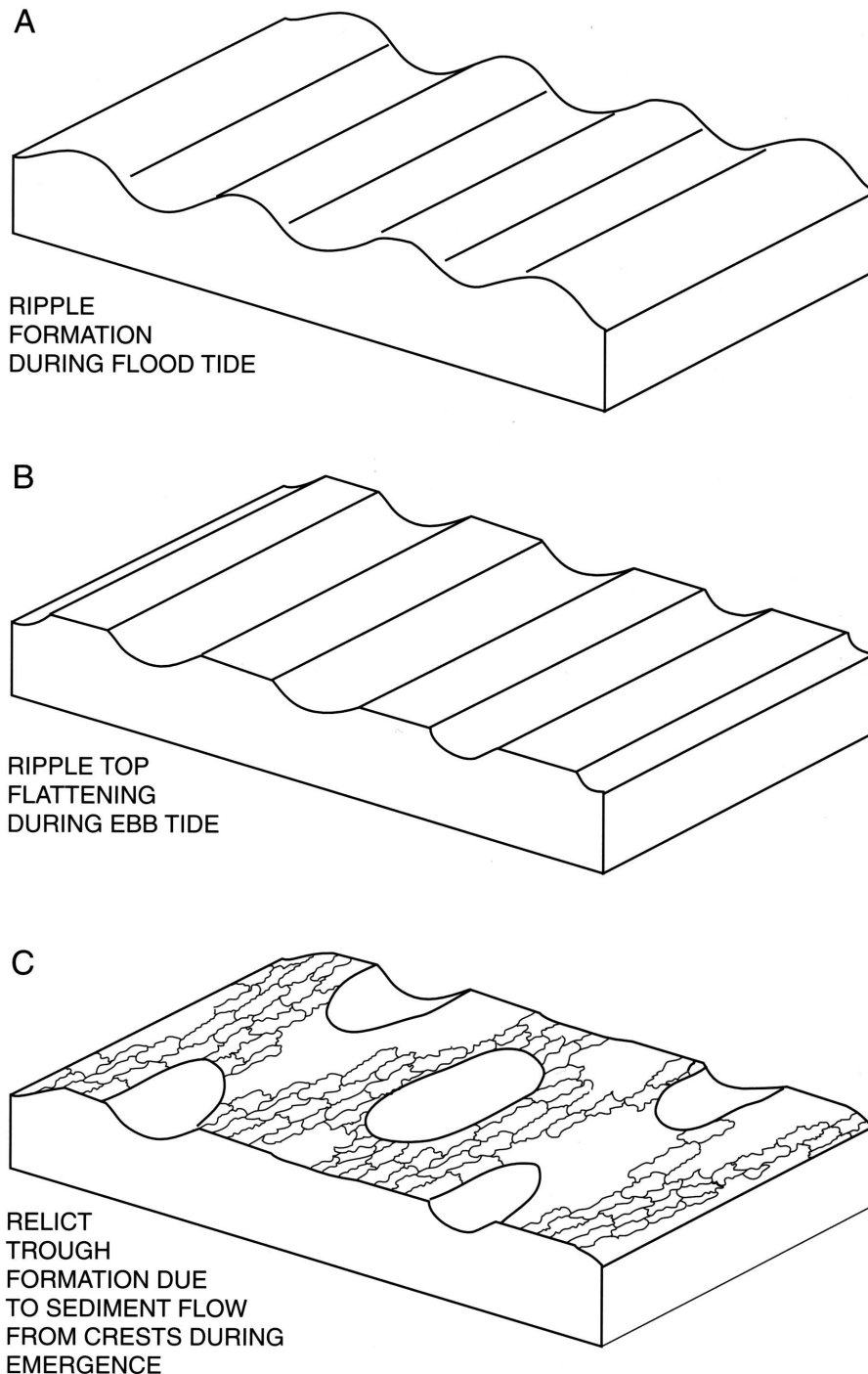
FIGURE 13—Origin of relict troughs. **A**. Generation of ripples during the flood tide. **B**. Flattening of ripple tops during the subsequent ebb flow. **C**. Stabilization of substrate by microbial binding, formation of wrinkle marks, flowing of sand from the adjacent ripple crests, increased flattening of ripple tops, and infilling of parts of the troughs during emergence.

ripples (figs. 14A–B, 15A–D). Ripple crests may bifurcate locally and include different types, including straight, sinuous in-phase, and sinuous out-of-phase. Lenticular bedding with connected flat lenses, wavy bedding, and wavy-flaser bedding are the most common bedding types. Low-angle cross lamination is present locally. Bedforms tend to show remarkable lateral variation at a scale of a few meters, forming multidirectional ripples (fig. 15A–B).

On one very well exposed bedding surface, interference ripples are replaced laterally, 2 m to the east, by discontinuous relict troughs, which in turn rapidly grade into more continuous relict troughs. Water-falling marks (fig. 16A–B) have been observed locally. Tool marks and flute marks are present on some sandstone soles (fig. 17A–B), where they occur in groups with a heterogeneous pattern of distribution. Most flute marks are of the simple conical
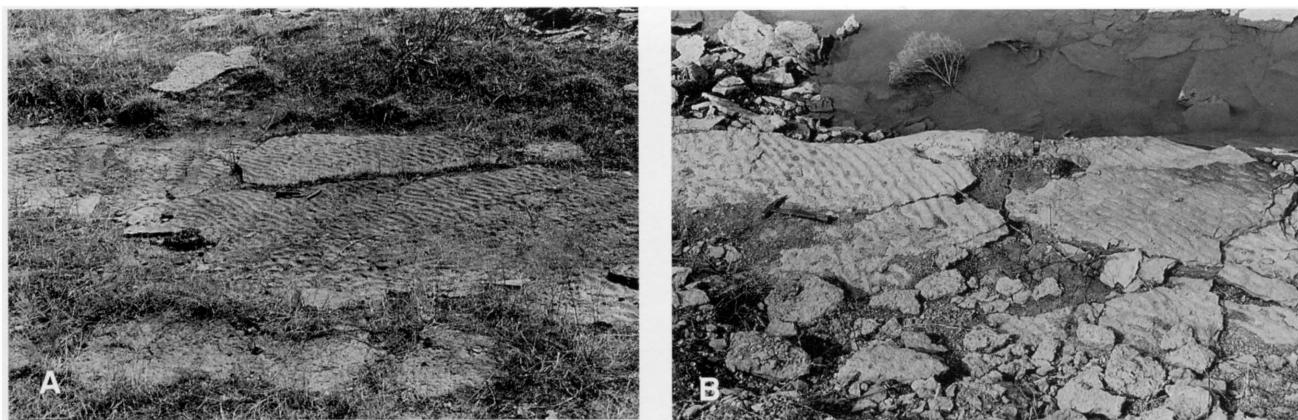
FIGURE 14—Rippled bedding planes in unit B1. **A**. Laterally extensive bedding planes with sinuous-crested ripples. **B**. Note upper level with strongly weathered sandstone tops. Hammer length is 33.5 cm.
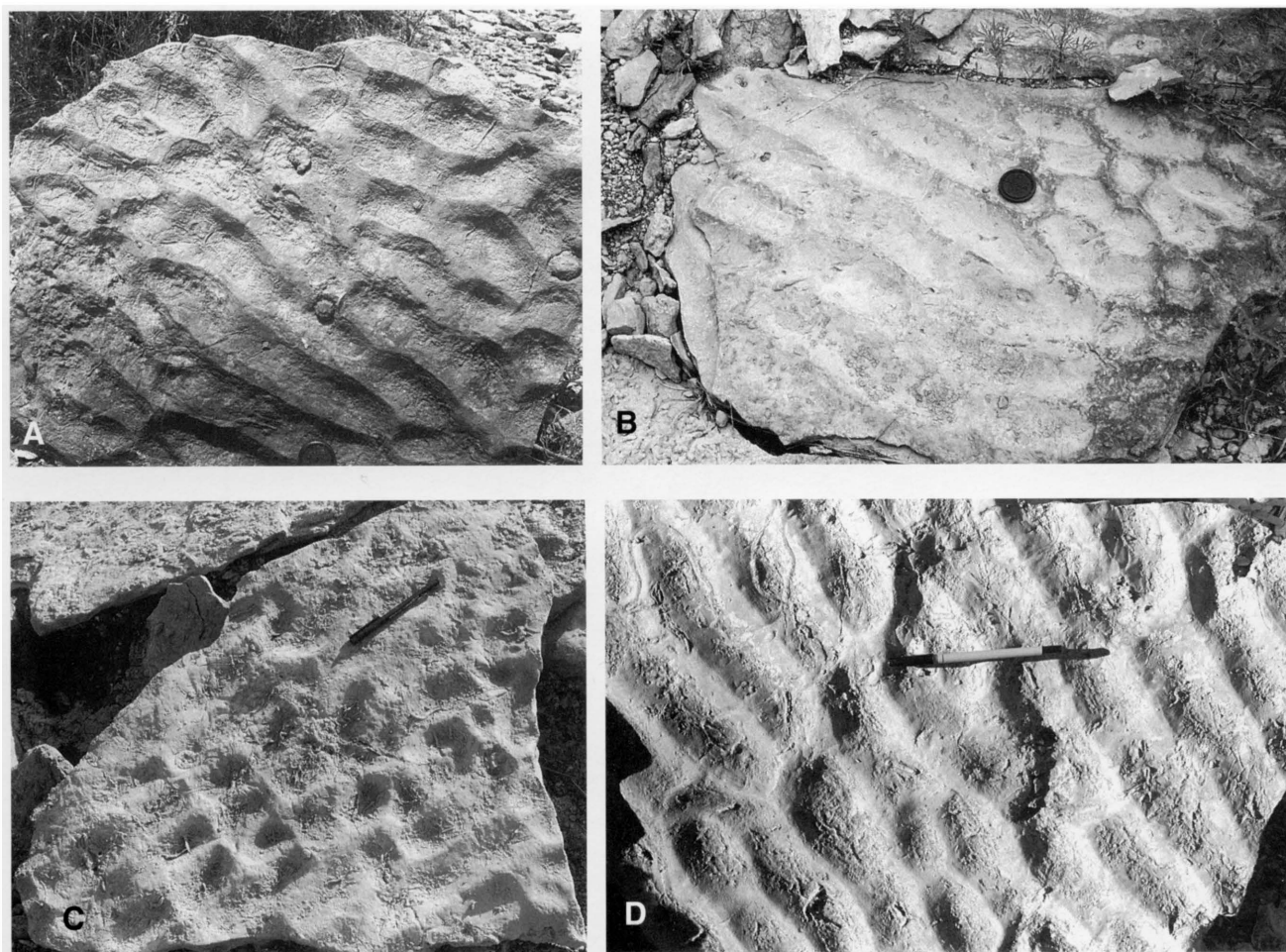
FIGURE 15—Ripple patterns in unit B1. **A, B**. Sinuous-crested ripples laterally becoming interference ripples. **C, D**. Interference ripples. Lens cap diameter is 55 mm and pen length is 150 mm.

type (the corkscrew form is less common) and range in width from 1.5 to 3.5 cm.

Soft-sediment deformation structures, including load casts and sand volcanoes, are present locally. Most load casts are small (up to 2 cm in diameter, but commonly less than 0.5 cm) and irregular in shape (fig. 17C–D). They are preserved on the bases of sandstone layers and are oriented parallel to ripple-crest trains on the tops of the sandstone beds ("load-casted ripple marks"). Sand volcanoes, up to 25 cm in width, occur at the base of this unit. A small dome at the center is surrounded by concentrically arranged rims, fringed by a circular depression and an outer lobe. They typically are associated with gutter casts eroded into the underlying unit (A1).

Desiccation cracks, consisting of irregular polygons, mostly pentagonal and quadrangular, ranging from a few millimeters to 12 cm in diameter and up to 1.5 cm deep, are present locally on the soles of sandstones (fig. 18A–B). In some cases, polygons of three different sizes are present on the same bedding plane (fig. 18B). The larger and deeper polygons occur only locally and crosscut all others. Intermediate-sized cracks consist of triangles and quadrangles and are relatively well developed. The small cracks

are irregular in shape and cover the whole surface. Irregularly branched to reticulate structures, preserved as positive reliefs, are concentrated on ripple troughs (fig. 19A–D). Large holes related to dissolution of shells are present (fig. 19D).

The uppermost rippled bedding planes of the sandstone package are characterized by prominent red mottles that become increasingly abundant and larger upward. The upper boundary of this sandstone unit is a distinctive irregular, iron-stained, weathered surface (fig. 14B). Primary sedimentary structures are hardly discernible on this surface; however, structures related to desiccation and dissolution are abundant. Root traces are observed locally (fig. 19B–C).

Horizontal trace fossils are abundant (up to degree 5) and diverse, including locomotion traces (*Cruziana problematica*, *Curvolithus multiplex*, *C. simplex*), resting traces (*Rusophycus* isp., *Asteriacites lumbricalis*), resting/feeding traces (*Lockeia ornata*), escape traces (*Protovirgularia rugosa*), dwelling structures (*L. siliquaria*, *Palaeophycus tubularis*), grazing traces (*Nereites missouriensis*, *N. cambrensis*, *N. jacksoni*, *N. imbricata*, *Psammichnites plummeri*, *P. implexus*,
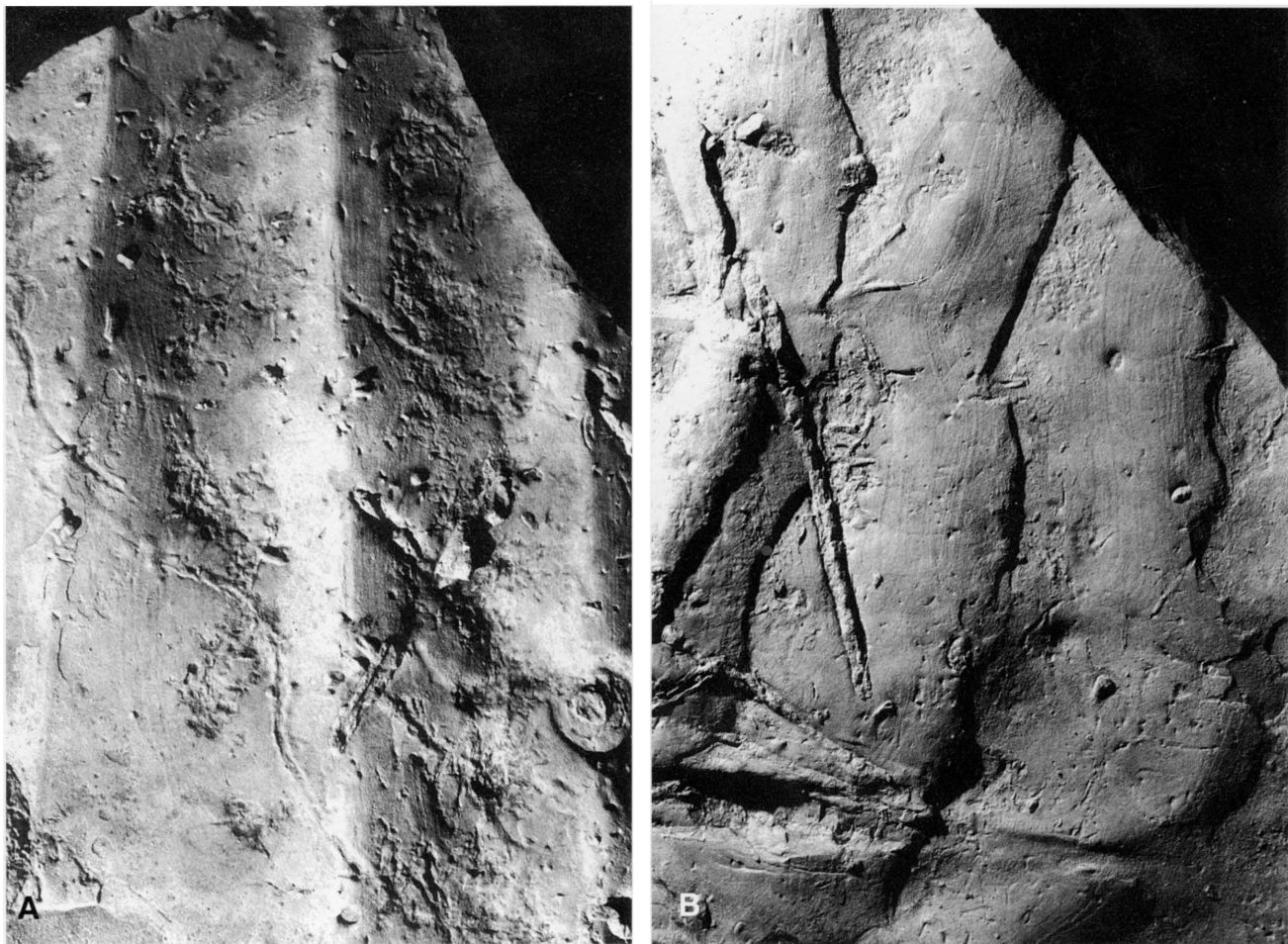
FIGURE 16—Water-falling marks in unit B1. **A**. Specimen of *Curvolithus simplex* (upper center) deflecting water-falling marks. Note shaft (lower right) with halo of deformed sediment. × 0.54. **B**. Water-falling marks associated with flat-top ripple crests and *Protovirgularia bidirectionalis*. × 0.71.
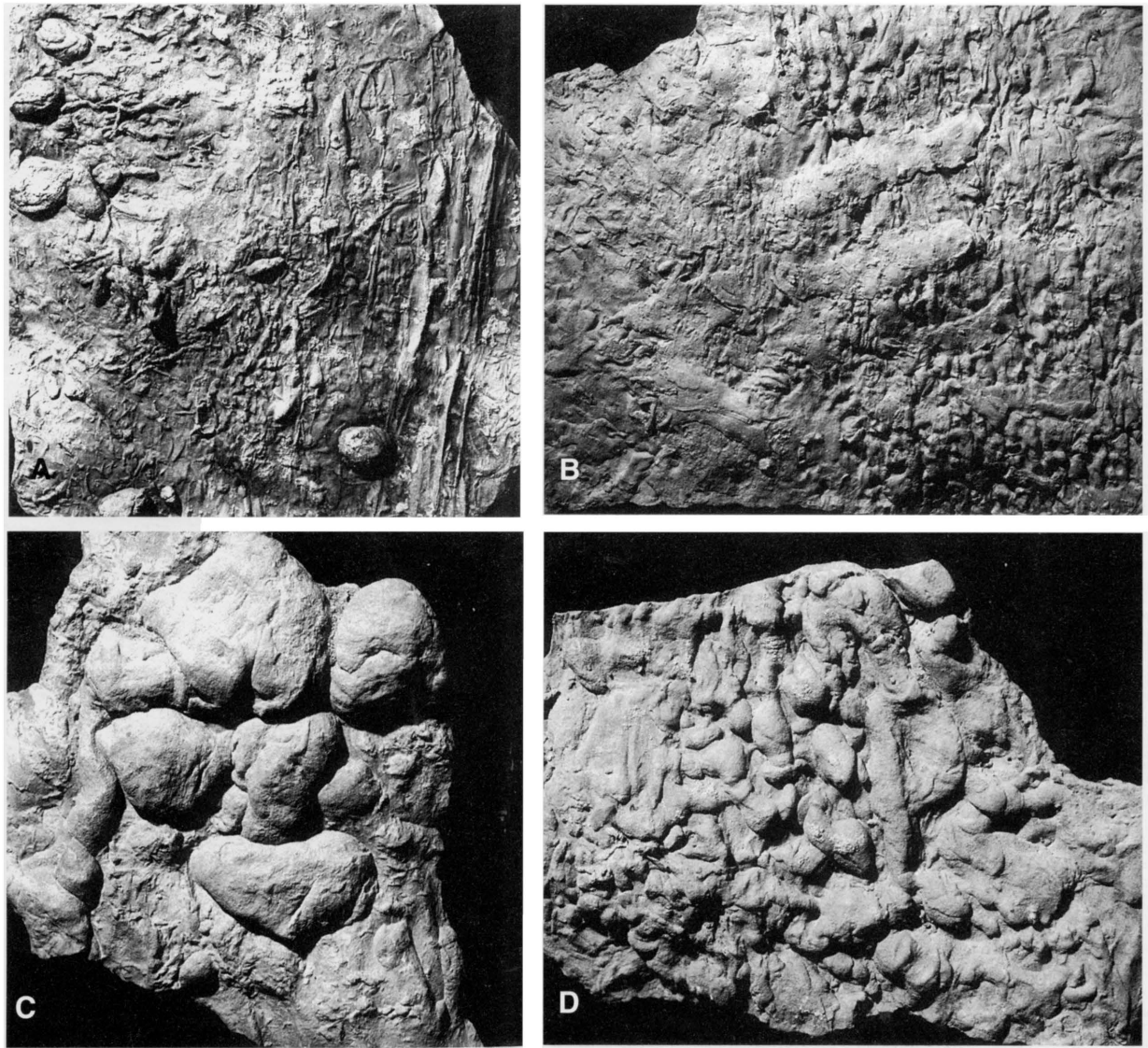
FIGURE 17—Sole marks on sandstones of unit B1. **A**. Groove marks. Note parallel orientation and associated deep bivalve burrows (*Lockeia siliquaria*). × 0.43. **B**. Adhesion structures (upper center) overprinted on load casts. Parallel orientation and fluted shape of load casts suggest that they originated from deformation of flute casts. × 0.28. **C**. Load casts. × 0.65. **D**. Load casts. × 0.71.
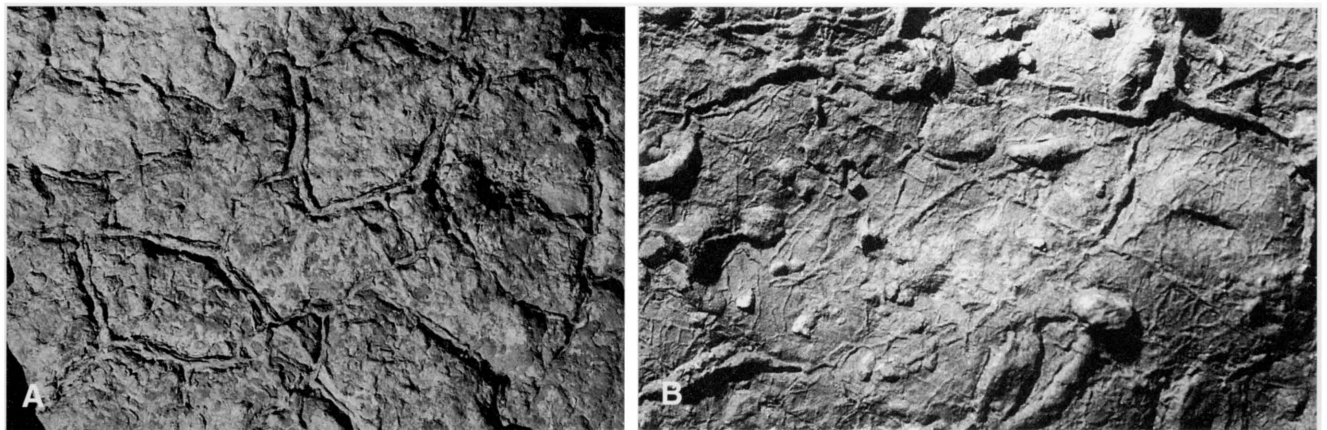
FIGURE 18—Desiccation cracks in sandstones at the top of unit B1. **A**. Large desiccation cracks. × 0.3. **B**. Three generations of desiccation cracks of different sizes. × 0.5.
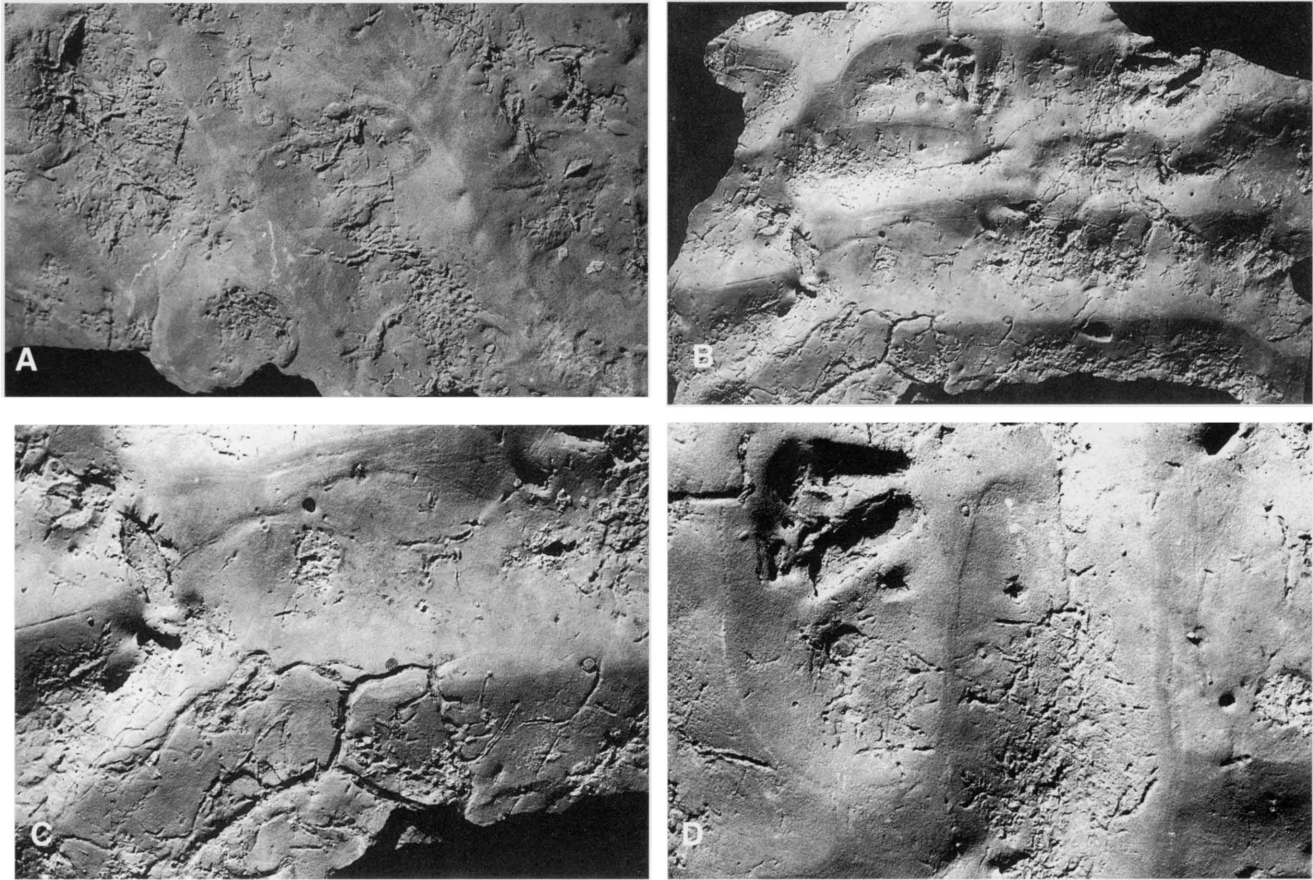
FIGURE 19—Desiccation and dissolution structures in sandstones at the top of unit B1. **A.** Irregularly branched and reticulate structures preserved in ripple troughs probably related to desiccation of mud that accumulated in the troughs. × 0.24. **B.** Desiccation structures concentrated in troughs of interference ripples. Note branched root trace on lower left. × 0.24. **C.** Close-up of root trace shown in B. × 0.47. **D.** Desiccation structures and dissolution holes (upper left). × 0.48.

Psammichnites? isp.), and feeding structures (*Halopoa* isp., *Teichichnus rectus*, *Rhizocorallium* isp., *Chondrites*? isp., *Trichophycus* isp., *Protovirgularia bidirectionalis*, *Phycodes palmatus*, *Phycodes* isp., *Phycosiphon incertum*). Rare vertical traces are represented by dwelling structures (*Diplocraterion* isp. A, *Arenicolites* isp., *Skolithos* isp., *Conichnus conicus*, *Pentichnus pratti*) and feeding traces (*Parahaentzschelinia ardelia*, *Rosselia socialis*). Because most traces are preserved on bedding planes, bioturbation is actually low, leaving the primary sedimentary fabric undisturbed. Some traces (e.g., *Chondrites*? isp.) tend to concentrate in ripple troughs, with others (e.g., *P. tubularis*, *C. simplex*) showing no preferential distribution. Basal terminations of U-shaped burrows referred to as *Diplocraterion* isp. B occur at the top of the unit, together with very rare *Planolites beverleyensis*. This unit also includes traces left in open nomenclature (chip-shaped burrows, pelletoidal chains, small horizontal cylindrical burrows, small vertical burrows, and undetermined trackways).

INTERPRETATION—Dominance of rippled sandstones indicates a substantial amount of bedload transport. However, alternation of tidal currents with settlement of suspended load during slack-water periods is indicated by lenticular, wavy, and wavy-flaser bedding (Reineck and Wunderlich, 1968; Klein, 1971). Absence of dune crossbedding and presence of ripples suggest low current speed (Dalrymple, 1992). Wave action was relatively important, as evinced by symmetrical ripples. Interference ripples suggest either a combination of waves and tidal currents or rapid changes in the direction of tidal flow. The latter is supported by sharp lateral changes in bedform morphology. The presence of multidirectional ripples suggests tidal action in very shallow water (Noffke et al., 1996). These authors interpreted multidirectional ripples as resulting from an interplay between physical processes and overgrowing of microbial mats that stabilized the substrate. Flat-topped ripples and relict troughs indicate a strong ebb outflow overprinted on the original flood-generated ripple morphology associated with subaerial emergence (Tanner, 1958; Klein, 1971). The peculiar set of sedimentary structures, bedding types, and grain size suggest that unit B1 represents an intertidal-sand flat.

Rapid sedimentation and differential compaction is indicated by load casts (cf. Van Straaten, 1954). Coincident orientation of load casts with respect to ripple crests suggests localized loading due to high pore-fluid pressures after bedform migration and differential deposition (Dzulinski and Walton, 1965; Allen, 1982). Presence of

sand volcanoes indicates liquefaction processes, particularly sand extrusion, flowage of liquefied sand, and subsequent sediment collapse in the central part of the structure. Additionally, preservation of sand volcano lobes suggests that extrusion and deposition occurred in quiet conditions, as such features commonly are reworked in high-energy settings (Collinson and Thompson, 1982).

Desiccation cracks indicate subaerial exposure. Collinson and Thompson (1982) illustrated two scales of crack patterns in the same horizon, and they suggested that the smaller cracks were associated with the drying out of a thin mud veneer, whereas the larger polygons reflect the drying of a thicker unit. In the present case, the small and intermediate-sized cracks probably record widespread drying and contraction of a thin surface veneer of mud. Larger cracks most likely are associated with desiccation of the entire unit. The irregularly branched and reticular structures concentrated in ripple troughs somewhat resemble inorganic structures described by Seilacher (1982a) as "Aristophycus." However, Aristophycus is a more regular dendroid structure, commonly radiating from ripple crests, and thought to be produced by the carving of tiny distributary channels in the mud during expulsion of pore water. In the case of the structures preserved at Waverly, an origin through desiccation of mud that accumulated in the troughs seems to be more likely.

The irregular morphology of the upper boundary of the sandstone unit is indicative of pedogenic processes associated with the formation of a paleosol in overlying unit B2. These processes led to substantial obliteration of the original sedimentary fabric. The mottled texture in the uppermost interval of the sandstone package may represent either early stages of nodule formation or, more probably, irregular patches of iron oxide staining due to infiltration from the paleosol horizon.

Abundance and diversity of biogenic sedimentary structures support the existence of a very active benthic fauna. Preservation of trace fossils on bedding planes was enhanced by the alternation of sand and mud layers. The abundance of biogenic structures also reflects breaks in sedimentation. Although the envisaged sedimentary environment is rigorous and fluctuating, organisms were able to cope with these stressful conditions, probably as a result of the predictable nature of such an ecosystem. High trace-fossil diversity suggests that the tidal flat occurred along an open coast under normal-marine conditions. Tidal flats in brackish-water estuarine or bay systems have a low trace-fossil diversity (Pemberton and Wightman, 1992), whereas the freshwater inner part of estuaries are characterized by a completely different set of biogenic structures (Buatois, Mángano, et al., 1997a).

Unit B2—Mottled Mudstone Facies

DESCRIPTION—Unit B1 grades upward into a poorly exposed interval of structureless reddish mudstones. Although this unit is laterally persistent (at a scale of tens of meters), it changes thickness laterally, from 15 cm to 6 cm. Primary sedimentary structures are not preserved, and the only structures discernible are red mottles and fine to medium tuberose- to spherical-ferruginous nodules (glaebules).

INTERPRETATION—The presence of nodular glaebules, the mottled texture, and the absence of primary sedimentary structures indicates edafic processes. Absence of well-developed horizons indicates that unit B2 represents a weakly developed paleosol. The paleosol most likely developed on a mudstone to sandy mudstone overlying the sand-flat deposits of unit B1. Pedogenic processes probably occurred on mixed- to mud-flat deposits. The poor exposure of this facies prevents further interpretation.

Parasequence C

This parasequence is 90 cm thick and is subdivided into two units: a rippled silty sandstone facies (unit C1) and a blocky mudstone facies (unit C2).

Unit C1—Rippled Silty Sandstone Facies

DESCRIPTION—Unit C1, which consists of strongly weathered, reddish, very fine grained, silty sandstones, is 20 cm thick and contains laterally discontinuous individual beds, 3–5 cm thick (fig. 20A). Poorly preserved asymmetrical and quasisymmetrical ripples are the only recognizable primary sedimentary structures (fig. 20B). Fragmented bivalve shells and crinoid ossicles are present locally. The dominant features of this facies are conspicuous red mottles and prominent, fine to medium, spherical to ellipsoidal ferruginous nodules (glaebules) (fig. 20C). An irregular and iron-stained weathered surface marks the top of this unit (fig. 20D).

INTERPRETATION—Unit C1 probably records deposition in an intertidal-mixed flat. The presence of nodular glaebules and the irregular upper surface of unit C1 indicate edafic processes associated with the development of a paleosol in the overlying unit (C2). These processes led to substantial obliteration of the original sedimentary fabric. As in the case of unit B1, the mottled texture may represent either early stages of nodule formation or irregular patches of iron oxide staining through infiltration from the overlying paleosol.

Unit C2—Blocky Mudstone Facies

DESCRIPTION—Unit C2 overlies the rippled silty sandstones of unit C1 and is a laterally continuous, 70-cm-thick interval of apparently structureless gray mudstones. Closer examination, however, reveals a set of soil aggregates and structures. The lower part of the unit displays coarse to very coarse subangular blocky peds that grade to medium and fine subangular and angular blocky peds in the upper part (fig. 21). Randomly arranged, thin very fine
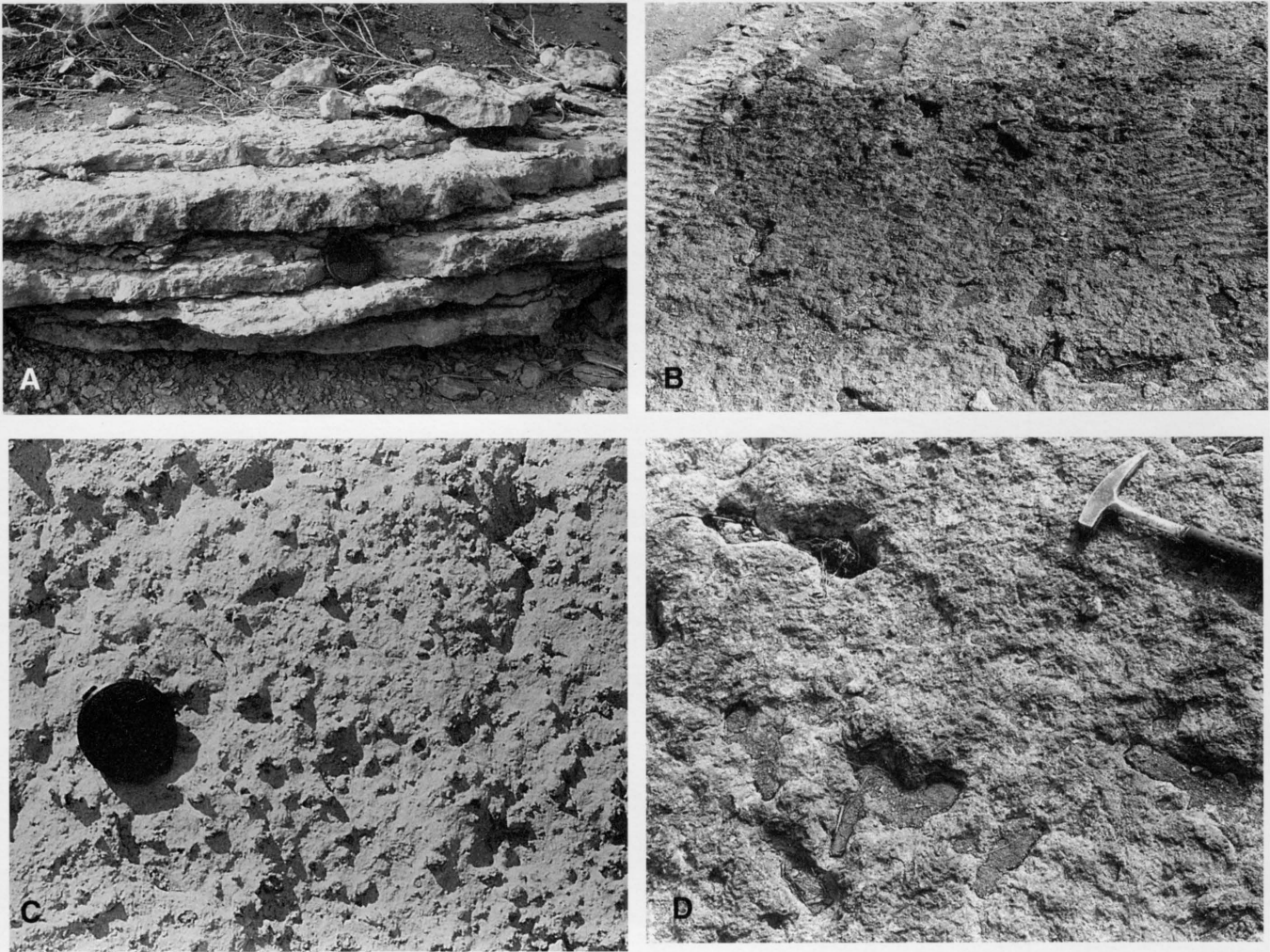
FIGURE 20—Sedimentary features of rippled silty sandstone facies (unit C1). **A**. Laterally discontinuous silty sandstone beds. **B**. Poorly preserved ripples at the top of the unit. Note patches of well-weathered rippled tops. **C**. Ferruginous nodules (glaebules). **D**. Iron-stained weathered surface at the top of the unit. Close-up of structures probably formed by decomposition of roots. Lens cap diameter is 55 mm and length of hammer head is 17 cm.

grained cutans with striated and smeared surfaces also are present.

INTERPRETATION—Features of unit C2 are unequivocally pedogenic in origin. The dominance of subangular over angular peds suggests erosion or coatings of ped margins (Retallack, 1990). Striated and smeared surfaces on cutans are regarded as slickensides, and the cutans therefore are stress cutans. Although stress cutans also form simply by crushing of peds against one another during compaction (Retallack, 1990), an origin by swelling and shrinking of clays during repeated wetting and drying episodes is here consistent with the envisaged depositional environment of the associated facies. Absence of very well defined horizons indicates a weakly developed paleosol.

The paleosol seems to have developed on a mudstone overlying the mixed-flat deposits represented by unit C1. Although primary sedimentary structures of the parent material are not preserved, the fine-grained texture of the unit and the stratigraphic position of the paleosol suggest that edafic processes probably developed on mud-flat
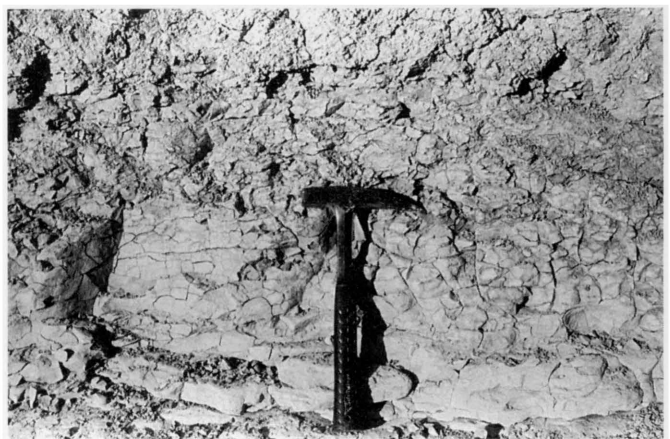
FIGURE 21—Blocky mudstone facies (unit C2). Note the coarse to very coarse subangular blocky peds grading to medium and fine subangular and angular blocky peds in the upper part. Length of hammer is 33.5 cm.

deposits. The paleosol therefore is regarded as recording maximum progradation and is thought to have developed in a supratidal marsh environment. Absence of bioturbation is probably related to harsh conditions typical of marsh settings, characterized by intermittent flooding, extreme temperature variations, and salinity fluctuations (Weimer et al., 1982). However, a taphonomic reason, most likely obliteration of previous biogenic structures by rooting, cannot be ruled out.

Parasequence D

Parasequence D is 1.10 m thick and consists of three units: siltstone and mudstone heterolithic facies (unit D1), inclined-heterolithic stratified silty sandstones and siltstones (unit D2), and trough cross stratified sandstones (unit D3).

Unit D1—Siltstone and Mudstone Heterolithic Facies

DESCRIPTION—Unit D1 is 1.10 m of laterally persistent, heterolithic-bedded siltstones and mudstones. The lower 20 cm are siltstones with asymmetric ripple cross-lamination and mud drapes. Flaser and wavy bedding are dominant near the base of the unit, but are replaced upward by lenticular bedding. The upper 90 cm is lenticular bedded in the lower part, but it is dominated by massive mudstones upward. Trace fossils have not been observed.

INTERPRETATION—Unit D1 is interpreted as a prograding intertidal mixed- to mud-flat environment. Flaser, wavy, and lenticular bedding indicate alternation of bedload transport due to tidal currents and suspension fallout during slack-water periods (Reineck and Wunderlich, 1968; Klein, 1971). Upward replacement of tractive bedforms (i.e., current ripples) by mud deposited from suspension indicates decreasing tidal energy, which is consistent with progressive shallowing.

Unit D2—Inclined Heterolithic Stratified Silty Sandstones and Siltstones

DESCRIPTION—Unit D2 is encased in the fine-grained deposits of unit D1. It consists of two, stratigraphically equivalent, but individual channelized bodies. The dominant structure in this unit is inclined heterolithic stratification, which laterally grades into parallel stratification (fig. 22A, B). Lateral-accretion sets are 6–11 cm thick. Inclined units are silty sandstones and siltstones with ripple cross stratification and thin mud drapes on the lee faces (fig. 22C). Single and bifurcated flaser and wavy bedding also are present (fig. 22D). In some cases, adjacent sets of cross lamination display opposed dip directions. One of these channels is 38 cm thick and 4 m wide. In this channelized body, lateral-accretion surfaces

dip 5° with an azimuth of 30°. The other channel is 40 cm thick and 30 m wide. Inclined surfaces dip 2° with an azimuth of 240°. No trace fossils have been found.

INTERPRETATION—This unit is interpreted as having been deposited in small-scale, intertidal runoff channels. Inclined-heterolithic stratification is interpreted as point-bar accretion, a dominant structure in upper-intertidal channels (e.g., Reineck, 1958; Bridges and Leeder, 1976; de Mowbray, 1983; Thomas et al., 1987). Additionally, the stratigraphic relation with the underlying mixed- to mud-flat deposits supports this interpretation. Presence of flaser and wavy bedding records alternation of bedload transport during tidal flow and suspension settlement during slack-water periods (Reineck and Wunderlich, 1968; Klein, 1971). Absence of trace fossils is problematic, because intense to moderate bioturbation has been recorded in modern (e.g., Bridges and Leeder, 1976) and ancient (e.g., Ranger and Pemberton, 1992) tidal point bars, but the absence of bioturbation here probably is related to high rates of sedimentation along unstable channel margins (cf. Gingras et al., 1999).

Unit D3—Trough Cross Stratified Sandstones

DESCRIPTION—This facies is a 30-cm-thick, channelized, light-brown, medium- to fine-grained sandstone body (fig. 23A), with an erosive base that cuts into one of the unit D2 channels and is encased upward by the upper half of unit D1. This sandstone body is 66 m wide and is oriented north-south with stratification gently dipping (3°) toward the channel axis. The dominant sedimentary structure is trough cross lamination, commonly expressed as rib and furrow structures on bedding planes (fig. 23B). Rib and furrow structures consist of a series of curved laminae arranged in parallel zones up to 15 cm wide. Small-scale trough cross lamination, with sets up to 3 cm thick, has concave-upward bases and sharply truncated tops. Asymmetrical ripple bedforms are preserved locally. Large trackways up to 30 cm wide, assigned to the ichnospecies *Diplichnites cuithensis*, occur on the top of this unit.

INTERPRETATION—Internal and bedding-plane structures indicate migration of unidirectional, current ripples. The trackway *D. cuithensis* currently is regarded as locomotion traces produced by the giant myriapod *Arthropleura* (Briggs et al., 1979). *Arthropleura* is considered a terrestrial arthropod and *D. cuithensis* has been recorded exclusively from late Paleozoic subaerial deposits, commonly exposed fluvial bars, silted channels, and desiccated sheetflood deposits (Briggs et al., 1979; Briggs et al., 1984; Ryan, 1986). Assuming a terrestrial environment for this ichnotaxon, its presence eliminates a subtidal origin for these channels. An alternative interpretation is that they are intertidal runoff channels. However, absence of physical structures indicative of tidal action also argues against a tidal origin for this channel. Accordingly, this sandstone body is interpreted as a channel-fill in a coastal
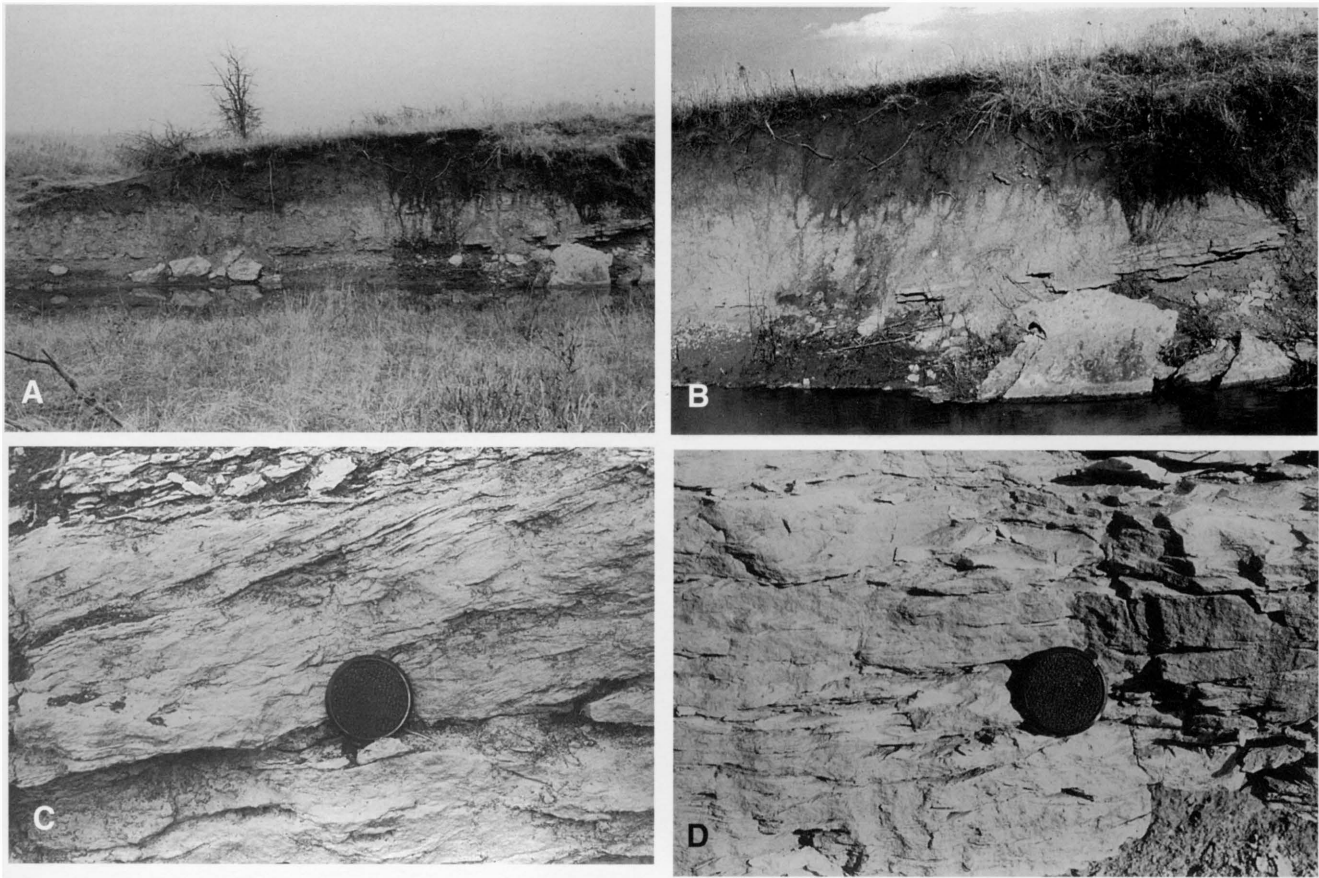
FIGURE 22—Inclined heterolithic stratified silty sandstones and siltstones (unit D2). **A**. General view of one of the intertidal runoff channels encased in fine-grained deposits of unit D1. Inclined heterolithic stratification grades laterally into parallel stratification (to the left). **B**. Close-up showing inclined heterolithic stratification. **C**. Close-up of internal features of stratification showing silty sandstones and siltstones with ripple cross stratification and thin mud drapes on the lee faces. **D**. Flaser- and wavy-bedding in inclined heterolithic strata. Lens cap diameter is 55 mm.
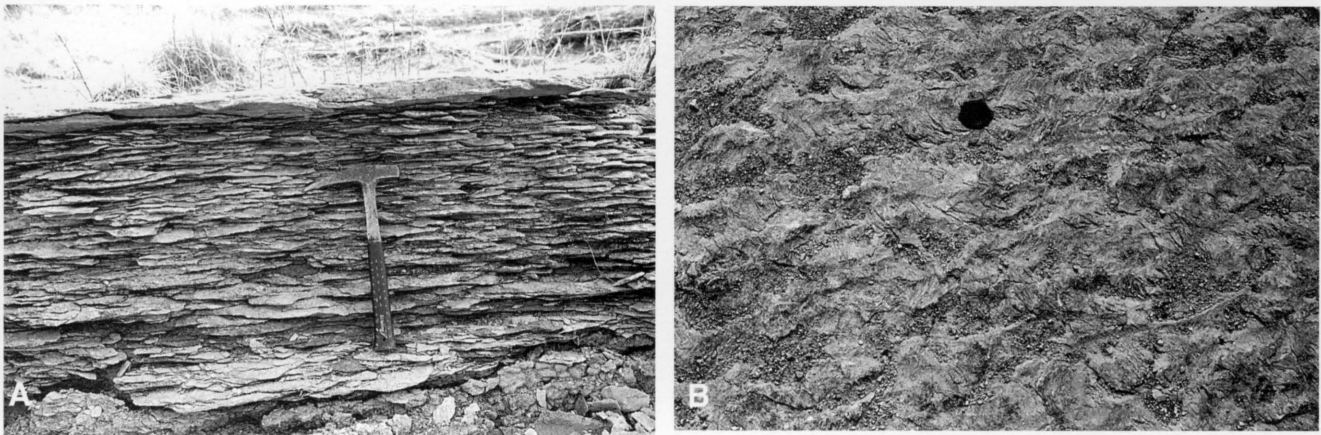
FIGURE 23—Trough cross stratified sandstone (unit D3). **A**. Channelized sandstone body with an erosive base. **B**. Ribs and furrows on bedding plane. Hammer length is 33.5 cm and lens cap diameter is 55 mm.

fluvial system. Absence of marine taxa also supports a fluvial origin. Absence of major erosive or reactivation surfaces within the sandstone body may suggest rapid infilling during a single sedimentary event. The basal surface of the channel cuts into unit D2 deposits, which suggests capture of upper intertidal channels by a fluvial system.

Systematic Ichnology

Taxonomic Philosophy

The Waverly ichnofauna represents a real challenge to ichnotaxonomists. The biogenic structures are extremely abundant and the morphologic variability of the trace fossils is striking. In modern ichnology, contrasting philosophical perspectives have been adopted by different authors. As in the case of body-fossil taxonomists, the lumpers and the splitters represent two opposing ways of weighting trace-fossil morphology (Pickerill, 1994). In a simplified characterization, lumpers will tend to cluster all existing forms in a few essential ichnogenera, and splitters will find visible morphologic differences significant enough to create a plethora of new forms. From a philosophical perspective, lumpers can be characterized as more inferential, splitters as more empirical. Lumpers tend to favor behavior over morphology, trying to define the basic behavior that relates a group of structures, while splitters remain reluctant about the invisible links among morphologically dissimilar forms. This confrontation is a revisitation of the old debate about the roles of observation and theory in science.

Most ichnologists will agree with Bromley (1996, p. 166) that "in the final analysis, it is the morphology of the trace as an expression of animal behavior that is the basis of the name." To decipher the behavior of the tracemaker, however, may be quite a difficult task. Very frequently morphology in itself is considered sufficient to define new ichnotaxa, although its ethologic meaning is hardly understood. Some morphologic features can be objective in the sense of being observable and easily recognizable, and they may still not deserve any consideration at any ichnotaxonomic level. A drastic difference in morphology may actually provide evidence of extrinsic controls rather than behavioral determinants (see section on "Substrate"). Only morphologic characters that are known to reflect significant behavioral traits should be considered (i.e., ichnotaxobases; Bromley, 1996).

While morphology is observed, behavior must be inferred. The degree of behavioral inference varies with each particular case. For example, in the simplest case, there is almost a continuum from the morphologic observation of clearly preserved ventral anatomic features to the interpretation of a trace as a resting structure. However, analysis of most traces requires a larger inferential jump, involving knowledge of a complex array of biological, taphonomic, and environmental determinants.

Advantages of a dual nomenclature (i.e., two separate names for biotaxa and ichnotaxa) as well as the risks involved in the biotaxonomic identification of the tracemaker have been stressed by Bromley (1996). In some instances, inclusion of the actual taxonomic identification of the tracemaker as an essential component of naming trace fossils (e.g., Seilacher, 1985; Hasiotis and Bown, 1992) has led to circular reasoning. Introduction of a biologically (or environmentally) based ichnotaxonomy will lead to a dual nomenclature for marine and continental trace fossils. Buatois, Jalfin, et al. (1997) noted that if biologic or sedimentologic criteria are applied to ichnotaxonomy, it will be virtually impossible to escape from circular reasoning when using trace fossils as an aid to interpret ancient depositional environments. In these situations, such a taxonomic system undercuts the information potential of trace fossils in sedimentology, stratigraphy, and paleoecology (Buatois, Jalfin, et al., 1997).

The importance of the biology of the tracemakers in understanding the ethologic significance of biogenic structures, however, is not always straightforward. Constructional possibilities are determined by intrinsic biologic factors, and therefore should be helpful in evaluating the relative significance of behavioral traits as reflected by trace-fossil morphology. In this sense, the biology of the tracemaker plays a role, albeit indirect, in trace-fossil taxonomy. Ethologic interpretation of a morphologic feature requires this broad biological framework. Similarly, an accurate understanding of the environmental conditions under which a trace fossil is created should enlighten our understanding of the structure, even if those factors are not formally considered in the nomenclature of trace fossils (cf. Goldring et al., 1997). Both paleobiological and environmental analyses provide significant clues that help decipher behavior and propose more robust taxonomic schemes.

In our efforts to characterize the Waverly ichnofauna, we have been conservative to avoid creating names with little ethological significance. At the same time, we have tried to provide an appropriate biological and environmental framework to maximize the information potential of the Waverly trace fossils. We have erected only one new ichnospecies, *Protovirgularia bidirectionalis*, whose distinctive morphology undoubtedly reflects a unique behavioral pattern. When possible, we have used a formal name to characterize a structure, which will lead to direct comparisons with other ichnofaunas. However, where morphology was indistinct or the available specimens were insufficient to recognize significant morphological and behavioral traits, we have used open nomenclature.

General Comments

In this section, trace fossils are described and discussed in terms of ichnotaxonomy, environmental and stratigraphic range, and possible tracemakers. Ichnotaxa are listed alphabetically and ichnofossils in open nomenclature are described at the end of the section. Associated ichnofauna refers to the other traces most commonly recorded on the same bedding plane. Descriptions are based on the analysis of more than one hundred collected rock slabs and additional specimens examined in the field. Specimens are housed at the Museum of Invertebrate Paleontology at the University of Kansas.

Ichnogenus *Arenicolites* Salter, 1857

DISCUSSION—The ichnogenus *Arenicolites* includes vertical U-shaped burrows lacking spreiten, thus differing from the spreiten U-burrow *Diplocraterion* (Fürsich, 1974a; Hakes, 1976). A related ichnotaxon, *Solemyatuba* Seilacher, 1990a, is distinguished from *Arenicolites* by its elliptical cross section, indicative of a bivalve tracemaker.

Arenicolites is interpreted as dwelling structures (domichnia) commonly produced by polychaetes (Goldring, 1962; Fürsich, 1974b), crustaceans (Goldring, 1962), and holothurians (Seilacher, 1990a; Bromley, 1996). Bromley (1996) discussed *Arenicolites*-like structures formed in modern environments by the polychaetes *Chaetopterus variopedatus*, *Lanice conchilega*, *Amphitrite ornata*, and *Arenicola marina*, the echiuran worms *Urechis caupo* and *Echiurus echiurus*, the holothurian *Leptosynapta tenuis*, and the enteropneust *Balanoglossus clavigerus* (see also Howard and Dörjes, 1972 for a discussion of the latter genus). U-shaped

burrows also are produced by the polychaete *Glycera alba* (Ockelman and Vahl, 1970). Bromley (1996) cautioned against assuming that *Arenicolites* indicates a suspension-feeder, because in modern environments such burrows are produced by both suspension-feeders (e.g., *Urechis caupo*) and deposit-feeders (e.g., *Echiurus echiurus*). Ronan (1977) also criticized the assumption that U-shaped burrows are invariably produced by filter-feeders, providing several examples of *Arenicolites*-like burrows constructed by omnivorous polychaetes. Bajard (1966) also figured U-shaped burrows of *Arenicola marina*.

Although more typical of high-energy shallow-marine facies (e.g., Carey, 1978; Heinberg and Birkelund, 1984; Dam, 1990a; Pemberton, MacEachern, et al., 1992), *Arenicolites* also has been recorded in deep-marine (e.g., Crimes et al., 1981; Buatois and Mángano, 1992), marginal-marine (e.g., Hakes, 1976; Chaplin, 1982; Eagar et al., 1985), and continental (e.g., Bromley and Asgaard, 1979, 1991; Mángano et al., 1994) facies. Examples of this ichnogenus in tidal-flat facies have been mentioned by Hakes (1976), Ireland et al. (1978), Chamberlain (1980), Pollard (1981), and Narbonne (1984), among others. *Arenicolites* ranges in age from Cambrian to Holocene (e.g., Crimes, 1994; Bromley, 1996).

Arenicolites isp.
Fig. 24A–B

SPECIMENS—Four specimens on slabs KUMIP 288500, KUMIP 288531, KUMIP 288532, and KUMIP 288552.

DESCRIPTION—Simple, U-shaped, vertical burrows without spreiten. Walls are smooth with a thin lining. Burrow fill is identical to host rock. Burrow depth is 17.2–40.0 mm; arm width is 4.0–11.4 mm; spacing between is arms 71.4–201.7 mm. Preserved as full relief.
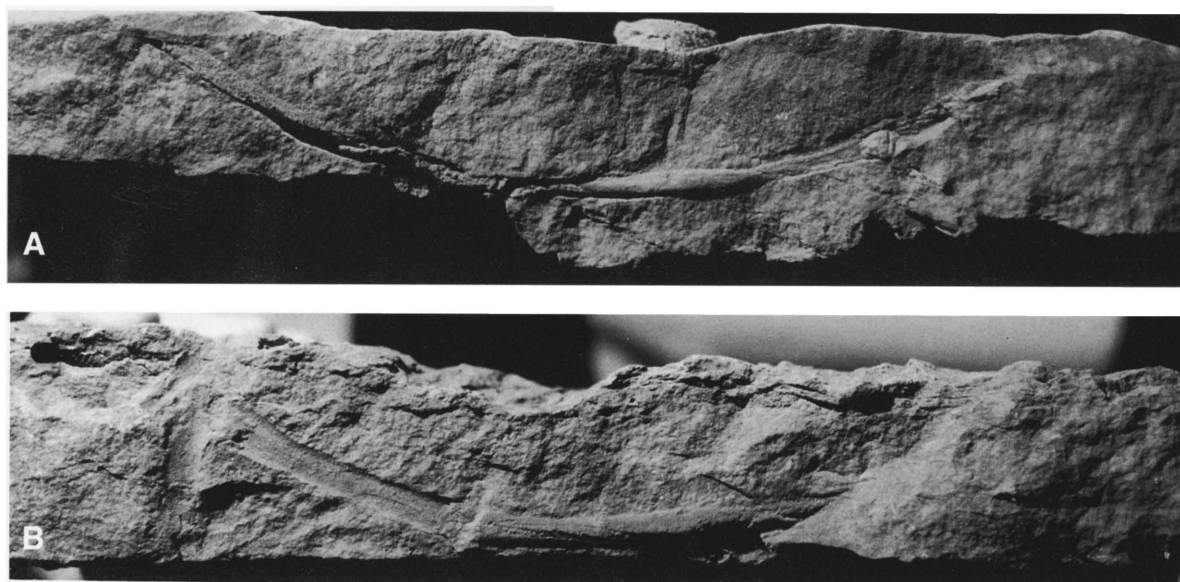
FIGURE 24—*Arenicolites* isp. Cross sectional view. **A.** Note associated *Rosselia socialis* (center). KUMIP 288552. × 0.5. **B.** Burrow-fill partially preserved, showing thin wall lining. KUMIP 288531. × 0.6.

ASSOCIATED ICHNOFAUNA—*Nereites missouriensis, Protovirgularia bidirectionalis, P. rugosa, Curvolithus simplex, Conichnus conicus, Rosselia* isp.*, Lockeia siliquaria, Psammichnites implexus, Halopoa* isp.*, Palaeophycus tubularis, Cruziana problematica*, and small cylindrical burrows.

REMARKS—The ichnotaxonomy of the different ichnospecies of *Arenicolites* is unclear and this ichnogenus is a candidate for taxonomic revision. *Arenicolites* isp. differs from *A. carbonarius* Binney, 1852, in the absence of successive subdivisions in one of the arms, from *A. stather* Bather, 1925, in being very thinly lined and having curved arms, and from *A. variabilis* Fürsich, 1974b, in having curved arms. In the absence of any consistent ichnotaxobases for *Arenicolites*, and because no bedding-surface expression of the U-burrow is available, we prefer to leave the designation of this form at the ichnogeneric level.

Our specimens are similar to *A. curvatus* figured by Goldring (1962, fig. 11). However, this ichnospecies has been included in *Solemyatuba* by Seilacher (1990a), who considered *A. curvatus* a junior synonym of *Solemyatuba* (*Arenicolites*) *subcompressa. Solemyatuba* includes two ichnospecies, *S. subcompressa* (Eichwald, 1860) and *S. ypsilon* Seilacher, 1990a. *Solemyatuba subcompressa* lacks a lower extension tube and has been recorded only from the Paleozoic, while *S. ypsilon* has a lower extension tube and is typically found in Mesozoic strata (Seilacher, 1990a). An ichnotaxon similar to *S. subcompressa* is the smaller *Arenicolites graptolithoformis* Hundt, 1831, from the Silurian of Germany. Nonetheless, re-examination of the type specimens is necessary to establish its affinity with *Solemyatuba*. Specimens from Waverly have smooth walls and longer diameters in the plane of the U, which are features present in *Solemyatuba*. However, we prefer to include our specimens in *Arenicolites*, because elliptical cross sections cannot be demonstrated because of partial preservation.

Ichnogenus *Asteriacites* von Schlotheim, 1820

DISCUSSION—The first comprehensive study of stellate trace fossils was accomplished by Seilacher (1953). His study dealt with both experimental neoichnology and Mesozoic specimens, and it provided a detailed account of ophiuroid and asteroid burrowing techniques. *Asteriacites* differs from the asterozoan burrow *Pentichnus* Maerz, Kaesler, and Hakes, 1976, in the subcylindrical to subconical morphology of the latter, which represents permanent to semi-permanent domiciles rather than resting traces (Mángano et al., 1999).

Asteriacites commonly is interpreted as resting traces (cubichnia) of asterozoans, including ophiuroid and asteroid traces (Häntzschel, 1975). Aquarium experiments with *Ophiura texturata* and *Astropecten aurantiacus* led Seilacher (1953) to interpret *A. lumbricalis* as an ophiuroid resting trace and *A. quinquefolis* as an asteroid resting

structure. In addition, Seilacher (1953, fig. 3) analyzed an occurrence of *A. lumbricalis* that ethologically corresponds to fugichnia (cf. Seilacher, 1953, figs. 3a and b). Ophiuroids are known to escape successfully from storm sedimentation events (Schäfer, 1972). Mángano et al. (1999) recently analyzed several occurrences of *Asteriacites* from Pennsylvanian units in Kansas, and they interpreted them either as escape (vertical repetition) or as hunting structures (horizontal repetition) of omnivorous epifaunal ophiuroids.

Occurrences of *Asteriacites* traditionally have been attributed to asterozoans without further distinction (e.g., Santos and Campanha, 1970; Brito, 1977; Muniz, 1979). More recently, some authors have related explicitly *Asteriacites* to ophiuroid tracemakers (e.g., Hakes, 1976; Mikuláš, 1990; West and Ward, 1990; Twitchett and Wignall, 1996; Wilson and Rigby, 2000). In two of these cases, *Asteriacites* is associated directly with ophiuroid body fossils (Mikuláš, 1990; West and Ward, 1990). *Asteriacites* commonly is produced by deposit feeding or omnivorous ophiuroids (Mángano et al., 1999).

Asteriacites has been reported from shallow-marine (e.g., Dam, 1990a) to deep-marine facies (e.g., Crimes and Crossley, 1991). Although some authors (e.g., Seilacher, 1983) have considered this ichnogenus as an indicator of normal-salinity conditions, West and Ward (1990) and Mángano et al. (1999) have shown that *Asteriacites* may be present in brackish-water, marginal-marine environments. *Asteriacites* is a common component of tidal-flat ichnofaunas (e.g., Hakes, 1976; Howard and Singh, 1985; Miller and Knox, 1985; West and Ward, 1990; Mángano et al., 1999), and ranges in age from Cambrian to Holocene (Mikuláš, 1992).

Asteriacites lumbricalis von Schlotheim, 1820
Figs. 25A–F, 26A–C

SPECIMENS—Eighty-seven specimens on 23 slabs (KUMIP 288500, KUMIP 288503, KUMIP 288510, KUMIP 288511, KUMIP 288517, KUMIP 288519, KUMIP 288520, KUMIP 288521, KUMIP 288522, KUMIP 288523, KUMIP 288527, KUMIP 288528, KUMIP 288530, KUMIP 288535, KUMIP 288538, KUMIP 288542, KUMIP 288544, KUMIP 288546, KUMIP 288553, KUMIP 288556, KUMIP 288568, KUMIP 288570, KUMIP 288571), many incomplete specimens (i.e., partial disc impressions with less than five arms), and several other specimens examined in the field.

DESCRIPTION—Star-like convex hyporeliefs (fig. 25A–F) or, less commonly, concave epireliefs (fig. 26A–C) of small to moderate size. The central disc commonly is poorly defined. Disc diameter is 5.3–8.5 mm, but typically 5.3–6.0 mm. A central depression is observed in a few specimens. Arms are moderately long (6.7–16.8 mm). Arm width (1.0–5.3 mm.) depends on arm shape. Arms display a wide variety of morphologies, and an individual specimen can show significant differences between arms. Arms
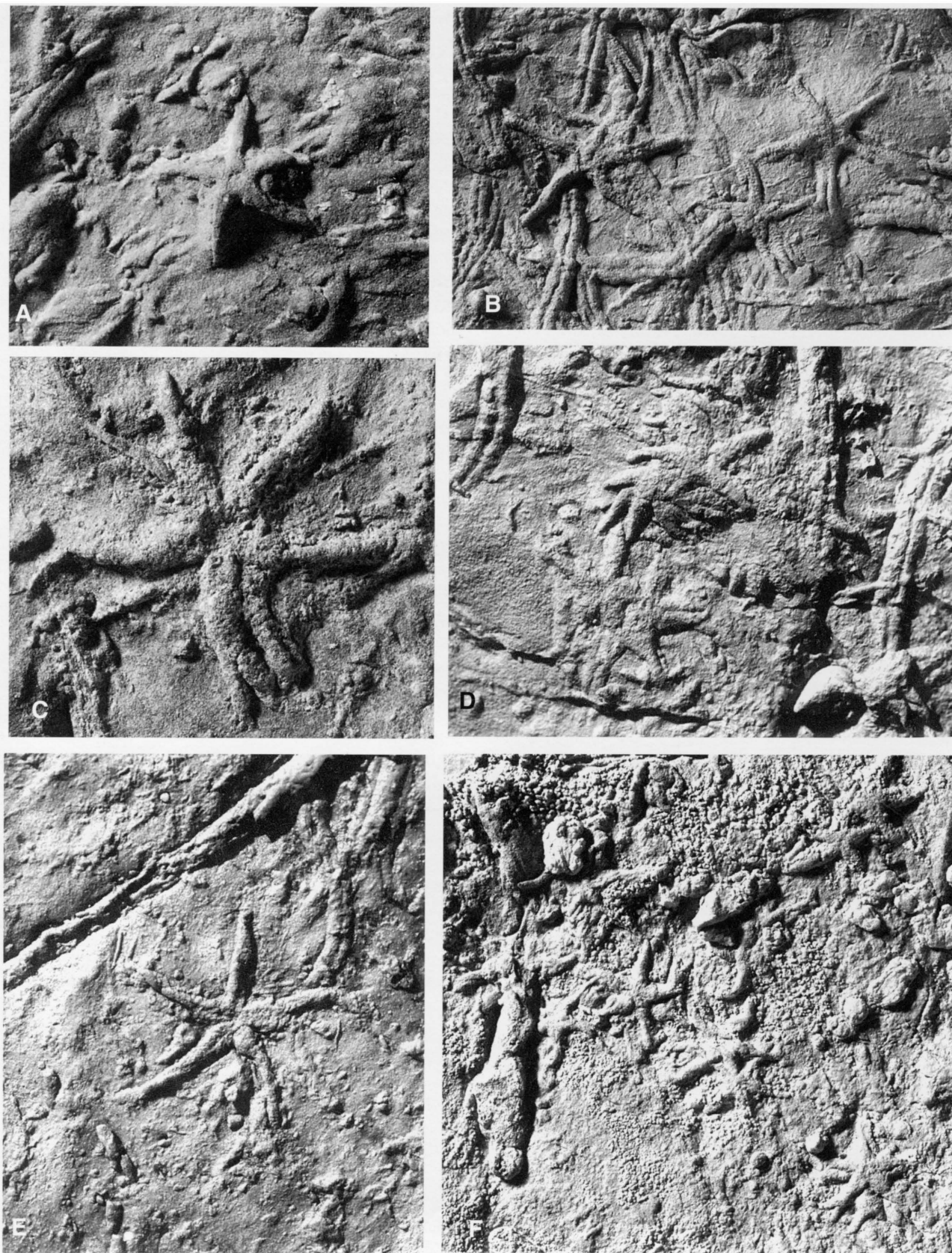
FIGURE 25—*Asteriacites lumbricalis*. Hypichnial preservation. **A**. Specimen with deep central disc and the arms extending upward. KUMIP 288519. × 1.4. **B**. Cluster of several specimens associated with *Cruziana problematica*. Note transverse striae in some of the specimens and branched arms. KUMIP 288519. × 1.3. **C**. Specimen with central depression and branched arms. KUMIP 288522. × 1.9. **D**. Note lateral repetitions and associated *Cruziana problematica*. KUMIP 288510. × 1.5. **E**. Specimen with central depression associated with *Cruziana problematica*. KUMIP 288500. × 1.2. **F**. Cluster of several specimens showing lateral repetition. KUMIP 288520. × 0.9.

may expand proximally and taper toward the tip, resulting in a lanceolate shape (cf. Seilacher, 1953, fig. 2a). In such cases, delicate longitudinal striations may cover the arms; transverse striations also are present. Other specimens show arms divided into two subparallel ridges covered by a regular transverse sculpture. In general, the distal part of the arm may bifurcate into twos or, more rarely, threes; may widen ending in a funnel-like shape; or may end in a single tip of a progressively tapering arm. Free arm length is typically two to three times the disc diameter, irrespective of size and arm morphology. Vertical repetition (*sensu* Seilacher, 1953) is recorded by successive impressions at different depths on the soles of some current-rippled sandstones. In most cases, repetition is partial, involving part of the central disc and arms. No clear "horizontal repetition" (*sensu* Seilacher, 1953) has been detected.

ASSOCIATED ICHNOFAUNA—*Asteriacites lumbricalis* commonly forms a dense shallow-tiered assemblage with *Cruziana problematica*. Other traces commonly associated are *Lockeia siliquaria, L. ornata, Curvolithus simplex, Protovirgularia rugosa, P. bidirectionalis*, small cylindrical burrows, and small vertical burrows.

REMARKS—Analysis of mainly Mesozoic specimens of *Asteriacites* led Seilacher (1953) to recognize two ichnospecies, *A. lumbricalis* von Schlotheim, 1820, and *A. quinquefolis* Quenstedt, 1876, both being distinct in convex hyporelief. However, almost all re-examined specimens (Seilacher, 1953, Plate 10, Figs. 1 and 2 excepted) were placed in *A. lumbricalis*. *Asteriacites lumbricalis* includes relatively small star-like traces with a distinctive or poorly defined central disc, relatively narrow arms that may display proximal expansions, or bifurcated rays. Seilacher (1953) made an innovative characterization of the different preservational variations of *A. lumbricalis*, relating the proximal expansion and the regular sculpture of longitudinal and transversal striations to the circular movements of the disc and the digging activity of the tube feet, respectively (see Seilacher, 1953, Fig. 2, for further explanation). On the other hand, *A. quinquefolis* is less well defined in terms of its distinctive features. It is somewhat larger, with a very regular stellate outline, typically with a more inflated shape and shorter arms than *A. lumbricalis*. In convex hyporelief, *A. quinquefolis* typically shows an irregular raggy aspect that contrasts with the regularity of *A. lumbricalis* (cf. Seilacher, 1953, Table 10, Fig. 1a).

Subsequent work on new collections led to the recognition of three additional ichnospecies, *A. stelliformis* Osgood, 1970, *A. gugelhupf* Seilacher, 1983, and *A. aberensis* Crimes and Crossley, 1991. *Asteriacites stelliformis* is characterized by arms showing a distinctive chevron-like sculpturing (Osgood, 1970). *Asteriacites gugelhupf* is characterized by its conical shape and represents deep domiciles (Seilacher, 1983). As noted by Mikuláš (1990), however, permanent or semi-permanent deep burrows representing dwelling traces should not be included within *Asteriacites*. Accordingly, *A. gugelhupf* is regarded more appropriately as *Pentichnus gugelhupf* (Mángano et al., 1999). *Asteriacites aberensis* is represented by small five-rayed impressions with the diameter of the central area large compared to the length of the rays (Crimes and Crossley, 1991).

Taking into account Seilacher's (1953) characterization, the Waverly specimens must be included in *A. lumbricalis*, which display multiple preservational variations related to the digging technique. Specimens of *Asteriacites* at Waverly were probably produced by an ophiuroid. Depth of excavation, digging technique, and typical behavior of an ophiuroid tracemaker can explain morphologic differences between and within specimens. When digging into the sediment, the central disc and proximal arms twist back and forth, resulting in the disappearance of the disc contour and enlargement of the proximal arms that misleadingly looks asteroid-like in outline (Seilacher, 1953, Fig. 2.2). Very fine longitudinal striations are evidence of sideways arm movements, whereas transverse striations resulted from the digging activity of tube feet. Arms with funnel-like open tips indicate that, although the disc and proximal arms were completely hidden in the sand, the arm tips extended above the substrate, sweeping sediment sideways. This behavior has been recorded in recent ophiuroids inhabiting shallow waters (Thorson, 1957). General configuration and depth of the structure suggest that epifaunal ophiuroids, rather than infaunal burrowers, were responsible for *Asteriacites lumbricalis*.

Ichnogenus *Chondrites* von Sternberg, 1833

DISCUSSION—The taxonomy of *Chondrites* has been reviewed by Fu (1991). A somewhat similar form is *Phymatoderma* Brongniart, 1849. However, *Phymatoderma* is distinguished from *Chondrites* by a more complex branching pattern that includes secondary tunnels (Miller, 1998).

Historically considered a feeding trace (fodinichnion), recent work suggests that *Chondrites* may represent specialized feeding behavior that involves chemosymbiosis, being interpreted as a sulfide pump (Fu, 1990; Seilacher, 1990; Bromley, 1996). Seilacher (1990a) suggested lucinoid bivalves, such as *Thyasira*, as modern analogues of the *Chondrites* tracemaker.

Chondrites is a facies-crossing form, recorded in marginal-marine (e.g., Archer and Maples, 1984), shallow-marine (e.g., Frey, 1990), and deep-marine facies (e.g., Buatois and Mángano, 1992; Orr, 1995). It has been regarded that the *Chondrites* animal developed adaptations to cope with oxygen-depleted conditions (Bromley and Ekdale, 1984; Savrda, 1992). *Chondrites* has also been reported in tidal-flat facies by Chamberlain (1980). *Chondrites* ranges in age from Cambrian to Holocene (Crimes, 1987; Ekdale, 1977).
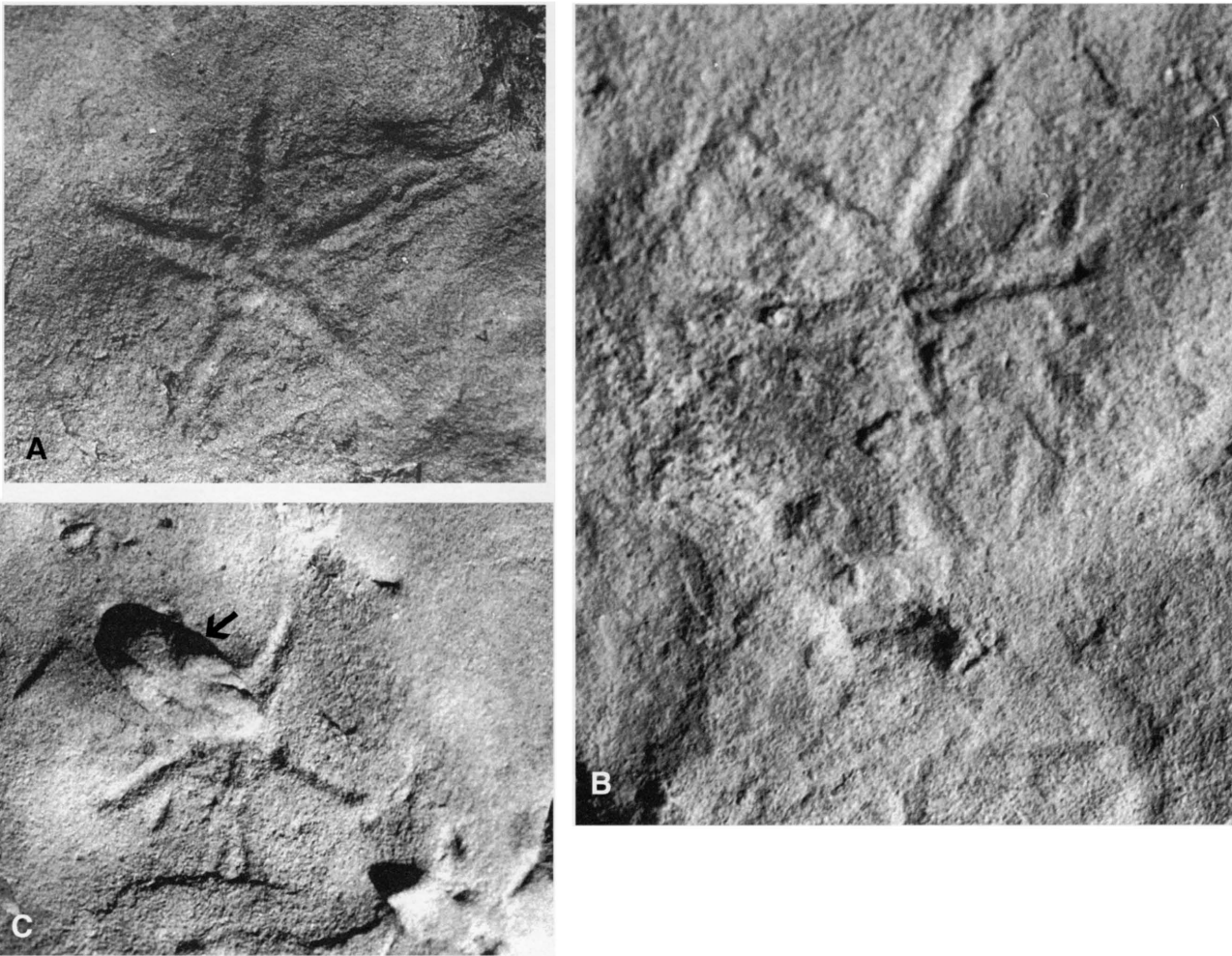
FIGURE 26—*Asteriacites lumbricalis*. Epichnial preservation. **A.** Very shallow impression with straight arms and poorly preserved morphological details. KUMIP 288528. × 2.3. **B.** Note lateral repetition. KUMIP 288528. × 3.14. **C.** Specimen of *A. lumbricalis* crosscut by *Curvolithus simplex* (arrow). KUMIP 288527. × 1.2.

FIGURE 27—*Chondrites*? isp. preserved at the top of a sandstone bed with flat-topped ripples. KUMIP 288563. × 1.3.

Chondrites? isp.
Fig. 27

SPECIMENS—Five slabs (KUMIP 288500, KUMIP 288527, KUMIP 288537, KUMIP 288542, KUMIP 288563) containing numerous specimens, the actual number of which is not possible to assess.

DESCRIPTION—Regularly branching system forming a dendritic network. Tunnel fill different from host rock. Tunnel width is 0.6–1.4 mm. Preserved as positive epireliefs or, more rarely, negative epireliefs in ripple troughs.

ASSOCIATED ICHNOFAUNA—*Chondrites*? isp. commonly is associated with *Curvolithus simplex* and *Protovirgularia bidirectionalis*, but other ichnotaxa may also be present (e.g., *Asteriacites lumbricalis*, *Nereites missouriensis*).

REMARKS—The Waverly specimens are only tentatively assigned to *Chondrites* because the typical branching pattern of this ichnotaxon is not completely evident. The specimens analyzed are always concentrated in ripple troughs. An identical preferential distribution was observed in Carboniferous tidal-flat deposits in roadcuts exposures along Kansas Highway 166 in Chautauqua County, southeastern Kansas. Differentiation of *Chondrites*? isp. from the inorganic branched and reticular structures described previously is extremely difficult in some cases. It also is possible that some of the inorganic structures were initiated by cracking along the traces themselves, a situation commonly observed in modern tidal flats (e.g., Bajard, 1966; Baldwin, 1974).

Ichnogenus *Conichnus* Männil, 1966

DISCUSSION—The taxonomy of *Conichnus* and related plug-shaped burrows has been discussed by Pemberton et al. (1988). *Conichnus* has been considered a senior synonym of *Amphorichnus* Männil, 1966, by Frey and Howard (1981) and Pemberton et al. (1988). However, subsequent re-examination of the type specimen of *Amphorichnus* suggests that this is a valid ichnogenus (A. Ekdale, written communication, 2000). *Conichnus* is characterized by its conical to subcylindrical geometry, rounded base, and lack of ornamentation.

Conichnus commonly is interpreted as a dwelling structure (domichnion) or a resting trace (cubichnion) of anemones or anemone-like organisms (Pemberton et al., 1988). Presence of a thin lining is suggestive of a more or less permanent domicile (domichnia).

Conichnus typically has been reported in shallow-marine environments (e.g., Frey and Howard, 1981; Vossler and Pemberton, 1988; Nielsen et al., 1996; Curran and White, 1997), although examples have been recorded in intertidal facies (Hiscott et al., 1984; Weissbrod and Barthel, 1998). *Conichnus* ranges in age from Cambrian to Holocene (Hiscott et al., 1984; Curran and Frey, 1977).

Conichnus conicus Männil, 1966
Fig. 28A–B

SPECIMENS—Two slabs (KUMIP 288509, KUMIP 288568) containing two specimens and one slab (KUMIP 288552) having two possible other specimens.

DESCRIPTION—Vertical, conical, very thinly lined burrows circular in cross section. Burrow-fill apparently is identical to host rock, although more resistant to weathering. Burrow wall displays corrugations that may suggest a crude funnel-like layering. Where the base of the burrow is visible, a small, planar, apical disc without ornamentation is observed. Height is up to 45.5 mm. Burrow diameter is 25.0–32.2 mm. Apical disc diameter is 10.2–16.6 mm. Preserved as full relief protruding from base and top of sandstone beds.

ASSOCIATED ICHNOFAUNA—*Lockeia siliquaria, L. ornata, Cruziana problematica, Asteriacites lumbricalis,* and *Protovirgularia rugosa.*

REMARKS—*Conichnus conicus* is distinguished from *C. papillatus* (Männil, 1966) by the lack of an apical protuberance, and from *C. conosinus* Nielsen et al., 1996, by the absence of an upper dish-shaped depression.

Ichnogenus *Cruziana* d'Orbigny, 1842

DISCUSSION—*Cruziana* is distinguished from *Didymaulichnus* Young, 1972, by the presence of transverse striations representing scratch marks (Aceñolaza and Buatois, 1993; Keighley and Pickerill, 1996). Poor preservation and the generally smooth lobes of the Waverly specimens cloud their distinction from *Didymaulichnus*, particularly *D. lyelli*. However, careful examination of the specimens shows the presence of transverse striations locally, placing these traces in *Cruziana*.

In marine deposits, *Cruziana* is interpreted as produced by trilobites (e.g., Seilacher, 1970). Long ploughs of *Cruziana* are related either with locomotion (repichnia) or grazing (pascichnia) activities within the sediments (Seilacher, 1970). In continental environments other arthropods, such as notostracan crustaceans, also produce *Cruziana* (Bromley and Asgaard, 1972, 1979; Pollard, 1985). Pollard (1985) noted that *Cruziana* (and its cubichnion companion *Rusophycus*) also occurs in Devonian and Carboniferous continental strata that predate the first occurrence of notostracan body fossils, and therefore their biologic affinities are unknown. In recent tidal flats, some detritus-feeding amphipods are able to produce bilobated structure comparable to *Cruziana*.

Although more typical of shallow-marine facies (e.g., Crimes et al., 1977; Fillion and Pickerill, 1990; Mángano et al., 1996), *Cruziana* also has been recorded from deep-marine (e.g., Pickerill, 1995), marginal-marine (e.g., Buatois and Mángano, 1997), and continental deposits (e.g., Bromley and Asgaard, 1972, 1979). *Cruziana* is a
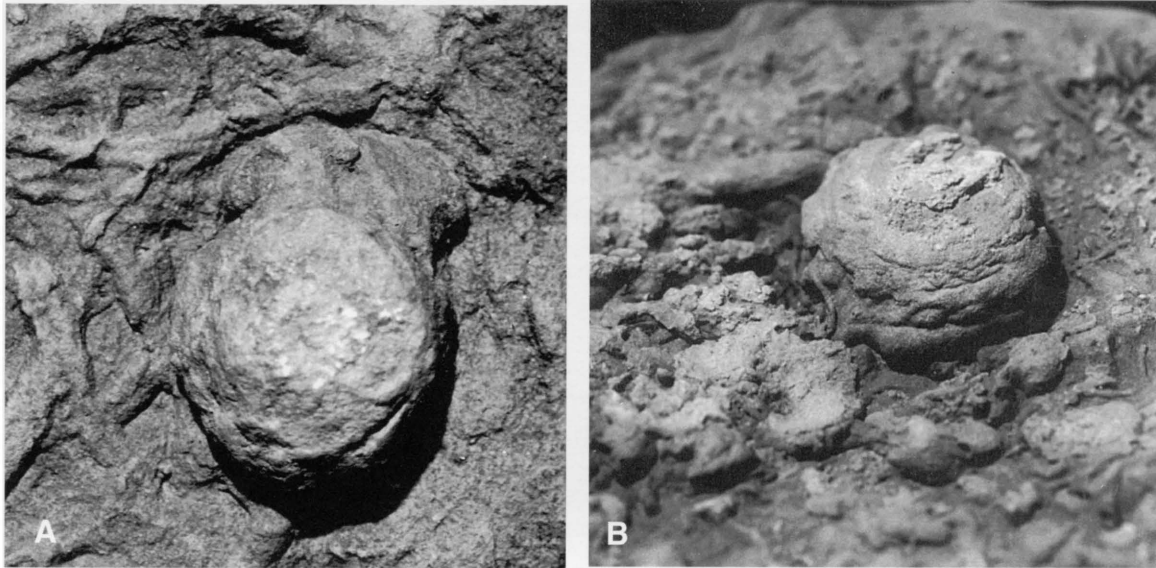
FIGURE 28—*Conichnus conicus.* Both are basal bedding-plane views. **A.** Basal view of a specimen showing unornamented apical disc. KUMIP 288509. × 1.4. **B.** Oblique view of a specimen with lateral corrugations. KUMIP 288568. × 1.26.

common element in Paleozoic tidal-flat environments (e.g., Baldwin, 1977; Narbonne, 1984; Durand, 1985; Legg, 1985; Mángano et al., 1996; Mángano et al., 2001; Stanley and Feldmann, 1998; Mángano and Buatois, 2000; Mángano and Astini, 2000; Astini et al., 2000) and ranges in age from Cambrian to Cretaceous (e.g., Crimes et al., 1977; Fregenal–Martinez et al., 1995; Buatois et al., 2000).

Cruziana problematica
(Schindewolf, 1921)
Fig. 29A–F

SPECIMENS—Forty-seven slabs (KUMIP 288500, KUMIP 288501, KUMIP 288502, KUMIP 288503, KUMIP 288505, KUMIP 288506, KUMIP 288507, KUMIP 288505, KUMIP 288509, KUMIP 288510, KUMIP 288511, KUMIP 288512, KUMIP 288513, KUMIP 288514, KUMIP 288515, KUMIP 288516, KUMIP 288517, KUMIP 288518, KUMIP 288519, KUMIP 288521, KUMIP 288522, KUMIP 288523, KUMIP 288527, KUMIP 288531, KUMIP 288533, KUMIP 288534, KUMIP 288535, KUMIP 288536, KUMIP 288538, KUMIP 288540, KUMIP 288541, KUMIP 288542, KUMIP 288543, KUMIP 288545, KUMIP 288546, KUMIP 288552, KUMIP 288554, KUMIP 288556, KUMIP 288559, KUMIP 288563, KUMIP 288565, KUMIP 288567, KUMIP 288568, KUMIP 288569, KUMIP 288570, KUMIP 288571, KUMIP 288572) containing approximately 727 specimens and several others examined in the field.

DESCRIPTION—Straight to gently sinuous bilobate traces. Lobes are mostly smooth and symmetrical, with lateral margins slightly curved. Median longitudinal furrow is narrow and shallow. Poorly preserved transverse striations are visible in some specimens. Trace width is 1.4–6.6 mm, but commonly 2.5–5.8 mm. Length is 27.0–230.0 mm, but typically 80.0–150.0 mm. Axial terminations commonly are lacking. A few specimens display partial preservation as negative hyporeliefs, revealing the unilobate upper surface of the trace. Depth is variable, but most specimens are very shallow structures. Preserved mostly as positive hyporeliefs.

Some bed soles exhibit almost a monospecific assemblage of *C. problematica* in multiple preservational variants. Some specimens are partially or completely represented by an irregular unilobated string of rock (fig. 29D). In many cases, these irregular strings become more regular unilobated traces or poorly bilobated structures. In these crowded surfaces, specimens commonly crosscut each other. Locally, they may display different patterns of distribution, such as several subparallel specimens following ripple topography (fig. 29A).

Cruziana problematica commonly is not connected to well-developed resting structures. Some specimens, however, show incipient resting features, commonly associated with a shift in the vertical direction of movement. These structures are slightly wider than the connected locomotion trace and are consistently 4.6–8.6 mm long. They are comparable with *Rusophycus carbonarius*, but they do not display the typical coffee-bean shape of that ichnospecies.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica* either forms monospecific assemblages or is associated with *Asteriacites lumbricalis* in dense assemblages, and commonly is crosscut by *Lockeia siliquaria, Nereites imbricata, Protovirgularia bidirectionalis, P. rugosa, Curvolithus simplex, Conichnus conicus,* and *Psammichnites grumula,* among many other ichnotaxa.

REMARKS—The studied specimens are similar to *C. problematica* described by Fillion and Pickerill (1990) and to the type specimens described by Schindewolf (1921) as *Ichnium problematicum. Isopodichnus osbornei* recorded by Glaessner (1957) displays a wider median furrow and is
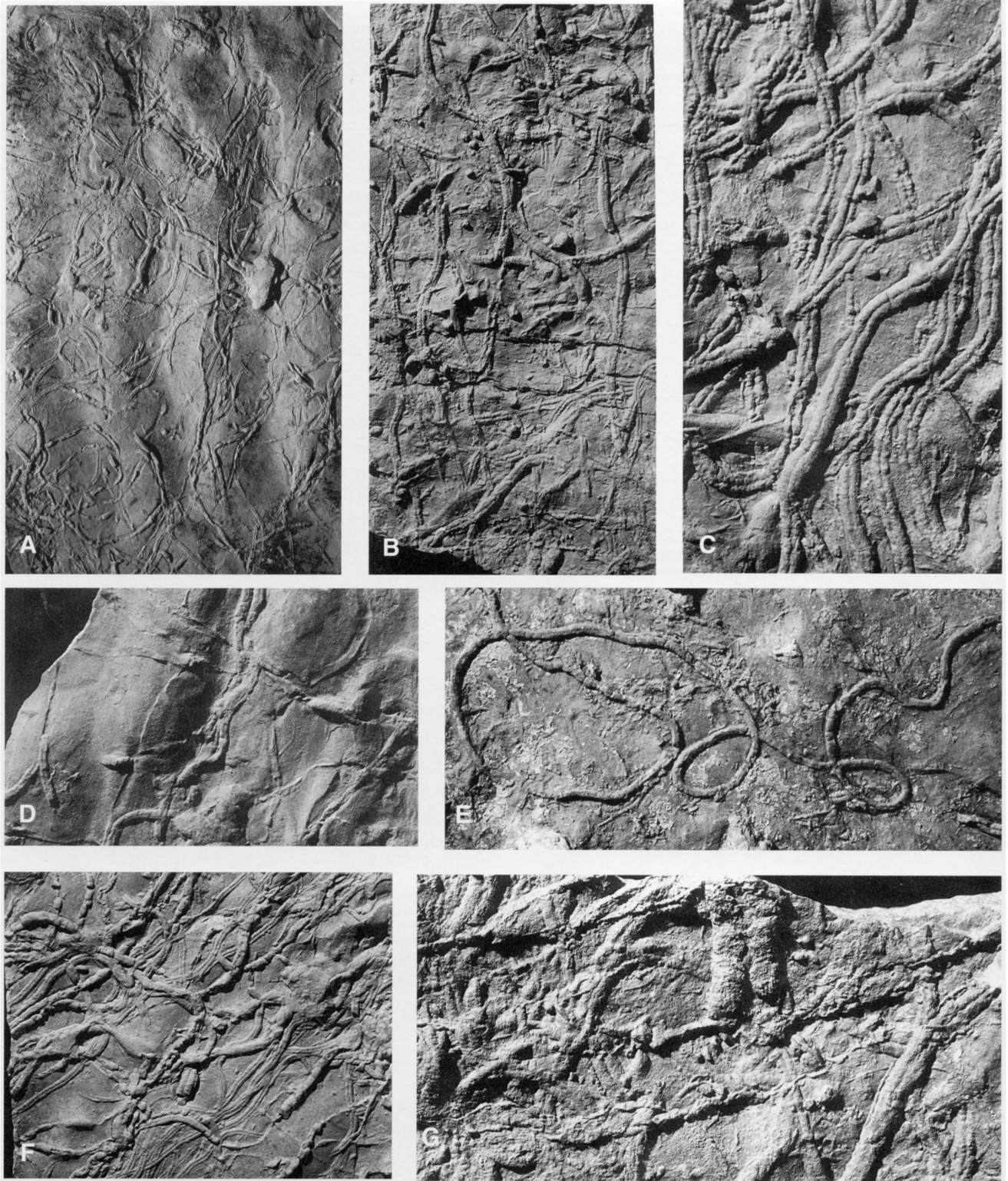
FIGURE 29—*Cruziana problematica* and *Cruziana* isp. All are basal bedding-plane views. **A**. General view of a monospecific assemblage of *Cruziana problematica*. Note specimens oriented parallel to ripple crests and troughs, whose morphology is casted from the underlying bed. KUMIP 288508. × 0.26. **B**. Close-up view. Note overcrossing among different specimens of *Cruziana problematica*. KUMIP 288510. × 0.38. **C**. Detailed view of some specimens of *Cruziana problematica* showing poorly developed scratch marks. KUMIP 288511. × 0.79. **D**. Specimens of *Cruziana problematica* preserved as strings showing only locally the bilobate structure. KUMIP 288513. × 0.52. **E**. Specimen of *Cruziana problematica* displaying self-overcrossing in a *Gordia*-like fashion. KUMIP 288540. × 0.46. **F**. Multiple overcrossing among different specimens of *Cruziana problematica* at different depths. KUMIP 288515. × 0.4. **G**. Larger specimen of *Cruziana* isp. associated with several poorly preserved individuals of *Cruziana problematica*. KUMIP 288510. × 0.86.

commonly preserved as shallow furrows in epirelief, resembling *Diplopodichnus biformis* (Buatois et al., 1998c). Jensen (1997) analyzed the type specimens of *Fraena tenella* Linnarsson, 1871, and concluded that this ichnospecies is identical to *Cruziana problematica*. He therefore regarded *Cruziana problematica* as a junior synonym of *Cruziana tenella*. However, because *Cruziana tenella* is a poorly known ichnospecies, we prefer to retain the widely used *Cruziana problematica* to promote nomenclatorial stability.

Some specimens of *C. problematica*, such as those at the base of gutter casts, most likely represent simple locomotion structures. However, crowded occurrences of *C. problematica* may well record grazing within the sediment (pascichnia).

Cruziana isp.
Fig. 29G

Specimens—One slab (KUMIP 288510) containing a single specimen.

Description—Straight horizontal trace consisting of two lobes separated by a relatively shallow, but well-defined median furrow. Lobes are relatively flat. Faint, thin, discontinuous transverse scratch marks cover the lobes. External ridges are absent. Length is 29.7 mm; width is 12.4–14.4 mm. Width changes slightly along the specimen. Preserved in positive hyporelief.

Associated ichnofauna—*Cruziana problematica, Asteriacites lumbricalis,* and *Lockeia siliquaria.*

Remarks—This single specimen of *Cruziana* isp. clearly differs in morphology and size range from *C. problematica*. Although size commonly is not a good ichnotaxobase, *C. problematica* has a consistently smaller size range and a distinctive mode of occurrence (i.e., long, straight to sinuous, commonly overlapping bilobated ridges). Discontinuous transverse endopodal scratches are not distinctive enough to allow a detailed ichnotaxonomic evaluation.

Ichnogenus *Curvolithus* Fritsch, 1908

Discussion—*Curvolithus* is distinguished from similar forms (e.g., *Gyrochorte, Psammichnites*) by its trilobate upper surface. However, traces with variable morphology usually have been included in *Curvolithus*, resulting in a rather complex ichnotaxonomic situation (cf. Fillion and Pickerill, 1990). Although *Curvolithus* has a trilobate upper surface, its lower surface has been regarded either as quadralobate (e.g., Maples and Suttner, 1990), trilobate (e.g., Webby, 1970; Hakes, 1976, 1977), bilobate (e.g., Heinberg, 1970; Fürsich and Heinberg, 1983; Heinberg and Birkelund, 1984; Lockley et al., 1987), and even unilobate (e.g., Chamberlain, 1971; Badve and Ghare, 1978). Confusion resulted in part because, other than Mikuláš (1992) and Rindsberg (1994), little attention has been paid to the original specimens described by Fritsch

(1908). In comparing his Carboniferous specimens with the types, Rindsberg (1994) noted some differences between the type specimens of *Curvolithus* and traces subsequently assigned to this ichnogenus by later authors. In an attempt to resolve these problems, Buatois, Mángano, Mikuláš, et al. (1998) redescribed the type specimen of *Curvolithus* and reviewed the taxonomy of this ichnogenus. These authors mentioned six ichnospecies recognized in the stratigraphic record: *C. multiplex* Fritsch 1908, *C. gregarius* Fritsch 1908, *C. davidis* Webby 1970, *C. annulatus* Badve and Ghare 1978, *C. aequus* Walter et al. 1989, and *C. manitouensis* Maples and Suttner 1990. Additionally, they defined another ichnospecies, *Curvolithus simplex*. Buatois, Mángano, Mikuláš, et al. (1998) retained *C. multiplex* for specimens with a smooth trilobate upper surface and a quadralobate lower surface and removed *C. gregarius* from *Curvolithus*. Buatois, Mángano, Mikuláš, et al. (1998) also regarded *C. davidis* and *C. annulatus* as *nomina dubia*, and they considered *C. manitouensis* as a junior synonym of *C. multiplex*. *Curvolithus aequus* has a bilobate lower surface and was interpreted as washed-out specimens of *Didymaulichnus*.

Curvolithus is regarded as a locomotion trace (repichnion) of carnivores, most likely gastropods, flatworms, or nemerteans (Lockley et al., 1987; Buatois, Mángano, Mikuláš, et al., 1998). The internal structure and production of this ichnogenus was analyzed by Heinberg (1973), who demonstrated that sediment excavated by the *Curvolithus*-animal was transported along its sides and packed in pads behind it.

Curvolithus commonly is associated with shallow-marine facies, both normal salinity and brackish, and it typically occurs in the *Cruziana* ichnofacies (Buatois, Mángano, Mikuláš, et al., 1998). Lockley et al. (1987) defined the *Curvolithus* ichnofacies as a subset of the *Cruziana* ichnofacies (actually *Curvolithus* association; see Bromley, 1990, 1996) that indicated delta-influenced nearshore environments. Occurrences of *Curvolithus* in tidal-flat deposits were reported by Hakes (1976, 1977, 1985) and Martino (1989, 1996). We are unaware of deep-marine occurrences of *Curvolithus*. Badve and Ghare (1978) noted that *C. annulatus* from the Jurassic Gajansar Beds of India occurred in the *Zoophycos* and *Nereites* ichnofacies. However, a critical analysis of the ichnotaxa present in the association (e.g., *Arenicolites, Monocraterion, Scolicia, Planolites, Nereites, Thalassinoides*) and the overall aspect of the assemblage suggests the *Cruziana* ichnofacies. Chamberlain (1971) and Häntzschel (1975) also regarded grooved tubes described by Keij (1965) from Miocene brackish-water deposits of Borneo as *Curvolithus*. Specimens from the Cambrian of Poland were questionably included in *Curvolithus* by Fedonkin (1977); they are bilobate and probably belong to another ichnogenus. *Curvolithus* ranges in age from Precambrian to Miocene (Webby, 1970; Keij, 1965).

Curvolithus multiplex Fritsch, 1908
Fig. 30

SPECIMENS—A single specimen on slab KUMIP 288500.

DESCRIPTION—Horizontal, straight to curved trace. Lower surface consists of four flat smooth lobes. Lobes are 1.9–2.6 mm wide. Total trace width is 7.0–7.5 mm. Maximum observed length of the trace is 56.3 mm. Lobes are separated by three narrow angular furrows. Laterally, inner lobes gradually merge to form a single central lobe. Trace-fill is identical to the host rock. Upper surface cannot be observed. Preserved as positive hyporelief.

ASSOCIATED ICHNOFAUNA—*Asteriacites lumbricalis, Diplocraterion* isp. A., *Protovirgularia bidirectionalis, Curvolithus simplex*, and *Cruziana problematica*.

REMARKS—*Curvolithus multiplex* is distinguished from the other *Curvolithus* ichnospecies by having a smooth trilobate upper surface and a quadralobate lower surface (Buatois, Mángano, Mikuláš, et al., 1998).

Curvolithus simplex Buatois, Mángano, Mikuláš and Maples, 1998
Fig. 31A–F

SPECIMENS—Twenty-six slabs (KUMIP 288500, KUMIP 288514, KUMIP 288516, KUMIP 288519, KUMIP 288522, KUMIP 288527, KUMIP 288528, KUMIP 288531, KUMIP 288533, KUMIP 288534, KUMIP 288541, KUMIP 288542, KUMIP 288543, KUMIP 288544, KUMIP 288548, KUMIP 288549, KUMIP 288550, KUMIP 288551, KUMIP 288552, KUMIP 288554, KUMIP 288555, KUMIP 288558, KUMIP 288559, KUMIP 288561, KUMIP 288569, KUMIP 288571) containing approximately 202 specimens and several others recorded in the field.

DESCRIPTION—Horizontal to oblique or, more rarely subvertical, straight to curved to sinuous, endostratal trace consisting of three smooth lobes on lower and upper surface. The central lobe ranges from 2.0 to 7.9 mm in width. Outer lobes are narrower and flatter than the central one, ranging from 1.4 to 4.0 mm in width. Total trace width is 2.7–14.5 mm. Maximum observed length of the trace is 77.6 mm. Each outer lobe is separated from the central lobe by a narrow angular furrow. In certain specimens, outer lobes gradually taper toward the center, enveloping the central lobe and giving the appearance of a narrower bilobate structure. Trace-fill is identical to the host rock. Segments preserved on ripple tops are usually very short, while those preserved on sandstone soles are long. Preserved as full relief, as well as positive hyporeliefs and epireliefs.

ASSOCIATED ICHNOFAUNA—*Asteriacites lumbricalis, Diplocraterion* isp. A, *Protovirgularia bidirectionalis,*

FIGURE 30—*Curvolithus multiplex*. Basal bedding-plane view. KUMIP 288500. × 1.6.

Curvolithus multiplex, and *Cruziana problematica*, as well as other ichnotaxa.

REMARKS—Buatois, Mángano, Mikuláš, et al. (1998) noted that there was no available ichnospecific name to cover the most common specimens of *Curvolithus* (i.e., with a trilobate smooth upper surface and a trilobate to unilobate smooth lower surface), which either were assigned erroneously to *C. multiplex* or classified as *Curvolithus* isp. Therefore, they proposed the ichnospecies *C. simplex* for such traces. *Curvolithus simplex* includes specimens with both concave and convex lower surfaces.

Ichnogenus *Diplichnites* Dawson, 1873

DISCUSSION—Considerable confusion persists regarding the use of the ichnogenus *Diplichnites*. It was erected by Dawson (1873) to name trackways reported from deltaic Carboniferous deposits of Nova Scotia, which were believed to be produced by crustaceans, annelids, or myriapods. Subsequently, Seilacher (1955) applied this name to trilobite trackways from the Cambrian of Pakistan. However, Briggs et al. (1979, 1984) suggested restricting *Diplichnites* to nontrilobite trackways. The name *Diplichnites* is applied herein regardless of the tracemaker identity and based strictly on trackway morphology. However, it should be stated that the ichnotaxonomy of arthropod trackways, and of the ichnogenus *Diplichnites* in particular, is in need of revision.
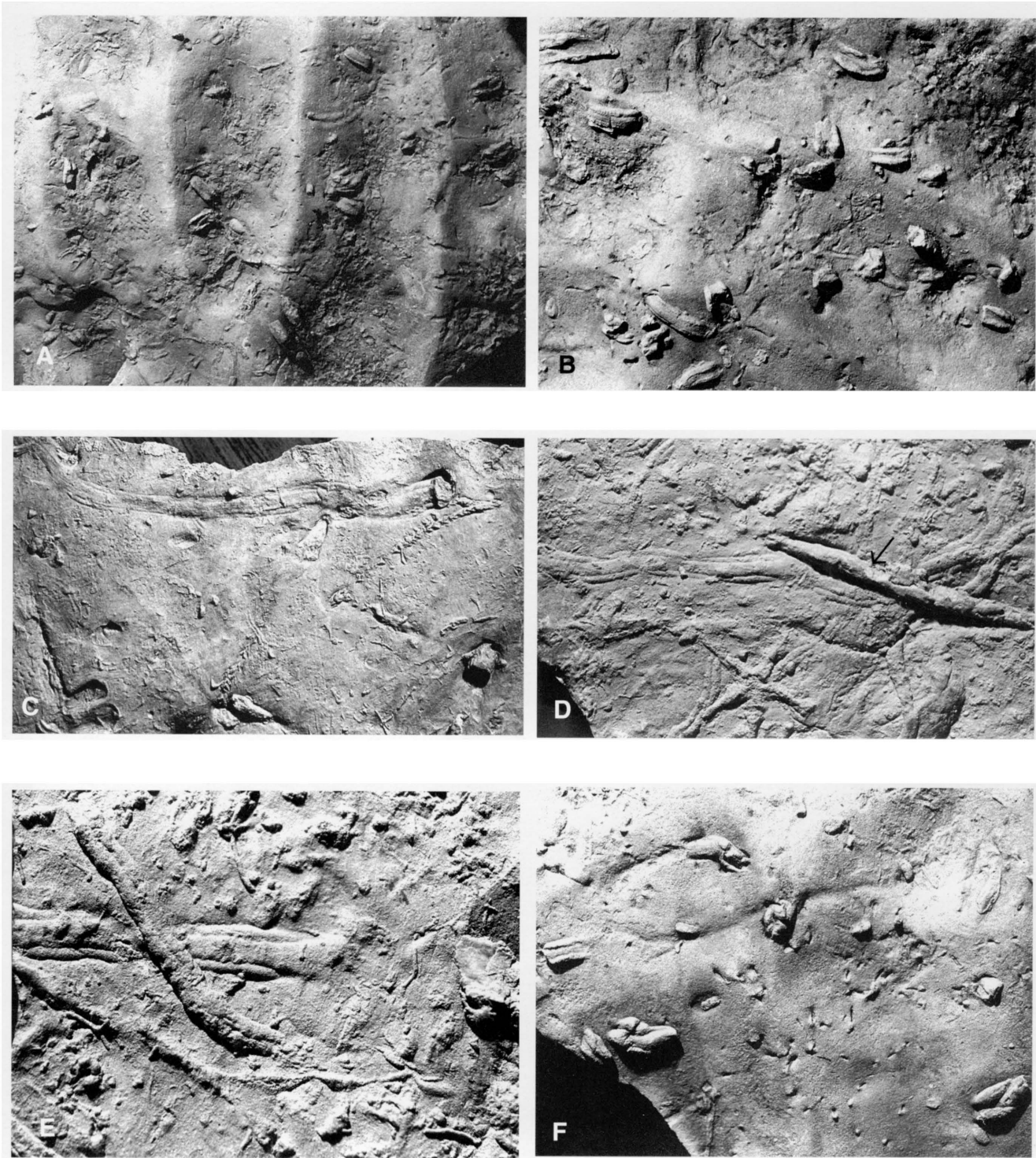
FIGURE 31—*Curvolithus simplex*. **A**. Several specimens preserved on the top of rippled sandstone. Specimens in the upper right with outer lobes tapering toward the center and enveloping the central lobe. KUMIP 288550. × 0.3. **B**. Close-up of top of rippled sandstone showing specimens preserved on both crests and troughs. KUMIP 288549. × 0.5. **C**. Large specimen of *C. simplex* preserved on the base of sandstone bed. KUMIP 288531. × 0.37. **D**. Large specimen of *C. simplex* overprinting a background association of *Cruziana problematica* and crosscut by a deeper structure, possibly *Protovirgularia bidirectionalis* (arrow). Basal bedding-plane view. KUMIP 288500. × 0.62. **E**. Specimen of *C. simplex*, preserved on the base of sandstone bed, crosscut by a bilobate structure (probably *Protovirgularia rugosa*). KUMIP 288500. × 1.22. **F**. Top of bed view showing specimens with the outer lobes enveloping the inner lobe. KUMIP 288549. × 0.62.

Diplichnites cuithensis Briggs, Rolfe, and Brannan, 1979
Fig. 32A–C

SPECIMENS—Three specimens on three slabs (KUMIP 288576, KUMIP 288577, KUMIP 288578) and three additional specimens studied in the field.

DESCRIPTION—Straight trackways consisting of two parallel rows of similar tracks preserved as positive hyporelief or negative epirelief. Individual trackways traced up to 440 mm long. Width of trackway is 233.0–302.4 mm. Space between rows is 101.6–177.7 mm. Imprints represented by elongated and sigmoidal ridges oriented normal to the axis of the trackway. In most cases, details of individual imprints not preserved due to super-position of imprints, soft-sediment deformation, or both. In well-preserved forms, each imprint tends to be sharply defined, shallow, and tapers toward axis. Imprints 49.1–96.7 mm long; width 6.5–22.4 mm. Imprints closely spaced between 9.5–37.1 mm. Superposition due to coalescing of adjacent footfalls is common. In one specimen, individual imprints cannot be identified because they coalesce into a single ridge that forms the row (fig. 32B).

ASSOCIATED ICHNOFAUNA—No other traces are associated with D. cuithensis.

REMARKS—Diplichnites cuithensis is interpreted as a locomotion trace (repichnion) produced by the giant myriapod Arthropleura (Briggs et al., 1979). A detailed analysis of the morphology of this ichnospecies can be found in Briggs et al. (1979). These authors discussed several potential arthropod tracemakers, including myri-apods, eurypterids, and scorpions, concluding that D. cuithensis was produced by the former. Assuming the estimation of Ryan (1986) that the body length of Arthropleura is 3.75 times the width, the Waverly arthropleurids would be at least 1.13 m long. This estima-tion falls within the Arthropleura range suggested by other authors.

Diplichnites cuithensis has been recorded from Namurian deltaic channel-fill deposits of Arran, Scotland (Briggs et al., 1979); Westphalian alluvial deposits of New Brunswick (Briggs et al., 1984); and Westphalian to Early Permian channel-bar facies of Nova Scotia (Ryan, 1986). The depositional environment of Diplichnites cuithensis is typically subaerial, commonly exposed fluvial bars, silted channels, and desiccated sheetflood deposits. Diplichnites cuithensis ranges in age from Namurian to Early Permian (Briggs et al., 1979; Ryan, 1986).

Ichnogenus Diplocraterion Torell, 1870

DISCUSSION—The presence of spreiten connecting the arms distinguishes Diplocraterion from the related U-burrow Arenicolites (Fürsich, 1974a). Rhizocorallium, another U-shaped trace, also has spreiten, but it differs from Diplocraterion in its horizontal to subhorizontal orientation. Corophioides Smith, 1893 and Polyupsilon Howell, 1957a are considered junior synonyms of Diplocraterion (Goldring, 1962; Frey and Chowns, 1972; Fürsich, 1974a; Fillion and Pickerill, 1990).

Functional analysis of the spreiten provides a key to the ethologic significance of Diplocraterion. Fürsich (1974a) concluded that the spreiten may result either from growth of the inhabitant or vertical movement of the structure by the inhabitant to maintain an optimum distance from the sediment-water interface. Diplocraterion may be regarded as a dwelling structure or domichnion (Cornish, 1986; Ekdale and Lewis, 1991), or as an equilibrium structure or equilibrichnia (Bromley, 1996). Although Diplocraterion usually has been considered as the work of suspension feeders (Cornish, 1986; Mason and Christie, 1986; Dam, 1990b; Ekdale and Lewis, 1991; Jensen, 1997), Bromley (1996) has shown that this is not always the case and that the origin of vertical U-spreiten traces may be considerably more complex. Bromley (1996) contrasted the activities of the amphipod Corophium volutator, a detritus feeder that constructs Diplocraterion-like burrows in muddy sediments, with the suspension feeder Corophium arenarium that produces similar, but mucus-lined, structures in sand. Polychaete annelids also have been suggested as tracemakers of Diplocraterion (Arkell, 1939).

Diplocraterion is especially common in high-energy, shallow-water environments. However, it is a facies-crossing ichnotaxon that ranges from deep-marine (e.g., Crimes, 1977) to shallow-marine (e.g., Bromley and Hanken, 1991; Chaplin, 1996; Paczesna, 1996; Orlowski and Zylinska, 1986) and marginal-marine environments (e.g., Chaplin, 1985; Mángano and Buatois, 1997). Although most occurrences are restricted to marine settings, Diplocraterion recently has been recorded in continental deposits (Kim and Paik, 1997; Zhang et al., 1998). Diplocraterion is a common component of tidal-flat environments, being particularly abundant in high-energy, lower-intertidal sand flats (e.g., Ireland et al., 1978; Chamberlain, 1980; Pollard, 1981; Narbonne, 1984; Cornish, 1986; Mason and Christie, 1986; Weissbrod and Barthel, 1998). Diplocraterion ranges in age from Cam-brian to Holocene (Jensen, 1997; Bromley, 1996).
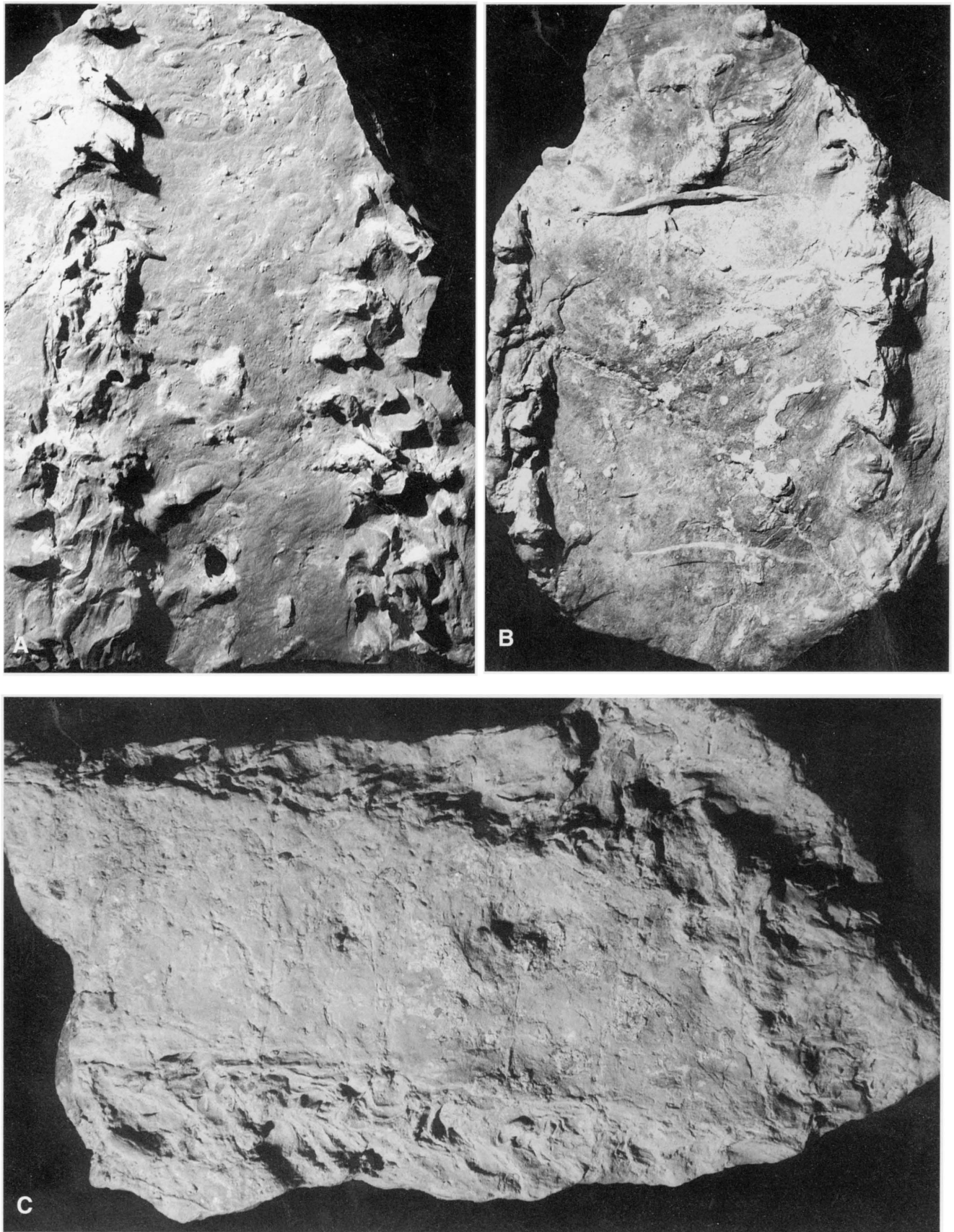
FIGURE 32—*Diplichnites cuithensis*. **A**. Specimen preserved as positive hyporelief. KUMIP 288578. × 0.27. **B**. Superposition of imprints due to coalescing of adjacent footfalls in specimen preserved as positive hyporelief. KUMIP 288576. × 0.36. **C**. Specimen preserved as negative epirelief. KUMIP 288577. × 0.36.

Diplocraterion isp. A
Fig. 33A

SPECIMEN—One specimen on a single slab (KUMIP 288500).

DESCRIPTION—U-shaped burrow observed as dumbbell semirelief. Spreite is protrusive. Arms are very thinly lined and are filled with the same lithology as the host rock. Burrow surface displays corrugations. Arm terminations are separated by a zone of reworking representing bedding-plane expression of spreiten. Width is 19.8 mm. Arm thickness is 6.6–8.5 mm. Preserved as positive hyporelief.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica, Protovirgularia bidirectionalis, Curvolithus simplex, C. multiplex,* and *Asteriacites lumbricalis.*

REMARKS—Terminology follows that proposed by Fürsich (1974a). The Waverly specimen compares favorably with other occurrences of dumb-bell semireliefs (e.g., Fillion and Pickerill, 1990, fig. 7.5; Zhang et al., 1998, fig. 11B). Preservation is restricted to the bedding plane, which precludes ichnospecific assessment. Hypichnial preservation and larger size distinguishes this ichnospecies from *Diplocraterion* isp. B.

Diplocraterion isp. B
Fig. 33B–D

SPECIMENS—Seven slabs (KUMIP 288514, KUMIP 288516, KUMIP 288519, KUMIP 288529, KUMIP 288539, KUMIP 288541, KUMIP 288554) with approximately 84 specimens and many others examined in the field.

DESCRIPTION—U-shaped burrow observed as dumbbell depressions on bedding planes. Arms are very thinly lined. Burrow surface is smooth and lacks ornamentation. Arm terminations typically are separated by a furrow reflecting reworked sediment that records the bedding-plane expression of the protrusive spreiten. In some cases, both arms appear isolated as paired small circles with no apparent spreiten. Unequal development of limbs is
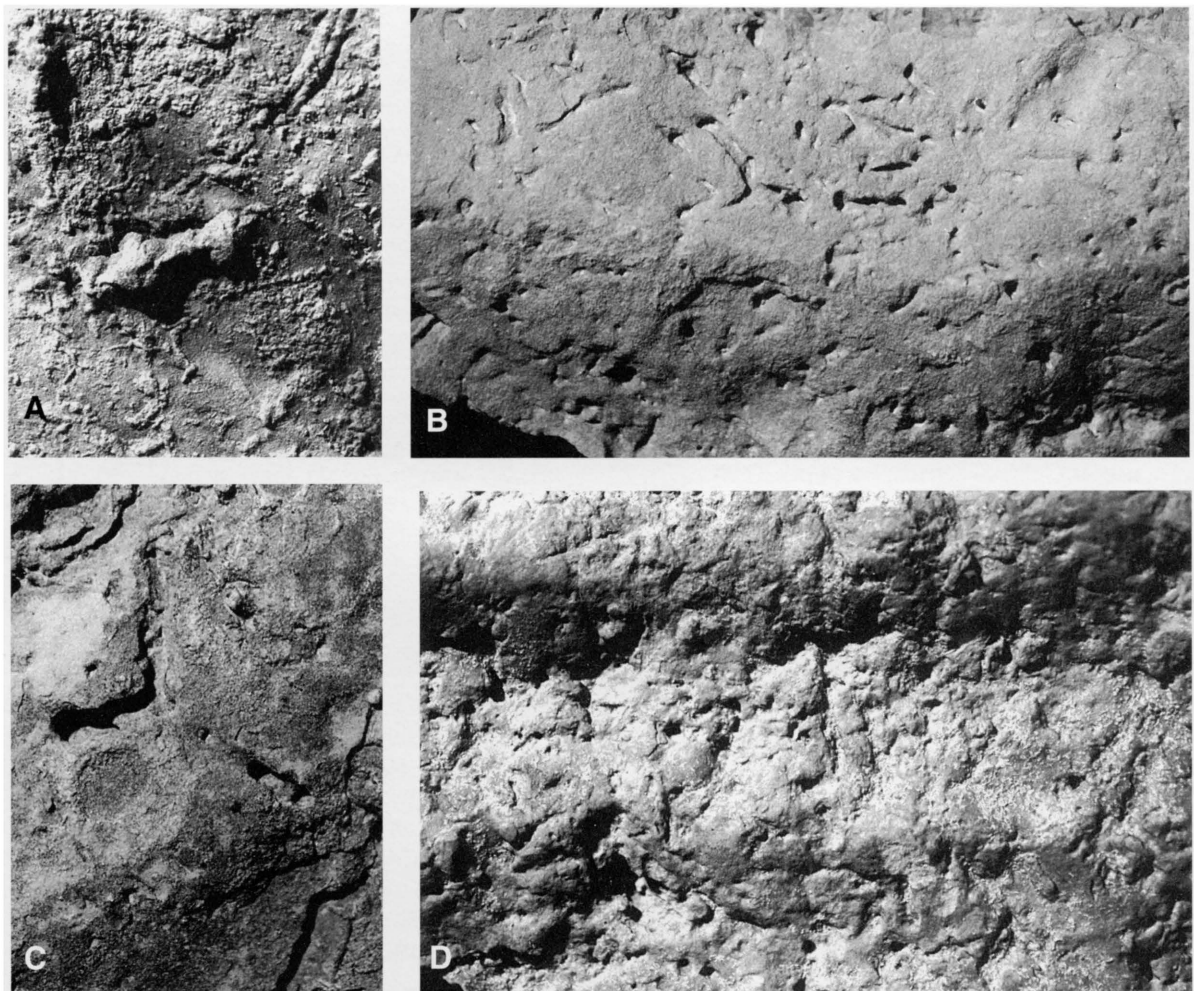
FIGURE 33—Ichnospecies of *Diplocraterion*. **A.** *Diplocraterion* isp. A. U-shaped burrow preserved as dumb-bell hyporelief. KUMIP 288550. × 0.99. **B.** *Diplocraterion* isp. B. Cluster of several specimens preserved at the top of a rippled sandstone. KUMIP 288529. × 0.75. **C.** *Diplocraterion* isp. B. Small specimens preserved as negative epirelief. KUMIP 288514. × 1.03. **D.** *Diplocraterion* isp. B. Poorly preserved specimens in a well-weathered rippled sandstone top. KUMIP 288554. × 0.52.

common. Width is 5.8–13.0 mm. Arm thickness is 1.1–3.8 mm. Preserved as negative epireliefs.

Associated ichnofauna—Commonly associated with *Curvolithus simplex* and *Protovirgularia bidirectionalis*, and, more rarely, with *Halopoa* isp., and arthropod tracks.

Remarks—Specimens of *Diplocraterion* isp. B described here are similar to those figured by Arkell (1939, pl. VII, figs. A–B), Mason and Christie (1986, fig. 2), and Bromley and Hanken (1991, figs. 10 and 11) preserved on bedding planes. Our specimens probably represent the bases of U-shaped burrows. Preservation restricted to bedding planes precludes ichnospecific assessment. In contrast to *Diplocraterion* isp. A, *Diplocraterion* isp. B is smaller, preserved as negative epireliefs, and typically occurs in high densities.

Ichnogenus *Halopoa* Torell, 1870

Discussion—The ichnogenus *Halopoa* recently was reviewed by Uchman (1998). It includes predominantly horizontal traces covered with longitudinal ridges or wrinkles and composed of overlapping cylindrical probes. *Asterosoma* von Otto, 1854, also has longitudinal wrinkles, but it is characterized by a radial morphology (Seilacher, 1969; Häntzschel, 1975; Pemberton, MacEarchen, et al., 1992). The ichnogenus *Asterophycus* Lesquereux, 1876, also is star-shaped and has longitudinal wrinkles, and is most likely a junior synonym of *Asterosoma* (Chamberlain, 1971; Schlirf, 2000).

Halopoa is interpreted as a feeding structure (fodinichnion) produced by deposit-feeding crustaceans (Nathorst, 1881). Książkiewicz (1977) suggested priapulid worms as tracemakers, but his proposal was rejected by Uchman (1998). Uchman (1998, 1999) noted that the origin of the longitudinal striation and wrinkles may be diverse, including microfaulting due to tension caused by the producer (cf. Osgood, 1970; Seilacher, 1990).

Halopoa is present in open marine environments, both shallow (Torell, 1870; Jensen, 1997) and deep (Książkiewicz , 1977; Buatois et al., 2001) water. *Halopoa* ranges in age from Cambrian to Miocene (Seilacher, 1955; Crimes and McCall, 1995).

Halopoa isp.
Fig. 34A–F

Specimens—Thirteen slabs (KUMIP 288519, KUMIP 288531, KUMIP 288532, KUMIP 288534, KUMIP 288535, KUMIP 288538, KUMIP 288544, KUMIP 288550, KUMIP 288551, KUMIP 288554, KUMIP 288555, KUMIP 288572, KUMIP 288575) containing twenty-five specimens.

Description—Horizontal to rarely oblique traces characterized by longitudinal wrinkles or striae. Trace segments have an inflated shape, pinching out laterally. Striae are commonly laterally continuous, but they may anastomose or merge in some specimens. Trace segments

occur alone or branch to form pairs. Tunnels are thickly lined and have a concentric fill. Trace segments are 6.0–27.7 mm wide and up to 160.9 mm long. Striae are 0.3–2.6 mm wide and up to 79.9 mm long. Wall lining is up to 3.2 mm thick. Preserved in full relief on both tops and bases of sandstone beds.

Associated ichnofauna—*Asteriacites lumbricalis, Cruziana problematica, Protovirgularia bidirectionalis, Curvolithus simplex,* and *Trichophycus* isp.

Remarks—Two ichnospecies of *Halopoa* were recognized by Uchman (1998): *H. imbricata* Torell, 1870, and *H. annulata* (Książkiewicz, 1977). *Halopoa imbricata* is unbranched and has relatively long and continuous furrows and wrinkles, while *H. annulata* is branched and has perpendicular constrictions. The Waverly specimens are classified at the ichnogeneric level because the overall morphology of the trace cannot be detected. The specimens studied differ from single concentrically filled traces, such as *Rosselia* or *Cylindrichnus*, in their horizontal orientation. Concentric fill, inflated trace segments, and continuity of striation distinguish the Waverly specimens from *Palaeophycus striatus*.

Ichnogenus *Lockeia* James, 1879

Discussion—Although *Pelecypodichnus* Seilacher, 1953, still is used as an ichnogenus by some authors (e.g., Eagar and Li, 1993), it should be abandoned, because it is a junior synonym of *Lockeia*. *Lockeia* James, 1879, was once considered as a *nomen oblitum* rather than the senior synonym of *Pelecypodichnus* (Hakes, 1977; Bromley and Asgaard, 1979; Wright and Benton, 1987). The status of *Lockeia*, however, was revised by Maples and West (1989). Based on the Principle of Priority (ICZN, 1985), they considered *Lockeia* to be the senior synonym of *Pelecypodichnus*. *Umbonichnus* Karaszewski 1975 is a poorly known junior synonym of *Lockeia* (Rindsberg, 1994). *Lockeia* is distinguished from *Sagittichnus* Seilacher, 1953, by the arrowhead shape of the latter (Gluszek, 1995).

Several ichnospecies of *Lockeia* have been proposed: *L. siliquaria* James, 1879, *L. amygdaloides* (Seilacher, 1953), *L. ornata* (Bandel, 1967a), *L. czarnockii* (Karaszewski, 1975), *L. elongata* Yang, 1984, *L. avalonensis* Fillion and Pickerill, 1990, *L. triangulichnus* Kim, 1994, *L. cordata* Rindsberg, 1994, and *L. hunanensis* Zhang and Wang, 1996. *Lockeia siliquaria*, the most widespread ichnospecies, is oval to almond-shaped, typically tapering only at one end with the other end somewhat rounded. However, *L. siliquaria* may display very irregular outlines, corrugated sides, or a peripheral rim (Mángano et al. 1998). All these features are related to the paleobiologic affinity of the bioturbator or substrate fluidity, and do not involve modifications of behavior. *Lockeia siliquaria* is considered the senior synonym of *L. amygdaloides* (Seilacher and Seilacher, 1994). *Lockeia czarnockii* is indistinguishable from almond-shaped *L.*
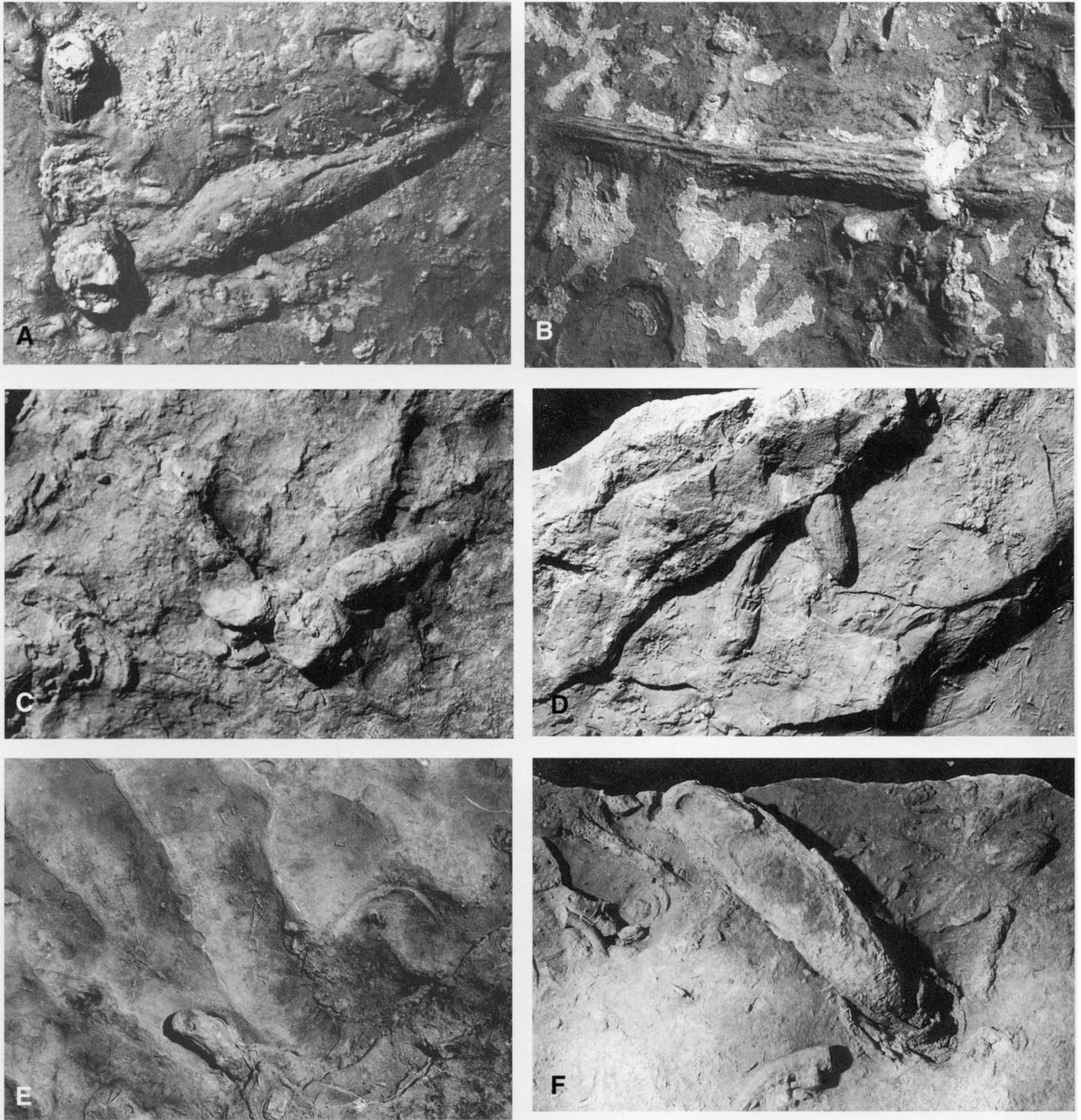
FIGURE 34—*Halopoa* isp. All photos are of base of beds with the exception of C and E, which show preservation at the top of sandstone beds. **A**. Specimen showing two branches oriented oblique to the bedding plane. KUMIP 288554. × 0.8. **B**. Large trace segment with laterally persistent striations. KUMIP 288555. × 0.8. **C**. Trace segments at the top of sandstone bed. Note associated *Nereites missouriensis* (upper right). KUMIP 288531. × 0.7. **D**. Paired striated trace segments. KUMIP 288531. × 0.5. **E**. Trace segment at the top of a sandstone bed with interference ripples. KUMIP 288544. × 0.3. **F**. Trace segment showing concentrical fill. KUMIP 288575. × 0.5.

siliquaria. Fillion and Pickerill (1990) suggested that *L. ornata* was a questionable form that probably should be included in *Walcottia*. Our observations of Bandel's specimens, including the types, indicate that *L. ornata* is a distinct ichnotaxon, and its diagnostic feature is the presence of a concentrically ornamented surface. Many specimens of *L. ornata* are often in physical continuity with *Protovirgularia rugosa*, forming a compound trace fossil. *Lockeia cordata* probably is a preservational variant of *L. siliquaria*, and is not distinctive enough in terms of ethology to warrant recognition as a separate ichnospecies. *Lockeia avalonensis* is spheroid to sub-ovate in form with steep margins and, rarely, a shallow carinal crest (Fillion and Pickerill, 1990). Observations of the Waverly specimens suggest that distinguishing among spheroid, sub-ovate, and almond-like *Lockeia* can be quite difficult. Data on *L. siliquaria* from Waverly clearly show that small specimens of *L. siliquaria* tend to be more spherical, and they resemble the "stuffed burrows" of Pollard (1981). Accordingly, more spherical specimens may record structures of juvenile forms or a different biologic species rather than real behavioral variants. The question of whether or not this subtle change in shape deserves a different ichnospecies name remains problematic.

Lockeia triangulichnus is most likely an inorganic structure. In any case, the solely subtriangular outline would not be of behavioral significance, but would be a feature more related to the paleobiology of the tracemaker (e.g., its foot morphology, shell form). The taxonomic validity of *L. hunanensis* is difficult to evaluate, because the quality of the illustrations of the type specimens is very poor.

Lockeia typically occurs as convex hyporeliefs on the soles of sandstones, occasionally displaying an overlying shaft (cf. Seilacher, 1953). *Lockeia* historically has been interpreted as a resting structure (cubichnion) (Seilacher, 1953; Osgood, 1970, Fillion and Pickerill, 1990; Rindsberg, 1994). However, some specimens of *Lockeia*, particularly those representing the lower end of relatively deep structures, may document semi-permanent domiciles (i.e., domichnia). Bivalves are the typical tracemakers of *Lockeia* (Seilacher and Seilacher, 1994). However, conchostracans also may produce similar traces in continental settings (Pollard and Hardy, 1991).

Lockeia has been reported from shallow-marine (e.g., Seilacher, 1953; Osgood, 1970; Fillion and Pickerill, 1990; Kim, 1994), marginal-marine (e.g., Bandel, 1967; Hakes, 1977; Wright and Benton, 1987; Rindsberg, 1994; Mángano and Buatois, 1997), and deep-marine facies (e.g., Crimes et al. 1981; Yang et al., 1982), in addition to continental environments (e.g., Bromley and Asgaard, 1979; Gluszek, 1995). Hakes (1976, 1977, 1985), Rindsberg (1994), and Mángano et al. (1998), among others, recognized *Lockeia* in tidal-flat facies. *Lockeia* ranges in age from Late Cambrian/Early Ordovician to Pleistocene (Fillion and Pickerill, 1990; Pemberton and Jones, 1988). Specimens reported from the Vendian (Late

Precambrian) as *Lockeia* isp. by McMenamin (1996) do not display the characteristic morphology of this ichnogenus.

Lockeia ornata (Bandel, 1967a)
Fig. 35A–D

SPECIMENS—Eight slabs (KUMIP 288521, KUMIP 288543, KUMIP 288549, KUMIP 288552, KUMIP 288557, KUMIP 288558, KUMIP 288562, KUMIP 288568) with approximately 217 specimens.

DESCRIPTION—Elongate, relatively small almond-shaped structures preserved as positive hyporeliefs. Delicate, sharp, concentric ridges resembling growth interruptions in a bivalve shell are diagnostic (fig. 35B). Length is 12.0–26.8 mm; width is 6.5–13.4 mm. In some specimens, a longitudinal median ridge (carina) occurs. Chevroned, smooth or roughly bilobated locomotion traces commonly are connected to *L. ornata* (fig. 35A). This form typically exhibits a gregarious mode of occurrence, with local patches of high density. Looping, radial, and rosary patterns formed by serial alignment of *Lockeia* commonly are observed (fig. 35C–D).

ASSOCIATED ICHNOFAUNA—*Lockeia ornata* typically is associated with *Protovirgularia rugosa, P. bidirectionalis, Cruziana problematica, Asteriacites lumbricalis,* and *Palaeophycus tubularis*.

REMARKS—Bandel (1967a) found specimens of *Lockeia* exhibiting similar ornamentation, and he proposed the ichnospecies *Pelecypodichnus ornatus* (= *Lockeia ornata*). It can be argued, however, that specific substrate conditions are required for preservation of *Lockeia ornata*. Although the presence of concentric ornamentation was the diagnostic feature selected by Bandel (1967a), *L. ornata* exhibits a unique mode of occurrence, which suggests a pattern of behavior that differs significantly from that depicted by *L. siliquaria*. Connection of *Lockeia ornata* with spicate locomotion traces indicates a high degree of mobility along horizontal planes. Rosary structures (i.e., individual *Lockeia* aligned one behind the other) have been noted by several authors (e.g., Linck, 1949; Osgood, 1970; Wright and Benton, 1987; Seilacher and Seilacher, 1994). Seilacher and Seilacher (1994) proposed a new ichnospecies, *L. serialis*, based on the serial alignment of structures. These authors also suggested that *L. serialis*, first documented from the German Keuper (Triassic), has environmental significance (i.e., continental environments). However, our observations of Pennsylvanian tidal-flat facies indicate that serial alignment is quite common in brackish and normal-marine settings. Radial arrangements and looping record a patterned feeding strategy with constant repositioning in search for food. Seilacher and Seilacher (1994, Pl. 1, Figs. c-e) illustrated radial structures produced by the modern bivalve *Macoma*.

In its movement, the *L. ornata* tracemaker cut the sand-mud casting interface at different angles, resulting in
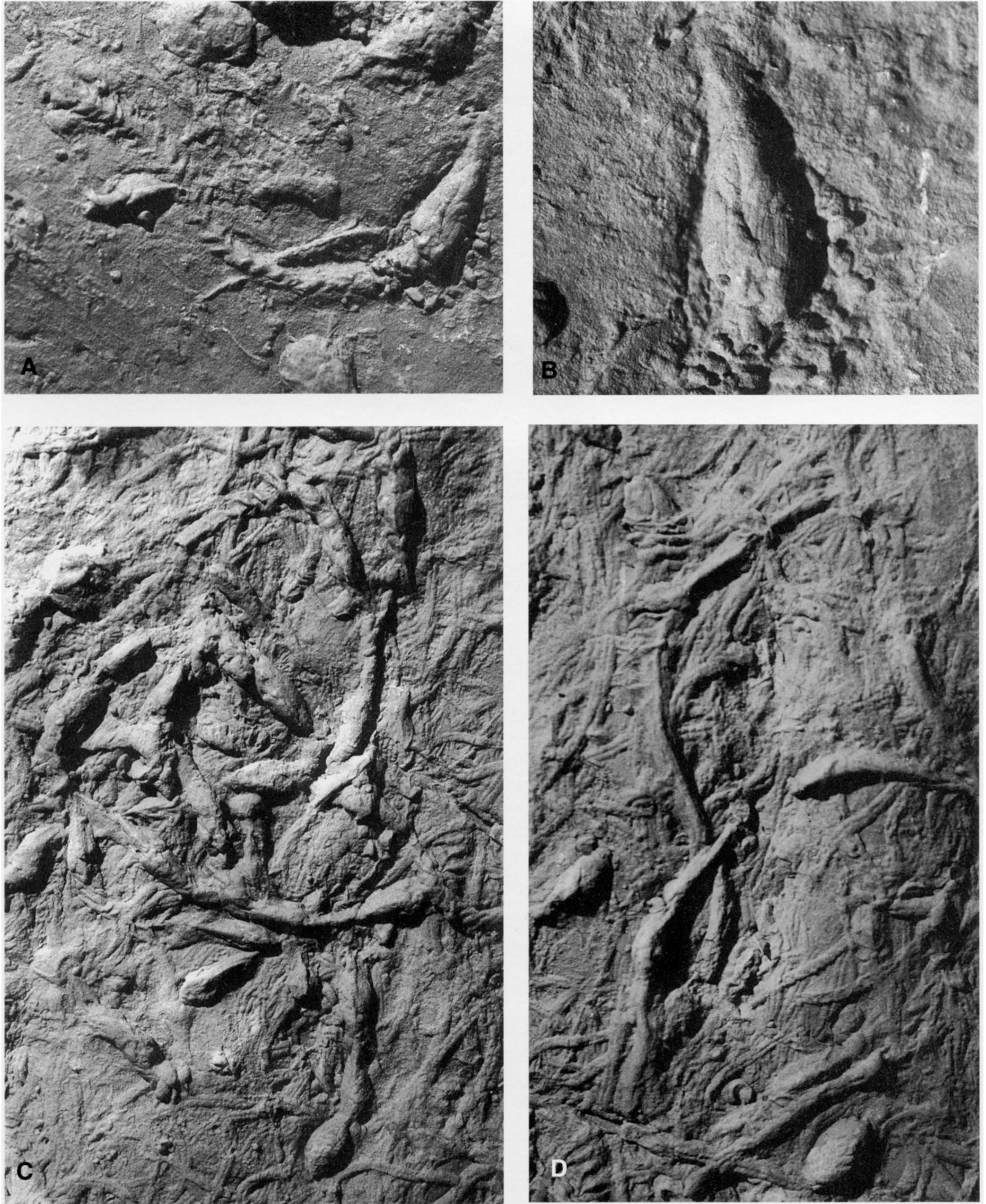
FIGURE 35—*Lockeia ornata*. All photos are of base of KUMIP 288552. **A**. Specimen of *L. ornata* connected with chevron locomotion traces. Chevron orientation indicates that the animal exited the resting structure. × 0.88. **B**. Close-up of specimen in A showing concentric ornamentation. Delicate, fine longitudinal ridges present on both sides of *Lockeia siliquaria*. × 1.9. **C**. Rosary structures resulting from the alignment of several specimens of *Lockeia ornata* and radial or fan-like patterns. × 0.8. **D**. Localized high density of *L. ornata* superimposed on a background assemblage of *Cruziana problematica*. × 0.89.

a highly variable range of length-to-width ratios (L/W) (fig. 36; see also Mángano et al., 1998, Fig. 11). *Lockeia ornata* records ventral and antero-ventral areas of the bivalve tracemaker. Elongate forms represent almost horizontal orientations, whereas less elongate forms suggest inclined to subvertical orientations. Other specimens of *L. ornata* are connected to relatively short chevroned structures (*Protovirgularia rugosa*) that reveal a bifurcate foot. These structures can be interpreted as escape structures related to tidal sedimentation (see "Remarks" of *P. rugosa*). In the late Paleozoic, this mode of life was exploited almost exclusively by nuculoid protobranch bivalves (Stanley, 1968). Mángano et al. (1998) suggested *Phestia*, a Pennsylvanian nuculanid with concentric ornamentation, as the most likely tracemaker of *L. ornata* in the Waverly tidal flat.

Lockeia siliquaria (James, 1879)
Fig. 37A–F

SPECIMENS—Eighteen slabs (KUMIP 288508, KUMIP 288509, KUMIP 288510, KUMIP 288511, KUMIP 288514, KUMIP 288522, KUMIP 288528, KUMIP 288531, KUMIP 288540, KUMIP 288541, KUMIP 288551, KUMIP 288552, KUMIP 288553, KUMIP 288554, KUMIP 288556, KUMIP 288569, KUMIP 288571, KUMIP 288572) containing 91 specimens and several others examined in the field.

DESCRIPTION—Almond-like or oval-shaped traces. Typically, these forms taper toward one end with the other end more rounded. However, some specimens exhibit irregular shapes. Length is 12.3–45.2 mm and width is 8.9–22.7 mm. Large specimens display hypichnial ridges up to 17.9 mm deep, but typically the depth is about 10 mm. The surface usually is smooth, although some specimens show corrugated lateral sides. A marginal rim is observed in a few specimens. A longitudinal ridge, or carena, is present occasionally. Some large specimens are strongly tilted to one side. Large specimens may occur singly (particularly some large specimens) or in patches, forming groups of three or more. Overlap between specimens is quite common, particularly in densely covered sandstone soles (fig. 37D). No preferred long-axis orientation has been detected. Alignments of one form behind the other, forming chainlike structures similar to those described by Seilacher (1953) from the Triassic of Germany ("pseudo-preferred orientation" of Osgood, 1970), have not been observed. Cross sectional views of some specimens show two basic patterns of preservation: (1) hypichnial ridges connected to endichnial shafts that cut across thin sandstone beds, and (2) hypichnial ridges connected to short endichnial shafts that are truncated by physical sedimentary structures. The burrow fill may be massive, suggesting a passive filling of the structure, or the burrow fill may show a poorly defined meniscus-like structure in the lower part of the shaft.

ASSOCIATED ICHNOFAUNA—*Lockeia siliquaria* is present throughout the sequence, and it is associated with such other forms as *Curvolithus simplex, Asteriacites lumbrica-*
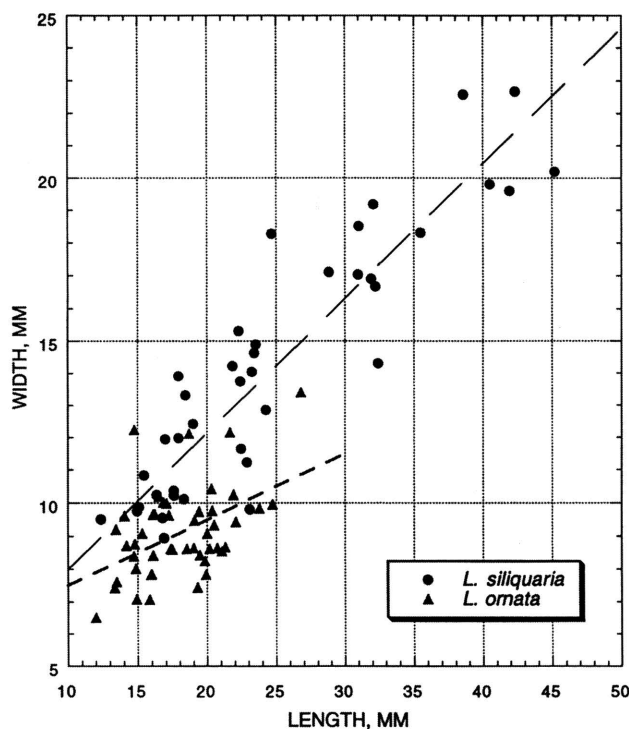
FIGURE 36— Width/length regression curves of *Lockeia ornata* (triangles) and *Lockeia siliquaria* (circles). Note high degree of variability in witdh/length ratio for *L. ornata* versus *L. siliquaria*. The wider range of *L. ornata* reflects the undulating movements of its deposit-feeding producer that crossed the sand-mud interface with different orientations.

lis, and *Cruziana problematica*. A few stratigraphic horizons, however, are characterized almost exclusively by high densities of *L. siliquaria*.

REMARKS—Morphologic variability and mode of occurrence of these traces are consistent with *L. siliquaria*. *Lockeia siliquaria* commonly occurs in connection with inclined or vertical shafts, suggesting that the bioturbator was able to move vertically. *Lockeia siliquaria* records either the anterior area of the tracemaker or the foot compressing the sediment. Morphologic variability and corrugated sides suggest the second possibility as more plausible. Ethologically, *L. siliquaria* either represents dwelling structures (domichnia) of suspension feeders or fugichnial responses to changing environmental conditions, rather than short-lived resting traces (cubichnia). Absence of intergradation with locomotion structures (*Protovirgularia*) suggests a bivalve tracemaker with a wedge-shaped foot rather than one with a bifurcated foot. The abundance and multiple modes of preservation of *Lockeia siliquaria* in time-averaged surfaces also suggest relatively deep structures that survived, at least partially, the destructive effects of coastal erosion. In the late Paleozoic very few bivalves, probably only primitive lucinids and a few anomalodesmatids, were capable of burrowing to intermediate depths (Stanley, 1968). At Waverly, the pholadomid *Wilkingia* is the most likely tracemaker of *L. siliquaria* (Mángano et al., 1998).

Ichnogenus *Nereites* MacLeay in Murchison, 1839

DISCUSSION—*Nereites* has been the subject of a continuous controversy regarding its relationship with other forms, particularly *Neonereites* Seilacher, 1960, and *Scalarituba* Weller, 1899. Some authors have argued that these three ichnotaxa represent preservational variants of the same form (e.g., Seilacher and Meischner, 1965; Chamberlain, 1971; D'Alessandro and Bromley, 1987; Rindsberg, 1994; Uchman, 1995), while others retained them as separate ichnogenera (e.g., Hakes, 1976; Fillion and Pickerill, 1990; Pickerill, 1991; Crimes and McCall, 1995). Chamberlain (1971) demonstrated that a single specimen is preserved as hypichnial biserially arranged lobes or pustules (*Neonereites biserialis*-like) and an epichnial median furrow with lobes on both sides (*Scalarituba missouriensis*, *Nereites* isp., and *Neonereites uniserialis*-like). Recently, Uchman (1995) discussed this problem in detail, stressing the importance of a central tunnel surrounded by a zone of reworked lithology as a diagnostic feature. He concluded that the type of preservation cannot be regarded as an ichnotaxobase at the ichnogeneric level, and he suggested that *Neonereites* and *Scalarituba* should be considered as junior synonyms of *Nereites*. Other ichnogenera synonymized with *Nereites* are *Myrianites*, *Nereograpsus*, *Phyllodicites*, *Maldanidopsis*, *Delesserites*, and *Paleohelminthoida*

(Häntzschel, 1975; D'Alessandro and Bromley, 1987; Uchman, 1995). The ichnotaxonomic status of *Radionereites* Gregory, 1969, is somewhat problematic. According to Gregory (1969), *Radionereites* differs from *Nereites* by occurring in radiating clusters. Because the internal structure of *Radionereites* is identical to that of *Nereites*, it probably should be included in this ichnogenus, perhaps as a distinctive ichnospecies. Until a comprehensive review of all the ichnospecies of *Nereites* and similar forms is undertaken, this problem will remain unsolved.

Partial reviews and descriptions of some ichnospecies of *Nereites* were presented by Benton (1982), Crimes and McCall (1995), and Orr and Pickerill (1995). Uchman (1995) provided an extensive synonymy of *Nereites*, suggesting that accessory preservational features can be used to distinguish among different ichnospecies. Additionally, he proposed that ichnospecies formerly included in *Neonereites* (*N. uniserialis*, *N. biserialis*, and *N. multiserialis*) are better considered as ichnosubspecies of *Nereites missouriensis*. Uchman (1995) also placed *Helminthoida irregularis* Schafhäutl, 1851, in *Nereites* as a separate ichnospecies (*N. irregularis*). Orr and Pickerill (1995) analyzed the type specimens of some ichnospecies of *Nereites* originally described by Emmons (1844), as well as additional specimens. These authors considered *N. macleayi* (Murchison, 1839), *N. cambrensis* (Murchison, 1839), *N. jacksoni* Emmons, 1844, and *N. pugnus* Emmons, 1844 as distinctive ichnospecies. Mángano et al. (2000) noted that *Nereites jacki* Pek et al., 1978, though properly placed in *Nereites*, is most likely a *nomen dubium*, because the type material does not warrant creation of a new ichnospecies. *Nereites murotoensis* Katto, 1960 and *N. tosaensis* Katto, 1960 probably represent *Protovirgularia*-like structures, most likely *P. longespicata* (Mángano et al., 2000).

Nereites represents combined locomotion and feeding activities, and therefore it is considered to be a grazing trace (pascichnion) (Seilacher, 1983, 1986; Orr, 1995). Seilacher (1986) suggested that *Nereites* is produced by a wormlike sediment-feeder, probably an enteropneust that separates the coarse sediment with its protosoma and stows it in backfill lobes around the median tunnel.

Although the namesake of the deep-marine *Nereites* ichnofacies (Seilacher, 1967), this ichnogenus actually is a facies-crossing form that commonly is recorded in shallow-marine deposits, particularly in the Paleozoic (e.g., Conkin and Conkin, 1968; Hakes, 1976; Seilacher, 1983; Chaplin, 1985; Fillion and Pickerill, 1990; Rindsberg, 1994). Examples of *Nereites* in tidal-flat facies were recorded by Hakes (1976, 1977, 1985), Miller and Knox (1985), and Rindsberg (1994), among others. *Nereites* ranges in age from Late Precambrian/Early Cambrian to Miocene (Aceñolaza and Durand, 1973; Gregory, 1969). Lacustrine specimens recorded as *Nereites* from Jurassic lacustrine deposits of the Anyao Formation, central China, by Bin et al. (1998) do not display the
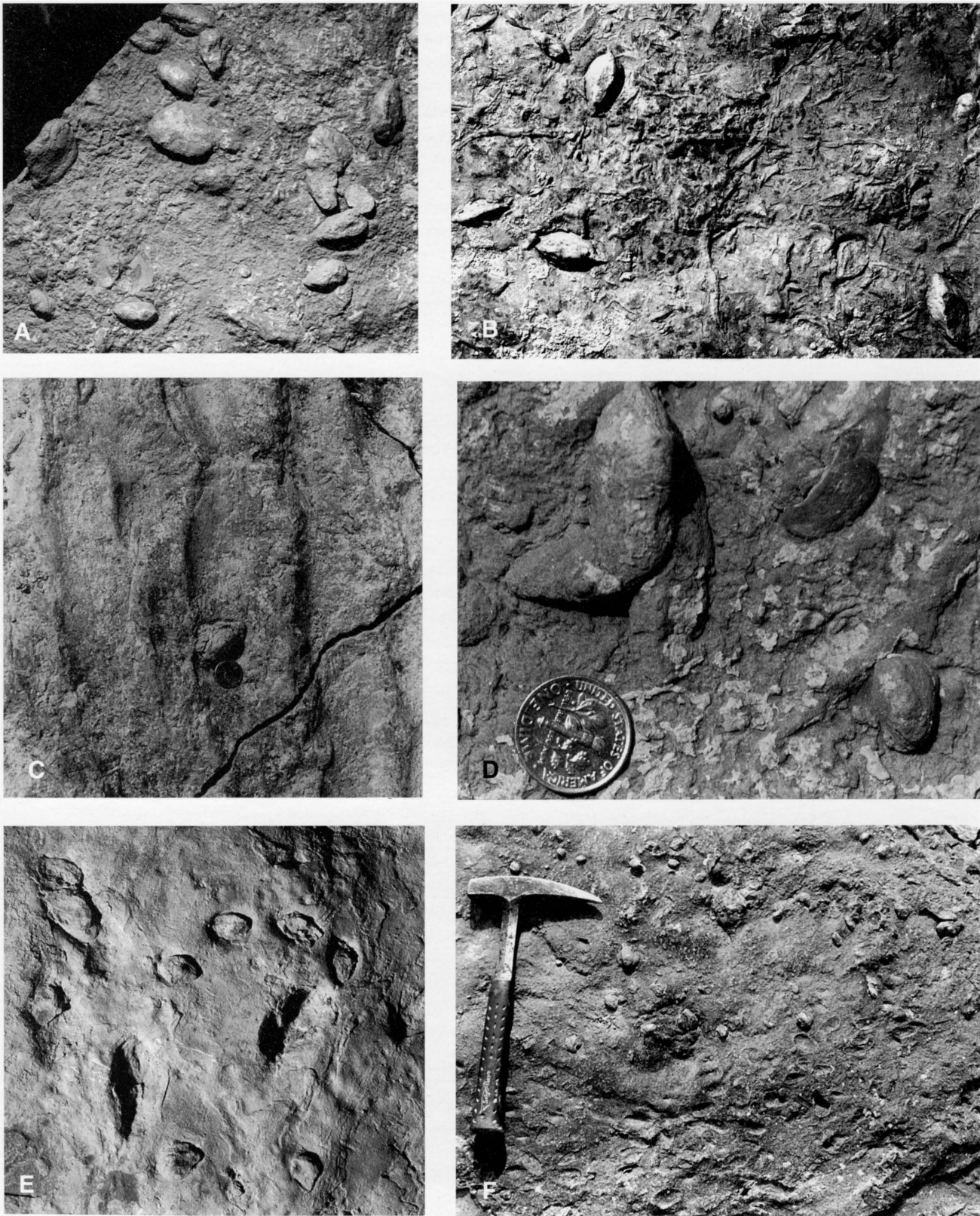
FIGURE 37—*Lockeia siliquaria*. **A**. Several specimens preserved as positive hyporelief on the sole of a sandstone bed. KUMIP 288553. × 0.29. **B**. Several specimens of *Lockeia siliquaria* associated with *Cruziana problematica* and preserved as positive hyporelief. KUMIP 288572. × 0.3. **C**. Specimen preserved as protruding shaft on the top of a rippled sandstone bed. Field photo. **D**. Superposition of three specimens at the base of a sandstone bed. KUMIP 288553. × 1.1. **E**. Differential preservation of *Lockeia siliquaria* at the top of a sandstone bed. Small protruding shafts are preserved together with large depressions. KUMIP 288553. × 0.44. **F**. Several specimens of *Lockeia siliquaria* with associated bivalve shells on the base of a sandstone bed. Field photo. Length of hammer is 33.5 cm.

diagnostic features of this ichnogenus. The constricted aspect of their specimens suggests placement in *Vagorichnus anyao*, which is the most abundant component of the Anyao ichnofauna (Buatois et al., 1995, 1996).

Nereites cambrensis Murchison, 1839
Fig. 38A–C

SPECIMENS—Seven slabs (KUMIP 288521, KUMIP 288524, KUMIP 288527, KUMIP 288549, KUMIP 288551, KUMIP 288552, KUMIP 288562) containing nine specimens. One of these specimens intergrades with *N. jacksoni*.

DESCRIPTION— Horizontal, meandering traces with ovate to lanceolate, lateral lobes. Adjacent lobes touch each other or partially overlap. Lobes of different rows are arranged alternately or slightly offset. Where visible, internal structure is a median back-filled tunnel. Trace width is 13.2–28.7 mm. Axial tunnel width is 3.8–7.8 mm. Lobes are 5.3–6.5 mm wide and 8.0–15.5 mm long. Preserved as positive hyporelief.

ASSOCIATED ICHNOFAUNA—*Nereites cambrensis* is commonly associated with *Lockeia ornata, Protovirgularia bidirectionalis*, and *Cruziana problematica*, although other ichnotaxa also may be present (e.g., *Asteriacites lumbricalis, Palaeophycus tubularis*).

REMARKS—*Nereites saltensis* Aceñolaza and Durand, 1973, has lateral lobes similar to those of *N. cambrensis*, but those in *N. saltensis* are commonly less well developed than those in *N. cambrensis*. Mángano et al. (2000) tentatively suggested that the following ichnospecies, proposed by Delgado (1910), are junior synonyms of *N. cambrensis*: *Nereites barroisi, N. marcoui, N. roemeri, N. liebei, N. barrandei, N. lorioili*, and *N. castroi. Nereites fengxianensis* Cui, Yu, Mei, and Meng, 1996, also is a probable junior synonym of *N. cambrensis*.

Nereites imbricata Mángano, Buatois, West, and Maples, 2000
Figs. 39A–F, 40A–F

SPECIMENS—Six slabs (KUMIP 288503, KUMIP 288517, KUMIP 288535, KUMIP 288536, KUMIP 288537, KUMIP 288538) with 11 specimens of different preservational variants.

DESCRIPTION—Predominantly horizontal, curved to slightly sinuous traces commonly preserved as imbricated subspherical pads arranged in uniserial rows. Shape and length (measured parallel to the trace axis) of pads are highly variable among specimens and reflect the degree of packing. Individual pads aligned in a row are commonly subequal in size. Pads are 12.8–17.2 mm wide and 3.6–14.9 mm long. Nested pads in some specimens do not display the characteristic subspherical shape. These traces commonly are relatively short, 27.8–37.8 mm, highly

convex, and formed by tightly packed pads, resulting in an annulated appearance. Trace length is up to 119.6 mm. In a few specimens, the internal structure is clearly visible. A thin median tunnel, 1.2–2.9 mm wide, is flanked by transverse backfill menisci, 0.5–1.2 mm wide. In weathered specimens, the axial channel is lacking and a median depression can be observed. Trace walls are distinctive, but no visible lining is observed. Preserved as positive hyporelief or full relief.

ASSOCIATED ICHNOFAUNA—*Nereites imbricata* is commonly associated with *Asteriacites lumbricalis* and *Cruziana problematica*, but other forms (e.g., *Palaeophycus tubularis*) also may be present.

REMARKS—*Nereites imbricata* differs from other *Nereites* ichnospecies by the characteristic external morphology of uniserial imbricate sediment pads and the poorly specialized nonmeandering pattern. *Nereites imbricata* winds in horizontal planes and undulates in vertical planes, resulting in tightly packed overlapping pads, producing an annulated appearance. Internally, this ichnospecies is characterized by an overlapped, obliquely arranged lamination that envelops the axial tunnel. Additionally, the enveloping-sediment-width / axial-tunnel-width ratio is remarkably larger than in the other *Nereites* ichnospecies (Mángano et al., 2000).

Nereites jacksoni Emmons, 1844
Fig. 38C–E

SPECIMENS—Three slabs (KUMIP 288545, KUMIP 288552, KUMIP 288557) with three specimens, one of which intergrades with *N. cambrensis*.

DESCRIPTION—Horizontal, curved to sinuous traces with circular to subcircular, alternately arranged, lateral lobes. Lobes are smooth and envelop an axial tunnel. Trace is 17.4–24.8 mm wide. Individual lobes are 8.1–10.3 mm wide. Axial tunnel is 3.5–11.7 mm wide. Adjacent lobes touching each other or separated by up to 6.7 mm. Preserved as positive epirelief and hyporelief.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica, Palaeophycus tubularis*, and *Lockeia ornata*.

REMARKS—*Nereites jacksoni* is characterized by its circular to subcircular lobes (Orr and Pickerill, 1995). Specimens from Waverly are very similar to that figured as *Nereites* isp. by Hakes (1976, pl. 9, fig. 2d) from the Virgilian Tecumseh Shale in eastern Kansas.

Nereites missouriensis (Weller, 1899)
Fig. 41A–E

SPECIMENS—Ten slabs (KUMIP 288531, KUMIP 288535, KUMIP 288540, KUMIP 288548, KUMIP 288557, KUMIP 288558, KUMIP 288561, KUMIP 288562, KUMIP 288564, KUMIP 288573) containing at least 32 specimens.
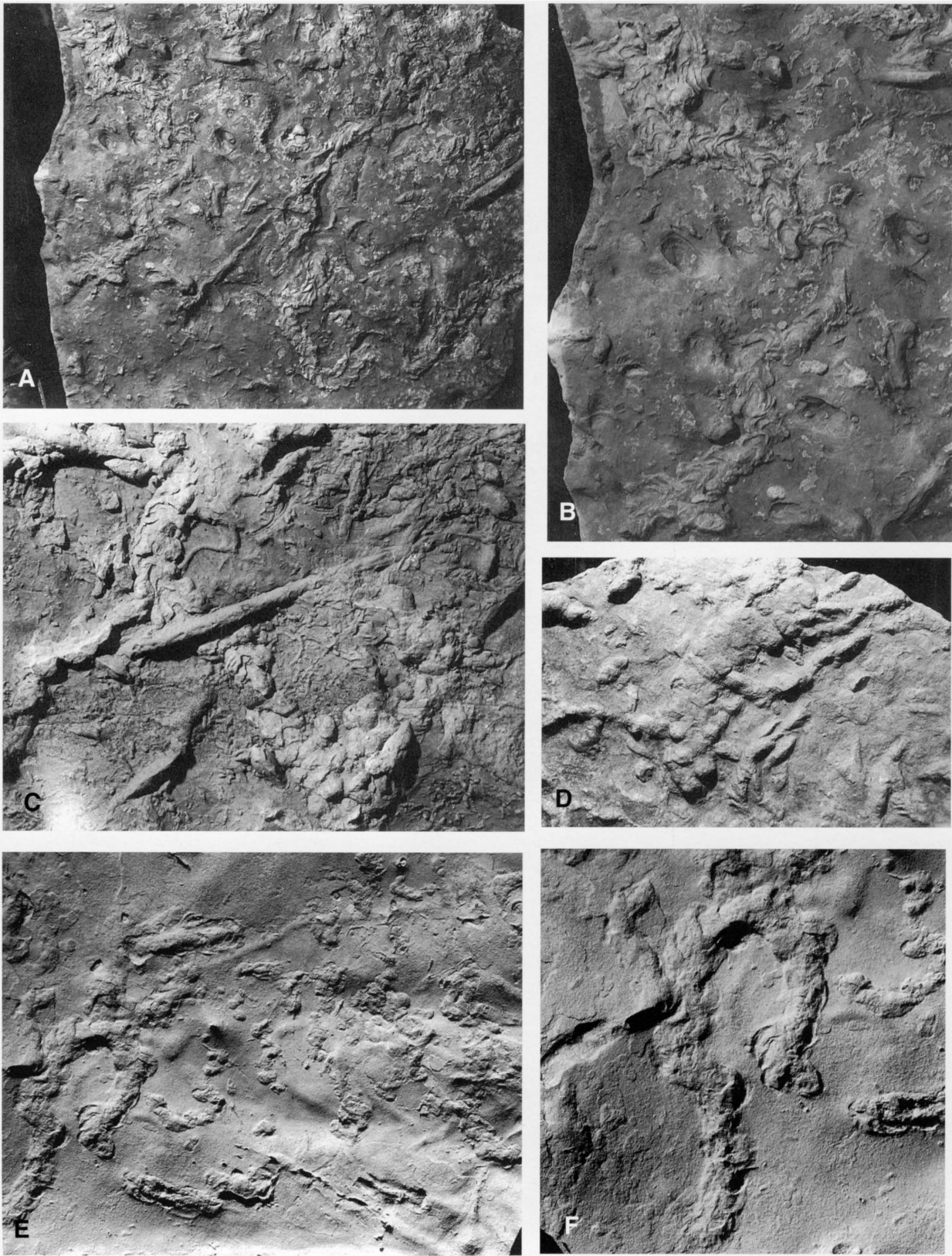
FIGURE 38—*Nereites cambrensis* and *Nereites jacksoni*. **A**. *Nereites cambrensis*. Large slab with a meandering specimen. Positive hyporelief. KUMIP 288562. × 0.2. **B**. *Nereites cambrensis*. Close-up view of specimen in A. Positive hyporelief. KUMIP 288562. × 0.34. **C**. *Nereites cambrensis* (upper left) intergrading with *Nereites jacksoni* (lower right). Positive hyporelief. KUMIP 288552. × 0.48. **D**. *Nereites jacksoni*. Note circular shape of the lobes. Positive hyporelief. KUMIP 288557. × 0.4. **E**. *Nereites jacksoni* preserved at the top of a sandstone bed. KUMIP 288521. × 0.34. **F**. *Nereites jacksoni*. Close-up of some specimens shown in E. KUMIP 288521. × 0.6.
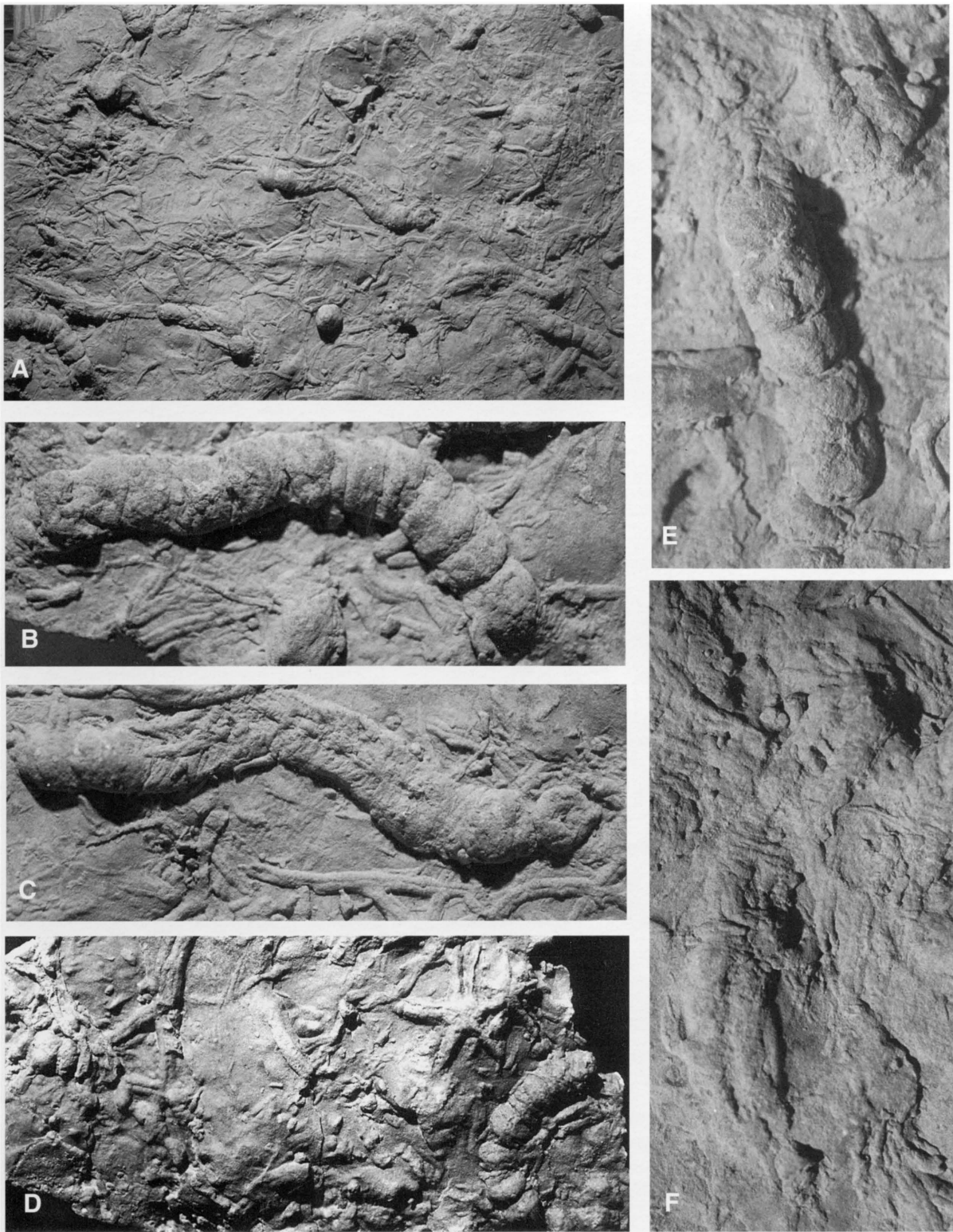
FIGURE 39—*Nereites imbricata*. All specimens preserved as positive hyporelief. **A**. General view of sandstone sole with several specimens of *N. imbricata*. KUMIP 288535. × 0.28. **B**. Detailed view of the specimen illustrated in the lower left of A. Note imbrication of subspherical sediment pads. KUMIP 288535. × 0.86. **C**. Internal structure of the specimen of *N. imbricata* illustrated in the center of A, showing a thin axial tunnel, flanked by transversally arranged backfill menisci. KUMIP 288535. × 0.86. Holotype. **D**. Two specimens of *N. imbricata*. Note associated *Asteriacites lumbricalis* and *Cruziana problematica*. KUMIP 288503. × 0.65. **E**. Detailed view of the specimen illustrated in the lower right of A. KUMIP 288535. × 0.91. **F**. Detailed view of the weathered specimen, illustrated in the lower right of A, with the axial channel lacking and a longitudinal furrow present. KUMIP 288535. × 0.85.
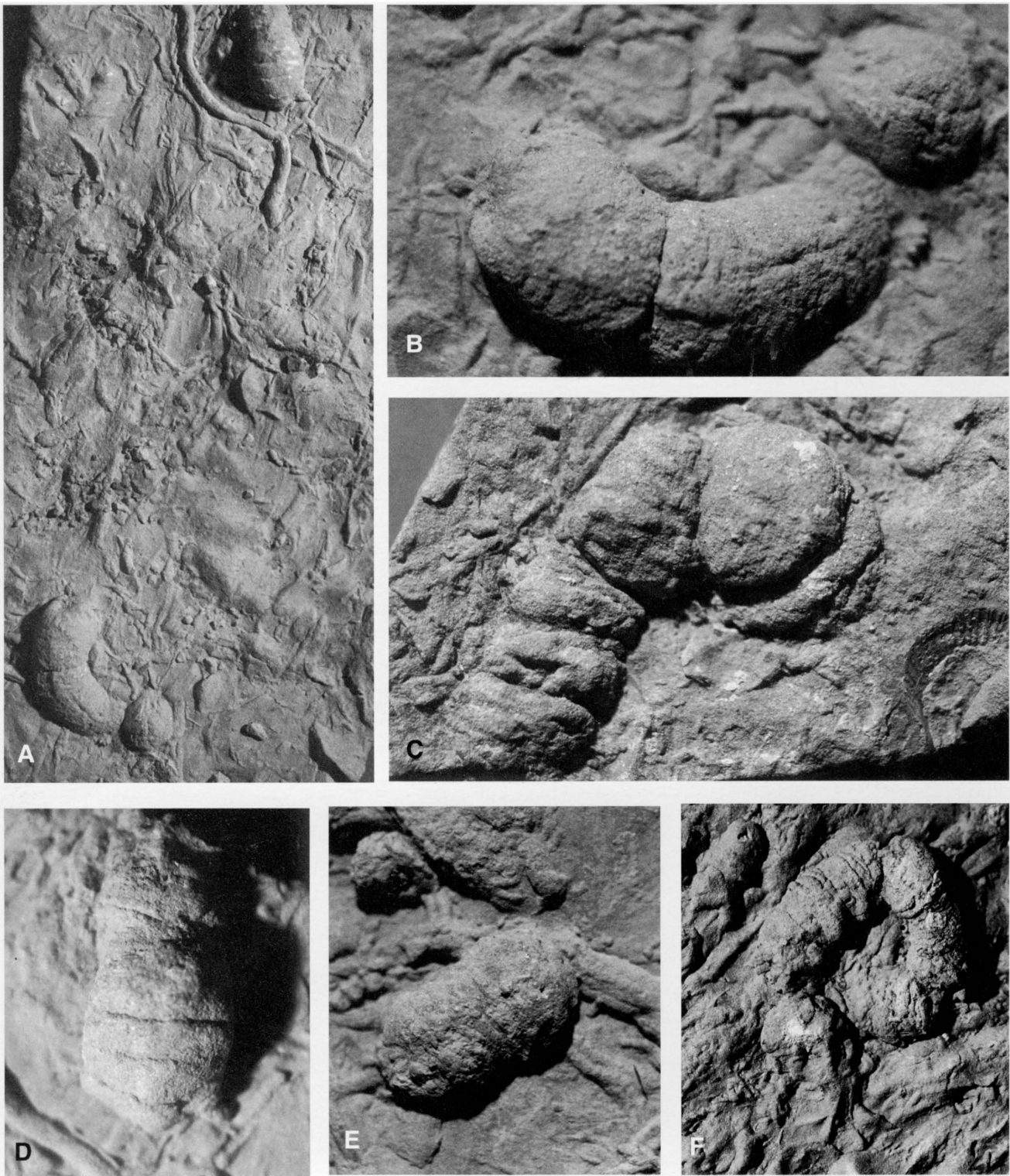
FIGURE 40—*Nereites imbricata*. All specimens preserved as positive hyporelief. **A**. General view of a sandstone base, preserving short specimens with tightly packed pads. KUMIP 288538. × 0.71. **B**. Detailed view of the specimen illustrated in the lower left of A. Note short trace composed of annulated pads re-emerging into a subspherical pad. KUMIP 288538. × 1.6. **C**. Specimen displaying change in pad morphology from annulated to subspherical, coincident with a change in orientation of trace. KUMIP 288536. × 1.6. **D**. Detailed view of the specimen illustrated on the upper right of A. Note highly convex specimens formed by tightly packed pads, resulting in an annulated appearance. KUMIP 288538. × 1.46. **E**. Highly convex and very short specimen. KUMIP 288538. × 1.2. **F**. Specimen having a spiralled course. KUMIP 288537. × 0.92.
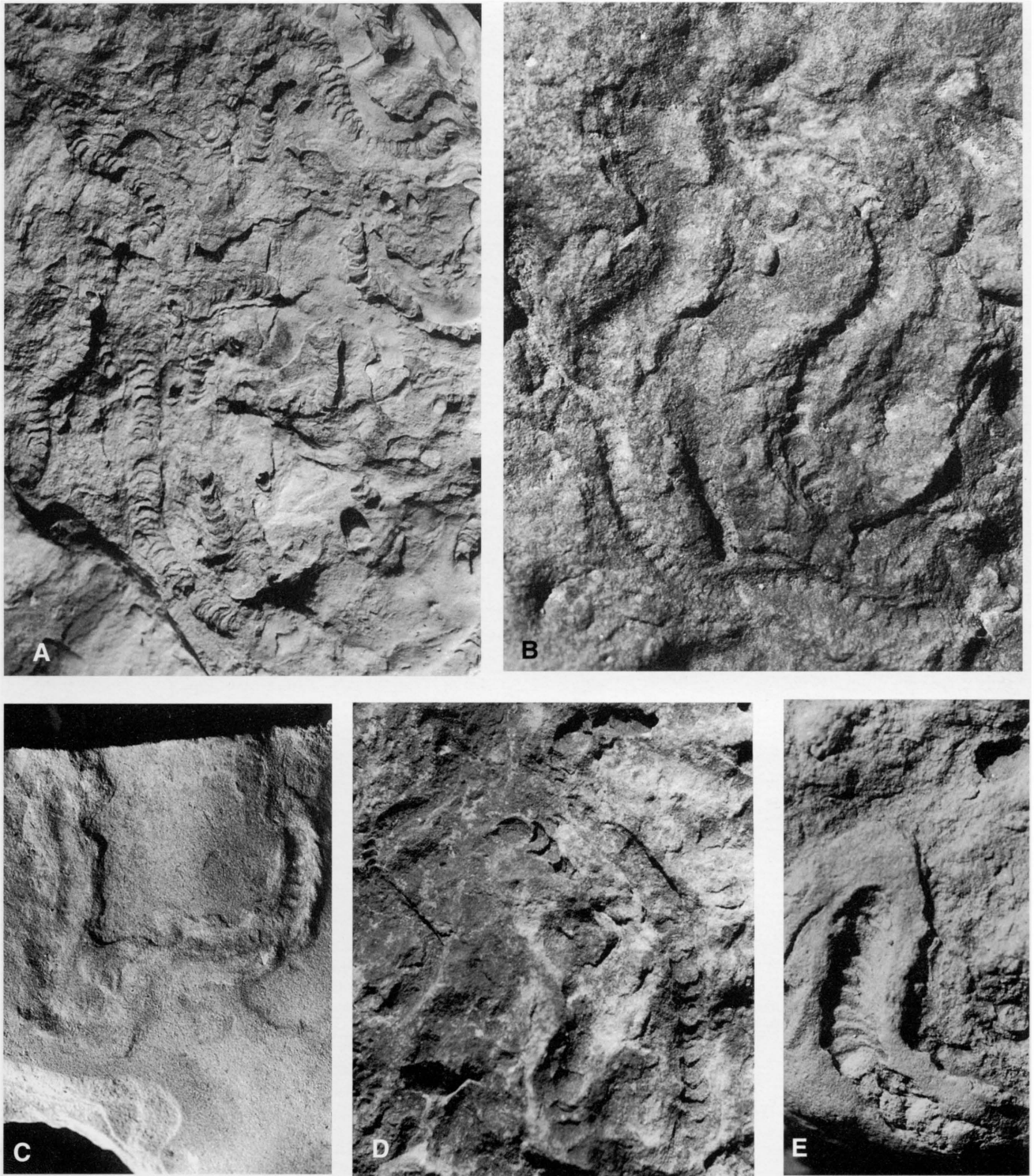
FIGURE 41—*Nereites missouriensis*. All specimens preserved at the top of a sandstone bed. **A**. Dense association of meandering specimens. KUMIP 288561. × 0.6. **B**. Close-up showing scalariform ridges. KUMIP 288558. × 1.4. **C**. Specimen with well developed lateral lobes. KUMIP 288573. × 0.87. **D**. Specimens with sharply defined scalariform ridges. KUMIP 28864. × 1.05. **E**. Close-up of a specimen having a single row of spherical pustules. KUMIP 288561. × 1.4.

DESCRIPTION—Horizontal to rarely oblique, winding, meandering to exceptionally coiled traces composed of transverse scalariform ridges along entire length of trace. Envelope zone consisting of sand lobes commonly present on both sides of the tunnel. In one specimen, trace-fill locally preserved as a single row of gray clay pustules, displaying the external sculpture of *Neonereites uniserialis*. Trace diameter highly variable within a single specimen. Traces are 3.2–10.3 mm wide. Envelope zone up to 6.7 mm wide. Scalariform ridges 0.4–1.6 mm wide and separated from each other by 0.6–4.1 mm. Preserved as negative epireliefs.

ASSOCIATED ICHNOFAUNA—*Nereites missouriensis* commonly occurs in monospecific assemblages. In other cases, it is associated with *Phycosiphon incertum, Curvolithus simplex*, and *Protovirgularia bidirectionalis*.

REMARKS—Originally described as *Scalarituba missouriensis*, this ichnospecies is included herein under *Nereites* following the suggestions of Seilacher and Meischner (1965), Chamberlain (1971), D'Alessandro and Bromley (1987), Rindsberg (1994), and Uchman (1995). Seilacher and Meischner (1965) noted that the lateral lobes are hardly visible. Weller (1899) did not describe lateral lobes, but his figured specimens (Weller, 1899, pl. VI, fig. 1) have sediment lobes locally along the margins of the trace. Uchman (1995, Text-fig. 8B) illustrated different preservational variations of *N. missouriensis,* and specimens from Waverly compare favorably with the thick-meniscate form of Uchman (1995). *Nereites missouriensis* is typified by its scalariform ridges (Conkin and Conkin, 1968). A synonym for *N. missouriensis* was provided by Uchman (1995). We agree with Conkin and Conkin (1968), who regarded *Scalarituba*? *atoka* Branson, 1966, as a junior synonym of *Nereites missouriensis. Akinereites kannouraensis* Katto, 1965 and *Notaculites toyomensis* Kobayashi, 1945 also are junior synonyms of *Nereites missouriensis. Scalarituba welleri* Branson, 1938, does not exhibit the scalariform ridges of *Nereites missouriensis* and it should be removed from this ichnogenus, as originally suggested by Conkin and Conkin (1968). *Scalarituba indica* Chiplonkar and Tapaswi, 1972, is a back-filled trace that should be removed from the *Nereites* group and be included in *Taenidium.* As noted by Uchman (1995), *Scalarituba darvaseana* Vialov, 1979, also is a junior synonym of *N. missouriensis*, as is *Maldanidopsis meandriformis* (Müller, 1966), which was redescribed by Plicka (1973). *Scalarituba lungmaxiensis* Yang, 1984, should be removed from the *Nereites* group because it represents a form similar to *Protovirgularia. Scalarituba michlensis* Mikuláš, 1992, does not display the diagnostic features of *N. missouriensis* and is of uncertain taxonomic affinities. Conkin and Conkin (1968) reviewed occurrences of *N. missouriensis* in Paleozoic strata of North America and concluded that this form occurs in prolific numbers in tidal-flat settings. *Nereites missouriensis* also has been recorded in slope to deep-marine environments (e.g., Buatois and Mángano, 1992; Uchman, 1995).

Ichnogenus *Palaeophycus* Hall, 1847

DISCUSSION—The taxonomy of *Palaeophycus* has been discussed by Pemberton and Frey (1982) and by Keighley and Pickerill (1995). *Palaeophycus* is distinguished from *Planolites* by the presence of wall linings and by a burrow-fill identical to the host rock (Pemberton and Frey, 1982), and from *Macaronichnus* by the active burrow-fill of the latter (Clifton and Thompson, 1978; Curran, 1985). Jensen (1997) noted the problems of differentiating *Palaeophycus* from *Planolites* in the case of concealed bed-junction preservation.

Pemberton and Frey (1982) regarded five ichnospecies of *Palaeophycus* as valid: *P. tubularis* Hall, 1847, *P. striatus* Hall, 1852, *P. heberti* (de Saporta, 1872), *P. sulcatus* (Miller and Dyer, 1878a), and *P. alternatus* Pemberton and Frey, 1982. Subsequent to that review, seven additional ichnospecies have been proposed: *P. ferrovittatus* Hofmann, 1983, *P. subornatus* Ghare and Kulkarny, 1986, *P. annulatus* Badve, 1987, *P. anulatus* McCann and Pickerill, 1988, *P. canalis* Walter et al., 1989, *P. serratus* McCann, 1993, and *P. crenulatus* Buckman, 1995. Additionally, Jensen placed *Halopoa imbricata* Torell, 1870, in *Palaeophycus* as *P. imbricatus*. Recently, Buckman (1995) discussed the taxonomy of annulate ichnospecies of *Palaeophycus*, and considered *P. annulatus, P. anulatus, P. canalis*, and *P. serratus* as *nomina dubia. P. subornatus* is characterized by a thick wall and transverse markings. However, ornamentation is not displayed clearly in the illustrated holotype, so Mángano et al. (1996) considered this ichnospecies a *nomen dubium. Rituichnus* Yang, Song, and Liang, 1982, has been regarded as a junior synonym of *Palaeophycus striatus* by Fillion and Pickerill (1990).

Palaeophycus is a passively filled open burrow that is interpreted as the dwelling structure (domichnion) of predaceous or suspension-feeding animals (Pemberton and Frey, 1982). Osgood (1970) suggested the predaceous polychaete *Glycera* as a modern analog for the *Palaeophycus* tracemaker.

The ichnogenus *Palaeophycus* has been recorded in nonmarine (e.g., Buatois and Mángano, 1993a), marginal-marine (e.g., Wightman et al., 1987), shallow-marine (e.g., Maples and Suttner, 1990), and deep-marine (e.g., Miller, 1993) settings. Occurrences of *Palaeophycus* in tidal-flat settings has been recorded by several authors (e.g., Narbonne, 1984; Mángano et al., 1996; Stanley and Feldmann, 1998). It ranges in age from Precambrian to Pleistocene (Narbonne and Hofmann, 1987; D'Alessandro and Bromley, 1986).

Palaeophycus tubularis Hall, 1847
Fig. 42A–D

SPECIMENS—Ten slabs (KUMIP 288500, KUMIP 288514, KUMIP 288521, KUMIP 288538, KUMIP 288543, KUMIP 288544, KUMIP 288545, KUMIP
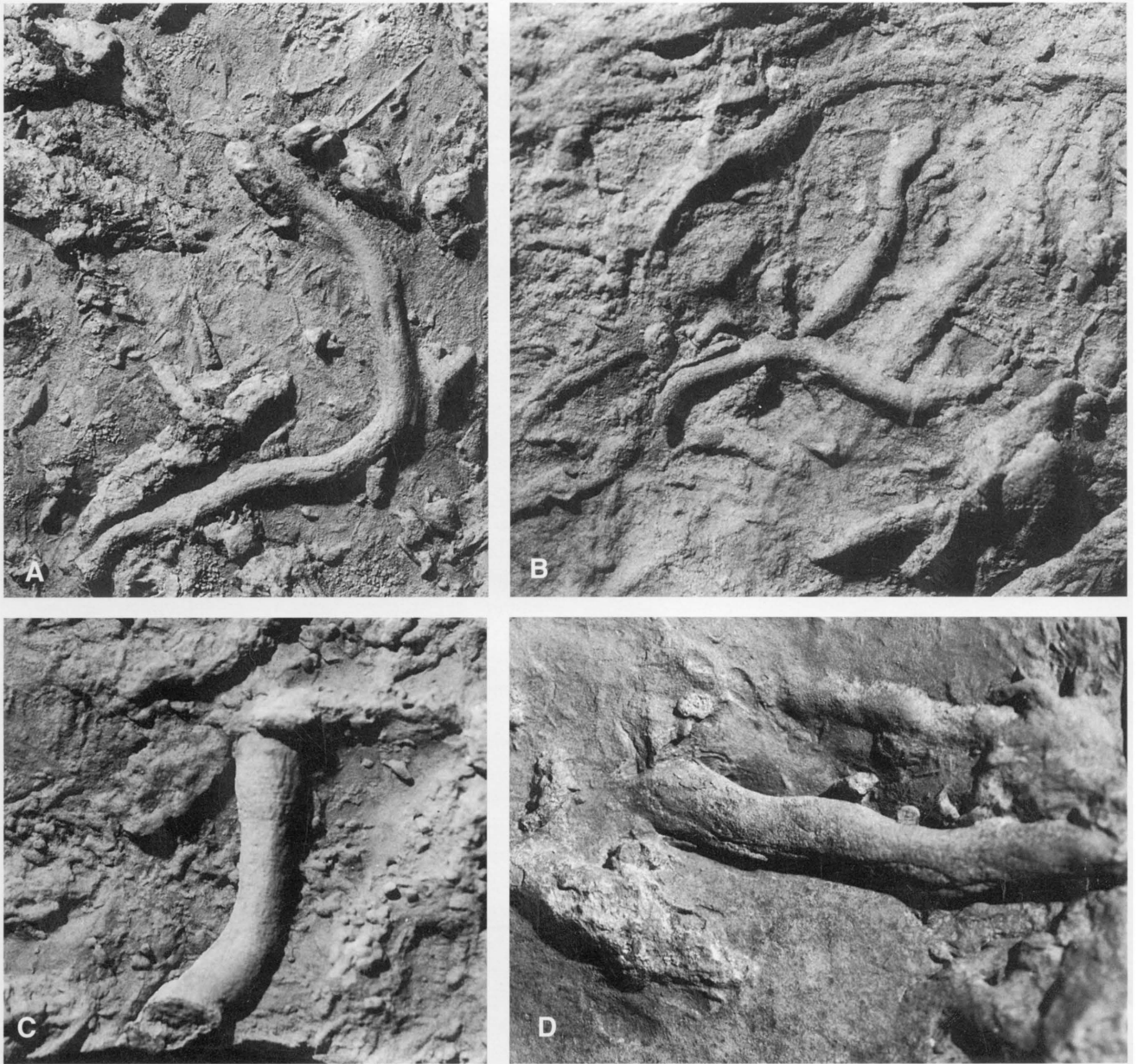
FIGURE 42—*Palaeophycus tubularis*. All are base of bed views. **A**. Curved specimen of *P. tubularis*. KUMIP 288543. × 0.99. **B**. Specimens with secondary successive branching. KUMIP 288514. × 1.4. **C**. Specimen showing elliptical cross section. KUMIP 288552. × 1.28. **D**. Slightly sinuous specimen. KUMIP 288504. × 0.9.

288555, KUMIP 288561, KUMIP 288574) with 20 specimens.

DESCRIPTION—Straight to sinuous, horizontal, commonly unbranched, thinly lined to unlined, smooth-walled cylindrical, endichnial burrow. Some specimens display primary or secondary successive branching. Burrow diameter is 5.1–11.3 mm. Maximum length observed is 91.0 mm. Burrow-fill is similar to the host rock and massive. No evidence of burrow collapse has been detected. Preserved as both positive hyporelief and epirelief.

ASSOCIATED ICHNOFAUNA—*Palaeophycus tubularis* commonly is associated with *Protovirgularia bidirectionalis*, *Curvolithus simplex*, *Lockeia siliquaria*,

and *Parahaentzschelinia ardelia*, but other forms also may be present.

REMARKS—*Palaeophycus tubularis* is typified by its thin, smooth walls (Pemberton and Frey, 1982).

Ichnogenus *Parahaentzschelinia* Chamberlain, 1971

DISCUSSION—*Parahaentzschelinia* was created by Chamberlain (1971) to include shafts radiating from a vertical central tunnel. *Parahaentzschelinia* differs from *Arborichnus* Ekdale and Lewis, 1991, in having all shafts radiating from a central tunnel; however, in the latter the shaft splits at irregular intervals into multiple branches.

Altichnus Bromley and Hanken, 1991, is similar but the shafts in this ichnogenus expand upward (Bromley and Hanken, 1991). Two ichnospecies have been recognized: *P. ardelia* Chamberlain, 1971 and *P. surlyki* Dam, 1990b.

Chamberlain (1971) regarded *Parahaentzschelinia* as a feeding trace (fodinichnion). Dam (1990b) interpreted the main tunnel in his specimens as an escape structure (fugichnion) on the basis of its association with hummocky cross stratified beds. However, he considered the whole biogenic structure as a dwelling trace (domichnion), an interpretation supported by the thick lining of the tunnel walls. Uchman (1995) recognized three different types, informally named "A, B, and C," but he suggested that form B may represent part of a graphoglyptid system (agrichnion), which therefore could be included in some other ichnogenus. Specimens from Waverly ethologically resemble those described by Chamberlain (1971). Absence of thick linings and presence of systematic branching support a fodinichnia interpretation. According to Chamberlain (1971), the structure is produced by a worm that repeatedly extends up and outward from a fixed central point in search of food. Polychaete annelids are the potential tracemakers.

Parahaentzschelinia is known from both deep-marine (e.g., Chamberlain, 1971; Uchman, 1995; Tunis and Uchman, 1996) and shallow-marine facies (e.g., Dam, 1990a). The Waverly occurrence is the first report of this ichnotaxon in tidal-flat facies. *Parahaentzschelinia* ranges in age from Carboniferous to Miocene (Chamberlain, 1971; Uchman, 1995).

Parahaentzschelinia ardelia Chamberlain, 1971
Fig. 43A–D

SPECIMENS—Four specimens on three slabs (KUMIP 288514, KUMIP 288524, KUMIP 288555).

DESCRIPTION—Structures consisting of numerous oblique to rarely vertical, very thinly lined tubes of sandstone. Tunnel fill is structureless. Poorly preserved annulations are present in some trace walls. Individual tubes are 3.0–8.5 mm in diameter and up to 12.2 mm long. System consists of up to 25 tunnels and is 12.8–22.7 mm wide. In one specimen, tubes form an elongated cluster 8.3 mm wide and 36.5 mm long. Preserved as positive epirelief, positive hyporelief, or full relief.

ASSOCIATED ICHNOFAUNA—*Parahaentzschelinia ardelia* commonly is associated with *Protovirgularia bidirectionalis, Curvolithus simplex*, and *Cruziana problematica*.

REMARKS—Specimens from Waverly closely resemble the types described by Chamberlain (1971) in overall pattern, branching style, and absence of thick wall linings, and are therefore ascribed to *P. ardelia*. However, the Waverly specimens are larger than those from Oklahoma and lack a lateral gallery. *P. ardelia* differs from *P. surlyki*

in the absence of thick wall linings. Additionally, the type specimens of *P. surlyki* are deeper and wider.

Ichnogenus *Pentichnus* Maerz, Kaesler, and Hakes, 1976

DISCUSSION—*Pentichnus* was created by Maerz et al. (1976) for subcylindrical to subconical, vertical structures having pentameral symmetry. Rindsberg (1990) and Mángano et al. (1999) noted similarities between this ichnotaxon and *Asteriacites gugelhupf* Seilacher, 1983. Deep, permanent to semi-permanent burrows, such as *A. gugelhupf*, are remarkably different from the shallow, temporary resting traces that are typically included in *Asteriacites*. Accordingly, Mángano et al. (1999) removed *A. gugelhupf* from *Asteriacites* and placed it in *Pentichnus* as a separate ichnospecies (*P. gugelhupf*) characterized by lateral grooves.

Maerz et al. (1976) interpreted *Pentichnus* as a dwelling trace (domichnion) or a resting trace (cubichnion). Overall burrow morphology and penetration depth of the structures favor a domichnia interpretation. Maerz et al. (1976) noted that the pentameral symmetry indicates an echinoderm tracemaker, most likely an ophiuroid. Based on the presence of lateral grooves, Seilacher (1983) favored an asteroid origin for *P. gugelhupf*. Rindsberg (1994) even proposed stalkless crinoids as potential tracemakers.

Pentichnus has been recorded only from Carboniferous shallow-marine environments (Maerz et al., 1976; Seilacher, 1983, 1990b; Rindsberg, 1990).

Pentichnus pratti Maerz, Kaesler, and Hakes, 1976
Fig. 44A–B

SPECIMENS—Two slabs (KUMIP 288535, KUMIP 288540) with two specimens.

DESCRIPTION—Subconical structures vertically oriented, projecting from the sole of sandstone beds, characterized by pentameral symmetry. Apical end may have a poorly developed protuberance. Diameter is 16.3–31.5 mm. Facet width is 10.5–19.0 mm. Preserved as positive hyporeliefs.

ASSOCIATED ICHNOFAUNA—*Pentichnus pratti* is associated with *Cruziana problematica, Nereites imbricata, Rhizocorallium irregulare, Palaeophycus tubularis, Lockeia siliquaria*, and *Protovirgularia bidirectionalis*.

REMARKS—Absence of lateral grooves distinguishes the Waverly specimens from *P. gugelhupf*. Specimens of *Pentichnus* from the Stull Shale Member show the basic morphology of *Pentichnus pratti* Maerz, Kaesler, and Hakes, 1976, the type ichnospecies.
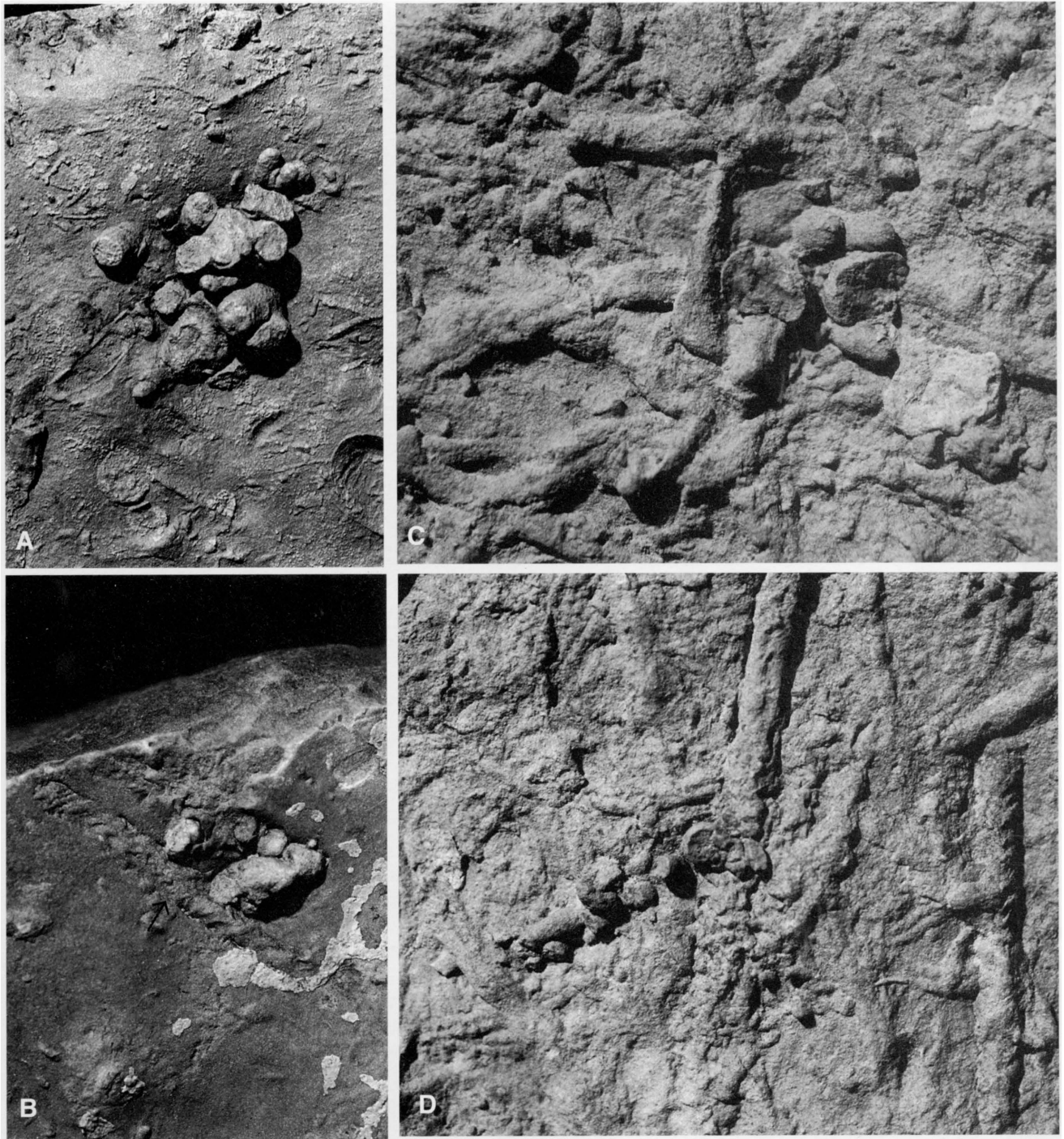
FIGURE 43—*Parahaentzschelinia ardelia*. All are base of bed views. **A.** Specimens protruding from the base of a sandstone bed. Note radial arrangement suggesting the presence of a central shaft. KUMIP 288524. × 0.97. **B.** Specimens of *P. ardelia* cross cutting *Protovirgularia bidirectionalis* (arrow). KUMIP 288555. × 1.27. **C.** *Parahaentzschelinia ardelia* crosscutting poorly preserved *Cruziana problematica*. KUMIP 288514. × 1.8. **D.** Specimens having a linear arrangement. KUMIP 288514. × 1.27.

Ichnogenus *Phycodes* Richter, 1850

DISCUSSION—Seilacher (1955) regarded *Arthrophycus* Hall, 1852, as a junior synonym of *Phycodes*. However, most authors recognize them as separate ichnogenera (e.g., Häntzschel, 1975; Han and Pickerill, 1994b). *Phycodes* was reviewed by Han and Pickerill (1994b) and Pickerill et al. (1995), who recognized the following valid ichnospecies: *P. palmatus* (Hall, 1852); *P. circinatus* Richter, 1853; *P. pedum* Seilacher, 1955; *P. reniforme* Hofmann, 1979; *P. curvipalmatum* Pollard, 1981; *P. yichangensis* Yang, 1984; *P. coronatum* Crimes and Anderson, 1985; *P. wabanensis* Fillion and Pickerill, 1990; *P. ungulatus* Fillion and Pickerill, 1990; *P. auduni* Dam,
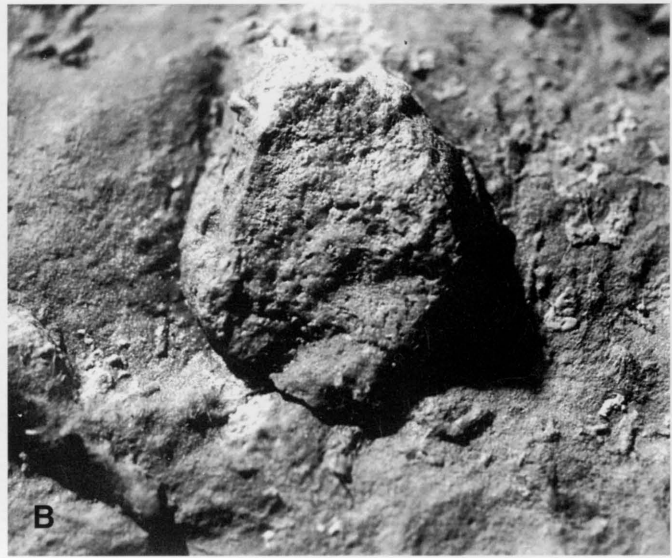
FIGURE 44—*Pentichnus pratti*. Both are base of bed views. **A**. Specimen with apical end having a poorly developed protuberance. KUMIP 288535. × 0.83. **B**. Specimen with well developed pentameral symmetry. KUMIP 288540. × 1.59.

1990; *P. bromleyi* Dam, 1990b; and *P. templus* Han and Pickerill, 1994b. The taxonomic position of *Phycodes pedum* remains controversial. Geyer and Uchman (1995) considered *P. pedum* as an ichnospecies of *Trichophycus*. However, Jensen (1997) placed *P. pedum* in *Treptichnus*, and he suggested affinities with *Treptichnus* for *P. yichangensis* and *P. templus*.

Phycodes is interpreted as a feeding trace (fodinichnion) (Seilacher, 1955; Osgood, 1970). The most likely tracemakers are annelids (Seilacher, 1955), although pennatulaceans (Bradley, 1980) and anthoptiloids (Bradley, 1981) also have been suggested. Specimens figured as *Phycodes* by Bradley (1980, figs. 3 and 4), however, should be assigned to *Chondrites*.

Although more typical of shallow-marine facies (e.g., Crimes and Anderson, 1985; Paczesna, 1996; Jensen, 1997), *Phycodes* is also known from nonmarine (e.g., Pollard, 1985), marginal-marine (e.g., Hakes, 1985), and deep-marine environments (e.g., Crimes et al., 1981; Buatois et al., 2001). *Phycodes* has been mentioned in tidal-flat environments by Martino (1996). It ranges in age from Cambrian to Miocene (Crimes and Anderson, 1985; Bradley, 1981).

Phycodes palmatus Hall, 1852
Fig. 45A

SPECIMENS—One slab (KUMIP 288555) with a single specimen.

DESCRIPTION—Horizontal branching system, consisting of a few branches developed from a single proximal tunnel and arranged in a digitate pattern. Branches taper laterally. Diameter of individual branches is highly variable. Tunnel fill similar to host rock. Trace diameter 5.3–8.1 mm. Length of the structure 66.4 mm. Preserved as positive hyporelief.

ASSOCIATED ICHNOFAUNA—*Halopoa* isp., *Parahaentzschelinia ardelia*, *Protovirgularia bidirectionalis*, *Palaeophycus tubularis*, and small horizontal cylindrical burrows.

REMARKS—*Phycodes palmatus* is characterized by having only a few branches arranged in a palmate or digitate form (Fillion and Pickerill, 1990). These diagnostic features are clearly observed in the Waverly specimen.

Phycodes isp.
Fig. 45B

SPECIMEN—One slab (KUMIP 288500) containing a single specimen.

DESCRIPTION—Horizontal branching system of a few branches developed from a single proximal tunnel and arranged in a fasciculate pattern. Proximal parts of the main tunnels are unbranched, but the distal parts branch at acute angles into recurved segments. Diameter of individual branches remains relatively constant. Tunnel fill is similar to host rock. Trace diameter 0.4–2.7 mm. Length of the structure 90.7 mm. Preserved as positive epirelief.

ASSOCIATED ICHNOFAUNA—*Teichichnus rectus*, *Protovirgularia bidirectionalis*, *Curvolithus simplex*, and *Palaeophycus tubularis*.

REMARKS—Partial preservation precludes a confident designation of the ichnospecies.

Ichnogenus *Phycosiphon* Fischer–Ooster, 1858

DISCUSSION—Controversy exists regarding the relationship among *Phycosiphon* Fischer–Ooster, 1858, *Helminthopsis* Heer, 1877, and *Anconichnus* Kern, 1978. The names *Phycosiphon incertum*, *Anconichnus horizontalis*, and *Helminthopsis horizontalis* have been used to designate essentially the same type of biogenic
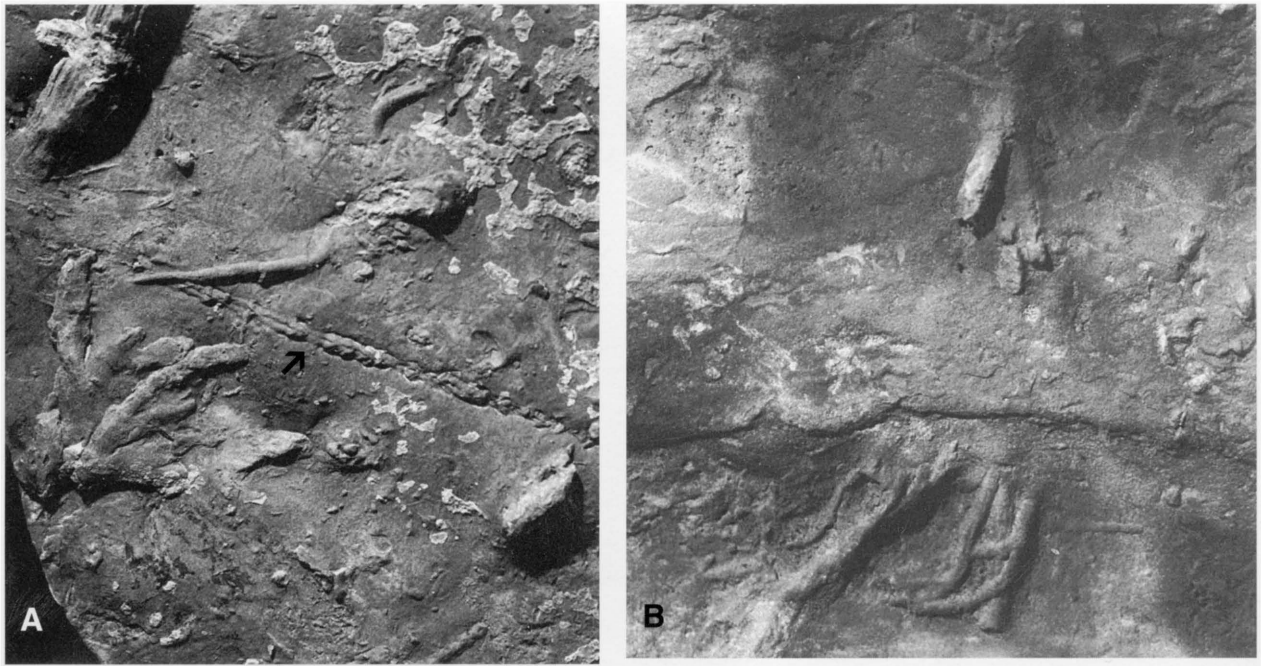
FIGURE 45—Ichnospecies of *Phycodes*. **A**. *Phycodes palmatus*. Note associated *Protovirgularia bidirectionalis* (arrow). Positive hyporelief. KUMIP 288555. × 0.6. **B**. *Phycodes* isp. preserved on a ripple top. Discontinuous specimen extending below the flat ripple crest. Positive epirelief. KUMIP 288500. × 0.85.

structure (e.g., Kern, 1978; Bromley, 1990; Goldring et al., 1991; Wetzel and Bromley, 1994). This taxonomic problem has been analyzed by Wetzel and Bromley (1994), who regarded *Anconichnus* as a junior synonym of *Phycosiphon*. Wetzel and Bromley (1994) emphasized the presence of a dark core and a pale mantle as a diagnostic feature of *Phycosiphon*, with poorly developed spreiten also present. *Helminthopsis* is best retained for irregularly meandering traces lacking spreiten and mantle (Han and Pickerill, 1995; Wetzel and Bromley, 1996).

Phycosiphon has been interpreted either as a grazing trail (pascichnion) or a feeding trace (fodinichnion) produced by a deposit feeder (Ekdale and Mason, 1988; Goldring et al., 1991; Fu, 1991; Wetzel and Bromley, 1994). Presence of a spreite supports a fodinichnial interpretation, though a spreite is typically not discernible. Goldring et al. (1991) suggested that *Phycosiphon* is produced by polychaetes that employ defecation of digested mud to create the central core and sorting of the sediment by parapodia to form the trace halo. *Phycosiphon* typically occupies shallow tiers and probably is produced by an opportunistic animal (Goldring et al., 1991; Wetzel and Bromley, 1994).

Phycosiphon is known only from marine environments, ranging from deep marine (e.g., Wetzel and Uchman, 1997) to shallow marine (e.g., Goldring et al., 1991) and marginal marine (e.g., Bradley and Pemberton, 1992). It ranges in age from Ordovician to Holocene (e.g., Häntzschel, 1975; Wetzel and Wijayananda, 1990).

Phycosiphon incertum Fischer–Ooster, 1858
Fig. 46A–B

SPECIMENS—Two slabs (KUMIP 288503, KUMIP 288564) with several specimens, the exact number of which is impossible to assess.

DESCRIPTION—Horizontal traces comprising recurving U-shaped lobes. Core of curved segments surrounded by a sediment mantle. Core is 0.9–1.4 mm wide. Mantle is 0.5–1.0 mm wide. Spreiten were not observed. Traces in high densities cover top of a very fine grained sandstone. Preserved as negative epirelief.

ASSOCIATED ICHNOFAUNA—*Nereites missouriensis*.

REMARKS—Spreiten are not apparent in the Waverly specimens. However, the traces show the typical recurving shape and the halo of *P. incertum*, and therefore they are assigned to this ichnospecies.

Ichnogenus *Planolites* Nicholson, 1873

DISCUSSION—*Planolites* differs from *Palaeophycus* by having an unlined wall and a fill different from the host rock (Pemberton and Frey, 1982), and it differs from *Macaronichnus* by the presence of a lined wall in the latter (Curran, 1985). Keighley and Pickerill (1995) regarded the absence of wall linings as the diagnostic feature of *Planolites*. Five ichnospecies of *Planolites* have been recognized: *P. beverleyensis* (Billings, 1862), *P. annularius* (Walcott, 1890), *P. montanus* Richter, 1937, *P. terraenovae* Fillion and Pickerill, 1990, and *P. constriannulatus* Stanley and Pickerill, 1994. *Planolites ballandus* Webby, 1970,
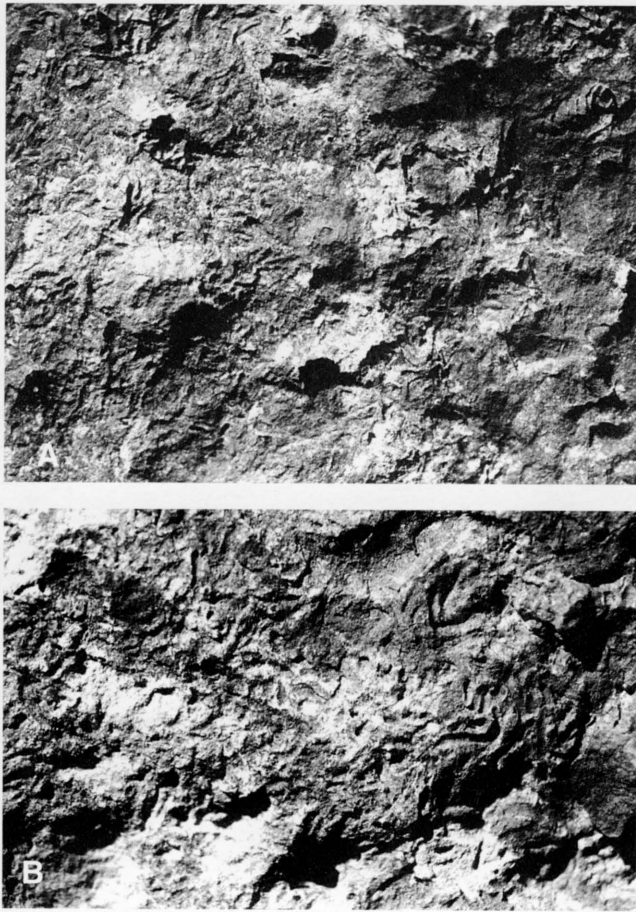
FIGURE 46—*Phycosiphon incertum*. Top of bed view. KUMIP 288564. **A**. General view of several, poorly preserved specimens. × 0.71. **B**. Close-up of some specimens on the slab illustrated in A. × 1.28.

regarded as a junior synonym of *P. montanus* by Pemberton and Frey (1982), subsequently was considered a valid ichnospecies by Walter et al. (1989). However, Mángano et al. (1996) placed it again in *P. montanus*. *Planolites nematus* Kowalski, 1987, also was regarded as a junior synonym of *P. montanus* by Orlowski and Zylinska (1996).

    Planolites is interpreted as feeding structures (fodinichnia) of deposit-feeders, most likely polychaetes (Pemberton and Frey, 1982). However, other phyla also may be responsible (Fillion and Pickerill, 1990).

    Planolites is a facies-crossing ichnotaxon that has been recorded in deep-marine (e.g., Buatois and Lopez Angriman, 1992), shallow-marine (e.g., Orlowski and Zylinska, 1996), marginal-marine (e.g., Archer and Maples, 1984), and continental facies (e.g., Pickerill, 1992). It is a common component of tidal-flat ichnofaunas (e.g., Ireland et al., 1978). *Planolites* ranges in age from Precambrian to Pleistocene (Gibson, 1989; Wetzel, 1981).

Planolites beverleyensis (Billings, 1862)
Fig. 47A–B

SPECIMEN—A single specimen on slab KUMIP 288539.

DESCRIPTION—Horizontal, subcylindrical, unlined, slightly curved trace. Trace fill different in color and grain size from the host rock. Trace surface typically smooth. Diameter fairly constant within the specimen. Maximum length observed is 87.12 mm. Diameter is 13.7–21.6 mm. Preserved as full relief.

ASSOCIATED ICHNOFAUNA—*Planolites beverleyensis* is associated with *Diplocraterion* isp. B.

REMARKS—*Planolites beverleyensis* differs from *P. montanus* by the smaller size and contorted to curved course of the latter (Pemberton and Frey, 1982). Absence of ornamentation and/or annulations distinguishes *P. beverleyensis* from *P. terraenovae*, *P. annularius*, and *P. constriannulatus*.

Ichnogenus *Protovirgularia* McCoy, 1850

DISCUSSION—*Protovirgularia* has received considerable attention in recent years (e.g., Han and Pickerill, 1994c; Rindsberg, 1994; Seilacher and Seilacher, 1994; Uchman, 1998). McCoy (1850) established *Protovirgularia* for structures composed of a median line and lateral chevron-like markings. Han and Pickerill (1994c) revised this ichnogenus and concluded that *P. dichotoma* McCoy, 1850, the type species, was the only valid name. *Protovirgularia harknessi* Lapworth, 1870, *P. nereitarum* Richter, 1871, and *P. mongraensis* Chiplonkar and Badve, 1970, do not differ significantly from *Protovirgularia dichotoma*, their senior synonym (Han and Pickerill, 1994c). Han and Pickerill (1994c) also provided an interesting historical overview about the multiple and dissimilar origins ascribed to *Protovirgularia*. Originally interpreted as a body fossil, either an octocoral (McCoy, 1850; Alloiteau, 1952) or a graptolite (Richter, 1853), *Protovirgularia* was first recognized as a trace fossil by Häntzschel (1958). Rindsberg (1994) included subhorizontal traces with imbricated chevrons terminating in an oval- or almond-shaped structure in the ichnogenus *Walcottia* Miller and Dyer, 1878b.

    Rindsberg (1994) reduced the number of available names for describing essentially similar structures by synonymizing the ichnogenera *Biformites* Linck, 1949, *Imbrichnus* Hallam, 1970, and *Chevronichnus* Hakes, 1976, with *Walcottia*. However, Rindsberg (1994) did not comment on the similarities between *Walcottia* and *Protovirgularia*. Based on the association with *Lockeia*, Rindsberg (1994) also noted that bivalves were the most probable tracemakers of *Walcottia*, as well as *Sustergichnus* Chamberlain, 1971, which he did not include in *Walcottia*. However, because the mode of construction of *Protovirgularia* and *Walcottia* was not
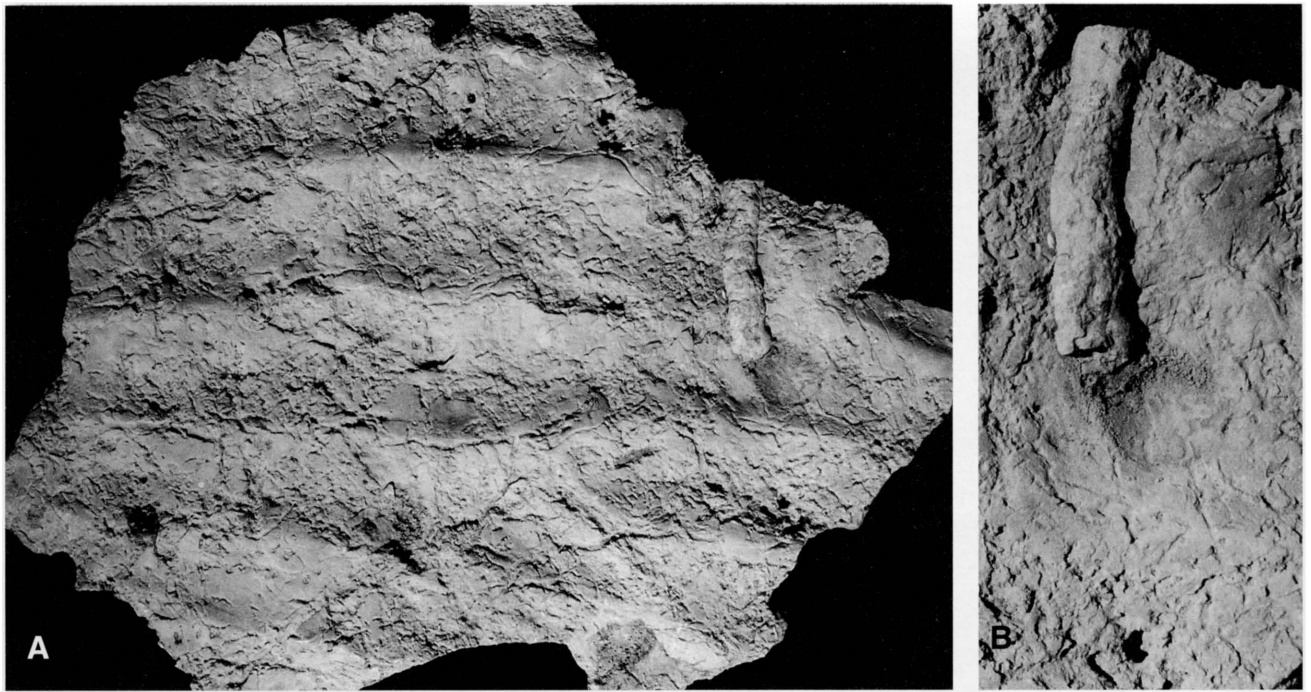
FIGURE 47—*Planolites beverleyensis*. Top of bed view. KUMIP 288539. **A**. General view of a strongly weathered rippled top with a specimen of *P. beverleyensis*. × 0.27. **B**. Close-up view of the specimen in A. × 0.45.

clearly understood, these ichnogenera remained somewhat enigmatic.

In an actuopaleontologic approach, Seilacher and Seilacher (1994) compared traces produced by the cleft-foot bivalve *Acila* with chevron structures known from the fossil record. Based on the unique basic pattern of behavior involved in the locomotion of cleft-foot bivalves, these authors revived the ichnogenus *Protovirgularia* as the senior synonym of *Walcottia, Pennatulites* de Stefani, 1885, *Paleosceptrom* de Stefani, 1885, *Biformites, Uchirites* Macsotay, 1967, *Imbrichnus*, and *Sustergichnus*. Following the same line of reasoning, *Chevronichnus* and *Polypodichnus* Ghare and Kulkarni, 1986, also should be considered junior synonyms of *Protovirgularia*. We generally agree with the Seilacher and Seilacher (1994) taxonomic scheme for *Protovirgularia*, although some adjustments and additions are needed. Seilacher and Seilacher (1994) recognized five ichnospecies of *Protovirgularia*: *P. dichotoma* McCoy, 1850, *P. triangularis* (Macsotay, 1967), *P. tuberculata* (Williamson, 1887), *P. rugosa* (Miller and Dyer, 1878b), and *P. longespicata* (deStefani, 1885). More recently, Uchman (1998) revised the Marian Książkiewicz collection and recognized three additional ichnospecies: *P. obliterata* (Książkiewicz, 1977), *P. vagans* (Książkiewicz, 1977), and *P. dzulynskii* (Książkiewicz, 1977).

Protovirgularia dichotoma, the type species, is a shallow *Protovirgularia* that is somewhat reminiscent of an arthropod trackway, but it is clearly symmetrical about the median axis. We had the opportunity to inspect casts of *P. dichotoma*, originally described by Richter (1941) as *Ichnia spicea* from the Devonian Hunsrück Shale. These specimens record the morphological variability of this form according to pore fluid content. In highly fluid substrate, chevrons of *P. dichotoma* display petaloid appearance. In slightly stiffer sediment *P. dichotoma* exhibits its classical symmetrical, delicate, V-shaped marks tangential to the median mark. *Protovirgularia dichotoma* is a straight, horizontal locomotion trace. None of the Hunsrück specimens is connected to *Lockeia*-like structures. Our observations on the type material of *P. triangularis* show that it is a mostly smooth, deeply impressed, tubular carinate structure with distinct triangular cross section. Chevrons are faint, closely spaced, but only very locally present. Material from Paleogene flysch deposits of Venezuela, referred to by Macsotay (1967) as *Nereites* (Pl. 5, Fig. 11, 13 and 14) and *Gyrochorte* (Pl. 5, Fig. 12), is herein included in *Protovirgularia*. The specimens from Venezuela display large, open chevrons, resulting in a vertebrae-like appearance, somewhat reminiscent of *P. longespicata*. However, this form does not display the morphological complexity of *P. longespicata* (cf. Seilacher and Seilacher, 1994, Pl. 2) and most likely represents a new ichnospecies. Notably, this material shows close similarities with specimens from the Tertiary of Trinidad, labelled as *Virgularia presbytes* and housed at the British Museum of Natural History (BMNH). *Protovirgularia tuberculata* is a deeply im-

pressed bilobated hypichnial structure with distinct chevrons that superficially resembles *Cruziana*. In their diagnosis of *P. tuberculata*, Seilacher and Seilacher (1994, p. 10) do not mention the presence of small tubercles on chevrons. Examination of Williamson's type material at the BMNH suggests that *Protovirgularia tuberculata* exhibits conspicuous, regularly spaced tubercles (see also Williamson 1887, p. 22 and Fig.2). Seilacher and Seilacher (1994) included *Sustergichnus lenadumbratus* in *Protovirgularia triangularis*. However, our observations on the type specimens of *S. lenadumbratus* indicate that this form shows affinities with *P. tuberculata* rather than with *P. triangularis*. *Sustergichnus lenadumbratus* displays small tubercles on chevrons, and its general morphology (i.e. bilobated structure with well-impressed, regular chevrons) is similar to *P. tuberculata*. Reexamination of the type specimens of *Imbrichnus wattonensis* Hallam, 1970, at the Oxford University Museum, allows placement of this ichnospecies in *P. rugosa*. *Protovirgularia rugosa* is a relatively short *Protovirgularia* connected to a smooth cylindrical to almond-shaped resting structure (Seilacher and Seilacher, 1994; Uchman, 1998). "Relatively short," in this context, is understood as subordinately horizontal, predominantly inclined structures that cross bedding planes. Some specimens of *P. rugosa*, however, can display significant horizontal locomotion; good examples are *P. rugosa* var. *Imbrichnus* and *P. rugosa* var. *Chevronichnus*. Chevrons are sharp, commonly tightly packed resulting in a wrinkled appearance. The Waverly material shows that the distinction between *P. dichotoma* and *P. rugosa* on strict morphological bases can be difficult in practice. Specimens exceedingly long (i.e. with significant horizontal displacement) can be, if partially preserved, within the expected morphological variability of *P. dichotoma*. The common gregarious occurrence of *P. rugosa* and invariable association with *Lockeia*, however, help to provide an appropriate assignment. This calls for identification based on a representative sample rather than a few, fragmentary specimens. Based on Miller and Dyer type specimens of *Walcottia rugosa*, Seilacher and Seilacher (1994) considered escape traces leading away from smooth resting structures as *P. rugosa*. Uchman (1998) also included short locomotion traces ending at *Lockeia*-like structures (Uchman, 1998, Fig. 67C). Seilacher and Seilacher (1994) interpreted *P. rugosa* as escape structures responding to episodic storm sedimentation; Uchman (1998) added also turbiditic sedimentation. Waverly specimens indicate that *P. rugosa* also can be related to rapid tidal sedimentation. *Protovirgularia longespicata* is a complex *Protovirgularia* characterized by strong papillate chevrons, the overall form of which may be palmate with spreiten-like structure (Seilacher and Seilacher, 1994, Pl.2).

Uchman (1998) revised the Marian Książkiewicz collection and placed in *Protovirgularia* several specimens included by Książkiewicz (1977) under various ichnogenera, such as *Rhabdoglyphus* Vassoevich, 1951,

Gyrochorte Heer, 1865, *Tuberculichnus* Książkiewicz, 1977, *Arthrophycus* Hall, 1852, and *Keckia* Glocker, 1841. This author considered *P. triangularis* similar to *P. pennatus* (Eichwald, 1860), which has priority, and therefore regarded *P. triangularis* as a junior synonym of *P. pennatus*. Although the general morphology of *P. pennatus* resembles *P. triangularis*-type material, chevrons are more conspicuous and deeply impressed in the former. Additionally, Uchman (1998) placed the following ichnospecies in *Protovirgularia*: *Gyrochorte obliterata* Książkiewicz, 1977, as *P. obliterata*; *Tuberculichnus vagans* Książkiewicz, 1977, and *Tuberculichnus meandrinus* Książkiewicz, 1977, as *P. vagans*; and *Arthrophycus* (?)*dzulynskii* Książkiewicz, 1977, as *P. dzulynskii*. *Protovirgularia obliterata* and *P. dzulynskii* are known from very fragmentary material. We agree with Uchman that *Gyrochorte obliterata* should actually be included in *Protovirgularia* (cf. Uchman 1998, Fig. 68C). The ichnospecies *P. obliterata*, however, is not very distinctive and is best considered a *nomen dubium*. *Protovirgularia dzulynskii* is a distinct form with strong, papillated, riblike chevrons. It is a complex structure reminiscent of *P. longespicata*, but the material is too fragmentary. *Protovirgularia vagans* was defined by Uchman (1998) as a smooth *Protovirgularia* having a strong carinate profile, undulating in the vertical plane and resulting in discontinuous ridges. This form lacks the distinctive chevronate pattern of *Protovirgularia* and is best considered as an ichnospecies of *Lockeia*. Seilacher and Seilacher (1994) created *Lockeia serialis* to include serial alignments of *Lockeia*-like structures. Linck's original material consists of a straight, continuous alignment of *Lockeia* (Linck, 1949, Pl. VIII, Fig. 1, 2). The Polish flysch specimens, however, record an undulating movement in the vertical plane and an open meandering pattern, warranting ichnospecific assignment as *Lockeia vagans*.

Bandel (1967a) described a wide variety of forms under *Crossopodia dichotoma*. As discussed by Mángano et al. (in press), *Crossopodia* is a problematic ichnotaxon and its abandonment is recommended. Han and Pickerill (1994) reassigned Bandel's material to *Protovirgularia dichotoma*. Although we agree with inclusion of these specimens within *Protovirgularia*, the wide variety of morphologies and size ranges exhibited by Bandel's material does not warrant inclusion within *P. dichotoma*. Our observations of Bandel's collection suggest that several distinct ichnospecies are present and that further detailed studies are needed. As outlined by Mángano et al. (1998), substrate conditions, particularly substrate consistency, play a major role in the morphology of *Protovirgularia*. Substrate character *per se*, however, is not considered a valid ichnotaxobase. Variability of Bandel's *Protovirgularia* collection cannot be explained in terms of a preservational bias. For example, the specimen of *P. dichotoma* KUMIP 25104 exhibits a peculiar chevron pattern resulting in apparent bifurcated chevrons (Bandel 1967, Pl. 3, Fig. 7).

Protovirgularia has been interpreted as a locomotion structure (repichnion). This ichnogenus, however, embraces many combined behavioral forms. For instance, *P. rugosa* can be interpreted as an escape structure (fugichnion), and *P. tuberculata* and *P. longispicata* are locomotion/feeding structures (pascichnia). Different possible tracemakers have been proposed for *Protovirgularia*, including arthropods (Gümbel, 1879; Richter, 1941; Volk, 1961), annelids (Richter, 1941; Claus, 1965), and bivalves (Bandel, 1967a; Hallam, 1970; Hakes, 1977, Maples and West, 1990; Han and Pickerill, 1994c; Rindsberg, 1994; Seilacher and Seilacher, 1994). A better understanding of the constructional techniques and functional limitations of these different types of organisms supports cleft-foot bivalves as the most likely tracemakers (Seilacher and Seilacher, 1994; Mángano et al., 1998). Seilacher and Seilacher (1994) also mentioned the possibility of scaphopods as producers, particularly if the chevroned locomotion traces are not associated with *Lockeia*-like resting structures.

Although originally described from deep-marine facies (e.g., McCoy, 1851a; Volk, 1961; Macsotay, 1967; Chamberlain, 1971; Benton, 1982b; Han and Pickerill, 1994c; Uchman, 1998), *Protovirgularia* also is well-represented in shallow open-marine and marginal-marine facies (e.g., Bandel, 1967a; Osgood, 1970; Hallam, 1970). Examples of this ichnogenus in tidal-flat facies have been documented by Bandel (1967a), Hakes (1976), and Mángano and Buatois (1997), among many others. *Protovirgularia* ranges from Ordovician to Holocene (e.g., Osgood, 1970; Seilacher and Seilacher, 1994).

Protovirgularia bidirectionalis n. isp.
Figs. 48A–C, 49A–G, 50

SPECIMENS—Thirty-seven slabs (KUMIP 288500, KUMIP 288501, KUMIP 288504, KUMIP 288509, KUMIP 288514, KUMIP 288519, KUMIP 288520, KUMIP 288522, KUMIP 288523, KUMIP 288524, KUMIP 288527, KUMIP 288530, KUMIP 288531, KUMIP 288532, KUMIP 288533, KUMIP 288534, KUMIP 288538, KUMIP 288540, KUMIP 288541, KUMIP 288542, KUMIP 288543, KUMIP 288544, KUMIP 288548, KUMIP 288549, KUMIP 288550, KUMIP 288551, KUMIP 288552, KUMIP 288554, KUMIP 288555, KUMIP 288556, KUMIP 288558, KUMIP 288559, KUMIP 288560, KUMIP 288561, KUMIP 288562, KUMIP 288569, KUMIP 288570) containing 231 specimens and several others recorded in the field.

TYPE SPECIMENS—Specimen illustrated in fig. 49B (KUMIP 288559) is designated as the holotype; all the other specimens are considered paratypes.

DIAGNOSIS—Relatively shallow, U-shaped traces with basal V-shaped markings oriented in opposite directions. Tunnels display oval cross section and thick, mucus-lined wall. Cross sectional views or exhumed tunnels may show a laminar spreiten structure. Preserved as full reliefs.

DESCRIPTION—Shallow, U-shaped endichnial structures. Tunnels with oval cross section and distinctive wall, 0.6–1.6 mm thick. The wall is particularly evident in some collapsed, or exhumed structures (fig. 48A–B). Fill is similar to that of the host rock. Width of tunnel is 4.7–11.3 mm. Some exhumed shafts, protruding from the upper surface of sandstone beds, exhibit a cross sectional view with spreiten. Closely spaced, V-shaped markings cover the basal part of the structure. Some tunnels display a bilobed internal structure. Length of basal structures is 5.8–21.7 mm, but typically between 7.8 and 16.0 mm. Locally, chevrons appear grouped (fig. 49E–F). Many tunnels display chevron markings in one predominant orientation (fig. 49C, E, F), but careful examination commonly reveals V-shaped markings in opposite directions. Some structures exhibit two segments with chevrons oriented in opposite directions meeting at a central point (fig. 49A–B). In other specimens, V-shaped markings are superimposed at slightly different levels (fig. 49G), or a smooth segment connects oppositely directed chevrons (fig. 49D). Some tunnels merge into another specimen, resulting in successive branching (fig. 49C, E). The width of the joined tunnel may remain unaffected (fig. 49C) or may be increased considerably (fig. 49E). Crosscutting of traces on sandstone soles is common (fig. 49F–G). Traces occur in densely packed assemblages with tunnel orientations forming an angle of 20° to 45° relative to ripple crests (fig. 48A–C). When two orientations occur, they commonly are in relation to interference ripples on the upper surface.

REMARKS— Mángano et al. (1998) discussed the role of the substrate in *Protovirgularia* morphology and assigned a wide range of chevroned structures to *P. dichotoma*. Further taxonomic analysis, however, suggests that two other ichnospecies are actually involved. We reassigned the studied material to *P. rugosa* and *P. bidirectionalis*. *Protovirgularia bidirectionalis* is a new ichnospecies that exhibits complex affinities with two different groups of bivalve structures, *Protovirgularia* and *Solemyatuba*. Although it originally was compared with *Uchirites* (*Protovirgularia*) *triangularis* by Maples and West (1990), *Protovirgularia bidirectionalis* is more closely related in constructional terms to *P. longespicata*, which was described by Seilacher and Seilacher (1994). Both forms have sharp, distinct chevrons, spreiten-like structure, and full-relief preservation. The chevrons of *P. bidirectionalis*, however, do not show the diagnostic papillar impressions that characterize *P. longespicata*, and they display opposite directions coexisting in the same structure. On the other hand, the shallow U-shaped form of the burrow and the oval cross section relate *Protovirgularia bidirectionalis* to *Solemyatuba*, which Seilacher (1990a) interpreted as a chemosymbiotic bivalve structure. The thick wall and apparent passive infill of *Protovirgularia bidirectionalis* indicate a mucus lining and that the structures were kept open by their occupants. Successive branching also suggests unfilled tunnels.
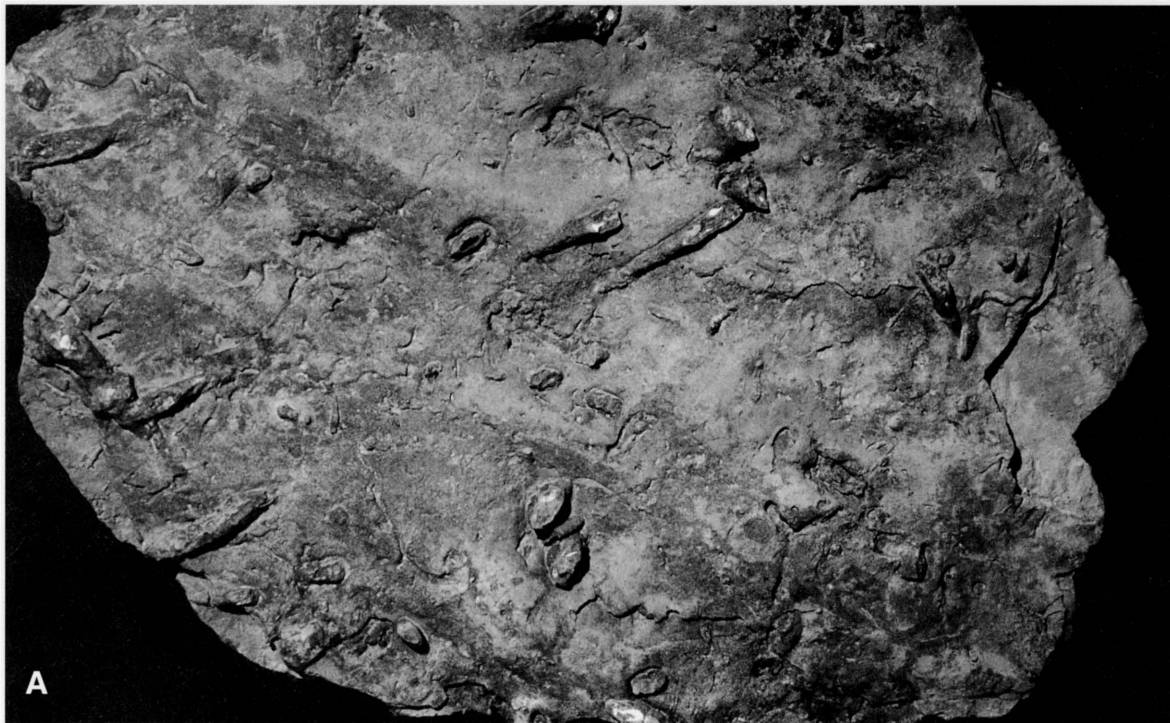
FIGURE 48—*Protovirgularia bidirectionalis*. General views. **A**. Several specimens with very thickly lined walls and U-shaped geometry, oriented oblique to ripple trend. Top of bed view. KUMIP 288514. × 0.41. **B**. Dense assemblage of shafts of *P. bidirectionalis* with very thick walls, preserved on the top of a rippled sandstone bed. Note exhumed burrows crosscutting each other on the left. KUMIP 288544. × 0.34. **C**. Base of a sandstone slab with a dense assemblage of *P. bidirectionalis*. Note subparallel orientation. Most burrows oriented approximately 35° relative to ripple train. KUMIP 288534. × 0.17.
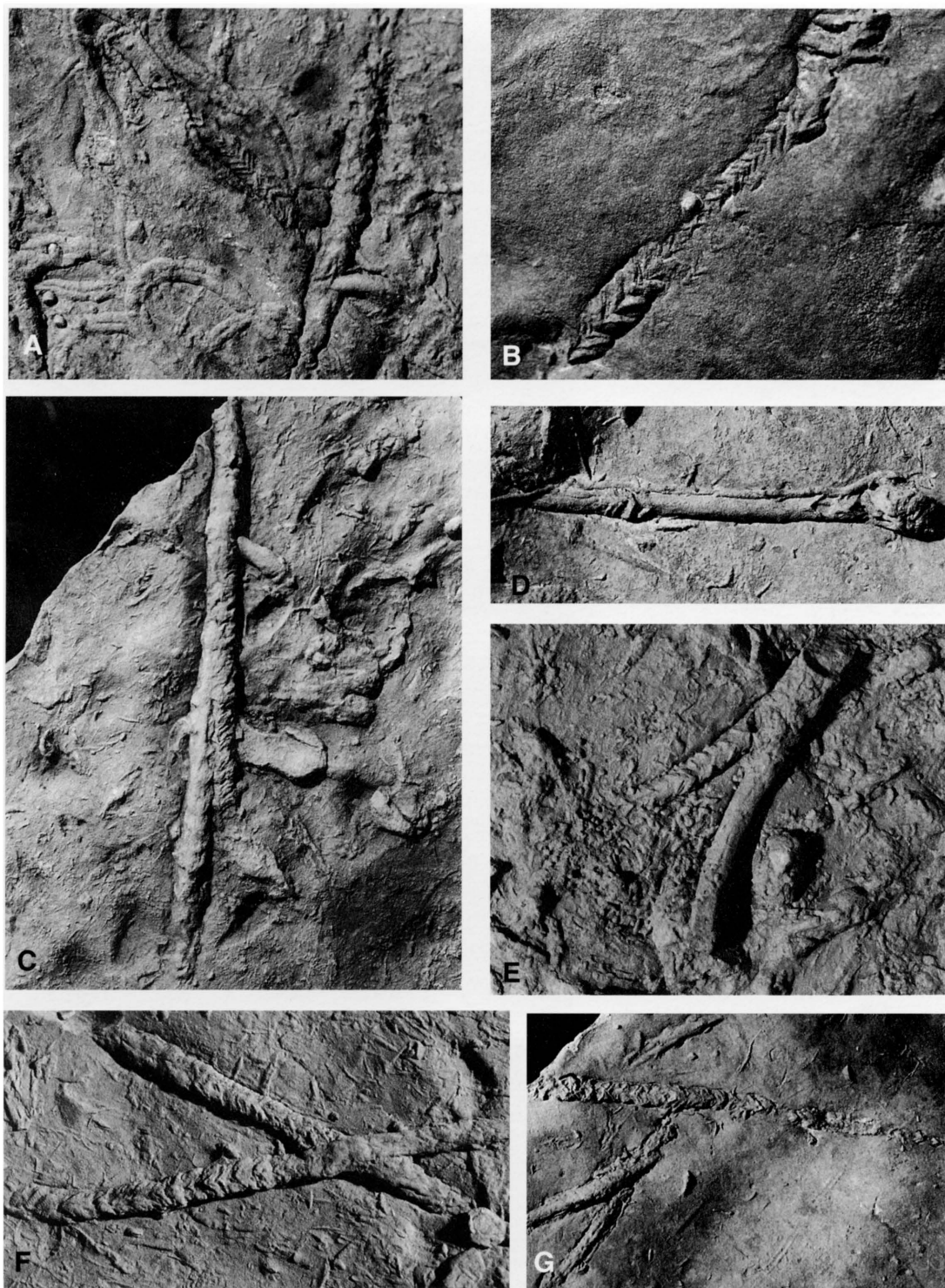
FIGURE 49—*Protovirgularia bidirectionalis*. Close-up views of base of burrows. **A**. Small burrow showing V-shaped markings with opposite directions meeting at a central point. Note that the direction of movement is from the center to the ends. KUMIP 288500. × 0.97. **B**. Burrow showing V-shaped markings with opposite directions at different levels. Note that at the lowermost level the direction of movement is toward the center of the structure (opposite of A). KUMIP 288559. × 0.97. **C**. Low-angle secondary successive branching without significant widening of the resulting structure. Burrow on the right seems to enter the structure on the left. KUMIP 288544. × 0.69. **D**. Burrow showing V-shaped markings with opposite directions connected by a smooth central segment. KUMIP 288531. × 0.69. **E**. Y-shaped secondary successive branching with significant widening of the resulting structure. Burrow on the left seems to deviate from the main structure on the right. KUMIP 288552. × 0.69. **F**. Crosscutting of two specimens showing one predominant direction of V-shaped markings. KUMIP 288544. × 0.69. **G**. Complex crosscutting relationships between specimens. Note bilobate internal structure (lower left specimen) and superimposed chevrons oriented in the opposite direction (upper specimen). KUMIP 288531. × 0.44.
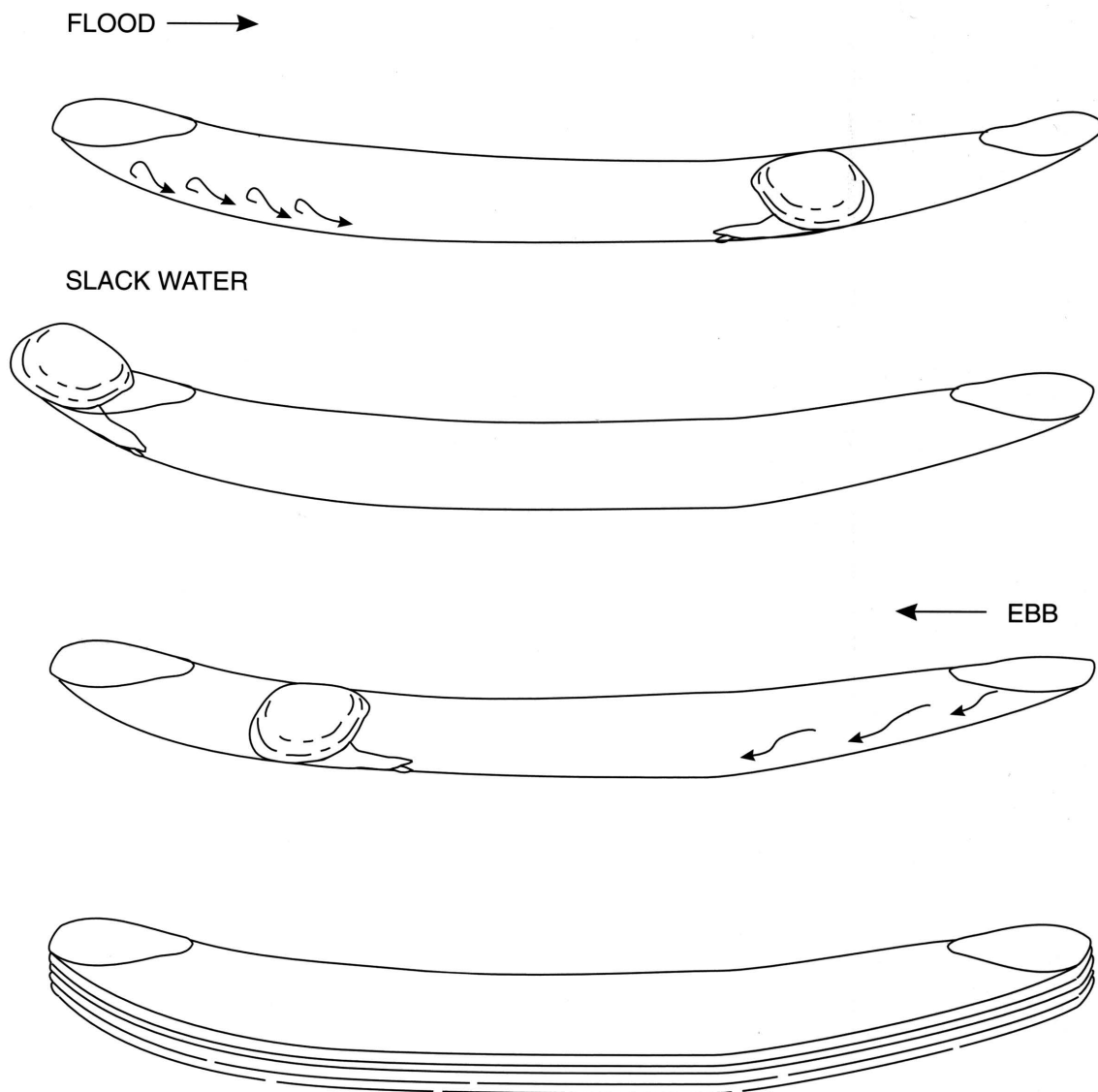
FIGURE 50—Behavioral reconstruction of *Protovirgularia bidirectionalis*. The bivalve constructed a U-shaped burrow in which it grazed organic debris transported by the tidal flood. It apparently turned around, perhaps during the slack-water period, and grazing was re-established during the ebb flow. Repetition of this activity led to the formation of a vertical spreiten structure.

The oval cross section and V-shaped imprints of *Protovirgularia bidirectionalis* are the fingerprints of a protobranch bivalve tracemaker (Seilacher, 1990a; Seilacher and Seilacher, 1994). Protobranch bivalves are well known detritus and deposit feeders that exploit the uppermost tiers of the substrate (Stanley, 1970). No representative is known to be a suspension feeder or a chemosymbiont.

The preferred orientation of the structures relative to ripple crests may be related to a feeding strategy. As tidal currents flow in and out the shallow U-shaped burrows, they transport organic debris that is trapped in the mucus lining, to be subsequently grazed by the animal. The spreiten structure and chevrons facing opposite directions within a single structure indicate that the animal re-entered the tunnel successively. Considering the hazards of the intertidal area, the turnaround at the surface had to be performed during the slack-water period. During flood and ebb, the animal was protected within the structure. The angular orientation of burrows relative to current axis may have prevented scouring and may have increased the smooth inflow of detritus into the structure. This complex, bipolar pascichnial strategy may have resulted in a *Teichichnus*-like pattern (fig. 50).

Protovigularia rugosa (Miller and Dyer, 1878)
Fig. 51A–D

SPECIMENS—Eight slabs (KUMIP 288523, KUMIP 288525, KUMIP 288526, KUMIP 288527, KUMIP 288543, KUMIP 288552, KUMIP 288566, KUMIP 288568) with 65 specimens.

DESCRIPTION—Horizontal to inclined structures crossing bedding planes. Morphological features are best recorded on bedding surfaces. Traces are straight to curved epichnial grooves or hypichnial ridges with chevron markings. Length is highly variable, some structures are only a couple of centimeters in length but others are considerably long, up to 194.7 mm (fig. 51A). Width is 1.7–12.8 mm, but typically 2.8–7.3 mm. In hypichnial preservation, the trace may be composed of a median ridge with well-developed, chevron-like lateral ridges (fig. 51D) or may display a more tubiform morphology with closely spaced, wrinkle-like chevrons (fig. 51C). Epichnial preservations have a prominent median groove and V-shaped imbricated sheets of sediment (fig. 51A–B). Distance between successive chevrons is 0.4–5.3 mm. V-angle is 60° to nearly 180°. Some structures are asymmetrical, with oblique to perpendicular markings only present on one side. Most specimens of *Protovirgularia rugosa*, including those with *Chevronichnus*-type preservation, begin or end in small specimens of *Lockeia* isp. or *L. ornata*.

REMARKS—Hakes (1976) created *Chevronichnus* to describe chevron epichnial trails, which should be included in *Protovirgularia* and are described herein as epichnial occurrences of *P. rugosa*. Material herein assigned to *P. rugosa* is almost invariably associated to *Lockeia*-like structures. Some specimens of *P. rugosa* connected to *L. ornata* (Mángano et al., 1998, Fig. 4) are relatively short and represent classic examples of *P. rugosa*. Other specimens, however, can be interpreted at first approach as within the morphologic variability of *P. dichotoma* (fig. 66A, see also Mángano et al., 1998, Fig. 13C, D). Nonetheless, the association with *Lockeia*-like structures and the mode of occurrence indicate that they most likely represent escape traces and are better included in *P. rugosa*.

In many cases the producer of *P. rugosa* moved across bedding planes resulting in short structures that can be interpreted as escape traces. The great length of some specimens, however, indicates significant horizontal locomotion along bedding planes. A detailed observation suggests slow upward migration related to high rates of tidal current tractive sedimentation, rather than rapid escape movements after episodic deposition (i.e. storms). Although these structures are not easily interpreted as efficient fugichnia, they most likely represent structures keeping pace with tidal sedimentation. Interestingly, individuals of *P. rugosa* associated with tempestites, such as the type specimens from the Ordovician of Cincinnati,

are shorter and mostly oblique to the bedding plane. It has been noted that vertical movements in bivalves require more energy than oblique movements (Brown and Trueman, 1991). Accordingly, vertical movements are most likely to be avoided by bivalves in the absence of episodic sedimentation.

At Waverly, nuculoid bivalves are the most likely tracemakers of *P. rugosa*. Specimens of *Protovirgularia rugosa* var. *Chevronichnus* are particularly small in size and commonly display a gregarious mode of occurrence (fig. 51A) similar to that observed in the *L. ornata* / *P. rugosa* assemblage. Epichnial preservation of *Lockeia* prevents ichnospecific assignment of *Lockeia*. Nevertheless, the size of the structures is out of the typical range recorded for *L. ornata* (Mángano et al., 1998) and shape is more oval than the almond-like shaped *L. ornata*. None of these morphologic observations, however, completely eliminates the possibility of a population of juvenile tracemakers of *Lockeia ornata*. These specimens of *Lockeia* isp., however, may have been produced by an alternative tracemaker of smaller size (e.g., *Nuculopsis*, Mángano et al., 1998).

Ichnogenus *Psammichnites* Torell, 1870

DISCUSSION—The taxonomy and internal structure of *Psammichnites* were clarified by Hofmann and Patel (1989), Seilacher and Gámez-Vintaned (1995, 1996), and McIlroy and Heys (1997), who documented its complex morphology. This ichnogenus typically consists of predominantly horizontal traces with transverse or arcuate internal structure and a distinct median dorsal structure. This dorsal structure commonly is represented by a sinusoidal or straight ridge/groove or regularly spaced circular mounds/holes (Mángano et al., in press).

A related form is *Plagiogmus* Roedel 1929. *Plagiogmus* is a complex endichnial structure, with different toponomic expressions (cf. McIlroy and Heys, 1997, fig. 7). Well-preserved specimens of *Plagiogmus arcuatus* exhibit four components: the basal "ladder trail," the internal backfill, the upper bedding surface "ribbon trail," and the lower surface arcuate structure (Walter et al., 1989; McIlroy and Heys, 1997). The internal structure of *Plagiogmus arcuatus* and *Psammichnites gigas* is strikingly similar (cf. Hofmann and Patel, 1989, fig. 5; McIlroy and Heys, 1997, fig. 7; Seilacher-Drexler and Seilacher, 1999, Fig. 8). The upper surface view of *Plagiogmus arcuatus* is hardly distinguishable from the upper surface of *Psammichnites gigas* (cf. Hofmann and Patel, 1989, fig. 3c; Walter et al., 1989, fig. 11c, d; McIlroy and Heys, 1997, fig. 5a-b). Mángano et al. (in press) noted that the "ladder trail" basal morphology, though commonly considered a diagnostic character of *Plagiogmus*, is a toponomic expression that may not be available in some preservational variants. Therefore, it should not be considered ethologically significant at the ichnogeneric
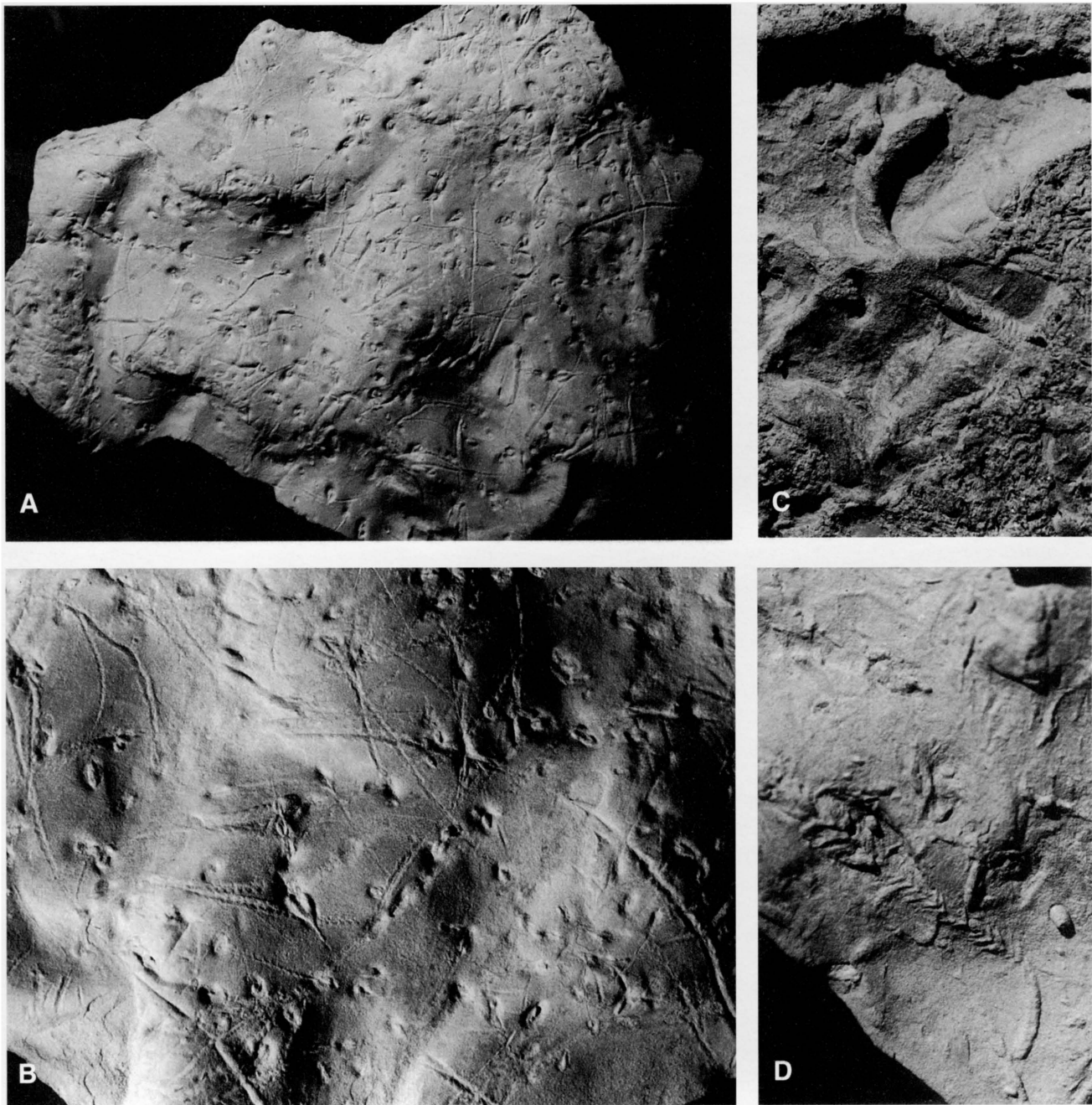
FIGURE 51—*Protovirgularia rugosa*. **A**. Dense assemblage of *P. rugosa* and associated resting traces on the upper surface of a sandstone bed. Note preservation as negative epireliefs in *Chevronichnus*-like fashion. KUMIP 288566. × 0.25. **B**. Close-up of some specimens in KUMIP 288566 showing sharp, V-shaped grooves and faint chevron impressions. × 0.5. **C**. Base of bed view of one specimen in KUMIP 288566, showing hypichnial preservation of *P. rugosa* and small *Lockeia siliquaria*. Chevron markings seem to lead toward the resting structure. × 1.16. **D**. Specimen with sharp chevrons. Direction of movement toward the upper left. Base of bed view. KUMIP 288569. × 1.16.

level. *Plagiogmus arcuatus* is most likely a junior synonym of *Psammichnites gigas* (Mángano et al., in press).

Confusion persists regarding the taxonomic status of the ichnogenus *Olivellites*. Some authors retain *Olivellites* as a valid ichnotaxon (Miller and Knox, 1985; Fillion and Pickerill, 1990; Brownfield et al., 1998), but others place it in synonymy with *Psammichnites* (Chamberlain, 1971; Maples and Suttner, 1990; Seilacher–Drexler and Seilacher, 1999; Mángano et al., in press). Chamberlain (1971) was the first to place *Olivellites* in synonymy with *Psammichnites*, regarding its type ichnospecies as *Psammichnites plummeri*, but without discussing his reasons. Subsequently, Yochelson and Schindel (1978) re-examined the type specimens of *P. plummeri*, described additional topotypes, and analyzed specimens from a new locality in Texas. However, they apparently were unaware of Chamberlain's study, and therefore they did not address the taxonomic status of *Olivellites*. Mángano et al. (in press) concluded that *Olivellites* represents a variant of the *Psammichnites–Plagiogmus* behavioral pattern (cf. Seilacher, 1986, 1997, p. 38–39). The ichnogenus *Psammichnites* has nomenclatural priority over *Olivellites* and *Plagiogmus* and therefore *Psammichnites* is considered their senior synonym.

Meandering trails identical to traces subsequently referred to as *Olivellites* in the United States have been recorded in United Kingdom since the 19th century (e.g., Wood, 1851a, b; Binney, 1852; Dixon, 1852; Hancock, 1858; Tate, 1859). Eagar et al. (1985) and Pollard (1986) noted that the name "*Crossopodia*" has been traditionally used by geologists from the British Geological Survey (e.g., Bromehead et al., 1933; Stephens et al., 1953) to describe traces similar to *P. plummeri*. Mángano et al. (in press) reexamined the type specimens of *Crossopodia* McCoy (1851a,b) and concluded that this ichnogenus does not show the characteristic morphology of *Psammichnites*. McCoy (1851a,b) erected two ichnospecies: *C. lata* and *C. scotica*; the latter subsequently designated as the type species by Häntzschel (1962, p. W189). Benton and Trewin (1980) later reassigned McCoy type material of *Crossopodia scotica* to *Dictyodora scotica*, and suggested *Crossopodia lata* as the type of the ichnogenus *Crossopodia*. Reexamination of the type material of *Crossopodia lata* reveals that this ichnotaxon is a trilobate structure, displaying well-developed, subequal lobes crossed locally by subtle transversal ridges (Mángano et al., in press). It is unclear whether the structure is preserved on the top or the sole of the bed. *Crossopodia lata* lacks the characteristic features of what was subsequently called "*Crossopodia*" in Great Britain. As summarized by Mángano et al. (in press), the confusing history of the different uses related to *Crossopodia* makes its abandonment the best alternative. The taxonomy of Carboniferous ichnospecies of *Psammichnites* was analyzed by Mángano et al. (2001b). These authors discussed three ichnospecies: *P. plummeri* (Fenton and Fenton, 1937), *P. grumula*

(Romano and Melendez, 1979), and *P. implexus* (Rindsberg, 1994).

Psammichnites is interpreted as a grazing trace (pascichnion) that records the feeding activities of a subsurface vagile animal using a siphon-like device (Mángano et al., in press). Seilacher (1997, p. 38) stated that "the animal moved through the sediment like a submarine, being connected to the sediment surface only by a narrow snorkel." Different tentative biological affinities have been proposed for Cambrian *Psammichnites*, including worms (Torell, 1868; Matthew 1888, 1890), annelids (McIlroy and Heys, 1997), echiurans (Runnegar, 1982), crustaceans (Torell, 1870), mollusks (Torell, 1870; Glaessner, 1969; McIlroy and Heys, 1997), and gastropods (Häntzschel, 1975). Recently, Seilacher–Drexler and Seilacher (1999) speculated that the producer of *Psammichnites* was probably related to halkieriids. Mángano et al. (in press) noted that evidence of a siphon-like device in Carboniferous *Psammichnites* reestablishes the possibility of a molluscan tracemaker.

Psammichnites is a common form in Lower Cambrian strata (e.g., Glaessner, 1969; Vortisch and Lindström, 1972; Hofmann and Patel, 1989; Walter et al., 1989; Pickerill and Peel, 1990; Goldring and Jensen, 1996; Seilacher, 1997; Alvaro and Vizcaïno, 1999), then it reappears in the Silurian (A. Seilacher, written communication, 1999; Mángano and Buatois, unpublished data), having another prolific record in the Carboniferous, probably reaching the Permian (e.g., Yochelson and Schindel, 1978; Eagar et al., 1985; Devera, 1989; Martino, 1989; Buckman, 1992; Greb and Chesnut, 1994; Brownfield et al., 1998; Eyles et al., 1998). It has been invariably recorded in shallow-water deposits; Carboniferous ichnospecies are common in intertidal settings (Mángano et al., in press).

Psammichnites grumula (Romano and Meléndez, 1979)
Fig. 52A

SPECIMEN—One specimen on slab KUMIP 288506.

DESCRIPTION—Predominantly horizontal, meandering trace bearing a series of holes or mounds in median line. Holes are subcircular in cross section and conical in three dimensions. Median ridge is visible only locally. Transverse fine ridges or arcuate marks, recording meniscate backfill, are present. Prominent levees are formed on both sides of the trace, and these are particularly evident in the hypichnial preservation. Trail width is 16.0–17.2 mm. Marginal levees are 2.1–5.2 mm wide. Holes or mounds are 2.0–2.8 mm wide, up to 2.7 mm deep and 5.5–9.2 mm apart. Transverse ridges are 1.7–2.3 mm wide. Maximum length observed is 331.9 mm. Preserved as negative hyporelief.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica*.

REMARKS—Romano and Meléndez (1979), who created the ichnospecies *Olivellites grumula* for two

specimens from the Carboniferous of northwest Spain, followed Häntzschel (1975) and included *Olivellites* within the *Scolicia* group. The specimen from Kansas shares with the Spanish specimens the presence of holes or mounds along the axis of the trace, which is diagnostic of this ichnospecies. Additionally, like one of the traces from Spain, the specimen studied is preserved as a negative hyporelief. Only the specimen preserved in positive epirelief displays a distinct median ridge (Romano and Meléndez, 1979, fig. 2.2). However, the ridge is hardly visible in the trace preserved as a negative hyporelief (Romano and Meléndez, 1979, fig. 2.3). Similarly, the median ridge in a specimen of *P. grumula* from the Stull Shale Member is present only locally. Although Romano and Meléndez (1979) stated that the specimens from Spain were meandering, illustrations show that the course of the traces is sinuous rather than meandering. In contrast, the specimen from Waverly clearly meanders. This difference, however, is not regarded as taxonomically significant. Romano and Meléndez (1979) also described two hyporeliefs with flat trilobate morphology and faint oblique striations as *Scolicia* type A. This morphology suggests that observed in rare specimens of *P. grumula* and *P. plummeri* exhibiting the ventral surface. Buckman (1992, p. 230) included in *Olivellites plummeri* one specimen with "1 mm pimples along its midline, spaced approximately every 10 mm along the axis," which fits the diagnosis of *Psammichnites grumula*. Another specimen of *P. grumula* was recorded from the Coal Measures by Atkinson (1839). Additional recordings of this ichnospecies were documented by Mángano et al. (in press).

Psammichnites grumula differs from other *Psammichnites* ichnospecies by the presence of holes or protruding mounds. Additionally, the presence of well-developed, fine transverse ridges or arcuate marks distinguishes *P. grumula* from the nearly smooth *P. implexus*. In the midcontinent, morphologically transitional forms indicate the biological affiliation of *P. plummeri* and *P. grumula*. The presence of mounds and holes in *P. grumula* confirms the presence of a siphon. *Psammichnites grumula* is interpreted as produced by a deposit feeder using the siphon for respiration, aspiration, or for chemosymbiotic purposes (Mángano et al., in press).

Psammichnites implexus (Rindsberg, 1994)
Fig. 52C–D

SPECIMENS—Four slabs (KUMIP 288507, KUMIP 288523, KUMIP 288531, KUMIP 288565) with nine specimens and several others examined in the field.

DESCRIPTION—Horizontal to subhorizontal traces with with a very faint meniscate structure and a sharp median ridge. Trace fill is similar to the host rock; meniscate internal structure is poorly preserved. The cross section is subtriangular to elliptical. Trace width remains relatively constant within specimens, but tends to broaden at turns.

Tear-shaped resting structures are connected to some traces. Some specimens display a meandering tendency with phobotaxis and almost guided meanders. Other specimens show numerous self-crosscutting backturns and a strong tendency to scribble. Crosscutting instances are relatively common. Trace width is 3.8 to 5.9 mm. Ridge width is 0.7 to 0.8 mm. Preserved as full reliefs at the top of sandstones.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica* typically is preserved on the soles of sandstones having *P. implexus* on the upper surfaces. *Psammichnites implexus* commonly occurs alone on upper surfaces of sandstone beds. In only one slab (KUMIP 288531), is *P. implexus* associated with *Nereites missouriensis, Curvolithus simplex, Rosselia* isp., and shafts of *Lockeia siliquaria* and *Protovirgularia bidirectionalis.*

REMARKS—Rindsberg (1994) proposed *Uchirites implexus* for epichnial traces having a median ridge from the Mississippian of Alabama. He noted that this ichnospecies differs from the type species *U. triangularis* in having a scribbling tendency. However, re-examination of the type specimens of *U. triangularis* originally described by Macsotay (1967) from the Paleogene of Venezuela confirms preservation in positive hyporelief on turbidite soles. Restudy of type specimens by Mángano et al. (in press) suggests that preservation at the top of beds, presence of a median ridge, and the meandering tendency favor assignment of *U. implexus* to *Psammichnites* as a separate and distinctive ichnospecies, *P. implexus.* Specimens described by Binney (1852) as "trail of a mollusc" and "trail of a bivalve shell" were tentatively assigned to *P. implexus* by Mángano et al. (in press). Greb and Chesnut (1994) have recorded identical forms as *Olivellites* from the Pennsylvanian of Kentucky. *Scolicia virgamontis* Chamberlain, 1971, resembles *P. implexus*, but further analysis of the type specimens is needed (Mángano et al., in press).

Psammichnites implexus is similar to some specimens of *Dictyodora*, especially the ichnospecies *Dictyodora scotica* (McCoy, 1851a). The ichnogenus *Dictyodora* Weiss, 1884, consists of highly complex three-dimensional structures composed of a basal trace and a dorsal vertical wall (Häntzschel, 1975; Benton and Trewin, 1980; Benton, 1982a). Ichnospecies of *Dictyodora*, however, have walls that range in height from 10 to 180 mm (Benton and Trewin, 1980), display vertical to oblique striation, and are much higher than the median ridge of *P. implexus* (Mángano et al., in press). The dorsal cord of *P. implexus* represents a simpler structure than that present in *Dictyodora*. Moreover, the path of *P. implexus* commonly is more irregular than that of *Dictyodora. Dictyodora* commonly is preserved as an endichnial trace fossil, with contrasting sediment infill and elliptical cross sections. Sectioning of *P. implexus* shows a diffuse lower surface and a sandy sediment infill almost indistinguishable from the host rock in cross sectional view. Mángano et al. (in press) suggested that *P. implexus* is not a preservational
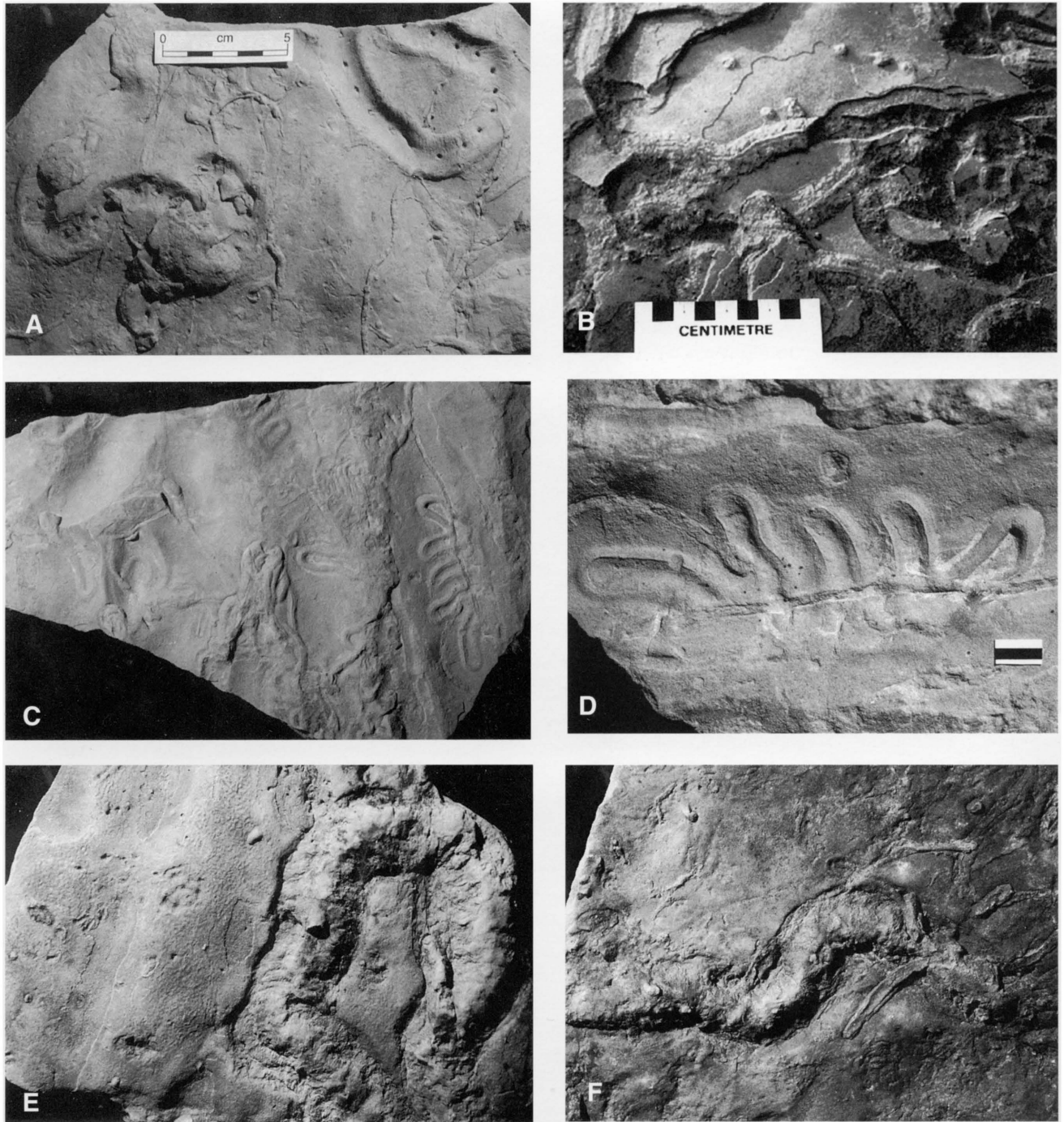
FIGURE 52—Ichnospecies of *Psammichnites*. **A**. *Psammichnites grumula* with well-developed holes along a median line and prominent levees on both sides of the trace. Base of bed view. KUMIP 288506. **B**. *Psammichnites plummeri*. Note central ridge and crenulated transverse ridges. Top of bed view. Field photo. **C**. *Psammichnites implexus* preserved on the top of a rippled sandstone bed. KUMIP 288507. × 0.27. **D**. *Psammichnites implexus*. Close-up of one of the specimens in C showing guided meanders. KUMIP 288507. Bar = 1 cm. **E**. *Psammichnites*? isp. with transverse ridges. Note associated, very small wrinkle marks. Top of bed view. KUMIP 288504. × 0.41. **F**. *Psammichnites*? isp. with poorly developed transverse ridges. Top of bed view. KUMIP 288522. × 0.48.

variant of *Dictyodora scotica*. However, when preserved on a bedding plane, distinction between the two ichnotaxa may be difficult. *Psammichnites implexus* is regarded as a shallow-tier structure that records a less specialized strategy than *Dictyodora* (Mángano et al., in press).

Horizontal traces described by Han and Pickerill (1994a) as *U. implexus* in Devonian turbidites in eastern Canada are preserved as positive hyporeliefs and closely resemble the types of *U. triangularis*. Specimens from Venezuela do not meander as do some of the traces from eastern Canada, and locally they display faint lateral striae. As suggested by Han and Pickerill (1994a), the absence of striae in the Devonian traces may be preservational. Consequently, the specimens from Canada should be regarded as conspecific with *U. triangularis*. Nonetheless, the taxonomic status of *Uchirites* remains problematic, as exemplified by Seilacher and Seilacher (1994), who synonymized it with *Protovirgularia*. *Psammichnites implexus* is distinguished from the other two *Psammichnites* ichnospecies by its less well developed meniscate structure, its consistently smaller size, and its tendency to scribble. Additionally, it differs from *P. grumula* by the absence of holes or protruding mounds in the latter.

Rindsberg (1994, p. 10) considered several possible explanations for the scribbling tendency of *P. implexus*, including superficial siphon detritus feeding, turns to face shifting currents, and disturbance caused by parasitic infection. Swennen (1969) documented winding paths produced by the modern bivalve *Macoma baltica* that apparently were caused by trematode infestation. Biological or environmental stress (e.g., high temperatures) may better explain the departures from the typical meandering pattern.

Psammichnites plummeri
(Fenton and Fenton, 1937)
Fig. 52B

SPECIMENS—Two specimens recorded in the field.

DESCRIPTION—Predominantly horizontal, sinuous to meandering trails bearing a distinct median ridge, and fine, crenulated transverse ridges. Meniscate structure is not apparent in weathered parts of specimens. Cross sectional view subcircular to elliptical. Trace width is 140.5 to 180.5 mm. Median ridge is 1.7–1.9 mm wide. Transverse ridges are 0.9 to 1.6 mm wide. Preserved as full reliefs at the top of sandstones.

ASSOCIATED ICHNOFAUNA—No other traces were recorded.

REMARKS—In a pioneering paper, Tate (1848) proposed the ichnospecies *Crassopodia embletonia* and *Crassopodia media* (error for *Crossopodia* McCoy) to name what he believed were body fossils of annelids. Tate type material is lost (J. Pollard, written communication, 2000), but reexamination of topotypes of *Crossopodia embletonia* indicates that this ichnotaxon displays all the diagnostic features of *Psammichnites plummeri* (Mángano et al., in press). Although the ichnospecies *Psammichnites embletonia* and *P. media* have priority over *P. plummeri*, Mángano et al. (in press) retained the more widely used *P. plummeri* to promote nomenclatorial stability. These authors regarded the second ichnospecies, *C. media*, as a *nomen dubium*.

Yochelson and Schindel (1978) analyzed the *Psammichnites plummeri* type specimen, as well as topotypes from the Wayland Shale Member of the Graham Formation (Pennsylvanian) and new specimens from another locality in Texas (Colony Creek Shale Member, Caddo Creek Formation). Their study provided details about the internal backfill structure and behavioral strategy. Although the internal structure of the Kansas specimens is less apparent, it closely resembles that of the type specimens from Texas.

Psammichnites plummeri is the most commonly encountered of the three *Psammichnites* ichnospecies (Mángano et al., in press). The presence of well-developed transverse ridges distinguishes *P. plummeri* from *P. implexus*. *Psammichnites plummeri* differs from *P. grumula* by the presence of holes or protruding mounds in the latter.

Psammichnites? isp.
Fig. 52E–F

SPECIMENS—Four slabs (KUMIP 288504, KUMIP 288515, KUMIP 288517, KUMIP 288522) containing four specimens.

DESCRIPTION—Horizontal, sinuous to meandering trails with transverse ridges. Cross sectional view elliptical. Trace width is 18.8–40.4 mm. Maximum length observed is 295.0 mm. Transverse ridges are 2.0–4.0 mm wide. Preserved as full reliefs at the top of sandstones or, more rarely, as negative hyporelief.

ASSOCIATED ICHNOFAUNA—Specimens of *Psammichnites*? isp. preserved on the top of sandstone beds are associated with *Palaeophycus tubularis*, *Lockeia siliquaria*, and *Protovirgularia bidirectionalis*. The single specimen preserved on the base of a bed is associated with *Cruziana problematica* and *Rusophycus* isp.

REMARKS—These specimens resemble *Psammichnites* in the presence of transverse ridges and their preservation as full reliefs at the top of sandstones or, more rarely, negative hyporelief. However, the absence of a median ridge precludes definitive placement of these specimens in *Psammichnites*.

Ichnogenus *Rhizocorallium* Zenker, 1836

DISCUSSION—*Rhizocorallium* is distinguished from other U-shaped traces, such as *Diplocraterion* and *Arenicolites*, by its horizontal to oblique orientation.

Sellwood (1970) suggested that the *Rhizocorallium* animal could be a deposit-feeder during trace construction

and a suspension-feeder afterwards. Fürsich (1974c) pointed out differences between the various ichnospecies, regarding *R. jenense* as a dwelling trace of suspension feeders, and *R. irregulare* and *R. uliarense* as feeding traces of deposit feeders. Specimens studied by Basan and Scott (1979) did not show characteristics suggestive of a suspension-feeding habit for the *Rhizocorallium* animal, so they suggested a deposit-feeding habit. Horizontal orientation of the spreiten in specimens from Waverly points to a deposit-feeding strategy. *Rhizocorallium* is probably produced by crustaceans (Fürsich, 1974c).

Although more common in shallow-marine settings (e.g., Fraaye and Werver, 1990), *Rhizocorallium* is a facies-crossing trace, and it has been reported from deep-marine (e.g., Uchman, 1991), marginal-marine (e.g., Hakes, 1976), and, more rarely, nonmarine environments (e.g., Fürsich and Mayr, 1981). Examples of *Rhizocorallium* in tidal-flat facies have been recorded by Farrow (1966) and El-Asa'ad (1987). It ranges in age from Cambrian to Miocene (Seilacher, 1955; Fürsich and Mayr, 1981).

Rhizocorallium irregulare Mayer, 1954
Fig. 53A–C

SPECIMENS—Two slabs (KUMIP 288530, KUMIP 288535) with two specimens and an additional one studied in the field.

DESCRIPTION—Endichnial, U-shaped trace parallel to slightly oblique to bedding plane. U-arms are nearly parallel and connected by spreiten. Thin striations perpen-dicular to arm axis are present locally. Arm width is 7.1–15.0 mm; maximum length observed is 120 mm. Spreiten are 9.5–27.0 mm wide.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica* and *Nereites imbricata*.

REMARKS—According to Fürsich (1974c), *R. irregulare* is distinguished from *R. jenense* and *R. uliarense* by its predominant horizontal orientation. *Rhizocorallium mongraensis* Chiplonkar and Ghare, 1975, *R. karaiensis* Chiplonkar and Ghare, 1979, *R. kutchensis* Ghare and Kulkarni, 1986, and *R. lixianensis* Zhang and Wang, 1996, are probably junior synonyms of *R. irregulare*.

Ichnogenus *Rosselia* Dahmer, 1937

DISCUSSION—*Rosselia* includes concentrically filled, funnel- to cone-shaped traces (Frey and Howard, 1985). *Monocraterion* is morphologically similar, but it lacks the characteristic concentric fill. *Cylindrichnus* has a concentric fill, but does not exhibit a funnel-shaped morphology (Frey and Howard, 1981, 1985). Three ichnospecies currently are ascribed to *Rosselia*: *R. socialis* Dahmer, 1937, *R. rotatus* McCarthy, 1979, and *R. chonoides* Howard and Frey, 1984.

Nara (1995) recently completed a detailed analysis of Pleistocene *Rosselia*, and he interpreted it as dwelling structures (domichnia) of deposit-feeding terebellid polychaetes.

Rosselia is particularly abundant in shallow-marine environments (e.g., Howard and Frey, 1984; Frey and
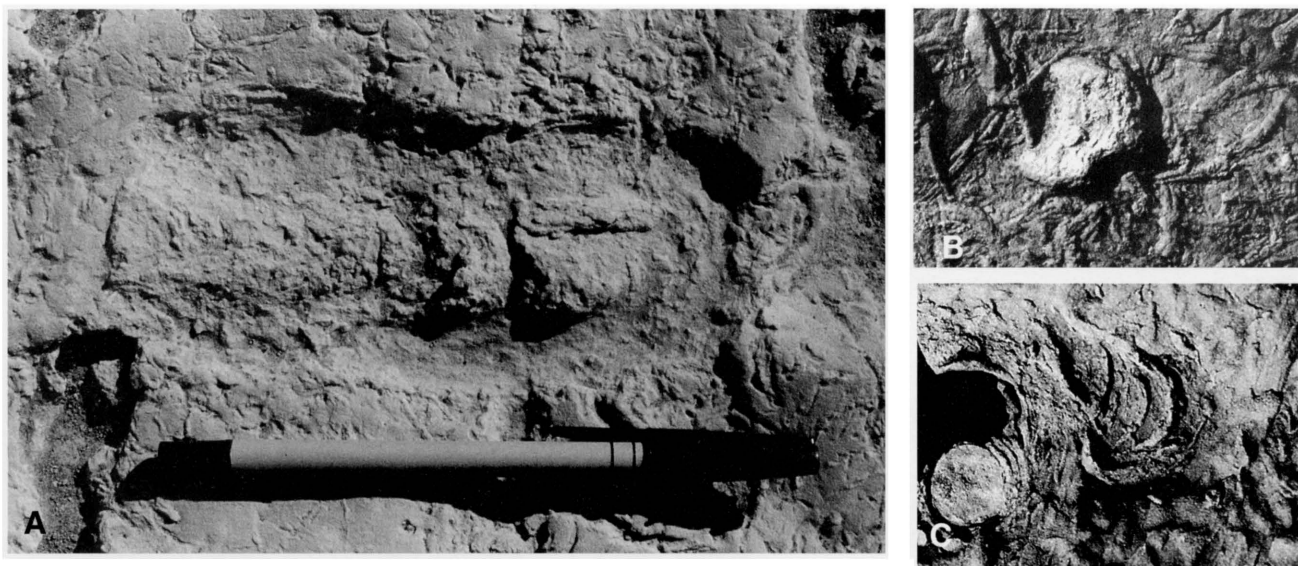
FIGURE 53—*Rhizocorallium irregulare*. **A.** Specimen with poorly preserved U trace. Top of bed view. Field photo. Pen is 150 mm long. **B.** Specimen oblique to the bedding plane. Poorly developed striations present in the tunnel arms. Base of bed view. KUMIP 288535. × 0.66. **C.** Specimen with well-developed spreiten. Note vertical *Skolithos* isp. cutting other structures. Base of bed view. KUMIP 288530. × 0.83.

Howard, 1985; Fillion and Pickerill, 1990; Nara, 1995; Jensen, 1997). However, it also has been recorded in brackish-water (Rindsberg and Gastaldo, 1990) and deep-marine environments (Książkiewicz, 1977). *Rosselia* ranges in age from Cambrian to Holocene (Jensen, 1997; Rindsberg and Gastaldo, 1990).

Rosselia socialis Dahmer, 1937
Fig. 54A–B

SPECIMENS—Two slabs (KUMIP 288531, KUMIP 288552) each with one specimen.

DESCRIPTION—Irregularly conical to funnel-shaped, very thinly lined, vertical trace with flat to slightly convex top. A vertical to inclined, central to sub-central tube is present within the trace. Tunnel fill consists of poorly developed concentric layers. Diameter is 24.9–37.9 mm. Height is 32.5–40.1 mm. Preserved as endichnia.

ASSOCIATED ICHNOFAUNA—*Arenicolites* isp., *Protovirgularia bidirectionalis*, *Lockeia siliquaria*, and *Curvolithus simplex*.

REMARKS—*Rosselia socialis* is distinguished from *R. chonoides* by the absence of helicoid swirls of sediment (Howard and Frey, 1984) and from *R. rotatus* by the absence of rotary twists of the trace (McCarthy, 1979).

Ichnogenus *Rusophycus* Hall, 1852

DISCUSSION—We follow the majority of authors (e.g., Osgood, 1970; Crimes, 1975; Aceñolaza, 1978; Webby, 1983; Fillion and Pickerill, 1990; Pickerill, 1994, 1995; Bromley, 1990, 1996; Jensen, 1997) in considering *Rusophycus* as separate from *Cruziana*, contrary to Seilacher (1970). *Isopodichnus*, an ichnogenus commonly used for arthropod resting traces in continental facies, is considered a junior synonym of *Rusophycus* (see Bromley, 1990, 1996, for discussion).

Rusophycus historically has been interpreted as the resting trace (cubichnion) of trilobites, although it also is common in continental facies, where it is produced by other arthropods such as notostracans or amphipods (Bromley and Asgaard, 1972; Pollard, 1985). Osgood (1970) found the trilobite *Flexicalymene meeki* situated directly on *Rusophycus pudicum* from the Upper Ordovician of the Cincinnati area.

Rusophycus is a common component of shallow-marine assemblages (e.g., Osgood, 1970; Webby, 1983; Rindsberg, 1994; Benton and Hiscock, 1996; Jensen, 1997), but also has been recorded from continental (e.g., Bromley and Asgaard, 1972, 1979; Pollard, 1985; Aceñolaza and Buatois, 1993) and deep-marine environments (e.g., Pickerill, 1995). Examples of *Rusophycus* in tidal-flat deposits have been recorded by Narbonne (1984), Legg (1985), Durand (1985), Fillion and Pickerill (1990), Mángano et al. (1996), and Mángano and Buatois (2000). *Rusophycus* ranges in age from Cambrian to Miocene (Jensen, 1997; Gámez Vintaned et al., 1998).

FIGURE 54—*Rosselia socialis*. KUMIP 288531. All illustrations are × 1.2. **A.** Top view of trace. **B.** Cross section view of the same specimen. **C.** Line drawing of trace as seen in cross section.

Rusophycus isp.
Fig. 55A–B

SPECIMENS—Two slabs (KUMIP 288505, KUMIP 288515) containing two specimens.

DESCRIPTION—Small hypichnial bilobed ridges, 14.8–15.8 mm long and 5.8–6.8 mm width. The traces are divided in two segments approximately equal in length. The anterior (?) part shows conspicuous, almost transversal clusters of endopodial scratches. Individual scratches are indistinct, but the clusters are well differentiated. They are about 0.8–0.9 mm in length. The posterior (?) part of
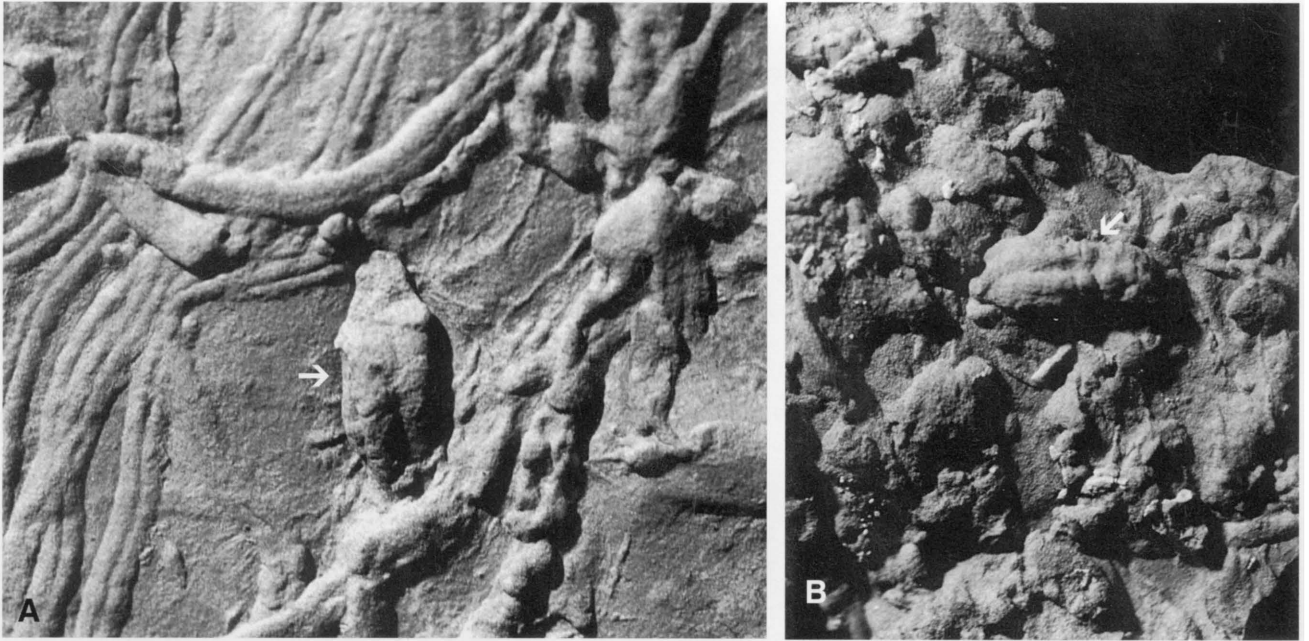
FIGURE 55—*Rusophycus* isp (arrow). Preserved at the base of beds. **A.** Bilobate specimen with poorly developed scratch marks. Note associated *Cruziana problematica*. KUMIP 288515. × 1.8. **B.** Specimen with clusters of endopodial scratches. Field photo. × 1.8.

the trace is smooth with a thin external lobe about 0.9 mm in width.

ASSOCIATED ICHNOFAUNA—*Cruziana problematica.*

REMARKS—Although the trace is slightly elongated, it shows the typical morphologic details of a resting structure. The poor preservation of scratches, however, makes it difficult to distinguish the front and the rear. The most distinctive features, transverse endopodal marks and pleural ridges, suggest affinities with *Rusophycus pudicum* Hall, 1852. Additionally, *Rusophycus pudicum* may exhibit an almost annulate appearance, generated by uneven concentration of scratches that closely resemble those observed in *Rusophycus* isp. Seilacher (1970) erected the *Cruziana pudica* group, characterized by strong, almost transversal endopodal scratches that are poorly individualized, and frequent genal or pleural marks. Seilacher (1970) noted that the *Cruziana pudica* group extends from the Lower Ordovician to the Carboniferous, and it includes several affiliated ichnospecies: *C. pudica, C. balsa, C. retroplana, C. rhenana*, and *C. carbonaria. Rusophycus* isp. differs from *C. balsa* and *C retroplana* in general form and the presence of external lobes. *Cruziana rhenana* shows strong pleural ridges, but the endopodal scratches are separated by a wide axial groove, which is absent in *Rusophycus* isp. Although *Rusophycus* isp. resembles *Rusophycus carbonarius* in its elongated shape and scratch pattern, the latter does not display pleural lobes. Specimens morphologically very similar to *Rusophycus* isp. are widespread in Pennsylvanian deposits along Kansas Highway 166 in Chautauqua County, Kansas, where

excellent preservation may allow identification to ichnospecies (Mángano and Buatois, unpublished observations).

Ichnogenus *Skolithos* Haldeman, 1840

DISCUSSION—*Skolithos* consists of simple, unbranched, vertical burrows, and it is distinguished from *Monocraterion* by the funnel-shaped upper portion of the latter. A detailed discussion of the relationship between both ichnogenera was provided recently by Jensen (1997). Eight ichnospecies of *Skolithos* currently are accepted: *S. linearis* Haldeman, 1840; *S. verticalis* (Hall, 1843); *S. serratus* (Salter, 1864); *S. magnus* Howell, 1944; *S. ingens* Howell, 1945; *S. annulatus* (Howell, 1957b); *S. bulbus* Alpert, 1975; and *S. gyratus* Hofmann, 1979.

Skolithos is interpreted as dwelling structures (domichnia), with phoronids and annelids the most likely tracemakers in marine environments (Alpert, 1974).

Skolithos is known from several depositional environments, including continental (e.g., Fitzgerald and Barrett, 1986), marginal-marine (Ranger and Pemberton, 1988), shallow-marine (Rindsberg, 1994), and deep-marine settings (Crimes, 1977). *Skolithos* is common in high-energy zones of intertidal areas (e.g., Mángano et al., 1996). It ranges in age from Precambrian to Holocene (Fedonkin, 1985; Howard and Frey, 1975).

Skolithos isp.
Fig. 56A–B

SPECIMENS—Four slabs (KUMIP 288530, KUMIP 288542, KUMIP 288558, KUMIP 288571) containing six specimens and several others recorded in the field.

DESCRIPTION—Vertical, unbranched, cylindrical, endichnial burrows preserved as protruding elements at the tops of beds. Diameter is 4.6–9.9 mm. Burrow walls are thinly lined and may exhibit corrugations. Burrow-fill typically is massive.

ASSOCIATED ICHNOFAUNA—*Protovirgularia bidirectionalis, Curvolithus simplex, Lockeia siliquaria,* and *Nereites missouriensis.*

REMARKS—Absence of cross sectional views precludes a confident identification of the ichnospecies.

Ichnogenus *Teichichnus* Seilacher, 1955

DISCUSSION—*Teichichnus* is similar to *Diplocraterion* in cross sectional view (Corner and Fjalstad, 1993). Although presence of a simple causative burrow is typically a diagnostic feature of *Teichichnus* that separates it from the U-shaped *Diplocraterion,* certain forms of *Teichichnus* display flattish U-shaped geometries that may be considered transitional with *Diplocraterion* (e.g., Corner and Fjalstad, 1993). *Phycodes,* a related ichnogenus, typically has a more complexly branched structure (Häntzschel and Reineck, 1968).

Teichichnus is a feeding structure (fodinichnion) of deposit feeders with the spreiten resulting from sediment mining (Seilacher, 1955; Häntzschel, 1975; Martino, 1989). Corner and Fjalstad (1993) favored an equilibrichnial origin for their specimens from the Holocene of Norway, in which the spreiten are produced to keep pace with an aggrading substrate. However, these Norwegian specimens seem to be more closely related to *Diplocraterion* than to *Teichichnus.* In all probability, many different animals produce *Teichichnus,* including annelids and arthropods (Häntzschel, 1975; Fillion and Pickerill, 1990). In modern environments, similar structures are produced by the polychaete *Hedista* (*Nereis*) *diversicolor* (Seilacher, 1957). Corner and Fjalstad (1993) suggested polychaete or sipunculan worms as tracemakers for their Holocene specimens.

Teichichnus is a facies-crossing ichnotaxon, which has been recorded in marginal-marine (e.g., Clifton and Gingras, 1997), shallow-marine (e.g., Pemberton and Risk, 1982), and deep-marine environments (e.g., Ekdale and Berger, 1978). *Teichichnus* is relatively common in tidal-flat environments (e.g., Hakes, 1976; Chamberlain, 1980; Martino, 1989, 1996; Fillion and Pickerill, 1990; Mángano and Buatois, 1997; Stanley and Feldmann, 1998). It ranges in age from Cambrian to Holocene (Jensen, 1997; Wetzel, 1981).
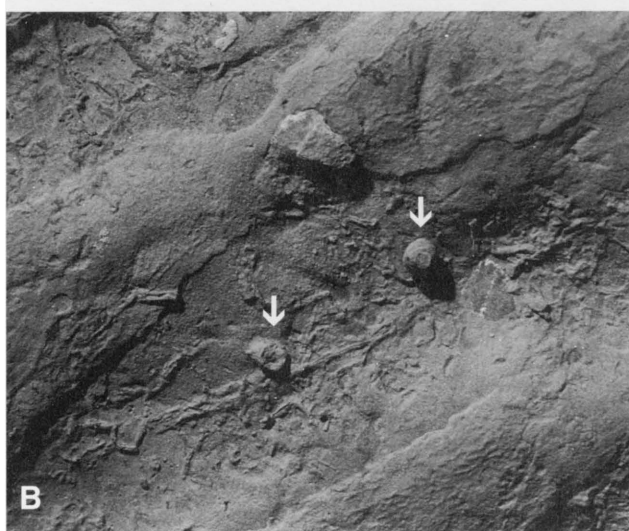
FIGURE 56—*Skolithos* isp (arrow). Preserved at the top of beds. **A.** Top of *Skolithos* burrows associated with shafts of *Protovirgularia bidirectionalis.* KUMIP 288530. × 0.42. **B.** Top of *Skolithos* isp. associated with wrinkle marks on ripple crest. KUMIP 288571. × 0.83.

Teichichnus rectus Seilacher, 1955
Fig. 57A–B

SPECIMEN—One specimen on a single slab (288500).

DESCRIPTION—Simple to flat U-shaped, horizontal, straight, unbranched, locally thickly lined trace having retrusive spreiten composed of vertically to subvertically stacked laminae. Causative burrow length is 88.9 mm. Causative burrow diameter is 5.4–6.5 mm. Spreite diameter is 7.6–8.9. Preserved as positive epirelief.

ASSOCIATED ICHNOFAUNA—*Curvolithus simplex.*

REMARKS—*Teichichnus* is a candidate for taxonomic review, because its ichnospecies remain poorly understood (Frey and Howard, 1985; Jensen, 1997). The specimen from Waverly clearly belongs to *T. rectus,* an ichnospecies

FIGURE 57—*Teichichnus rectus*. Both photos KUMIP 288500. **A.** Specimen preserved on top of a rippled bed. × 0.59. **B.** Cross sectional view of the same specimen showing retrusive spreiten and causative burrow. × 0.77.

characterized by a vertical to subvertical, unbranched, retrusive spreite composed of a pile of gutter-shaped laminae (Fillion and Pickerill, 1990). *Teichichnus pescaderoensis* Stanton and Dodd, 1984, which differs from *T. rectus* only in its larger size, was regarded as a junior synonym by Fillion and Pickerill (1990). *Teichichnus repandus* Chamberlain, 1977 was placed in *Rhizocorallium* by Buckman (1994). Buckman (1992, 1996) and Schlirf (2000) considered *T. ovillus* Legg, 1985, as a junior synonym of *T. rectus*.

Ichnogenus *Trichophycus* Miller and Dyer, 1878a

DISCUSSION—Originally described as a plant fossil by Miller and Dyer (1878a), *Trichophycus* subsequently was analyzed by Seilacher and Meischner (1965), Osgood (1970), Frey and Chowns (1972), Seilacher (1983), Fillion and Pickerill (1990), Geyer and Uchman (1995), and Jensen (1997). *Trichophycus* is made up of a series of U-shaped trace segments having *Teichichnus*-like spreiten. Five ichnospecies have been defined: *T. lanosus* Miller and Dyer, 1878a, *T. sulcatus* Miller and Dyer, 1878b, *T. venosus* Miller, 1879, *T. thuringicum* Volk, 1968, *T. tripleurum* Geyer and Uchman, 1995. *Trichophycus sulcatus* was considered an ichnospecies of *Palaeophycus* by Pemberton and Frey (1982) and synonymized with *Halopoa imbricata* by Uchman (1998). Osgood (1970) and Fillion and Pickerill (1990) considered *T. lanosus* to be an aberrant form of *T. venosus*. Although *T. lanosus* has priority, these authors retained *T. venosus* to maintain nomenclatural stability. Finally, Geyer and Uchman (1995)

placed *Phycodes pedum* in *Trichophycus*, although Jensen (1997) considered *P. pedum* as an ichnospecies of *Treptichnus*. *Trichophycus* is in need of an extensive review and its relation with *Halopoa* should be evaluated.

Trichophycus is interpreted as a feeding trace (fodinichnia). Seilacher and Meischner (1965) and Seilacher (1983) considered trilobites the most likely tracemakers. Fillion and Pickerill (1990) suggested that worms also may produce similar structures, using their setae to produce the striae. Jensen (1997) noted that the scratch pattern of specimens from the Cambrian of Sweden suggests the digging apparatus of a priapulid worm.

Trichophycus is known from shallow-marine environments (e.g., Osgood, 1970; Seilacher, 1983; Fillion and Pickerill, 1990; Geyer and Uchman, 1995; Jensen, 1997). In particular, occurrences in tidal-flat facies have been recorded by Fillion and Pickerill (1990) and Geyer and Uchman (1995). It reportedly ranges in age from Cambrian to Carboniferous (e.g., Geyer and Uchman, 1995; Seilacher, 1983).

Trichophycus isp.
Fig. 58A–B

SPECIMENS—Three slabs (KUMIP 288544, KUMIP 288550, KUMIP 288561) containing three specimens.

DESCRIPTION—Sinuous or straight, predominantly horizontal, cylindrical systems consisting of short segments that deviate laterally from the main course of the tunnel. Longitudinal, parallel, fine striae are visible locally, particularly at the sides of the structure. Trace segments are partially preserved, but they tend to curve slightly upwards distally. Some incipient retrusive spreiten, formed by a few, flattened U-shaped laminae, were observed. Total length is 7.6–14.4 mm. Up to four segments have been recognized forming one structure. Segments are 28.9 to 40.7 mm in length. Tunnel diameter is 5.6–12.4 mm; the widest segments are strongly flattened. Tunnel fill is similar to host rock. Preserved as full reliefs on soles of sandstone beds.

ASSOCIATED ICHNOFAUNA—*Protovirgularia bidirectionalis, Palaeophycus tubularis*, and *Halopoa* isp. are the most common traces associated with *Trichophycus* isp.

REMARKS—Partial preservation of the striae precludes ichnospecific assessment.

Chip-shaped Burrows
Fig. 59A–D

SPECIMENS—Five slabs (KUMIP 288505, KUMIP 288510, KUMIP 288511, KUMIP 288546, KUMIP 288567) containing 74 specimens.

DESCRIPTION—Small, vertical, funnel-shaped burrows. Burrow fill structureless and similar to host rock. Upper
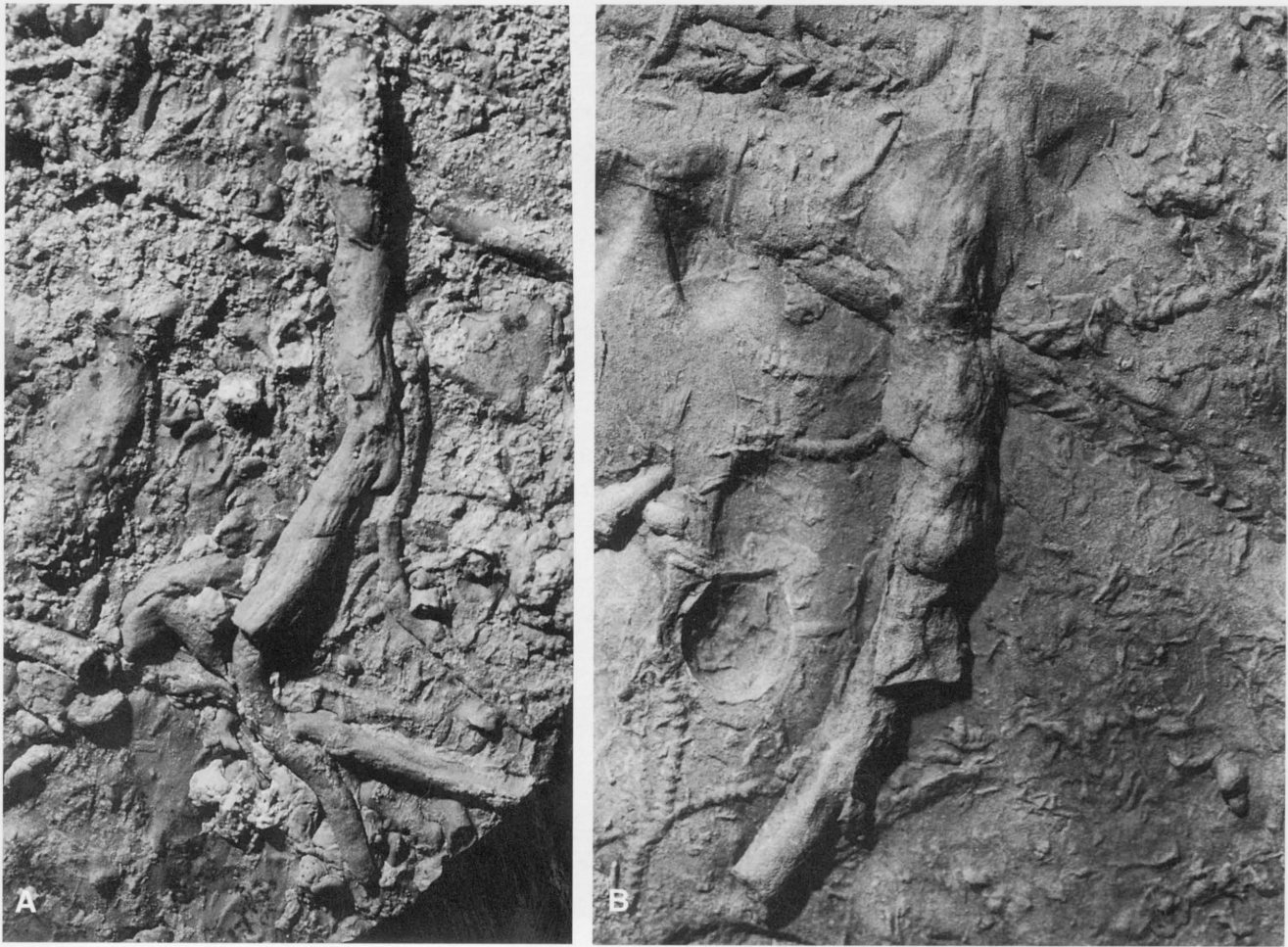
FIGURE 58—*Trichophycus* isp. Preserved at the base of beds. **A**. Specimen showing striations and *Teichichnus*-like spreite. KUMIP 288550. × 0.91. **B**. Specimen crosscutting a bivalve locomotion trace. KUMIP 288544. × 1.19.

section subcircular to oval, 2.6–7.5 mm in diameter. The lower tip of the structure is pointed, occasionally slightly flattened and folded toward one side (fig. 59A, C). The walls may be completely smooth or may display shallow, longitudinal, triangular grooves. Height is up to 8 mm on the bedding surface. Structures may cross more than one bed (fig. 59B). These burrows commonly occur in clusters of a few individuals (fig. 59A). Preserved as positive hyporeliefs (fig. 59A–C) or, more rarely, as negative epireliefs (fig. 59D).

ASSOCIATED ICHNOFAUNA—Chip-shaped burrows commonly are associated with *Asteriacites lumbricalis* and *Cruziana problematica*.

REMARKS—These structures resemble very small plug-shaped burrows, but they are difficult to include in any established ichnogenus. Although they do not display a duodecimal symmetry, the presence of a well-developed apical structure allies them with *Conostichus*, particularly *C. broadheadi* Lesquereaux, 1880. The prominent longitudinal fluting of *C. broadheadi*, however, contrasts with the almost smooth surface of the Waverly specimens. Presence of relatively smooth walls suggests some affinities with

Bergaueria. However, *Bergaueria* typically exhibits a shallow depression instead of a distinctive apical structure (Pemberton et al., 1988). Like many other Waverly ichnofossils, these tiny funnel-shaped structures have a wide range of preservational morphologies owing to substrate deformation related to fluidization.

Plug-shaped burrows currently are interpreted as resting or dwelling traces of sea anemones (Chamberlain, 1971; Pemberton et al., 1988). The small size of the Waverly burrows may indicate juvenile anemones.

Pelletoidal Chains
Fig. 60A–B

SPECIMENS—A single slab (KUMIP 288547) preserving tens of specimens.

DESCRIPTION—Small straight chains of pellets that cover the upcurrent side of ripple marks. The chains are more or less perpendicular to ripple crests, originating close to the top of the ripple and descend towards the trough. Chains are unbranched and subparallel, although they may crosscut each other. Chain length is up to 47.4
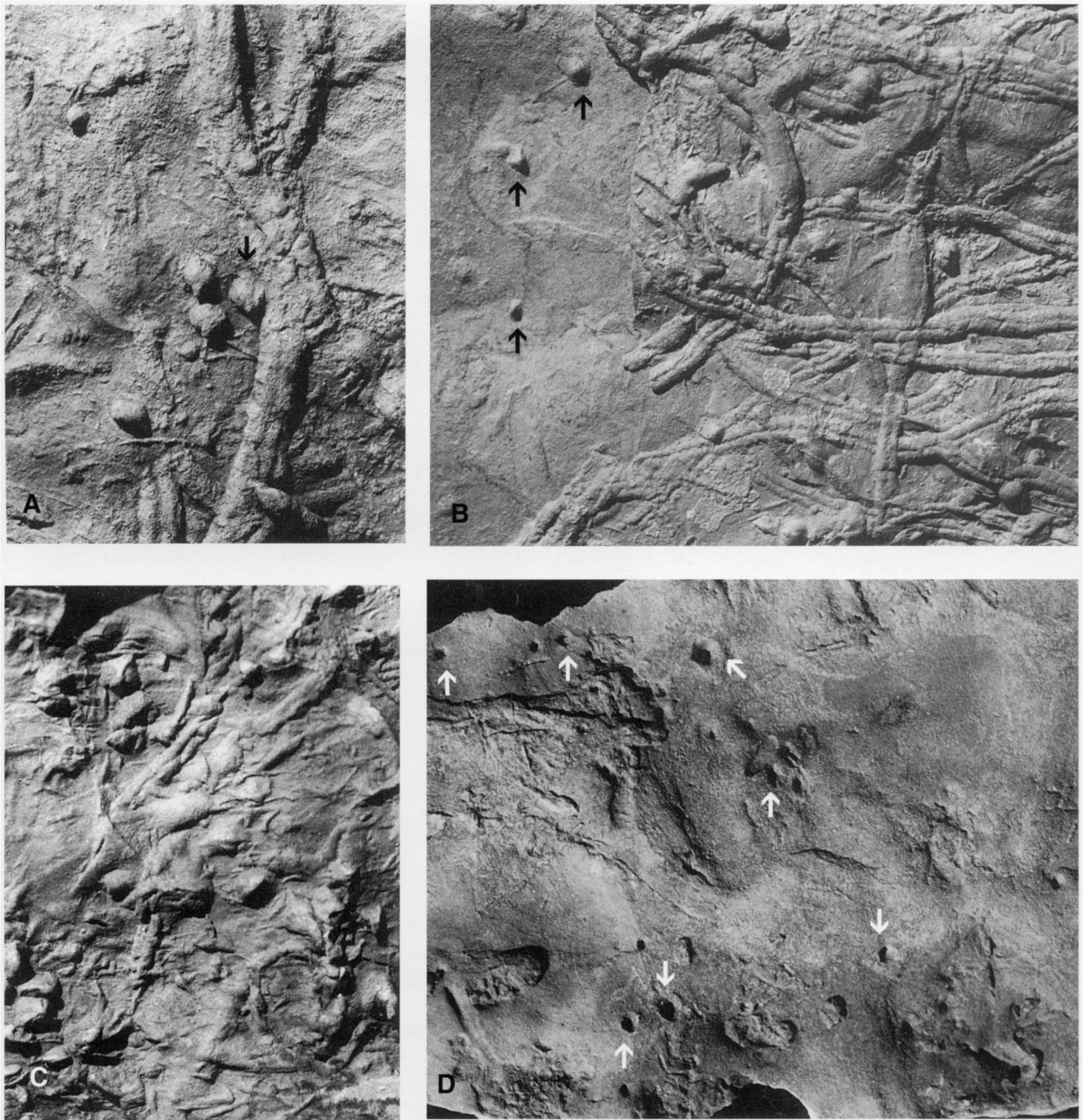
FIGURE 59—Chip-shaped burrows. **A.** Cluster of specimens (arrow) associated with *Cruziana problematica*. Base of bed view. KUMIP 288510. × 1.6. **B.** Specimens associated with *Cruziana problematica*. Note chip-shaped burrows preserved on the base of bed (arrow). KUMIP 288567. × 0.85. **C.** Cluster of chip-shaped burrows on the sole of a sandstone bed. KUMIP 288567. × 0.86. **D.** Specimens preserved as negative epirelief at the top of a sandstone bed (arrow). KUMIP 288567. × 0.85.

FIGURE 60—Pelletoidal chains. Preserved at the top of a rippled bed in KUMIP 288547. **A**. General view. × 0.47. **B**. Close-up showing internal pelletoidal structure. × 1.03.

mm, and width is 0.7 to 1.0 mm. Very fine grained sandstone pellets are cylindrical in shape and about 1mm in diameter. A fine-grained, darker-colored envelope surrounds the pellets.

ASSOCIATED ICHNOFAUNA—No other trace is associated with the pelletoidal chains.

REMARKS—Pelletoidal chains show slight similarities with *Microspherichnus linearis* Hakes, 1976.

Small Horizontal Cylindrical Burrows
Fig. 61A–C

SPECIMENS—Twenty slabs (KUMIP 288500, KUMIP 288511, KUMIP 288518, KUMIP 288523, KUMIP 288524, KUMIP 288527, KUMIP 288531, KUMIP 288532, KUMIP 288533, KUMIP 288534, KUMIP 288535, KUMIP 288538, KUMIP 288540, KUMIP 288544, KUMIP 288551, KUMIP 288555, KUMIP 288558, KUMIP 288565, KUMIP 288570, KUMIP 288571) containing several specimens, the actual number of which is impossible to assess.

DESCRIPTION—Predominantly horizontal, small, cylindrical burrows. Width is 0.6–1.7 mm. Cross section is subcircular. They typically occur as straight, short segments, less than 25.0 mm in length. The fill is essentially similar to the host rock, although carbonate cement may be more abundant within the burrow. Overcrossing of several individuals forming small isolated bunches is common. True branching in T's and Y's is rare. A few specimens curve. Preserved as full reliefs commonly on soles of sandstone beds.

ASSOCIATED ICHNOFAUNA—These burrows commonly are associated with *Asteriacites lumbricalis, Cruziana problematica, Protovirgularia bidirectionalis, Curvolithus multiplex*, among many other forms.

REMARKS—These small horizontal cylindrical burrows are abundant in several stratigraphic levels. In many cases, their presence seems to depend on preservation rather than ecologic causes. Small horizontal cylindrical burrows are easily differentiated from desiccation structures by their circular cross section and their hypichnial full relief preservation. Preferential concentration of carbonate cement within the tubes suggests the existence of a burrow microenvironment different from the surrounding conditions.

Although these traces may be roughly compared with *Chondrites*, they lack the regular branching and complex pattern of this ichnogenus (cf. Fu, 1991). Similar forms are *Dendrotichnium llarenai* Farrés, 1967, and *Dendrotichnium hantzscheli* Farrés, 1967. However, in both these ichnospecies, side branches diverge from a main stem.
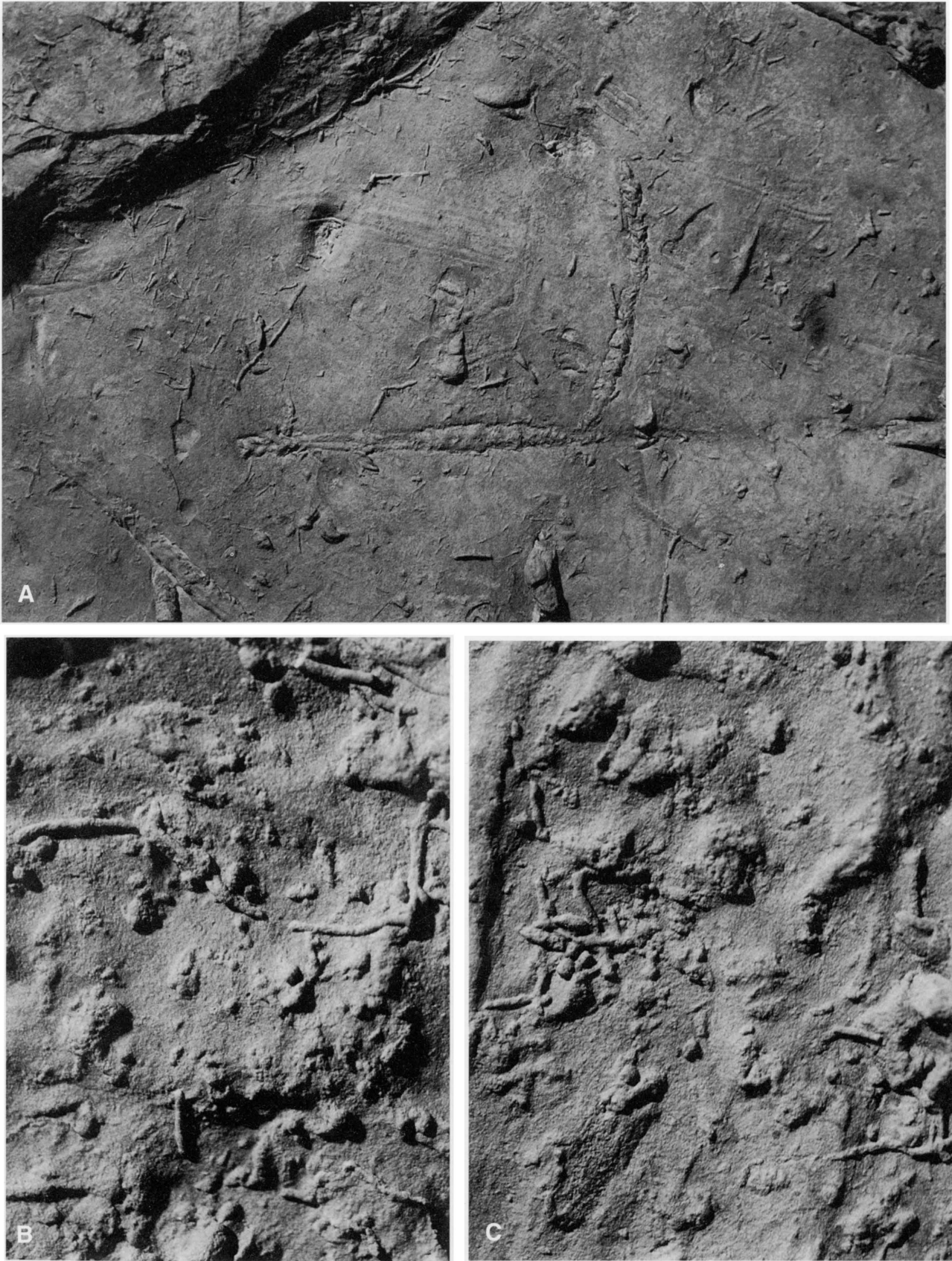
FIGURE 61—Small cylindrical horizontal burrows. Preserved at the base of beds. **A**. General view of specimens associated with *Protovirgularia bidirectionalis*. KUMIP 288531. × 0.65. **B**. Specimens associated with small vertical burrows. KUMIP 288500. × 2.5. **C**. Specimens showing branching at right angles. KUMIP 288500. × 2.5.

Small horizontal burrows are most likely the work of worms, probably polychaetes. Polychaete worms are significant components of many recent and fossil tidal flats, where they construct a wide variety of simple and branching structures (e.g., Frey and Howard, 1975; Craig, 1977). Newell (1979) noticed the presence of small horizontal burrows produced by juvenile polychaetes in sand-flat deposits. Interestingly, the adults of these organisms produce mostly vertical structures in the mixed and the mud flat.

Small Vertical Burrows
Fig. 62A–C

SPECIMENS—Ten slabs (KUMIP 288500, KUMIP 288510, KUMIP 288511, KUMIP 288516, KUMIP 288522, KUMIP 288533, KUMIP 288542, KUMIP 288552, KUMIP 288558, KUMIP 288574) with numerous specimens, the actual number of which cannot be determined.

DESCRIPTION—Small, vertical, unbranched, thinly lined burrows. Width is 0.8–2.2 mm. Cross section is subcircular. Fill is similar to the host rock. Several burrows occur together forming dense clusters. These small burrows often show an irregular distribution, being concentrated adjacent to or cutting other biogenic structures. Preserved as full relief or as positive or negative hyporeliefs.

ASSOCIATED ICHNOFAUNA—Small vertical burrows commonly are associated with *Protovirgularia bidirectionalis*, *P. rugosa*, *Lockeia siliquaria*, and *Lockeia ornata*. However, other ichnotaxa (e.g., *Asteriacites lumbricalis*, *Cruziana problematica*) also may be present.

REMARKS—Small vertical burrows are very similar to the ichnogenus *Pustulichnus* Ekdale and Picard, 1985, described from Jurassic eolianites. However, *Pustulichnus gregarius*, its single ichnospecies, is larger than the Waverly specimens and does not form clusters.

These burrows are probably produced by polychaetes. Vertical polychaete structures are very common in modern tidal-flat environments (e.g., Howard and Dörjes, 1972; Frey and Howard, 1975; Craig, 1977; Newell, 1979).

FIGURE 62 (right)—Small vertical burrows. Preserved at the base of beds. **A**. Cluster of small vertical burrows. KUMIP 288552. × 1.4. **B**. Base showing several clusters of vertical burrows. KUMIP 288552. × 1.3. **C**. Vertical burrows crosscutting *Lockeia ornata* (arrow). KUMIP 288552. × 1.5.

Undetermined Tracks
Fig. 63

SPECIMENS—Nine slabs (KUMIP 288519, KUMIP 288527, KUMIP 288533, KUMIP 288543, KUMIP 288549, KUMIP 288551, KUMIP 288555, KUMIP 288559, KUMIP 288568) with numerous specimens, the actual number of which cannot be determined.

DESCRIPTION—Isolated tracks consisting of elongate, scratch, or bifid imprints. Push-up mounds are present in some imprints. Imprint length is 1.5–5.6 mm. An internal continuous mark is observed locally. No clear trackway pattern is observed. Preserved as negative epireliefs on the tops of rippled sandstone beds.

ASSOCIATED ICHNOFAUNA—*Curvolithus simplex*, *Protovirgularia bidirectionalis*, and *Chondrites*? isp. are the most common structures associated with these tracks.

REMARKS—The internal mark could record the dragging of a telson. Poor preservation and presence of isolated tracks rather than continuous trackways prevent ichnotaxonomic classification. Local presence of a telson trace and bifid imprints suggests similarities with the ichnogenus *Kouphichnium* Nopcsa, 1923, a xiphosurid trackway (Caster, 1938; Goldring and Seilacher, 1971).

FIGURE 63—Undetermined tracks. Irregularly distributed tracks on the top of a rippled-sandstone bed. KUMIP 288533. × 0.56.

Trace-fossil Distribution

Relationships Between Trace Fossils and Sedimentary Facies

Trace fossils are distributed irregularly throughout the Stull Shale Member succession. Biogenic structures have been recorded in units A1 (parasequence A), B1 (parasequence B), and D3 (parasequence D), but they are most abundant in unit B1.

Trace fossils in **unit A1** (mud-dominated heterolithic facies) are restricted mainly to the sandstone interbeds. Sandstone soles contain low-diversity, but locally dense, assemblages of locomotion and grazing traces. *Cruziana problematica* is the dominant form, but *Protovirgularia rugosa* and *Psammichnites grumula* also are present. Monospecific assemblages or low-diversity assemblages are the rule, with traces often concentrated in small patches on certain bedding planes. Specimens of *Palaeophycus tubularis* are present in the mudstones, and they are filled with sand from overlying unit B1 and record a different bioturbation event (see section on "Ichnology of key stratal surfaces").

Unit B1 (sand-dominated heterolithic facies) displays an extraordinary abundance and diversity of trace fossils. This ichnofauna is dominated by bivalve resting (*Lockeia ornata, L. siliquaria*), escape (*Protovirgularia rugosa*) and feeding traces (*Protovirgularia bidirectionalis*), ophiuroid resting structures (*Asteriacites lumbricalis*), and arthropod locomotion traces (*Cruziana problematica*). Associated traces represent a wide variety of ethologic categories (domichnia, cubichnia, fodinichnia, pascichnia, and repichnia), and includes the following ichnotaxa: *Arenicolites* isp., *Asterosoma*? isp., *Chondrites*? isp., *Conichnus conicus, Cruziana* isp., *Curvolithus simplex, Curvolithus multiplex, Diplocraterion* isp. A, *Diplocraterion* isp. B, *Nereites cambrensis, Nereites imbricata, Nereites jacksoni, Nereites missouriensis, Palaeophycus tubularis, Parahaentzschelinia ardelia, Pentichnus pratti, Phycodes palmatus, Phycodes* isp., *Phycosiphon incertum, Planolites beverleyensis, Psammichnites implexus, Psammichnites plummeri, Psammichnites*? isp., *Rhizocorallium irregulare, Rosselia socialis, Rusophycus* isp., *Skolithos* isp., *Teichichnus rectus*, and *Trichophycus* isp. Biogenic structures left in open nomenclature include chip-shaped burrows, pelletoidal chains, small horizontal cylindrical burrows, small vertical burrows, and undetermined trackways. Most traces are preserved on bedding planes, and the degree of bioturbation is low, so the primary sedimentary fabric was not destroyed.

Unit D3 (trough cross stratified sandstones) contains a monospecific suite of *Diplichnites cuithensis*, a large trackway that may have been produced by the giant myriapod *Arthropleura* (Briggs et al., 1979). This ichnotaxon is present in the upper part of the sandstone.

Environmental Implications of Trace-fossil Vertical Distribution

Vertical distribution of trace fossils was controlled by substantial changes in environmental parameters, which in turn reflect the depositional evolution at the Waverly site.

Unit A1 is interpreted as having been deposited in a mixed- to mud-flat environment. This interpretation is supported by lenticular- and wavy-bedded deposits, wrinkle marks, relict troughs, and the near absence of body fossils. Scarcity of trace fossils may reflect severe living conditions and/or unfavorable preservational conditions. A low diversity of biogenic structures in mixed- to mud-flat facies is not surprising, because very few animals are able to inhabit the uppermost zone of tidal flats in tropical environments (Terwindt, 1988). Extremely high temperatures and desiccation usually prevent the establishment of diverse benthic communities in soft-sediment upper-intertidal zones (Newell, 1979; Reise, 1985). Taphonomic factors, however, also may have played a role. Preservation of trace fossils in tidal-flat deposits is favored by the presence of sandstone/mudstone interfaces. Lack of sandstone interbeds would inhibit preservation and visibility of biogenic structures, which is consistent with the concentration of trace fossils on the soles of interbedded thin sandstone beds. However, it is interesting to note that even at these interbeds, diversity is particularly low in comparison with the sandstone interbeds of Unit B.

Unit B1 reflects deposition in an intertidal-sand flat. Abundance and diversity of biogenic sedimentary structures in unit B1 record the activity of a diverse benthic community. Preservation of trace fossils on bedding planes was enhanced by the cyclic alternation of sand layers and mud partings. Some crowded bedding surfaces document time averaging, which records the activity of several communities (see section on "Evidence of time-averaged surfaces"). Although the envisaged sedimentary environment is rigorous and unstable, organisms were able to deal with these stressful conditions, probably as a result of the predictability of such an environment (see section on "Spatial heterogeneity").

Unit D3 represents the fill of an abandoned fluvial channel. The producer of the trackway *D. cuithensis* was most likely a terrestrial arthropod. *Diplichnites cuithensis* has been recorded exclusively from late Paleozoic sub-aerial deposits, commonly exposed fluvial bars, silted channels, and desiccated sheetfloods (Briggs et al., 1979; Briggs et al., 1984; Ryan, 1986).

Diversity and abundance of trace fossils abruptly decrease upward in the Waverly section, which reflects an overall shallowing-upward trend from lower-intertidal to fluvial facies. The highest ichnodiversity is recorded in the tidal-flat deposits, specifically in the sand-flat facies. Towards the upper part of the section, terrestrial deposition is indicated by the arthropod locomotion traces.

Spatial Heterogeneity

One of the most remarkable features of the Waverly tidal-flat deposits is the heterogeneous distribution of biogenic structures. Any casual observer inspecting the outcrop can find substantial differences in the trace-fossil content of different bedding planes. Furthermore, a detailed inspection of sandstone rippled tops or soles reveals patchiness or small-scale spatial heterogeneity. Although spatial heterogeneity is a major feature of modern tidal flats, it has not been recorded in the fossil record in previous ichnologic studies.

Zonation and patchiness of benthic communities and of the biogenic structures recording their behavior is a common characteristic of modern coastal environments (e.g., Schäfer, 1972; Anderson and Meadows, 1978; Newell, 1979; Reise, 1985; Tufail et al., 1989). This is particularly true for the intertidal zone, where the tidal cycles, tidal currents, river input, and wind processes result in a wide variety of salinity changes and hydrodynamic regimes (Meadows et al., 1998). In addition, the complex biogenic interactions of the intertidal zone produce further complexity in spatial and temporal heterogeneity (Reise, 1985; Bertness, 1999; Little, 2000). Heterogeneity occurs primarily at two scales.

At the larger scale, zonational distribution is expressed along the entire tidal range. This is shown by different animal communities living in different areas within the tidal flat, where substrate, exposure, temperature, and other environmental parameters differ substantially (i.e., sand, mixed, and mud flat). Only very few species are able to inhabit the entire tidal range (Reise, 1985). In general, biologic diversity and biomass decrease toward the level of high tide (Newell, 1979; Reise, 1985). Heterogeneity and predictability of the middle- to lower-intertidal environments result in high-species diversity containing species that are particularly adapted to utilize the resources of specific microhabitats (Sanders, 1968, 1969; Slobodkin and Sanders, 1969). In contrast, in the high-intertidal area conditions not only are more extreme, but they are characterized by high-temporal instability and unpredictability resulting in a decrease in species diversity. In this setting, physical factors, such as heating, frost, and water loss, play a crucial role on benthic macrofaunal communities. Although primary production by benthic microalgae increases in a landward direction, benthic consumers do not show a corresponding increase. This is related to difficulty for marine organisms to adapt to prolonged low-tide emersion (Reise, 1985). Arid climates cause more extreme upper intertidal conditions and corresponding impoverished communities than humid climates. In general, benthic organisms tend to be less specialized in their diet, often being trophic generalists.

Several authors have recognized tidal zonation based on biogenic sedimentary structures. For example, Frey, Howard, et al. (1987) distinguished three different ichnofaunas (brachyuran, molluscan, and holothurian assemblages) in low-energy, extensive macrotidal flats of the Yellow River, in South Korea, from the shore to more than 3.9 km seaward. Swinbanks and Murray (1981) recognized five sedimentological/floral zones in tidal flats of British Columbia, each characterized by different associations of animal structures. Different assemblages of biogenic structures also have been recognized in tidal flats from the North Sea by Gerdes et al. (1985), and the Bay of Mont-Saint-Michel in France by Larsonneur (1994). Aitken et al. (1988) discussed an interesting example of tidal-flat assemblages in a subarctic, ice-modeled coast. In fjord settings, coastal physiography plays a major role in organism distribution.

This scale of heterogeneity is reflected at Waverly by the broad vertical pattern in trace-fossil distribution previously discussed, where the mixed- and mud-flat assemblages are contrasted with the abundance and diversity of the sand-flat ichnofauna. Similar trends in trace-fossil distribution have been documented in a Silurian tidal flat by Narbonne (1984).

On a smaller scale, within each environment (e.g., on the sand flat), spatial segregation of species may reflect distinct microhabitats and partitioning of energy resources. Particular spatial array of organisms permits maximum utilization of available food resources (Newell, 1979). An example is the spatial separation of barnacles and limpets within the lower-intertidal zone of rocky shores (Lewis, 1961). Spatial partitioning patterns of intertidal organisms may be regarded as a mechanism by which organisms exploit particular food resources within the limits of their tolerance to environmental conditions, and at the same time minimize interspecific competition (Newell, 1979). In the middle and, particularly, in the lower-intertidal area, food resources are abundant and varied, but equally the organisms are bound by other species whose requirements may overlap with their own. Niche specialization, commonly reflected by patchiness, may effectively reduce interspecific competition. Selection commonly favors those behavioral responses that tend to restrict organisms to particular niches at which they convert energy more efficiently than their neighbors (Wolcott, 1973). Such adaptations are reflected by patterns of behavior, metabolism, or developmental changes (Newell, 1979).

Hogue and Miller (1981) recorded the existence of small patches of nematodes in ripple troughs, which they explained in terms of preferential accumulation of organic detritus (see section on "Substrate"). Reise (1985) documented segregation of assemblages of the amphipod *Corophium volutator*, the polychaete *Arenicola marina*,

and the prosobranch *Hydrobia* in the sandy-tidal flat at Köningshafen. Mounds are stabilized and inhabited by the tube-dwelling amphipods, the prosobranch tends to concentrate at the fringe of the mounds, and the polychaete causes high sediment turnover in the surrounding areas. This distribution pattern records trophic partitioning, ensuring maximum utilization of the available food resources. Interestingly, Reise (1985) explained this distribution pattern in terms of sediment stabilizers and destabilizers (see section on "Substrate"). Another example of small-scale spatial heterogeneity is recorded by the distribution of *Scolecolepsis squamata* and *Paraonis fulgens* on a foreshore profile (Röder, 1971; Bromley, 1996). *Scolecolepsis* constructs vertical shafts on slight topographic rises; meanwhile the spiral traps of *Paraonis* occur in nearby depressions. Bromley (1996, p. 126) noticed that subtle modifications in the environment could result in the two communities alternating in a stratigraphic sequence. To quantify spatial heterogeneity in the modern intertidal zone, Meadows et al. (1998) established three 50-m transects in the lower intertidal zone of a bay in the Clyde Estuary, Scotland. The first transect was at a right angle with the sand waves (peak/trough transect), the second and third crossed the peak (peak transect) and trough (trough transect), respectively. Correlation, cluster, and principal component analysis highlighted patterns of spatial patchiness in the sedimentary environment (micro-habitats) and macrobenthic community.

Heterogeneity related to local microtopography, typically bedforms or small positive areas within an isochronous horizon, is well represented at Waverly. Examples of patchiness are the mounds characterized by dense aggregations of U-shaped tubes (*Protovirgularia bidirectionalis*) and small vertical burrows (fig. 64A–D). These structures may be compared with *Corophium volutator* mounds (Reise, 1985) and tube-building polychaete worms (Jones and Jago, 1993), which increase sediment stability. U-shaped, mucus-lined bivalve structures can be interpreted as stabilizers, which trapped the tide-transported sediment resulting in small positive elements on the tidal-flat surface. The reason why the infaunal burrowers chose this particular spot of the substrate is more difficult to assess, but it must have been related to some particularly attractive feature of the sediment, as site selection is rarely random. Larvae preference for settlement in particular sites has been associated with specific features of the substratum, including physical properties (e.g., grain roundness) and

biological components (e.g., organic film induced by bacteria, type of interstitial organisms, presence/absence of seagrass) (Newell, 1979; Reise, 1985). Wilson (1954, 1955) showed that the most important factor in the settlement of *Ophelia bicornis* is the presence of a film of microorganisms on the surface of sand grains. Meadow and Anderson (1968) made a survey of microorganisms attached to grains of intertidal sand and found an uneven distribution, with microorganisms tending to concentrate in small pits and grooves within the surface. Microbial stabilization also plays a major role in creating topographic irregularities, such as erosive remnants, mounds, domal upheavals, and projecting bedding planes in tidal flats (Gerdes et al., 1994; Gerdes, Klenke, et al., 2000; Gerdes, Krumbein, et al., 2000; Noffke et al., 1996; Noffke, 1999).

Another example of patchiness is the preferential presence of *Psammichnites implexus* in ripple troughs. Small-scale spatial heterogeneity probably documents the effects of bedform topography on the partitioning of food resources (see section on "Substrate"). For example, specimens of *Psammichnites implexus* commonly are concentrated in ripple troughs, where they display almost a guided meandering pattern. Absence of self-overcrossing suggests phobotaxis. Specimens are isolated in separate troughs and do not overlap. Presence of guided meanders records a highly specialized feeding strategy comparable with that of *Helminthorhaphe* in deep-marine settings (Seilacher, 1977a; Uchman, 1995). This distribution may reflect food searching in ponded areas established in ripple troughs during the low tide. The searching pattern indicates that troughs acted as sites of accumulation of organic detritus, being organic-rich at the sediment-water interface and within the uppermost millimeters of the sediment.

Heterogeneity also is recorded by nuculoid bivalve structures (fig. 65). The paucispecific assemblage of *Lockeia ornata* and *Protovirgularia rugosa* on localized stratigraphic levels may be interpreted as recording tidal flat heterogeneity across the tidal range. Although the sand-dominated interval of the Waverly section represents a sand-flat environment, the mixed-flat transition is probably present. Stratigraphic changes in trace-fossil assemblages may record subtle shifts between adjacent zones of the intertidal area. Alternatively, physical or biological disturbance may result in temporal modifications of benthic community structure (see section on "Tiering structure and ichnoguilds").
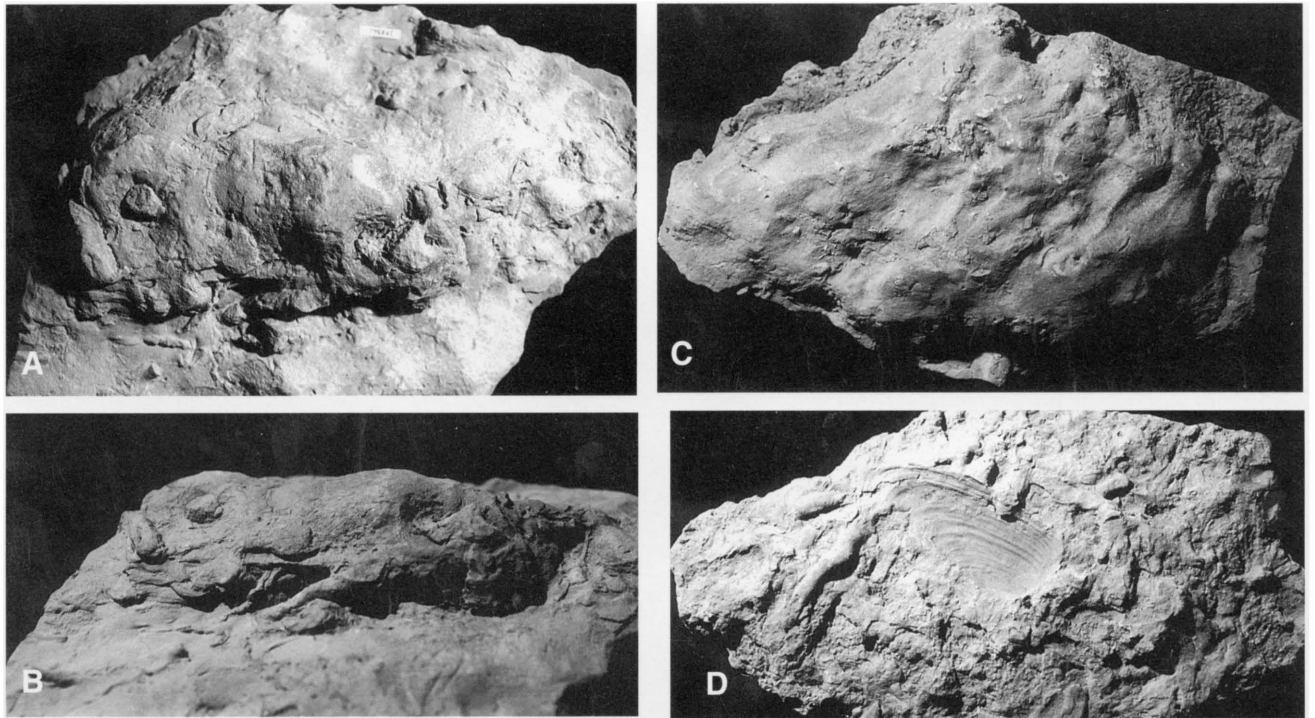
FIGURE 64—Sediment mounds. **A**. Upper view of an intensely bioturbated mound. KUMIP 288542. × 0.45. **B**. Lateral view of mound shown in A. Note shafts of *Protovirgularia bidirectionalis* and small cylindrical burrows. KUMIP 288542. × 0.45. **C**. Upper view of an irregular-shaped mound with smooth surface. KUMIP 288574. × 0.28. **D**. Basal view of mound shown in C. Note presence of *Palaeophycus tubularis* and abundant shell fragments. KUMIP 288574. × 0.28.
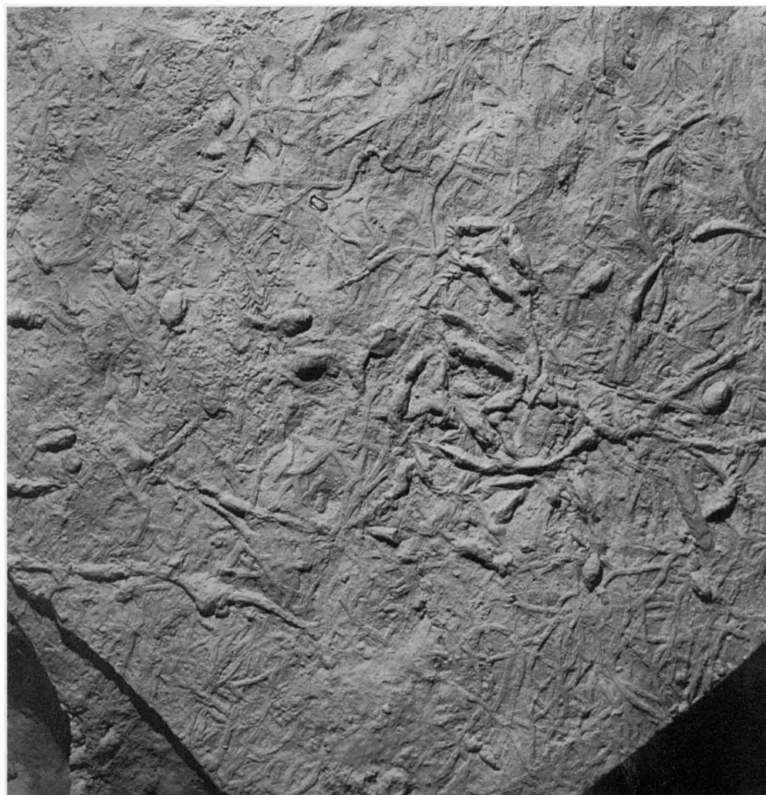
FIGURE 65—Heterogeneous distribution of *Lockeia ornata* preserved on the base of a sandstone bed. KUMIP 288552. × 0.23.

Trace-fossil Paleoecology

Environmental Controls

Many factors define the niche and survival range of animal species. Within a particular ecosystem, some of these factors are particularly relevant, becoming limiting factors (Brenchley and Harper, 1998). In the tidal zone, environmental controls acquire particular ecological significance. The tidal-flat zone represents a harsh environment where marine organisms often approach the survival boundaries of their tolerance range to environmental extremes. Although tidal flats are primarily a marine habitat, they are subject to the extremes of terrestrial climate, heating, frost, desiccation, and rain (Reise, 1985). Temperature, time of exposure to subaerial conditions, salinity, hydrodynamic energy, and substrate are effective limiting factors.

In this section, we discuss the role of environmental parameters as controlling factors of the Waverly ichnofauna. Although environmental factors are considered separately, it is important to understand that the limits of tolerance of intertidal invertebrates are defined in terms of multi-variable responses, rather than in terms of isolated factors (Newell, 1979). Salinity, temperature, and exposure to subaerial conditions are intimately linked and are strongly dependent on latitudinal position and climate. On the other hand, hydrodynamic energy and substrate conditions also are interconnected and dependent on coastal topography and physiography. The resultant ichnofauna therefore is shaped by the interplay of key environmental parameters overprinted by taphonomic factors.

Salinity

Coastal environments experience large fluctuations in salinity. Periodic emersions and submersions of the intertidal zone are matched by periodic fluctuations in salinity. Additionally, seasonal rains and drainage from the continent significantly affect the salinity and position of the water table. Salinity shifts, together with exposure and temperature, are typically drastic in the upper-intertidal area and diminish towards the lower-intertidal zone (Newell, 1979; Reise, 1985). In general, salinity tolerance controls the zonational distribution of intertidal animals, with the more euryhaline species occurring more abundantly in the upper-intertidal zones (Newell, 1979). Complex hydrologic conditions of the tidal flat promote particular behavioral strategies for protection, such as infaunalization. Inhabiting a burrow or temporary refuge in the sediment is an effective strategy in avoiding salinity variations (Howard, 1968; Pemberton and Wightman, 1992). In low-energy settings, close to the low-water mark, surface salinity changes have little effect on the salinity of

interstitial water below a depth of about 2 cm (Sanders et al., 1965; Johnson, 1967). Many tidal-flat inhabitants have developed biological rhythms (e.g., circa-tidal, circa-semilunar rhythms) of vertical or horizontal migration controlled by tide cyclicity (Palmer, 1995). Many species hide in their burrows during low tide and are active during high tide. For example, the modern crab *Sesarma reticulatum* hides in its burrow during low tides and roams the surroundings during high tides (Palmer, 1967, 1995; Seiple, 1981). Horizontal migration is a well-documented strategy to minimize the dramatic salinity shifts in the upper-intertidal zone. An example of tide-associated migration is the activity pattern of the modern predaceous isopod *Eurydice pulchra*, which lives buried in the sand flat during emersion, but rises into the water column with flood tide to swim at the water's edge and feed on epifauna, infauna, and debris. It retreats seaward with ebb tide and reburies itself for protection (Warman et al., 1991).

Marine invertebrate surface activity on the tidal flat is typically more intense during high tide (Pienkowski, 1983; Vader, 1964). In contrast, many semi-terrestrial and terrestrial animals (e.g., terrestrial crabs, the modern intertidal beetle *Thalassotrechus barbarae*) may display a peak of activity during low-tide emersions (Palmer, 1995). Other adaptations to stressful salinity conditions involve protection by organic substances (e.g., mucus), and osmoregulation (Kinne, 1964). Some animals combine several strategies for better protection. For example, the modern *Corophium* is a good osmoregulator and a well-known burrower that can tolerate salinities between 2‰ and 47‰.

In addition to the sedimentologic evidence, the diversity and complexity of forms recorded at Waverly indicate a sand-flat environment, probably very close to low-water level, where stress conditions were ameliorated by short-time exposure (cf. Swinbanks and Murray, 1981). From a biological perspective, lower intertidal animal communities resemble contiguous sub-wave base assemblages (Schäfer, 1972; Reise, 1985). The scarcity of biogenic structures in upper-intertidal deposits suggests that physico-chemical conditions were extreme, preventing the development of an abundant resident fauna. *Cruziana problematica* commonly is associated with other ichnotaxa in sand-flat deposits of the Stull Shale Member. Pauci-specific occurrences of *C. problematica* in the mud- and mixed-flat deposits may record either a wide environmental range of its producer or short-term incursions into this zone. High-density assemblages of these arthropod traces may not record upper-intertidal inhabitants, but landward migrations from the lower-intertidal zone. As in the case of many recent crustaceans, these migrations regulated by tidal cyclicity may have been connected to the search for food.

Temperature

Tidal flats commonly exhibit rapid changes in temperature related to periodic subaerial exposure. Several studies of modern environments have documented the relationships between temperature and animal-sediment interactions (e.g., Green and Hobson, 1970; Yeo and Risk, 1981; Aitken et al., 1988). However, application of these concepts to the study of fossil cases is still in its infancy. Commonly, the high-intertidal zone in tropical environments is an extremely inhospitable habitat for marine organisms due to very high temperatures, long time of exposure, and abnormal salinities. As a consequence, the highest density of biogenic structures in tropical tidal flats is in the lower-intertidal zone (Terwindt, 1988). On the other hand, tidal flats in colder areas may exhibit a high density of biogenic structures in the upper-intertidal zone (e.g., Yeo and Risk, 1981). Therefore, bathymetric displacement of certain species along latitudinal gradients is common (Reise, 1985). For example, the bivalve *Gemma gemma* lives in intertidal areas in northern North America and in subtidal areas in the south to avoid the hazards of high temperatures on tidal flats (Green and Hobson, 1970). Aitken et al. (1988) documented biogenic structures in modern subarctic tidal flats and noted a dominance of vertical domiciles of bivalves and polychaetes. These authors compared subarctic and temperate tidal flats in terms of biogenic structures and noted that some forms, such as *Corophium volutator*, were abundant in temperate tidal flats but absent from subarctic intertidal areas.

At Waverly, the highest density and diversity of ichnofossils is, by far, concentrated in lower-intertidal deposits, close to low tide. High temperatures and increased desiccation risk in the upper-intertidal zone were probably major limiting factors. This interpretation is consistent with paleogeographic reconstructions that suggest an equatorial position for Kansas during the Pennsylvanian (Scotese and McKerrow, 1990; West et al., 1997).

Substrate

Substrate control on trace fossil morphology of the Waverly ichnofauna is striking. Almost all forms were affected by the substrate and serve as useful tools for measuring substrate properties (fig. 66A–E). In general, it is possible to identify ichnotaxa irrespective of substrate effects (fig. 66A–D). In a few cases, however, deformation is so severe that accurate identification cannot be achieved (fig. 66E). Vertical and horizontal differences in substrate conditions influence the diversity, abundance, and distribution of intertidal organisms (Newell, 1979, Reise, 1985).

Morphologic variability of trace fossils between and along bedding planes reflects controls operating at different scales. Because tidal flats are regularly exposed and submerged by the tides, the concomitant pore-fluid content within the sediment will vary during a tidal cycle. On the other hand, the low-tide landscape commonly is characterized by the presence of tide pools within a generally emerged area, resulting in a range of substrate conditions along an isochronous surface.

The effects of microtopography on sediment grain size, sorting, and organic richness have been investigated. Thum and Griffiths (1977) analyzed the hydraulic circulation of water through the pore system of ripple marks in sand. They found that water entered through the troughs and exited through the crests along a pressure gradient. This circulation pattern results in a re-sorting of sediment with small grains and organic debris being drawn into the troughs. Organic matter is trapped in the sediment to a depth equal to the height of the ripple crest. The localized distribution of organics accounts for the aggregation of meiofauna and invertebrate grazers in troughs (Jansson, 1967; Harrison, 1977, Newell, 1979; see also section on "Spatial Heterogeneity").

Whereas the anatomy of body fossils is controlled by inherited genetic factors, the morphology of trace fossils is strongly controlled by external factors (Goldring et al., 1997). Substrate type and consistency are important extrinsic factors that determine both burrowing technique and infaunal community composition (Bromley, 1996). Substrate consistency embraces the intricate interplay of multiple factors (e.g., grain size, sorting, water content, organic matter content, shear strength, and mucus binding) that define the mechanical properties of the sediment (cf. Bromley, 1996). Sediment composition directly influences substrate consistency. Carbonate substrates may be subjected to progressive dewatering stages (soupground, softground, firmground, and hardground) associated with increasing compaction and cementation (Ekdale et al., 1984; Ekdale, 1985; Lewis and Ekdale, 1992). Goldring (1995) recently introduced the term "looseground" for soft sand and gravel as distinct from soft mud and silt (softground).

Most studies concerning trace fossils and substrate control have focused on the evolution of carbonate substrates and how this affects community composition (e.g., Bromley, 1975; Goldring and Kazmierczac, 1974; Mángano and Buatois, 1991; Lewis and Ekdale, 1992; Bromley and Allouc, 1992), or on the erosional exhumation of firm siliciclastic sediments (e.g., MacEachern et al., 1992; MacEachern and Pemberton, 1997). Recent work in siliciclastic ichnology, however, emphasizes that the process of dewatering and the concomitant changes in substrate properties is a continuum rather than a series of compartmentalized stages (cf. Buatois, Jalfin, et al., 1997). Therefore, a scale of morphologic variation of ichnofossils depicting substrate evolution can be constructed.

Maples and West (1990) suggested that morphologic variability of bivalve traces at Waverly was controlled by substrate fluidity. Protobranch bivalve traces at Waverly exhibit a complex array of relationships controlled by bivalve behavior and substrate character (Mángano et al.,
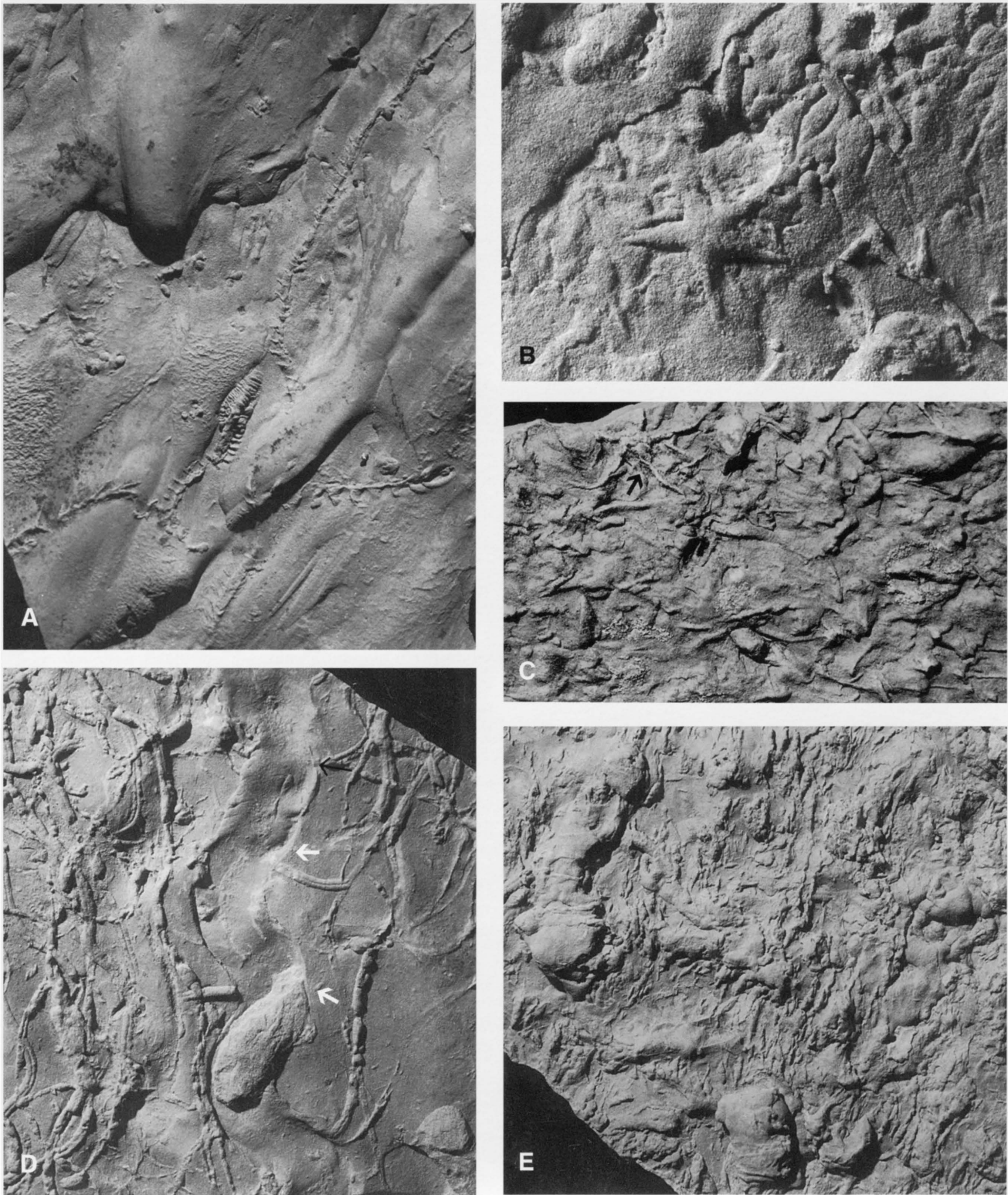
FIGURE 66—Substrate fluidity and morphology of trace fossils. All photos are base of bed views. **A**. Fluted base with deformed specimens of *Protovirgularia rugosa* connected to escape structures. KUMIP 288525. × 0.79. **B**. Load-casted surface with inflated, starfish-shaped *Asteriacites lumbricalis*. KUMIP 288523. × 1.66. **C**. Firm sandstone base with brittlestar-shaped *Asteriacites lumbricalis* (arrow). KUMIP 288530. × 0.79. **D**. Soft substrate with high pore-water content having poorly preserved sinuous trace (*Psammichnites*? isp. [arrow]) and *Cruziana problematica*. Note the gradation between bilobed forms and chains of knobs related to soft-sediment deformation. KUMIP 288515. × 0.55. **E**. Highly deformed sandstone base with large undetermined traces. KUMIP 288563. × 0.55.

1998). In defining a range of substrate conditions, presence of impregnated walls, sharpness of delicate morphologic details, and degree of deformation are important observations (Goldring, 1991). The sharp chevrons of *Protovirgularia bidirectionalis* suggest penetration in relatively firm, dewatered substrates. Structures with sharp, closely spaced chevrons represent what can be characterized as the firmer end of the softground range ("non-fluid sediments" of Maples and West, 1990).

Trueman et al. (1966) investigated the effects of substrate, particularly grain size, on the rate of burrowing. Paradoxically, it seems that the easier the penetration, the worse the anchorage, and vice versa. A dilatant medium becomes firm and more resistant to shear as increased force is applied, whereas a thixotropic system shows reduced resistance to increased rates of shear. As a consequence, anchorage requires a substance with dilatant qualities, whereas motion is facilitated by a thixotropic system (Trueman and Ansell, 1969). For example, in soft estuarine silts penetration is easy, but firm anchorage is difficult. Conversely, secure anchorage is attained in dilatant beach sands, but penetration is harder because of the increased resistance of the substrate. Factors involved in the penetration and protraction phase tend to compensate one another so that the difference in the rate of burrowing may not be determined solely by grain size. Trueman et al. (1966) noticed that compacted sediment is stiffer, which results in a decreased burrowing rate. Accordingly, the frequency of the digging cycle and depth of penetration in each sequential movement decreases as burrowing into deeper levels proceeds (Ansell, 1962). Although quantitative experimental work has not focused specifically on water content and how it affects the mechanical properties of the sediment, within any given grain-size range a more compacted sediment will be less fluid and stiffer, offering increased resistance to penetration.

In chevron locomotion traces, such as *Protovirgularia*, the distance between two chevrons represents each sequential set of movements, and each chevron indicates the site of anchoring of the foot flaps within the sediment. Sharp, closely spaced chevrons account for short steps, with the animal struggling to advance in a stiff, resistant sediment. Longer distances between chevrons, like those observed in some delicate *Protovirgularia rugosa*, may reflect relatively coherent, but less resistant substrates, resulting in lower shell friction and allowing smoother and easier movement during the protraction phase. Sediment that is too fluid may result in irregular and highly deformed trace morphologies, recording the difficulties of the foot in obtaining a secure anchorage. As the amount of pore water increases, neither the fine morphologic details of *L. ornata* nor its pedal flap anchor are cast by soft, fluid sand. This may explain the mostly smooth locomotion traces resembling *Palaeophycus tubularis* (*Planolites* of Maples and West, 1990) that are connected to poorly defined *L. ornata* structures. Intermediate, poorly cohesive, relatively fluid substrates lead to intermediate

morphologies, such as *Imbrichnus* (Hallam, 1970) and other forms that exhibit evidence of a bifurcated foot but display considerable deformation.

In short, dissimilar morphotypes respond to the same style of motion controlled by different substrate properties (Mángano et al., 1998). In other words, once intrinsic biologic factors were established (i.e., a bifurcated muscular foot), substrate consistency played the main role in the morphologic variability of trace fossils. Thus, *Protovirgularia, Walcottia, Uchirites, Imbrichnus*, and *Chevronichnus* do not represent major behavioral differences; they mainly record differences in the degree of dewatering and other related properties of the sediment. At a different scale, biologic diversity also could contribute to trace-fossil variability, as more than one bivalve species may have been involved in the production of biogenic structures. Species-level constraints, however, do not appear to have controlled the basic pattern of burrowing behavior.

The position of the tracemaker within the substrate, particularly in relation to the sand-mud casting interface, is also a major influence in trace fossil morphology (Goldring et al., 1997). Subtle up-and-down movements that result in different morphologic expressions of an ichnotaxon can sometimes explain gradational changes along locomotion structures. For example, some typical chevron specimens of *Protovirgularia* grade into bilobate *Didymaulichnus*-like structures that, in turn, grade into smooth-walled *Palaeophycus*-like burrows. Elsewhere, some chevron traces grade laterally into smooth-walled forms, or into bilobate structures that locally show some chevrons. These differences in morphology within a single trace are toponomic rather than morphoethologic, and accordingly only one name, the one that better reflects the ethology of the animal, should be applied to the whole structure. In deeper variants, chevrons disappear, resulting in bilobate or even apparently smooth simple burrows (cf. Seilacher and Seilacher, 1994, Pl. 1b).

The other important point about substrate is that animals are not passive to the physical properties of the sediment, but actually can substantially modify substrate attributes (Bromley, 1996). Woodin and Jackson (1979) and Woodin (1983) classified organisms into functional groups according to the effects, both direct and indirect, on the properties of the surrounding sediment, and the manner in which they make the environment more or less suitable for colonization by other organisms. Reise (1985) identified stabilization as promoting biologic interactions, whereas no benthic species will benefit directly from sediment destabilization. On this basis, two main functional groups can be distinguished: sediment stabilizers and sediment destabilizers. Mobile, mostly detritus-feeder infauna and epifauna, but also some sedentary organisms, whose feeding and defecation activities may provide abundant particles in suspension, destabilize the substrate (Rhoads and Young, 1970; Rhoads, 1974). In contrast, sedentary organisms that build mucus-lined tubes within the sediment reduce resuspension and erosion, and

represent sediment stabilizers. For example, the tube-building polychaete worm *Lanice conchilega* acts like the steel reinforcing rods in concrete and increase the rigidity and stability of the sand (Jones and Jago, 1993). Rhoads and Young (1970) proposed that one feeding group may affect negatively another trophic group to the point of making life impossible for the affected group. The expected result of trophic amensalism is that where deposit feeders are abundant, development of suspension feeders is limited. In this framework, Reise (1985) explained the incompatibility of dense assemblages of organisms in the sand flats of Königshafen in the North Sea.

At Waverly, bivalves that constructed mucus-lined, U-shaped burrows (*Protovirgularia bidirectionalis*), together with worms that produced lined vertical domiciles, most likely acted as sediment stabilizers. Evidence for this hypothesis comes from preferential concentration of these structures in small mounds (fig. 64A–B), resulting in the peculiar microtopography of some bedding surfaces. In contrast, dense concentrations of mobile detritus-feeding nuculanid bivalves (tracemakers of *Protovirgularia rugosa* and *Lockeia ornata*) may have acted as sediment destabilizers. Additionally, dense assemblages of *Nereites* may have changed significantly the nature of the substrate, encapsulating within the sediment significant amounts of defecation products. The intruding up-and-down movements of the *Curvolithus* tracemaker may have played a destabilizing role, particularly in some dense assemblages. Especially in the mud- and mixed-flat zones, microbial binding may have contributed significantly to stabilize the sediment because microbial mats shelter the substrate against erosion (see "Interpretation" of unit A1).

Another effect of infaunal burrowers on the chemical properties of the substrate is the increase in oxygen circulation through the sediment. The depth and abruptness of the redox potential discontinuity depends on the amount of oxidizable organic matter within the sediment and oxygen flow. Subsurface deposit feeders extend the oxic layer of sediment from close to the surface down to their depth of feeding in modern environments (e.g., Rhoads and Germano, 1982; Reise, 1985). According to sedimentologic and ichnologic evidence, both persistent wave action and burrowing activity within the sediment may have combined to provide good oxygen circulation in the sand flats at Waverly.

Hydrodynamic Energy

Hydrodynamic energy is a common limiting factor in coastal environments. High energy of tides, waves, and currents strongly controls patterns of trace-fossil distribution along tidal shorelines. High-energy zones of tidal flats are typically dominated by vertical burrows, commonly *Diplocraterion* or *Skolithos* (e.g., Cornish, 1986; Simpson, 1991). Overall features of the Waverly tidal flat, such as ichnotaxonomic composition and dominance of horizontal structures of deposit feeders and grazers, suggest a moderate- to low-energy coastal setting. Moderate- to low-

energy conditions also were prevalent in the lower, sandy-intertidal zone. Deep gutter-cast structures, flute marks, truncation of vertical shafts, palimpsest surfaces, and presence of transported burrows (fig. 67A–B), however, suggest occasional events of high energy that were able to sculpt the tidal-flat surface and move a considerable amount of sediment. These erosive events were most likely related to storms, or possibly to allocyclic changes of sea level (see section on "Ichnology of key stratal surfaces").

Evidence of Time-averaged Surfaces

Lockeia siliquaria is moderately abundant throughout the sand-flat deposits of unit B1. Some stratigraphic levels, however, exhibit a high density of structures with specimens crosscutting each other at the base and differentially preserved at the top, either as protruding shafts or as shallow epichnial depressions. Cross sectional views of some specimens show two basic modes of preservation: (1) hypichnial ridges connected to endichnial shafts that cut across thin sandstone beds, and (2) hypichnial ridges connected to short endichnial shafts that are truncated by physical sedimentary structures (e.g., low-angle tabular crossbedding). The burrow fill may be massive, suggesting a passive filling of the structure, or may show a poorly defined meniscus-like structure in the lower part of the shaft.

One distinctive stratigraphic horizon displaying segregation of bivalve traces is of particular interest. A sandstone lens composed of amalgamated thin sandstone layers and interbedded mudstone partings contains *L. siliquaria* associated with the ophiuroid resting trace *Asteriacites lumbricalis*. A slab collected from this bed provides a unique opportunity to analyze in detail the trophic type and behavioral response of the tracemaker of *L. siliquaria* to environmental dynamics. The bottom and top of the slab were mapped in detail, and the maps subsequently superimposed to outline crosscutting relationships between forms and vertical repetition (fig. 68A–E). Superposition of those maps shows that many sole structures correlate with structures on the upper surface (vertical repetition), commonly showing some component of lateral displacement. However, a closer look reveals that some crowded areas at the base are barely populated at the top; in other words, some *Lockeia* hypichnia are not connected to corresponding epichnia. Conversely, nearly all bivalve shafts whose openings are visible at the top reach the base. Crosscutting relationships between hypichnial ridges of *Lockeia* are very common at the base. Finally, *Lockeia siliquaria* on the upper surface can be preserved as large oval depressions (negative epirelief) or protruding shafts (positive epirelief).

The amalgamated sandstone lens with preferential preservation of *L. siliquaria* can be interpreted as a palimpsest fabric (fig. 69). Osgood (1970) attempted to explain the crosscutting of traces on bedding soles by a sequence of colonization events. Scouring followed a first colonization event. Then, new sedimentation and
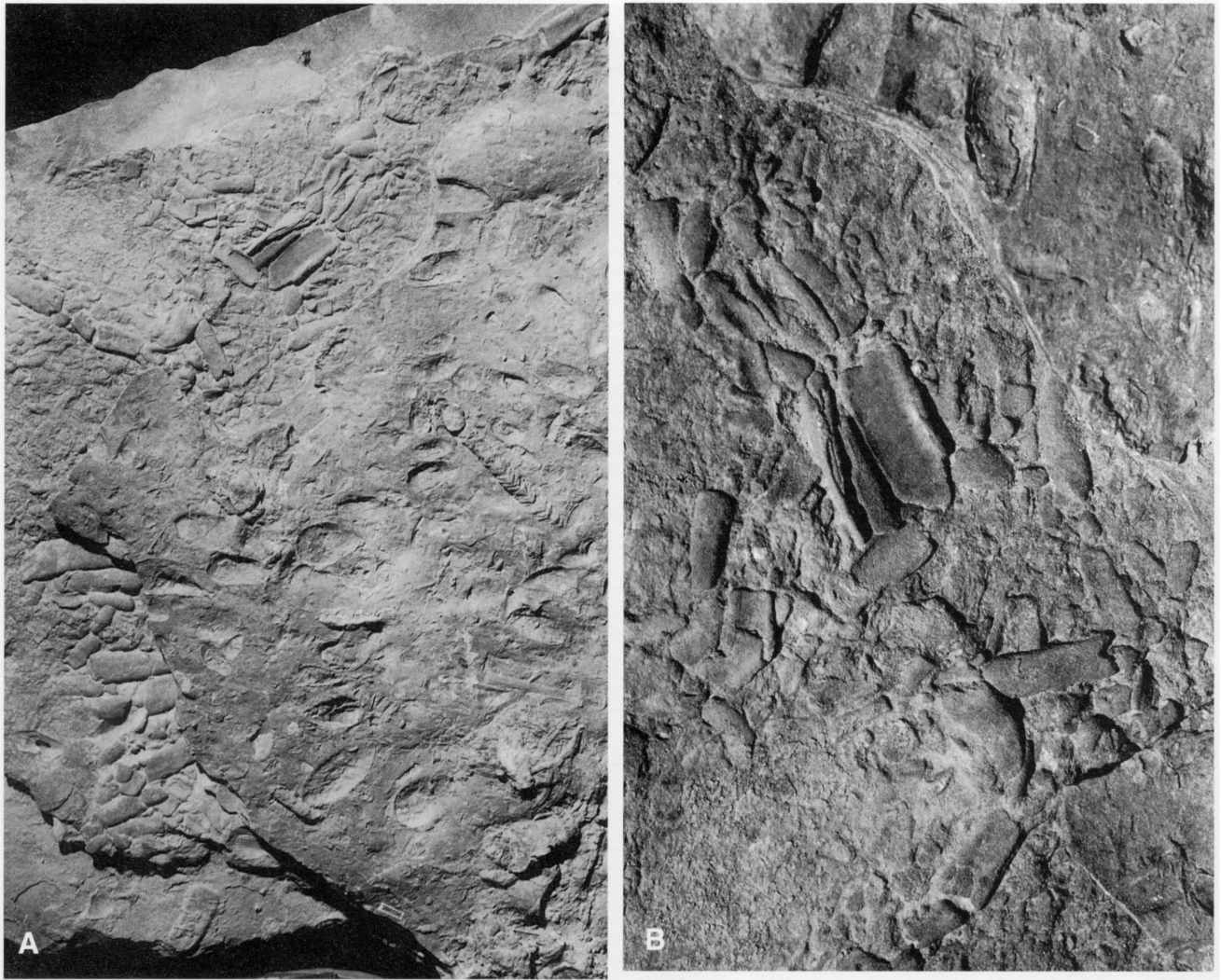
FIGURE 67—Transported burrows at the base of a sandstone bed. Both photos from KUMIP 288556. **A**. General view. Note molds of bivalve shells and associated locomotion traces of bivalves. × 0.36. **B**. Close-up. × 0.9.

recolonization resulted in a time-averaged surface that recorded the work of several communities of burrowers. At Waverly, *Lockeia siliquaria* preserved as hypichnial ridges and/or epichnial depressions or ridges further complicate the situation. Cross sectional views of polished slabs record at least two successive colonizations. A first generation of *Lockeia*, now preserved as hypichnial ridges, was eroded almost completely, and this episode was followed by traction deposition. Large specimens of *Lockeia* display negative epireliefs, suggesting shafts truncated by erosional events, with only their lower ends preserved. A second generation of *Lockeia* suggests a later colonization event. These are preserved as shafts protruding from the top of the bed, suggesting connection with a missing upper surface and the pumping up of sediment during upward movement. Palimpsest surfaces in intertidal environments also have been recognized on the basis of body-fossil analysis by West et al. (1990), who noted evidence of heterochronous community replacement in modern intertidal relict exposures of marsh surfaces and suggested analogous situations in the Carboniferous of the Appalachian basin and elsewhere.

Tiering Structure and Ichnoguilds

Tiering consists of the vertical stacking of organisms within a single habitat (Bromley and Ekdale, 1986). Marine infaunal communities typically are tiered as a consequence of vertical partitioning of the endobenthic habitat due to environmental and chemical gradients and also to the type and availability of food resources. Oxygen content, organic matter, and substrate consistency vary with respect to the sediment/water interface (Bromley and Ekdale, 1986; Bromley, 1990, 1996). Trace fossils can be grouped into ichnoguilds (Bromley, 1990, 1996). The **ichnoguild** concept involves three aspects, which result from adaptations of the guild concept in paleontology as proposed by Bambach (1983): (1) bauplan (whether a structure is stationary, semi-permanent, or transitory), (2) food source (trophic type), and (3) use of space (tier). The ichnoguild concept has been applied to the study of both marine (Ekdale and Bromley, 1991) and continental ichnofaunas (Buatois, Mángano, Genise, et al., 1998e).
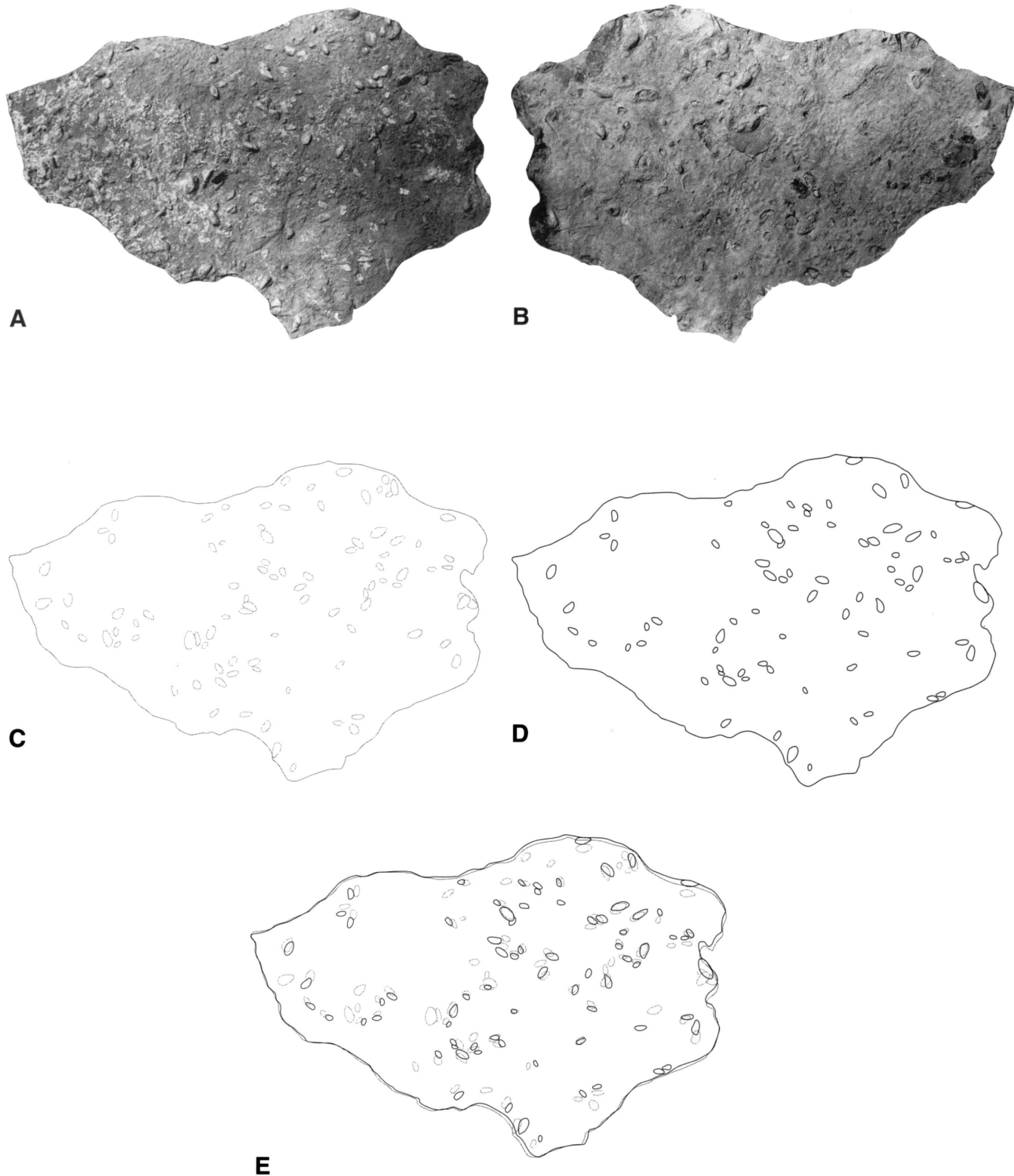
FIGURE 68—*Lockeia siliquaria* palimpsestic horizon. **A**. Photo of the base of a large slab with abundant *Lockeia siliquaria* preserved as positive hyporelief. **B**. Upper surface of the slab with *Lockeia siliquaria* preserved as large oval depressions (negative epirelief) or protruding shafts (positive epirelief). **C**. Map of base of slab. **D**. Map of top of slab. **E**. Superimposed map of specimens preserved on base (stipple) and top (white) of slab illustrating truncation between individuals, correspondence between basal and upper structures (with common horizontal displacement), and lack of a counterpart in some forms. All × 0.07.
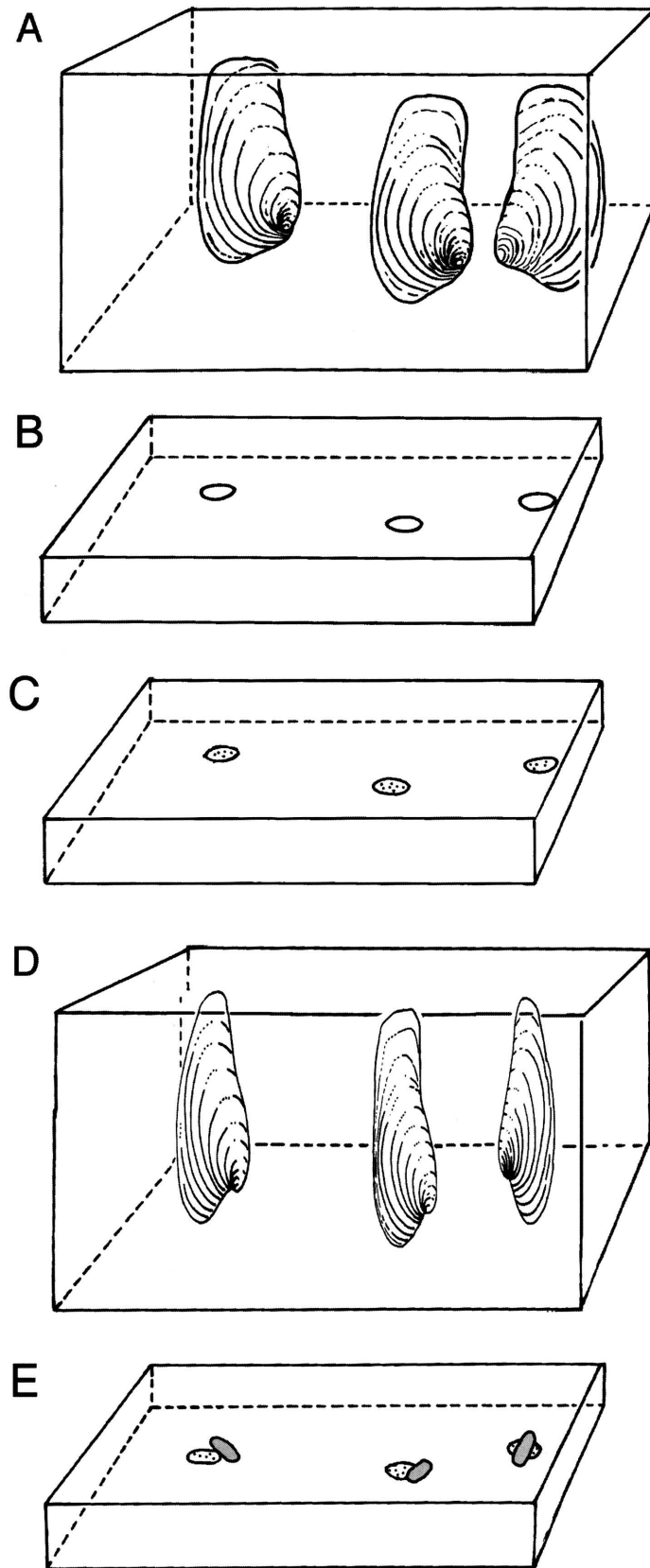
FIGURE 69—Sequence of events leading to a palimpsest fabric. **A**. First colonization event. **B**. Erosion event that scoured the structures leaving only their lower ends (typical *Lockeia* preservation). **C**. Renewed deposition and passive infill of structures. **D**. Second colonization event. **E**. New erosion episode resulting in a time-averaged horizon with palimpsest fabric. After Mángano et al. (1998).

Tiering and ichnoguild analysis has serious limitations in ancient tidal-flat settings due to temporal instability of community structure and time averaging of fossil faunas. Community structure in shoreline environments is shaped by the interaction of physical and biological forces. Significant changes may occur seasonally (e.g., as result of physical stress) or stochastically. For example, the introduction of a new predator may trigger a top-down effect modifying community composition (Bertness, 1999). Accordingly, what we reconstruct here as tiering structure is most likely an idealized time-averaged picture of the tidal-flat community.

Careful examination of crosscutting relationships, burrowing depth, and wall sharpness suggest a tiering structure for the benthic fauna of the Waverly tidal flat. This information has been integrated with trophic types and bauplan to define ichnoguilds. The tiering structure and ichnoguild model of the Waverly tidal flat (fig. 70) have been constructed using only information based on those traces that are abundant enough or that provide direct information about depth with respect to the sediment-water interface.

Horizontal sinuous to meandering trails of *Nereites missouriensis*, *Phycosiphon incertum*, and *Psammichnites implexus* represent the shallowest tier. This tier invariably is preserved at the tops of ripple-bedded sandstones and most likely reflects the work of animals moving at the mud-sand interface. The ophiuroid resting trace *Asteriacites lumbricalis* and arthropod horizontal locomotion burrows, *Cruziana problematica*, characterize a slightly deeper tier. This tier typically is preserved at the bases of sandstone beds and probably records burrowing immediately below the sand-mud interface. An intermediate tier is represented by horizontal to subhorizontal trails *Curvolithus simplex*, the bivalve resting/feeding trace

Lockeia ornata, and its associated escape trace *Protovirgularia rugosa*. *Curvolithus simplex* commonly crosscuts elements of the shallower tiers (e.g., *Asteriacites lumbricalis*) and is preserved both at the tops and bases of sandstones. *Lockeia ornata* and *Protovirgularia rugosa* are preserved on the soles of sandstone beds and usually crosscut shallower traces, such as *Cruziana problematica*. Preservation of fine sculpture in some specimens of *Lockeia ornata* indicates a firmer substrate. Finally, the deepest tier is occupied by dwelling and feeding structures of bivalves assigned to *Lockeia siliquaria* and *Protovirgularia bidirectionalis*, and the sea anemone burrow *Conichnus conicus*.

Four ichnoguilds have been recognized. Ichnoguild I consists of subsuperficial, vagile, deposit-feeder structures of worms and mollusks, represented by *Nereites missouriensis*, *Phycosiphon incertum*, and *Psammichnites implexus*. Ichnoguild II includes very shallow, vagile to semi-permanent, deposit-feeding structures of ophiuroids (*Asteriacites lumbricalis*) and arthropods (*Cruziana problematica*). Ichnoguild III consists of shallow, vagile, deposit-feeding and predaceous structures, recorded by *Curvolithus simplex*, *Protovirgularia rugosa*, and *Lockeia ornata*. Ichnoguild IV includes relatively deep, permanent to semi-permanent traces of suspension feeders, deposit feeders, and predators, represented by *Protovirgularia bidirectionalis*, *Lockeia siliquaria*, and *Conichnus conicus*.

With the exception of the relatively deep ichnoguild IV, the Waverly ichnofauna is dominated by shallow tiers. Preservation of shallow-tier structures is less common in post-Paleozoic tidal-flat assemblages, which are typically dominated by deep, elite traces of crustaceans. Ichnoguild analysis of the Waverly trace fossil assemblage provides a snapshot of the rich benthic fauna inhabiting the first few centimeters below the sediment/water interface.
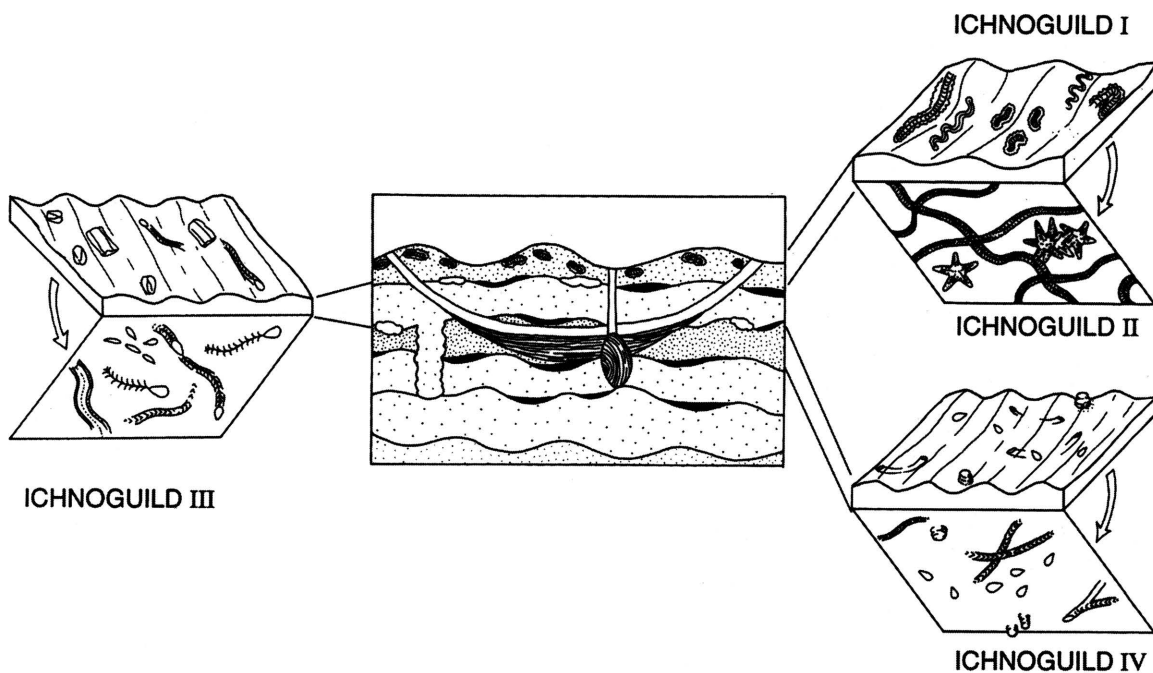

FIGURE 70—Tiering structure and ichnoguilds of the Waverly tidal-flat ichnofauna.

Sedimentary Environment

Paleocurrent Analysis

Paleocurrent data have been collected as part of the facies analysis. Integration of paleocurrent information and facies is essential, because paleocurrent patterns are controlled environmentally, with coastal settings displaying complex patterns resulting from the interaction of waves, tidal currents, and fluvial input (Klein, 1977). Paleocurrent orientations were determined from the azimuths of the axes of relict troughs in unit A1, the azimuths of the axes of gutter casts in unit A1, the azimuths of the ripple trains in unit B1, and the dip direction of cross-lamination in unit D2 (fig. 71). Additionally, the azimuth of the channel axis of unit D3 also was recorded.

Data from relict troughs were collected from two separate bedding planes. Orientation means from both surfaces do not show significant variations, ranging from 104° (or 284°) to 126° (or 306°). Paleocurrent data from ripple trains were measured from five different bedding planes. Orientation means range from 102° (or 282°) to 127° (or 307°). Orientations of ripple trains and relict troughs are therefore consistent and suggest that waves approached from a southwest-northeast direction. Assuming a northwest-southeast-oriented shoreline, as suggested by paleogeographic reconstructions, waves were approaching perpendicular to the intertidal zone. Although in situ gutter casts are relatively rare, available data indicate a north-northwest–south-southeast orientation with an orientation mean of 154° (or 334°). Additionally, gutter casts found as loose blocks commonly display ripple trains at the top oriented perpendicular to the axes of gutter casts. Trends in gutter casts suggest orientations oblique to perpendicular to the shoreline, indicating roughly downslope flows.

Data also were collected from cross-laminations in two intertidal runoff channels. One of these channels shows bipolar-bimodal distributions, indicating roughly north-south flood and ebb flows. The other channel displays unidirectional paleocurrent patterns, with a vector mean of 38°. Finally, the fluvial channel axis is oriented 10° (or 190°), suggesting a trend from perpendicular to oblique to the shoreline.

Klein (1967, 1977) noted that tidal-flat environments exhibit a quadrimodal paleocurrent pattern, with upper-intertidal zones displaying both landward- and seaward-oriented tidal flows and lower-intertidal zones having bipolar tidal currents flowing parallel to the shoreline. Data from the upper-intertidal facies at Waverly indicates tidal flow perpendicular to the coastline. However, ripple-train orientation in the lower-intertidal facies indicates flow perpendicular to the shore rather than parallel to depositional strike as suggested by the quadrimodal model. The latter probably reflects the direction of wave propagation rather than tidal flow.

Depositional Model

The facies model for siliciclastic tidal flats proposed by Klein (1977) was based on studies of modern tidal flats (e.g., Häntzschel, 1939; Van Straaten, 1952, 1954, 1961; Reineck, 1963, 1967, 1972). Examples in the fossil record are quite common (e.g., Klein, 1971; Sellwood, 1975; Carter, 1975; Ovenshine, 1975; Tankard and Hobday, 1977). Klein's facies model includes the upper-, middle- and lower-intertidal zones. Because tidal energy increases seaward, tidal flats in general are landward-fining, in contrast to wave-dominated shorelines. Therefore, a typical tidal-flat profile in a landward direction consists of a lower-intertidal sand flat, a middle-intertidal mixed (sand and mud) flat, and an upper-intertidal mud flat. Landward of the mud flat, supratidal salt marshes are present; the subtidal zone occurs seaward of the sand flat. Upper tidal flats are dominated by deposition of fine-grained suspended particles; lower tidal flats are characterized by bedload transport of sand-sized sediment. Middle-intertidal areas are typified by alternation of traction and fallout from suspension. Klein (1971) listed 10 phases involved in tidal sedimentation and subsequent modification of the deposits: (1) tidal-current bedload transport with bipolar-bimodal reversals of flow direction, (2) time-velocity asymmetry of tidal-current bedload transport, (3) late-stage ebb outflow and emergence with sudden changes in flow directions, (4) alternation of tidal-current bedload transport with suspension settlement, (5) tidal slack-water mud deposition, (6) tidal scour, (7) exposure and evaporation, (8) burrowing and organic diagenesis, (9) differential compaction, loading, and hydroplastic readjustment, and (10) high rates of sedimentation combined with regressive sedimentation.

Most of the phases of tidal transport mentioned above are recognized at the Waverly locality. Evidence of tidal-current bedload transport coupled with flow reversals is recorded by current ripples exhibiting bimodal-bipolar paleocurrent patterns in intertidal runoff channels of unit D2. Evidence of time-velocity asymmetry is typical of high-energy intertidal sand bodies and subtidal sand waves and is lacking in the lower-energy tidal-flat facies of Waverly. Late-stage emergence and sudden changes in flow directions are evidenced by interference ripples, flat-topped ripples, water-falling marks, and washout structures in units A1 and B1. Alternation of tidal-current bedload transport with suspension fallout is recorded by heterolithic bedding (flaser, wavy, and lenticular) and mud drapes in units A1, B1, D1, and D2. Evidence of tidal slack-water suspension fallout is represented by mud drapes and flaser bedding in units A1, B1, D1, and D2. Flute marks and gutter casts in units A1 and B1 record tidal scour. Exposure is indicated by wrinkle marks and mudcracks in units A1 and B1. Evidence of burrowing is

extensive, particularly in unit B1 and, to a lesser degree, in unit A1. Load casts and sand volcanoes in unit B1 record soft-sediment deformation. Finally, high rates of sedimentation coupled with regression are clearly evidenced by the four separate progradational parasequences, A, B, C, and D.

Six major subenvironments have been identified in the lower interval of the Waverly section (fig. 72): (1) sand flat, (2) mixed flat, (3) mud flat, (4) supratidal paleosols, (5) intertidal runoff channels, and (6) fluvial channel. The sand flat is represented by unit B1. Current-bedload transport was the dominant sedimentary process, but mud deposition during slack-water periods also occurred. Biogenic activity reached a maximum in this subenvironment. The mixed flat is represented, at least partially, by units A1, C1, and D1. Mixed-flat deposits originally may have been present in unit B2, but if so, they were obliterated subsequently by pedogenic processes. Tractional sand

deposition and mud settlement were equally important. Biogenic activity was relatively restricted. The mud flat is recorded, in part, by units A1 and D1. Mud-flat sediments also originally may have been present in units B2 and C2, but any evidence was completely destroyed by pedogenic processes. Deposition of mud from suspension was the dominant depositional process. Biogenic activity was remarkably scarce. Supratidal paleosols are represented in units B2 and C2. These paleosols developed in marshes landward of the intertidal zone, but as a result of the progradation, pedogenic processes affected underlying mud- to mixed-flat deposits. Intertidal runoff channels occur in unit D2, where they dissect mud- to mixed-flat deposits. There is no evidence of biogenic activity in these channels. The fluvial channel is represented by unit D3. There is no evidence of tidal influence in this channel and biogenic activity is restricted to abandoned channels.

A. GUTTER CASTS

N = 4
Class Interval = 10°
Vector Mean = 154°

B. RIPPLE TRAINS

N = 114
Class Interval = 10°
Vector Mean = 109°

C. RELICT TROUGHS

N = 42
Class Interval = 10°
Vector Mean = 114°

D. RIPPLE CROSS-LAMINATION

N = 17
Class Interval = 10°
Vector Mean = 34°
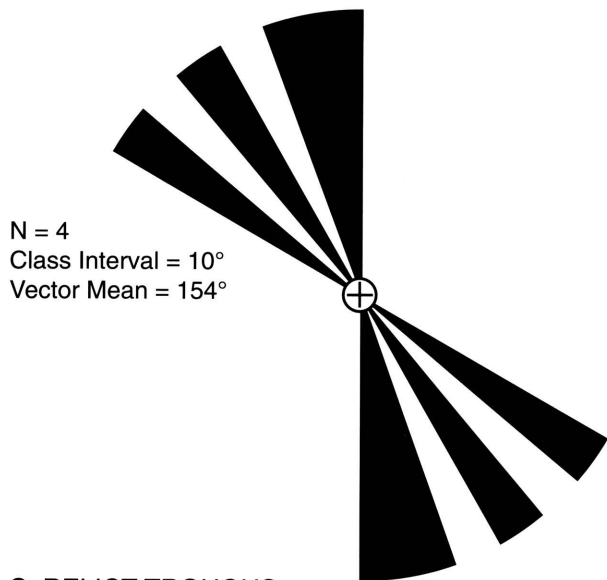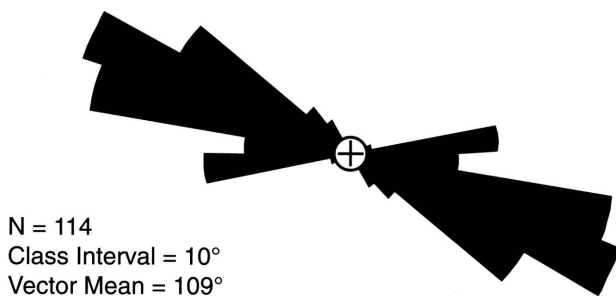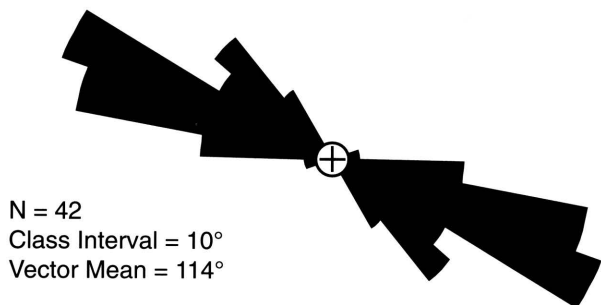
FIGURE 71—Equal-area paleocurrent rose diagrams in the Stull Shale Member at Waverly trace fossil site. **A**. Axis of gutter casts in unit A1. **B**. Ripple trains in unit B1. **C**. Axis of relict troughs in unit A1. **D**. Dip direction of cross-lamination in unit D2.

Tidal flats may develop in a number of depositional environments within the coastal setting, including fluvio-estuarine transitions, estuary bays, and open-marine shorelines (Buatois, Mángano, et al., 1997a; Mángano and Buatois, 1997). High diversity of trace fossils suggests that the tidal flat at Waverly was formed on the open coast under normal-marine conditions.

Paleotidal Range

Estimation of paleotidal range from tidal-flat sequences remains problematic. Klein (1971) provided a discussion of methods for determining paleotidal range, and he advanced his own method, which is based on measurement of the preserved thickness of the prograding tidal-flat succession. Terwindt (1988) discussed the shortcomings of the available methods and suggested some general criteria for estimating tidal ranges from ancient deposits. Simpson (1991) also discussed the associated problems and attempted to estimate the tidal range of a Cambrian tidal flat, taking into account paleorelief, thickness of tidal-flat deposits, trace fossils, and bedform amplitude.

Paleotopographic information is not available for the preserved deposits at Waverly. According to Klein (1971), the thickness of the sediment interval from low tidal-flat facies to high tidal-flat deposits is equivalent to the mean tidal range. Simpson (1991) noted that this method assumed constant sea level, lack of subsidence, insignificant sediment compaction, and a conformable succession.

The maximum recorded thickness of a tidal-flat progradational succession at Waverly is 1.10 m in parasequence D. This value, however, includes essentially upper-intertidal, mud-flat deposits. Although no detailed analysis of subsidence rates is available for the Waverly locality, isopach maps suggest renewed subsidence during deposition of the Shawnee Group (Lee, 1943). No evidence of soft-sediment deformation was observed in parasequence D, but in other parasequences (e.g., parasequences A and B) compaction due to sediment loading was relatively significant as evidenced by the presence of synsedimentary deformation structures. These factors undoubtedly influenced the resulting thickness preserved in the stratigraphic record. Although subsidence may lead to an overestimation of the tidal range, compaction may result in an underestimation of the actual range. Therefore, estimation of the paleotidal range based on thickness of the Waverly tidal-flat sequences is quite risky.

Simpson (1991) attempted to use trace fossils as a tool for defining tidal range, but he recognized that they are of limited value in constraining high- and low-tide lines. Actually, trace fossils may be only indirectly used to estimate tidal range because ichnologic information is basically a tool to refine facies interpretations based primarily on physical sedimentary structures. At Waverly, the highest diversity of biogenic structures is found in the sand-flat deposits, probably close to the low-tide line. Low ichnodiversity in the mixed- to mud-flat facies is probably related to a stressful regime associated with rigorous conditions.

Bedform amplitude was one of the criteria listed by Terwindt (1988) as useful in distinguishing between macro-, meso-, and microtidal settings. He suggested that thickness of crossbedded sets tend to be greater where tidal ranges are greater. Based on this criterion, the low amplitude of bedforms at Waverly suggests low tidal ranges. Simpson (1991) noted that bedform amplitude is problematic, because it also may be controlled by velocity and water depth.
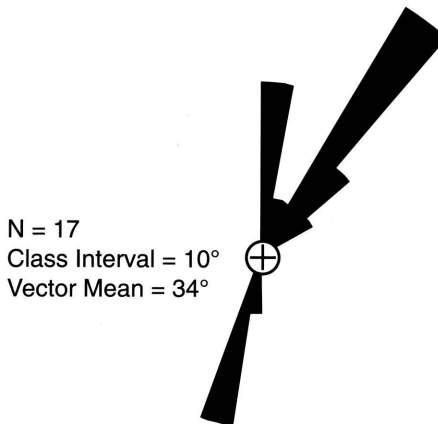
Terwindt (1988) also pointed out that the number and dimensions of intertidal drainage channels may yield insights into tidal range, with channels being small, widely spaced, or even absent under lower-tidal regimes. Intertidal channels at Waverly are rather small and are suggestive of lower paleotidal ranges.

In high-tidal ranges, tides influence fluvial systems; consequently diagnostic sedimentary structures and bedding types are present tens of kilometers landward from river mouths (e.g., Smith, 1988; Gastaldo et al., 1995). Fluvial-channelized deposits of unit D3 lack physical structures indicative of tidal action, suggesting low tidal ranges by default. Although most, if not all, criteria currently used to estimate paleotidal ranges are somewhat problematic, all the available evidence points to a microtidal regime for the Waverly tidal flat.

Effects of Climate on Deposition

Paleogeographic reconstructions suggest an equatorial position for Kansas during the Late Carboniferous (Scotese and McKerrow, 1990). Kansas underwent a northward migration from approximately 20°S in the Early Carboniferous to 15°N during the Late Permian (West et al., 1997) (fig. 73). West et al. (1997) analyzed the importance of climate to explain differences among the five different types of cyclothems recognized in the Permian–Carboniferous of Kansas. Study of lithofacies within the different cyclothem types (Cherokee, Kansas, Shawnee, Wabaunsee, and Permian) indicates a long-term Pennsylvanian–Permian drying trend. Virgilian Shawnee cyclothems are characterized by an abundance of fossiliferous mudrocks and limestones, with variegated mudrocks also present. In contrast to the underlying Kansas-type cyclothems, black mudrocks are rare. Coals are very thin or absent. Sedimentologic features of the Shawnee cyclothems suggest a transition from tropical-rainy and wet-seasonal climates to drier-seasonal climates (West et al., 1997).

Analysis of tidal-flat deposits at Waverly is compatible with the paleoclimatic situation for the Shawnee cyclothems suggested by West et al. (1997). Absence of evaporite deposits, little or no plant debris, high density of
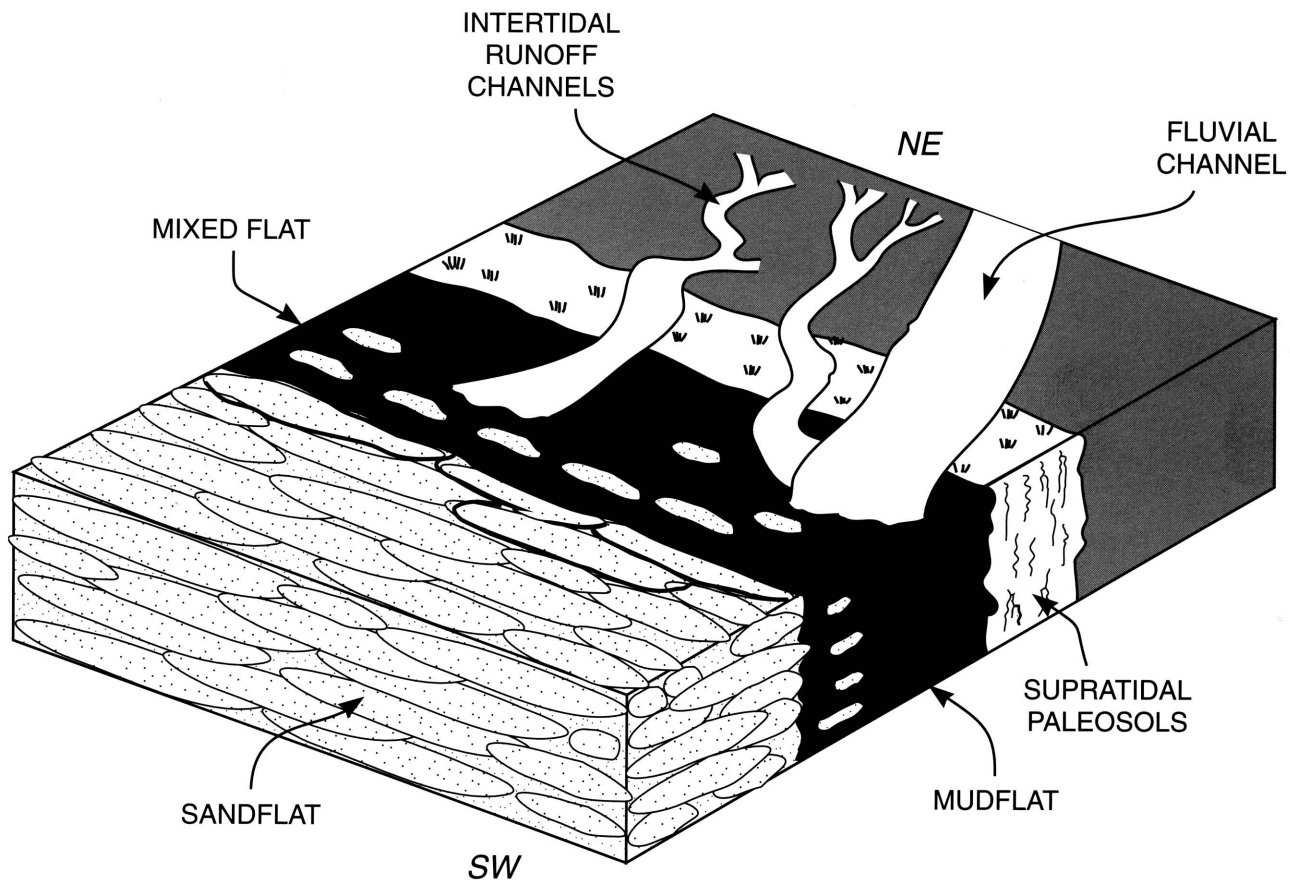
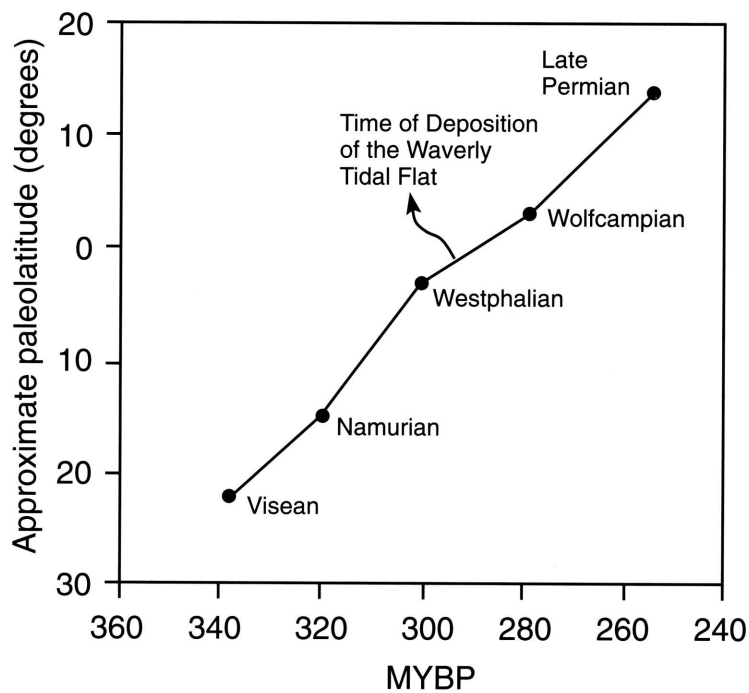FIGURE 72—Depositional model of the Stull Shale Member at Waverly.

FIGURE 73—Variation of paleolatitudinal position of Kansas during the late Paleozoic. Note equatorial position for Waverly during the Virgilian. Based on West et al. (1987).

trace fossils in a zone between the high- and low-water levels with few biogenic structures at the high-water level, and moderate mud accumulation suggest climatic condi-

tions that were intermediate between the humid regime of the earliest Virgilian and the more arid conditions that characterize the lower Permian.

Sequence Stratigraphy

Utility of Trace Fossils in Sequence Stratigraphy

The use of trace fossils in sequence-stratigraphic interpretations is a very promising field in ichnology (see reviews by Pemberton, MacEachern, et al., 1992, and Savrda, 1995). Trace fossils aid in sequence stratigraphy by allowing recognition of allostratigraphic surfaces (e.g., MacEachern et al., 1992), identification of system tracts (e.g., Pemberton, MacEachern, et al., 1992), and character-ization of parasequences (e.g., Pemberton, Van Wagoner, et al., 1992; Martin and Pollard, 1996).

At Waverly, ichnofossils are valuable tools for understanding the depositional evolution in relationship to sea-level history. In this section, we discuss the Stull Shale Member and related units within a sequence-stratigraphic framework. Trace-fossil information is integrated with sedimentologic and stratigraphic data to obtain a more accurate picture of the depositional history.

Parasequence Stacking Patterns

The sedimentary units of the lower part of the Waverly succession form four parasequences separated by successive flooding surfaces. A fifth parasequence is represented in the upper half of the Waverly succession, including the Spring Branch Limestone Member. Each of the parasequences records a regressive event of tidal-flat progradation. Typical tidal-flat successions constitute regressive fining-upward packages (e.g., Klein, 1971; Terwindt, 1988), and coarsening-upward successions are unusual, even in overall transgressive settings where fining-upward packages occur. This type of situation reflects local progradation of tidal flats (Sellwood, 1975; Dalrymple, 1992). A rare example of a coarsening-upward transgressive tidal-flat succession was described by Reineck (1972). A somewhat similar situation to that of Reineck (1972) was recorded by Kvale and Archer (1990) from the Pennsylvanian Brazil Formation, Indiana, where a coarsening-upward tidal sequence indicates transgression over a coastal peat swamp. This package is replaced upward by a fining-upward succession, which indicates a subsequent regression in the area (Kvale and Archer, 1990).

The four parasequences in the lower part of the Waverly succession form a parasequence set. Parasequence stacking patterns reflect the ratio between

rate of deposition and rate of accommodation space (Van Wagoner et al., 1988). Progradational parasequences are formed when the rate of deposition exceeds the rate of accommodation. Facies and trace-fossil analyses suggest a shallowing trend from parasequence A to D, indicating that the lower parasequence set is progradational. For example, lower-intertidal deposits are only present in the lower parasequences, and the fluvial facies is restricted to the top of parasequence D. Vertical distribution of trace fossils from highly diverse marine associations near the base (unit B1) to a monospecific suite of terrestrial trackways (Unit D3) also supports an overall regressive event. Facies and stratigraphic analyses indicate that the lower part of the Stull Shale Member represents part of a highstand systems tract.

A major transgressive surface separates the fluvial facies at the top of the lower parasequence set from the overlying subtidal orthomyalinid bivalve packstones and wackestones. This surface marks the base of the second parasequence set. In the Stull Shale Member, this set is represented by the orthomyalinid packstone and wackestone parasequence. Although this set is only partially exposed at Waverly and individual parasequences cannot be distinguished, a retrogradational pattern within an overall transgressive trend is evident. The transgressive *Orthomyalina* beds extend over an area of more than 2,000 km^2 in east and southeast Kansas (West et al., 1996). The transgressive aspect of the upper parasequence set also is evidenced by deposition of open-marine carbonate facies recorded by the Spring Branch Limestone Member. This upper part of the Waverly succession represents a trans-gressive systems tract.

The sequence-stratigraphic significance of the fluvial deposits is problematic. Two alternative hypotheses are suggested. The first is that establishment of the fluvial system may record maximum progradation during stillstands, representing the top of the highstand systems tract. In this interpretation the basal erosive surface resulted from autocyclic processes. The second alternative is that the fluvial body resulted from channel incision associated with a lowering of sea level. In this case, the base of the fluvial channel should be considered a se-quence boundary and the fluvial deposits part of the lowstand systems tract. Available information suggests that the first hypothesis is the most reasonable. Examination of coeval successions fails to reveal that this surface has regional, wide lateral extent. Additionally, the presence of fluvial deposits at the tops of regressive successions is more easily explained as the result of simple progradation

without invoking any discontinuity. Therefore, we infer that lowstand deposits were absent from this area. A sequence boundary is located at the inversion from the progradational to the retrogradational parasequence stacking patterns (Jackson et al., 1990). Accordingly, the base of the transgressive orthomyalinid packstones and wackestones is considered a co-planar surface, indicating amalgamation of lowstand and transgressive erosion.

Sequence-stratigraphic Significance of Outside Shales and Paleosols

Outside shales exhibit significant variability and include deltaic, paralic, and fluvial facies (Heckel, 1985, 1990, 1994; Watney et al., 1989). Although typically mudrock units, locally some outside shales may be sandstone dominated (Heckel, 1994). There is a general agreement that accumulation of cyclothems was controlled by sea-level changes, and that glacial eustasy related to the advance and retreat of Gondwanan ice sheets was the responsible mechanism (Heckel, 1994).

Heckel (1994) stated that outside shales were formed during lowstands of sea level. However, detailed analysis of vertical-facies changes and bounding surfaces suggest a different scenario for the Stull Shale Member at Waverly. At Waverly, progradational stacking patterns of tidal-flat strata and associated facies provide evidence that the lower part of the Stull Shale Member represents a highstand systems tract. Wackestones and packstones of the upper part of the Waverly section belong to a transgressive systems tract. No significant deposition occurred during the lowstand. Clearly, sea-level controls involved in the deposition of outside shales are more complex than envisaged by traditional cyclothem models.

Development of paleosols on mixed- to mud-flat facies overlying sand-flat deposits indicates progradation. Paleosols have been used as evidence for subaerial exposure in late Paleozoic cyclothems of the North American midcontinent (e.g., Heckel, 1986; Watney et al., 1989). Additionally, paleosols typically are considered to be part of lowstand systems tracts (e.g., Heckel, 1986). However, paleosols may occur in two different stratigraphic settings with contrasting implications in terms of sea-level position. When paleosols sharply overlie open-marine deposits, they most likely develop as a result of sea-level lowering (e.g., unconformity-based paleosols in valley interfluves). In contrast, when paleosols occur at the tops of regressive packages, where evidence of progradation from open-marine to coastal, deltaic, and even fluvial facies occurs, they probably record a regressive peak during the maximum highstand/stillstand. The latter situation seems to be very common within outside shales (Heckel, 1994, p. 69), and it suggests that part of what historically have been considered as lowstands actually represent highstand systems tracts. In the present

case, the stratigraphic position of the paleosol suggests that pedogenic processes occurred during a regressive maximum and that the paleosol is part of a highstand systems tract.

Ichnology of Key Stratal Surfaces

Trace fossils may help in the recognition of key stratal surfaces. Substrate-controlled ichnofacies are instrumental in the recognition of erosional discontinuities in the stratigraphic record (MacEachern et al., 1992; Pemberton, MacEachern, et al., 1992). Several such surfaces exist in the Waverly succession and two of them contain trace fossils.

The transgressive surface of erosion that separates parasequence A from parasequence B (TS1) marked the flooding of mud- and mixed-flat deposits (unit A1) and an increase in water depth with subsequent deposition of lower-intertidal sand-flat facies (unit B1). Mud- and mixed-flat deposits contain unlined burrows (*Palaeophycus tubularis*) passively filled by sand from the overlying sand-flat facies. This suite is considered an example of a poorly developed *Glossifungites* ichnofacies.

The *Glossifungites* ichnofacies is characterized by sharp-walled, unlined, passively filled, dwelling burrows of suspension feeders (MacEachern et al., 1992; Pemberton, MacEachern, at al., 1992). It develops in stable and cohesive substrates. Ravinement erosion associated with the transgression led to the exhumation of compacted and dewatered sediments, making a firm substrate available for colonization of the *Glossifungites* tracemakers. This surface may represent a high-energy parasequence boundary (MacEachern et al., 1992; Pemberton, MacEachern, at al., 1992; Pemberton and MacEachern, 1995). Similar surfaces in modern intertidal deposits were recognized by Pemberton and Frey (1985) in the Georgia coast, where they formed due to transgressive retreat of the beach. Firmground burrowers include various bivalves, crustaceans, nemerteans, and polychaetes. Burrows of the polychaetes *Nereis succinea* and *Drilonereis longa* tend to remain open and fill passively and, according to Pemberton and Frey (1985), might be preserved as *Palaeophycus* in the fossil record. These polychaete burrows are potential modern analogues of *Palaeophycus tubularis* in the Waverly section.

A more complicated situation occurs at the top of unit B1. This surface delineates the top of the sand-flat deposits, separating this facies from the overlying paleosol (unit B2). The surface is iron-stained, probably due to infiltration from the paleosol interval. Basal terminations of U-shaped *Diplocraterion* isp. are abundant on this surface. These burrows have unlined walls and commonly crosscut other traces. The sharpness of burrow margins gives these structures a boring-like appearance and may be confidently called pseudoborings. U-shaped burrows at the top of unit B1 probably record animals burrowing in

dewatered muds, reaching a level slightly below the sand/mud interface. Subsequent erosion of the muds removed most of the U traces leaving only the basal terminations of the burrows at the top of the underlying sandstone.

This surface is interpreted as a firmground recording an example of a composite ichnofabric (cf. Bromley and Ekdale, 1986). Explanation of the events that led to the formation of this firmground is difficult, because it involves erosional exhumation of a firm substrate and subsequent erosion of the burrowed sediments (i.e., two successive erosional events separated by one burrowing event). A further complication arises because the top of unit B1 does not seem to represent any discontinuity in the stratigraphic column, but only a boundary between genetically related facies within a prograding tidal-flat sequence. However, unequivocally gradational deposits between the sand-flat facies and the paleosol have not been observed. To explain this, it has been assumed that transitional mixed- to mud-flat sediments were deposited,

but their primary features were obliterated by pedogenic processes.

Although the presence of substrate-controlled ichnofacies, such as the *Glossifungites* ichnofacies, is considered suggestive of an allogenic origin (i.e., erosional exhumation due to a sea-level change), autocyclic processes also may exhume firm substrates. Pemberton and Frey (1985) noted that some of the *Glossifungites* surfaces in the Petit Chou Island were formed by tidal-stream erosion. Interestingly, similar small, vertical, U-shaped burrows have been documented from these firmground intertidal deposits of the Georgia coast (Pemberton and Frey, 1985). In modern semiconsolidated muds of Petit Chou Island, these structures are produced by the polychaete *Polydora ?websteri*. The complex origin of this firmground surface is consistent with evidence of palimpsest, time-averaged surfaces in the Waverly succession, discussed above.

The Waverly Ichnofauna in Regional Context

Introduction

The Waverly ichnofauna developed on a tidal flat connected with the open sea. Sedimentologic and ichnologic evidence from other exposures of the Stull Shale Member illustrate lateral variations in trace-fossil content and the environmental significance of the Waverly trace-fossil site in a broader regional context.

The Stull Shale Member crops out in a narrow belt across eastern Kansas. This unit contains numerous and excellent outcrops of tidal-flat deposits developed under contrasting paleoenvironmental conditions (Mángano and Buatois, 1997). Detailed stratigraphic sections were measured bed by bed, taking into account physical sedimentary structures, bed boundaries, geometry, and paleocurrents. Ichnologic information was added to data obtained from standard facies analysis. These tidal-flat deposits are stratigraphically equivalent, but they differ remarkably in trace-fossil content. Pennsylvanian successions in eastern Kansas are ideal for this type of study because horizontal, tectonically undisturbed strata can be followed for tens to hundreds of kilometers, allowing ichnologic comparisons along well-constrained time intervals. The Stull Shale Member is overlain by the Spring Branch Limestone Member, a laterally continuous transgressive unit that serves as a high-resolution marker bed. This situation allows comparisons with a degree of accuracy that usually is possible only in modern environments, but with the additional advantage of dealing with biogenic structures that already have passed through the taphonomic filter represented by the fossilization barrier.

Sedimentologic and ichnologic information of different Stull Shale Member localities north of the Waverly trace-fossil site is summarized below (fig. 74).

Sedimentology and Ichnology of Stull Shale Member Outcrops

East of Lyndon, Osage County, a 3-m-thick succession of the Stull Shale Member is exposed. At this locality the Stull Shale Member is dominated by fine-grained sandstones interbedded with thin mudstone partings. Soft-sediment deformation structures, including ball and pillow, pseudonodules, and convolute lamination, are dominant. Flat-topped ripples are present locally. Flaser and wavy bedding occur throughout the sequence. Intensity of bioturbation is low, and trace fossils are scarce, consisting almost exclusively of rare occurrences of the ichnogenus *Trichichnus*.

Excellent, laterally continuous outcrops of the Stull Shale Member, including its type section, are present in Douglas County. Most of these outcrops can be studied in roadcuts between the towns of Kanwaka and Stull, where this unit originally was defined. One of these outcrops was previously studied by Hakes (1976, his locality 8). Other outcrops are situated west/southwest of Clinton Lake, and along and adjacent to the Kansas Turnpike. Some of the latter also were described by Hakes (his localities 3, 5, 6, and 7). The Stull Shale Member is up to 9 m thick in this region. Sequences are dominated by thinly interbedded, very fine grained sandstones and mudstones displaying

flaser, wavy, and lenticular bedding. Sand- and mud-filled channels usually cut the tidal-flat deposits (fig. 75A–B). Gutter casts are present locally. Soft-sediment deformation structures are abundant in the upper part of the unit at some localities. A thin coal bed occurs at the top of the Stull Shale Member at most of the outcrops. In terms of ichnofaunas, these outcrops contain a moderate to low diversity of biogenic structures. *Teichichnus, Palaeophycus, Diplocraterion, Skolithos, Psammichnites, Lockeia, Nereites, Planolites*, and *Asteriacites* are the most common traces. Hakes (1976) also mentioned *Aulichnites* and *Chondrites* in this area. Intensity of bioturbation is low to moderate locally. Typically, heterolithic facies are stacked forming fining-upward cycles that record tidal-flat progradation from sand- to mixed- and mud-flat environments (fig. 76).

East of Perry Lake, in Jefferson County, the Stull Shale Member is up to 8 m thick and consists of flaser-, wavy-, and lenticular-bedded heterolithic facies. Gutter casts and sand-filled channels are common. Flat-topped ripples and convolute lamination are present locally. Poorly preserved plant fragments and carbonaceous debris increase in abundance toward the top of the section. Trace fossils are very rare and include only a few specimens of facies-crossing forms, such as *Palaeophycus*, and tiny specimens of bivalve traces (*Lockeia, Protovirgularia*). Intensity of bioturbation is low. Tidal-flat prograding successions are present.

Farther north, at the Jackson Park quarry, Atchison County, a complete sequence of the Stull Shale Member is exposed, with the Clay Creek Limestone Member and Spring Branch Limestone Member at base and top, respectively (fig. 77). At this locality, the Stull Shale Member is approximately 8.5 m thick and consists predominantly of massive siltstones. Very thin, current-ripple laminated, very fine grained sandstones occur
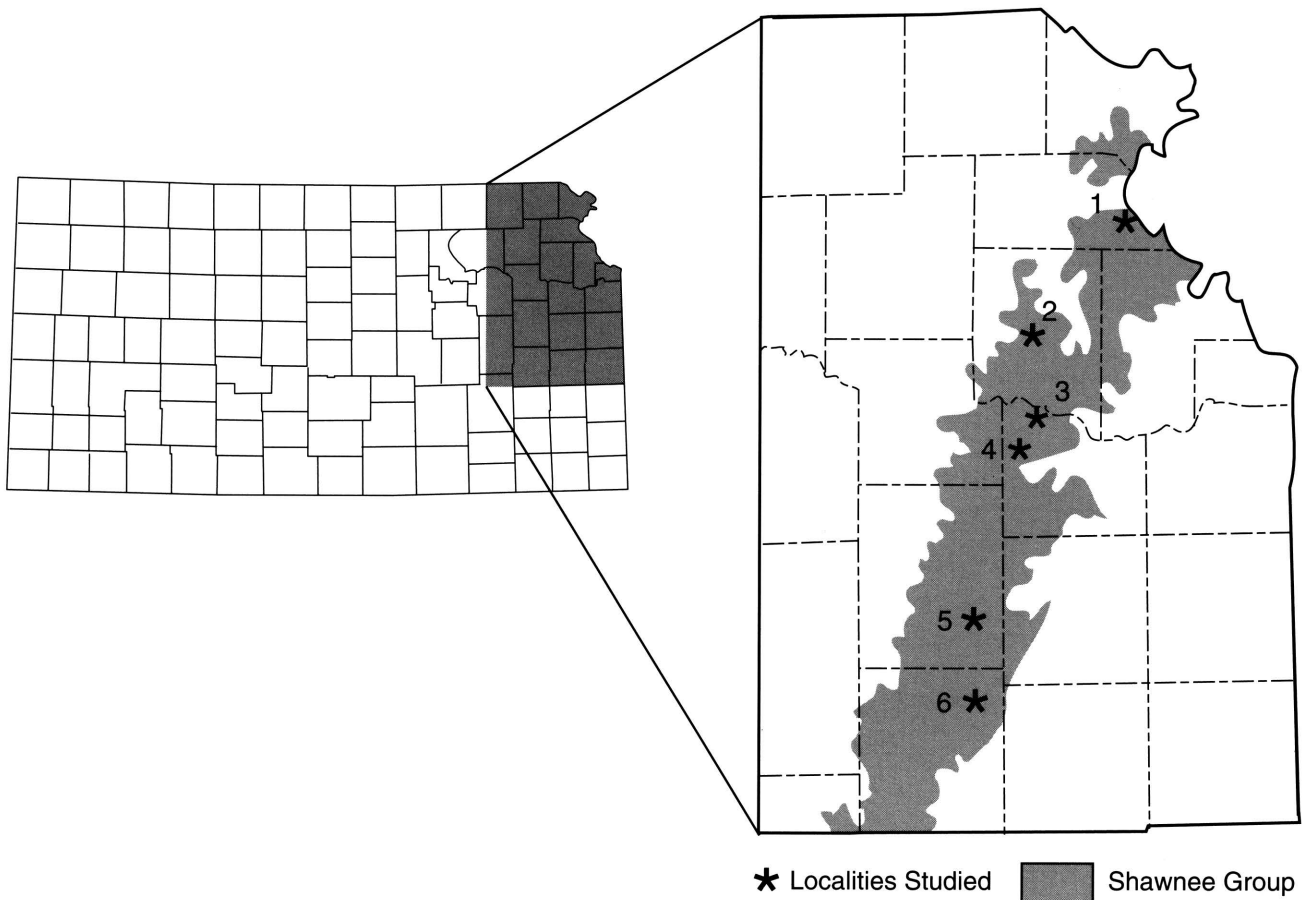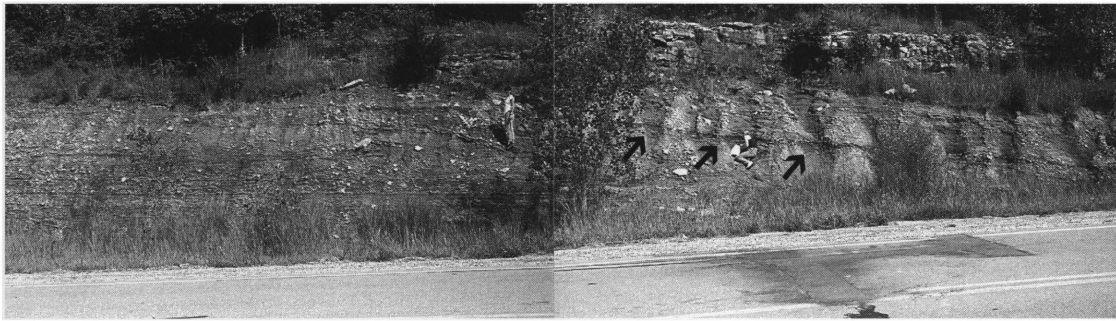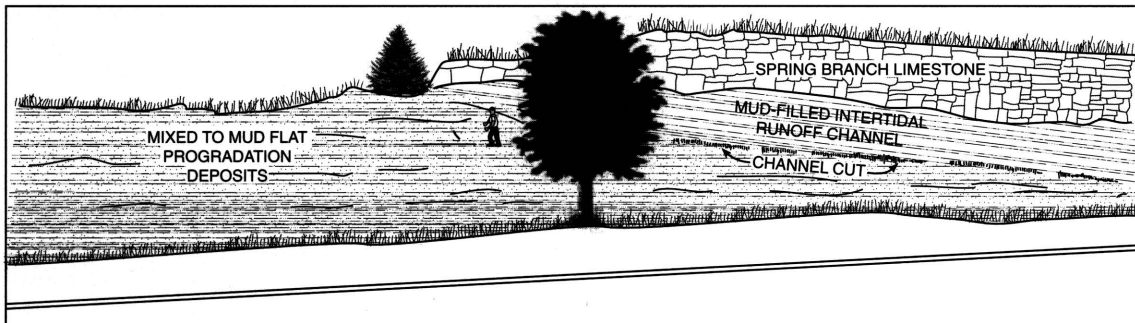

★ Localities Studied   ▦ Shawnee Group

FIGURE 74—Location map of the sections of the Stull Shale Member studied in eastern Kansas. **1**, Jackson Park quarry, Atchison County. **2**, East of Perry Lake, Jefferson County. **3**, Kansas Turnpike, Douglas County. **4**, Between Kanwaka and Stull, Douglas County. **5**, East of Lyndon, Osage County. **6**, Waverly, Coffey County.

A

B

FIGURE 75—Outcrop close to the town of Kanwaka. **A**. Photo. **B**. Drawing. Tidal-flat packages are cut by an intertidal runoff channel (arrows).

locally. Plant fragments are abundant. Trace fossils are scarce and are restricted to the sandstone interbeds. *Planolites* and *Palaeophycus* are the only forms recognized, and degree of bioturbation is very low.

Interpretation of Lateral Variability of the Stull Shale Member

Variation in trace-fossil types, ichnofossil diversity, burrow size, and degree of bioturbation reflect salinity gradients along an estuarine/embayment complex oriented northeast-southwest, with an open-marine system located to the southwest. In this model, outcrops in Atchison County represent the innermost facies of the embayment. In this area, fine-grained sediment accumulated on a mud flat close to the upper reaches of the estuary. Extreme fluctuations in salinity and temperature probably prevented the establishment of a significant benthic fauna. *Planolites* and *Palaeophycus* are very simple, facies-crossing forms that may be present in both marine and continental environments, and they therefore provide no clear evidence of marine influence.

In Jefferson County, tidal flats were most likely formed in an inner zone of the estuary bay (middle reaches). Low diversity of trace fossils indicates harsh conditions in a stressful environment, where extreme salinity fluctuations and freshwater influx make colonization by benthic fauna extremely difficult. However,

presence of nuculoid bivalve traces indicates brackish-water conditions. Size reduction due to dwarfism is a common phenomenon in stressful, brackish-water ecosystems (Hakes, 1985).

Tidal-flat successions in Douglas County are inferred to have occurred in the middle zone of the bay, still under brackish-water conditions. Ichnodiversity, however, is higher than in sections located farther north. Hakes (1976, 1977, 1985) first noticed the brackish-water nature of the Stull Shale Member ichnofaunas in this area.

Pertinent features in the outcrop in Osage County also suggest a restricted setting with sand-bar and tidal-flat facies developing in the sand-dominated outer zone of the embayment system. Low diversity may reflect in part high hydrodynamic energy and extreme soft-sediment deformation.

When compared with the other Stull Shale Member localities, the Waverly trace-fossil site is remarkable in abundance and diversity of biogenic structures. This uniqueness does not seem to be associated with any significant change in lithology or physical sedimentary structures. Essentially the same lithofacies (heterolithic tidal-flat facies) occurs at all localities studied. Therefore, salinity may have been the master factor in Stull Shale Member trace-fossil distribution.

Brackish-water ichnofaunas typically display: (1) low ichnodiversity, (2) ichnotaxa commonly found in marine environments, but produced by euryhaline organisms, (3) dominance of infaunal traces rather than epifaunal trails,

FIGURE 76—Outcrop close to the town of Stull. Parasequence of tidal-flat progradation, from sand- to mixed- and mud-flat deposits. Note Spring Branch Limestone Member at the top.

FIGURE 77—Outcrop at Jackson Park quarry. Both base and top of the Stull Shale Member are exposed. Clay Creek Limestone Member below, Spring Branch Limestone Member, above. Thickness of the Stull Shale Member is about 8.5 m.

(4) simple structures produced by opportunistic trophic generalists, (5) combination of vertical and horizontal traces from the *Skolithos* and *Cruziana* ichnofacies, (6) presence of monospecific associations, (7) variable density, and (8) small size (Pemberton and Wightman, 1992; Mángano and Buatois, 1997).

In contrast to brackish-water assemblages, the Waverly tidal-flat ichnofauna is characterized by: (1) high ichnodiversity, (2) marine ichnotaxa produced by both euryhaline and stenohaline forms, (3) presence of both infaunal and epifaunal traces, (4) presence of simple and complex structures produced by trophic generalists and specialists (e.g., *P. grumula*), respectively, (5) dominance of horizontal traces of the *Cruziana* ichnofacies, (6) presence of multispecific associations, (7) high density, and (8) variable size. Additionally, the Waverly tidal-flat ichnofauna differs from freshwater tidal-flat assemblages of fluvio-estuarine transitions, such as those discussed by Buatois, Mángano, et al. (1997).

Pertinent features of the Waverly ichnofauna suggest that the biota inhabited a tidal flat dominated by normal-marine salinities connected directly to the open sea (i.e., outside of embayments). This interpretation is consistent with paleogeographic reconstructions showing restricted facies occurring toward the northeast and more open-marine facies occurring in the southwest, where Waverly is located.

Some workers suggested that deltaic systems were active during deposition of the Kanwaka Shale (Wanless et al., 1970; Hakes, 1976). In particular, Wanless et al. (1970) interpreted siliciclastic units of the Kanwaka Shale in Kansas as having been deposited in prodelta settings. However, our facies analysis suggests deposition in an embayment rather than in a deltaic setting. Wanless et al. (1970, fig. 5) suggested that prograding systems extended from the south, but ichnologic evidence observed in this study indicates more open-marine conditions toward the south.

Implications for Ichnofacies Models

Ichnofaunas from Tidal Successions in the Fossil Record

A review of the available information on ichnofaunas from tide-dominated successions allows us to understand the Waverly ichnofauna in a broader context and provides implications for trace-fossil facies models. For this review, we have selected a number of papers that integrate trace fossils and sedimentary facies.

A substantial amount of information is known about lower Paleozoic quartzites that commonly contain abundant ichnofaunas in subtidal-sandwave and intertidal-flat facies. For example, Baldwin (1977) documented several ichnotaxa from the *Skolithos* and *Cruziana* ichnofacies in tidal successions of the Cambrian–Ordovician of Spain. He showed that trilobite traces characterized beach and tidal-flat deposits, whereas vertical burrows of suspension feeders were abundant in barrier and subtidal sandstones. He concluded that the dominance of trilobite traces in onshore areas results from both actual abundance of tracemakers and enhanced preservational potential of the structures.

Mángano et al. (1996) analyzed Cambrian–Ordovician tidal siliciclastic rocks of northwest Argentina, formed in intertidal-flat and subtidal-sandwave environments. These authors noted that assemblages typical of the *Cruziana* ichnofacies occurred in protected settings landward of the high-energy, subtidal *Skolithos* ichnofacies. They pointed out that this resulted in the vertical replacement of the onshore *Cruziana* ichnofacies by the subtidal-sandwave *Skolithos* ichnofacies in a transgressive succession, and they urged caution in the application of the classical ichnofacies model of nearshore successions to tide-dominated settings. A similar pattern of trace-fossil distribution was recorded in other lower Paleozoic tide-dominated successions of northwest Argentina (e.g. Mángano and Buatois, 2000; Mángano et al., 2001).

Durand (1985) presented an exhaustive sedimentologic and ichnologic study of Ordovician tidalites of France. He identified a low-diversity assemblage dominated by suspension feeders in subtidal-sandwave facies and a *Cruziana* association in heterolithic facies of intertidal- to upper-subtidal origin.

Fillion and Pickerill (1990) documented in detail the trace fossil content of Cambrian–Ordovician siliciclastic rocks of Canada. They recorded 89 ichnospecies in the tidal-flat facies, representing a highly diverse occurrence of the *Cruziana* ichnofacies. In contrast, only two ichnotaxa (*Skolithos* and *Diplocraterion*) were found in subtidal deposits.

Legg (1985) documented sedimentary facies and ichnofaunas from a Cambrian tide-influenced delta system in Spain. He noted that *Cruziana* was more abundant in low-energy heterolithic facies of intertidal origin and that vertical equilibrium structures, such as *Diplocraterion*, showed a preference for high-energy conditions. Notably, he also found that *Rusophycus* tends to be more abundant in high-energy tidal channels.

Crimes et al. (1977) discussed the ichnology of Precambrian–Cambrian shallow-water successions in Spain. They noted the dominance of elements of the *Skolithos* ichnofacies in high-energy, thick sandstone packages, and more varied ichnofaunas in low-energy, thinly bedded heterolithic facies, characterized by the *Cruziana* ichnofacies.

Bjerstedt and Erickson (1989) analyzed Cambrian–Ordovician deposits of the northern United States and Canada. The *Skolithos* ichnofacies was present in high-energy, herringbone crossbedded sandstones formed in low-intertidal to subtidal settings. The *Cruziana* ichnofacies occurred in shallow and protected intertidal facies.

Poire and del Valle (1996) documented trace fossils from a sandwave complex in Cambrian–Ordovician rocks of Argentina. Ichnofossils were very rare or even absent in subtidal-bar deposits, but a relatively diverse suite of the *Cruziana* ichnofacies was present in interbar and bar-margin facies.

Stanley and Feldmann (1998) provided a very detailed study of Cambrian–Ordovician rocks in northern United States. In this case, the highest trace-fossil diversity occurred in the subtidal and lower-intertidal areas. Subtidal zones were characterized by quiet-water conditions, although periodically disturbed by storm action. Scarcity of biogenic structures in the upper-intertidal zone was related to preservational conditions.

Various sedimentologic studies of lower Paleozoic tidalites mentioned the associated biogenic structures (e.g., Thompson, 1975; Jansa, 1975; Barnes and Klein, 1975; Rust, 1977; Tankard and Hobday, 1977; Hiscott et al., 1984). *Skolithos* is the dominant, if not exclusive, component of trace-fossil assemblages in high-energy environments, such as tidal inlets, intertidal sandflats and channels, and subtidal sandwaves. In some cases, however, *Skolithos* is replaced by *Diplocraterion* (e.g., Cornish, 1986; Simpson, 1991). An assemblage of *Arenicolites* and *Diplocraterion* is present in the Cambrian Flathead Sandstone Formation of Wyoming, where the tracemakers colonized reactivation surfaces in these subtidal-sandwave quartzites (Boyd, 1966; Mángano and Buatois, personal observations).

A relatively diverse ichnofauna has been described from Silurian carbonate tidal deposits of Arctic Canada by Narbonne (1984). This intertidal association is dominated by domichnia and fodinichnia, with cubichnia and repichnia being less common. Although Narbonne (1984) considered this association analogous to the *Skolithos* ichnofacies, the high ichnodiversity, abundance of horizontal traces of deposit feeders, and variety of ethologic groups indicate that this intertidal assemblage belongs to the *Cruziana* ichnofacies. Low-energy, subtidal-shelf environments also are characterized by abundant and diverse trace fossils, including feeding, dwelling, locomotion, and resting traces, representing an example of the *Cruziana* ichnofacies (Narbonne, 1984).

Another set of data comes from the study of late Paleozoic tidal deposits. For example, Miller and Knox (1985) documented a diverse trace-fossil assemblage of the *Cruziana* ichnofacies in Pennsylvanian tidal-flat facies of Tennessee. This trace-fossil assemblage includes representatives of most ethologic categories, and although

traces of suspension feeders are present, traces of deposit feeders represent the dominant trophic type.

Diemer and Bridge (1988) analyzed sedimentary facies of Carboniferous (Tournaisian) coastal deposits from Ireland. They mentioned a typical *Cruziana* assemblage in intertidal facies, with the highest diversity of trace fossils occurring in heterolithic tidal-flat facies.

Martino (1989) documented the ichnology of Pennsylvanian marginal-marine facies of West Virginia. In particular, biogenic structures are abundant and diverse in tidal-flat deposits. The assemblage was dominated by horizontal traces of deposit feeders and, to a lesser extent, grazers, reflecting a *Cruziana* ichnofacies.

High-diversity trace-fossil assemblages were recorded from Pennsylvanian tidal flats of Kentucky (Greb and Chesnut, 1994). This ichnofauna consisted of a mixture of vertical and horizontal traces, and included resting, dwelling, feeding, locomotion, and grazing traces. It is therefore considered to represent a *Cruziana* ichnofacies.

Tidal-flat trace fossils also were documented in Mississippian deposits in Illinois by Wescott and Utgaard (1987). This ichnofauna consisted of vertical traces of suspension and deposit feeders and horizontal traces of deposit feeders. Based on the dominance of vertical traces, these authors assigned this example to the *Skolithos* ichnofacies. However, the presence of horizontal feeding traces and trackways, existence of deposit feeders, ichnotaxonomic composition, and relatively high diversity observed in this study indicate instead that this assemblage is an example of the *Cruziana* ichnofacies that developed on intertidal flats.

Mesozoic and Cenozoic tidal ichnofaunas display similar onshore-offshore patterns to those of the Paleozoic. Triassic intertidal to supratidal deposits of British Columbia, described by Zonneveld et al. (1997) and Zonneveld et al. (2000), contain a low-diversity assemblage of feeding and dwelling traces. These authors suggested that extensive periods of exposure and fluctuations in salinity constrain development of the benthic fauna. Jurassic tidal-flat deposits of India also contain representatives of the *Cruziana* ichnofacies (Howard and Singh, 1985). The association includes dwelling, feeding, resting, and locomotion traces of deposit and, to a lesser extent, suspension feeders. The Alameda Avenue outcrop of Colorado is a well-known locality of the Cretaceous Dakota Group and has been described in a series of papers (e.g., MacKenzie, 1968, 1972; Weimer and Land, 1972; Chamberlain, 1980; Mángano and Buatois, personal observations). Tidal-flat deposits include abundant and varied biogenic structures, comprising both vertical traces of suspension feeders and horizontal traces of deposit feeders. Typical components are *Teichichnus, Diplocraterion, Rhizocorallium, Chondrites, Arenicolites, Thalassinoides, Planolites,* among many others, representing an example of the *Cruziana* ichnofacies. The *Skolithos* ichnofacies is present in higher-energy subtidal dunes and

channels. *Skolithos* and *Ophiomorpha* are typical components of this assemblage.

Pollard et al. (1993) analyzed trace fossil evidence of colonization in Eocene sandwave deposits of England. This facies displayed a colonization ichnocoenosis containing *Ophiomorpha* and *Macaronichnus*, which occur along foresets and reactivation surfaces. *Ophiomorpha* seems to replace *Skolithos* as the dominant form of the *Skolithos* ichnofacies in post-Paleozoic, high-energy, shallow-marine sandstones (Droser and Bottjer, 1989).

Examples of *Cruziana* ichnocoenoses also are very common in modern tidal flats (e.g., Bajard, 1966; Howard and Dorjes, 1972; Swinbanks and Murray, 1981; Ghare and Badve, 1984; Frey, Howard, et al., 1987). Preservational potential of biogenic structures in intertidal settings is highly variable with a clear bias in the fossil record towards deeper-tier structures.

Ichnofacies Gradients in Tide- and Wave-dominated Shorelines

Nearshore trace fossils in wave-dominated settings have received a lot of attention. On the basis of the analysis of Mesozoic ichnofaunas from the North American and Canadian Western Interior Seaway, an ichnofacies model of nearshore deposits has emerged (e.g., Howard and Frey, 1984; Frey and Howard, 1985; MacEachern and Pemberton, 1992; Pemberton, Van Wagoner, et al., 1992). In particular, MacEachern and Pemberton (1992) proposed a model of onshore-offshore ichnofacies gradients that represents a refinement of the classical scheme of Seilacher (1967). In this model, four ichnofacies are distinguished: (1) the *Psilonichnus* ichnofacies in backshore areas, (2) the *Skolithos* ichnofacies in foreshore to middle-shoreface facies, (3) the *Cruziana* ichnofacies in lower-shoreface to offshore deposits, and (4) the *Zoophycos* ichnofacies in shelf zones. These authors also noted onshore-offshore trends in the trophic types involved. This model has been used successfully to delineate environmental zonations of nearshore siliciclastic rocks of different ages (e.g., Buatois et al., 1999).

However, this model applies only to the analysis of wave-dominated shorelines where there is a net increase in energy shoreward. This shoreward increase of energy parallels an increase in oxygenation, sand content, amount of organic particles in suspension, and mobility of the

substrate. Nevertheless, this line of reasoning sometimes has been used erroneously in the analysis of ichnofaunas from tide-dominated environments. For example, studies of lower Paleozoic strata (e.g. Manca, 1986; Kumpa and Sánchez, 1988) commonly assumed a beach origin for large-scale, planar crossbedded quartzites with *Skolithos*, which were actually formed under subtidal conditions. In the same way, the presence of elements of the *Cruziana* ichnofacies in heterolithic facies commonly is regarded as evidence of subtidal conditions, although this is not necessarily the case.

Mángano et al. (1996) and Mángano and Buatois (1999) noted that the ichnofacies gradient in tide-dominated shallow seas is opposite to that in wave-dominated shallow-marine environments. As overall tidal energy increases from supratidal to subtidal settings, the *Skolithos* ichnofacies tends to occur seaward of the *Cruziana* ichnofacies. Analysis of the Waverly ichnofauna supports this conclusion. The Waverly assemblage is characterized by a mixture of horizontal, inclined, and vertical structures; dominance of crawling, feeding, and grazing structures of deposit feeders; high ichnodiversity and abundance; and presence of structures produced by mobile organisms. It therefore fulfills all the characteristics of the *Cruziana* ichnofacies (cf. Pemberton, MacEachern, et al., 1992).

Presence of the *Cruziana* ichnofacies in intertidal environments represents an occurrence in water shallower than expected according to standard ichnofacies models. This is the rule rather than the exception in tide-dominated settings. We therefore suggest that the classic onshore-offshore replacement model should be applied only in wave-dominated systems (fig. 78A) and that the opposite gradient is observed in tide-dominated systems (fig. 78B). This is consistent with information from modern tide-dominated environments, where the highest faunal diversity is present around mid-tide level (e.g., Beukema, 1976).

Needless to say, bathymetry is a second-order control in onshore-offshore ichnofacies gradients. Onshore-offshore replacement models work only when changes in the other environmental factors parallel water depth. In the case of tidal shorelines, the *Skolithos* ichnofacies may occur in very shallow water where local environmental conditions are favorable, such as where high energy conditions occur in intertidal runoff channels (e.g., Weissbrod and Barthel, 1998).
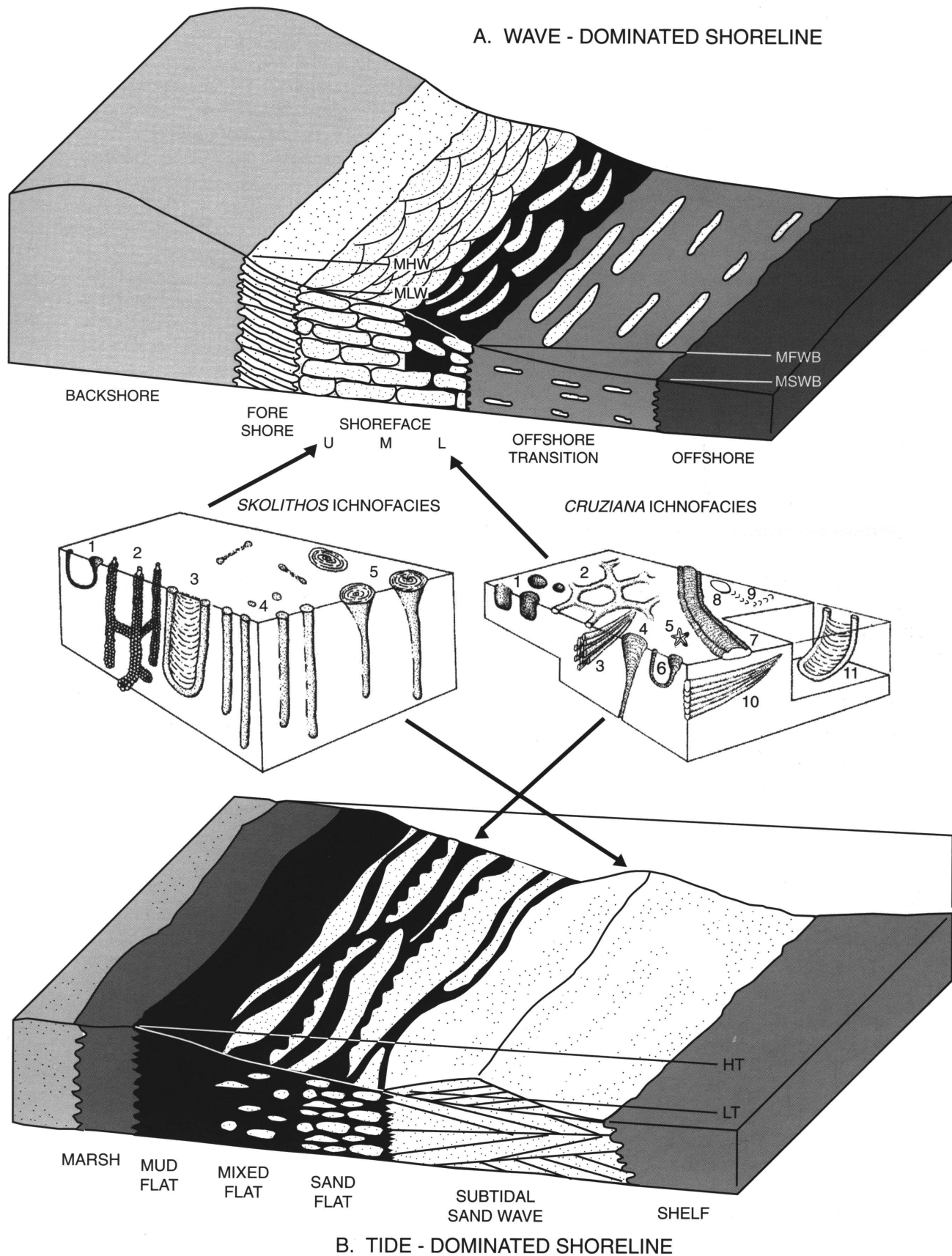
FIGURE 78—Trace-fossil facies models. **A**. Wave-dominated shoreline. **B**. Tide-dominated shoreline. Ichnofacies block diagrams based on Buatois et al. (2001). *Skolithos* ichnofacies: 1, *Arenicolites*. 2, *Ophiomorpha*. 3, *Diplocraterion*. 4, *Skolithos*. 5, *Monocraterion*. *Cruziana* ichnofacies: 1, *Bergaueria*. 2, *Thalassinoides*. 3, *Phycodes*. 4, *Rosellia*. 5, *Asteriacites*. 6, *Arenicolites*. 7, *Curvolithus*. 8, *Lockeia*. 9, *Protovirgularia*. 10, *Teichichnus*. 11, *Rhizocorallium*. Based on Buatois, Mángano, and Aceñolaza (2002).

Implications in Evolutionary Paleoecology

Introduction

During the past decade, trace fossils have become increasingly important in our understanding of the evolution of benthic communities. Bambach (1983) interpreted the history of life as a process of colonization that implies the exploitation of empty or under-utilized ecospace. Trace fossils may provide crucial evidence for the recognition of spatial and temporal patterns and processes associated with benthic colonization. In particular, ichnologic information has been used in evolutionary paleoecology to help understand a number of problems, including paleoenvironmental trends of individual ichnogenera through time (Bottjer et al., 1988); paleocommunity behavioral evolution within particular biotopes (Seilacher, 1974, 1977b); colonization and diversification patterns (Crimes, 1974; Crimes and Crossley, 1991; Crimes and Droser, 1992; Crimes and Fedonkin, 1994); onshore origination and subsequent migration of complex behavioral strategies (Crimes and Anderson, 1985); trends in the extent and depth of bioturbation (Thayer, 1983; Droser and Bottjer, 1988, 1989, 1993; Bottjer and Droser, 1994); and colonization of nonmarine environments (Maples and Archer, 1989; Buatois and Mángano, 1993a; Buatois, Mángano, Genise, et al., 1998e).

Ichnologic studies have shown that after a rapid diversification of shallow-water trace fossils, complex behavioral strategies (represented by graphoglyptids and ornate grazing traces) dispersed into the deep sea (Crimes, 1974; Crimes and Anderson, 1985). Additionally, body-fossil data show onshore evolutionary innovations and subsequent offshore migrations (Sepkoski and Sheehan, 1983; Sepkoski and Miller, 1985). However, not very much is known about the precise depositional environment where most of the evolutionary innovations occurred. Analysis of tidal-flat ichnofaunas may shed some light on current problems in evolutionary paleoecology.

Tidal Flats as Sites of Evolutionary Innovations

As noted by Reise (1985), tidal flats are geologically ephemeral systems. Depending on the transgressions and regressions of the sea, tidal flats of a given geographic region rarely last longer than 10^4 years (Reise, 1985). In contrast to the long-term temporal instability, tidal flats are, on a daily basis, highly predictable systems governed by tidal cyclicity. Tidal flats usually are regarded as harsh, heterogeneous, physically controlled environments. From a biological perspective, tidal flats are highly heterogeneous, "open systems" where interspecific interactions are poorly regulated and open to numerous possibilities

(Reise, 1985). Valentine (1976) related genetic variability in populations with physically controlled communities inhabiting unstable environments. In such a framework, selection will promote adaptive innovations. These ecologic attributes of tidal-flat communities, heterogeneity and unrefined interactions, together with predictability may have provided the appropriate ground for major steps in evolution (Reise, 1985).

Presence of large specimens of *Lockeia siliquaria* on the soles of Waverly lower-intertidal sandstones suggests that these traces were emplaced relatively deep below the sediment-water interface. As discussed previously, these burrows form palimpsest assemblages on time-averaged surfaces, which record repeated events of erosion, deposition, and recolonization. The presence of the bivalve *Wilkingia*, the most likely tracemaker of *L. siliquaria* at Waverly, reveals valuable information on evolutionary innovations (Mángano et al., 1998). *Wilkingia* may represent an evolutionary adaptation for siphon-feeding in the late Paleozoic, preceding the subsequent Mesozoic radiation of siphon-feeding infaunal bivalves (cf. Stanley, 1968, 1972). Stanley (1968) emphasized the role of mantle fusion and siphon formation as the key features that led to the Mesozoic infaunal bivalve radiation. Stanley (1972) argued that the virtual absence of deep burrowing bivalves in the Paleozoic was related to a non-siphonate condition and inefficient burrowing mechanisms. In extant rapid burrowers, siphons and ventral mantle fusion allow sealing of the mantle cavity, resulting in rapid foot extrusion and ejection of water that fluidizes the sediment around the shell (Trueman, 1966; Trueman et al., 1966; Stanley, 1970; Seilacher and Seilacher, 1994). Absence of ventral mantle fusion and true siphons (i.e., cylindrical tubes formed by fusion of the mantle edges at more than one point in the posterior region of the shell; Yonge, 1948, 1957) in late Paleozoic infaunal suspension feeders probably resulted in sluggish burrowers.

Wilkingia has an elongate shell and relatively deep pallial sinus, and it has been regarded as the first anomalodesmatan to be adapted to deep burrowing (Wilson, 1959; Runnegar, 1972). Whether or not *Wilkingia* was an efficient burrower that could cope with physical hazards of the coastal area is difficult to assess. In short, the presence of *Wilkingia* and associated relatively deep bivalve structures in this Carboniferous tidal flat may indicate incipient exploitation of the deep infaunal ecospace by bivalves, long before the Mesozoic revolution (Mángano et al., 1998).

Tidal-flat Ichnofaunas through Time

Comparison of the Waverly tidal-flat ichnofauna with other assemblages formed in similar environmental settings may be useful in addressing the problem of

onshore replacement and offshore migration of benthic faunas through time. Bivalve trace fossils are, by far, the dominant biogenic structures in the Waverly tidal-flat deposits. Similar ichnofaunas have been recorded in other late Paleozoic tidal flats (e.g., Rindsberg, 1994). These ichnofaunas are remarkably different from those recorded in early Paleozoic and post-Paleozoic tidal flats. Early Paleozoic tidal-flat ichnofaunas are dominated by trilobite traces. For example, Mángano et al. (1996) described an ichnofauna from Late Cambrian–Early Ordovician intertidal facies in northwest Argentina that includes a wide variety and abundance of trilobite traces, comprising several ichnospecies of *Cruziana, Rusophycus*, and *Monomorphichnus*. Similar trilobite-dominated ichnofaunas have been documented in other early Paleozoic tidal flats (e.g., Baldwin, 1977; Legg, 1985; Durand, 1985; Astini et al., 2000; Mángano and Buatois, 2000; Mángano and Astini, 2000; Mángano et al., 2001).

These observations suggest that trilobite faunas were replaced by bivalve faunas on tidal flats during the mid-Paleozoic. Sepkoski and Miller (1985) noted a correspondence between evolutionary faunas and local marine communities, namely the Cambrian (trilobite-rich), Paleozoic (brachiopod-rich), and Modern (molluscan-rich) faunas. Temporal changes in environmental distribution of each of these communities display onshore-offshore expansions. Based on a Q-mode factor analysis of body-fossil communities, Sepkoski and Miller (1985; fig. 6) documented a replacement of trilobite-rich communities by mollusk-rich communities in shallow-water niches throughout the Paleozoic. Ichnologic analysis of Paleozoic tidal-flat ichnofaunas supports this model and suggests the importance of tidal flats as nurseries of evolutionary innovations. Bivalves, in contrast to articulate brachiopods, were particularly adaptable to physically unstable, stressful nearshore settings (Steele–Petrovic, 1979). Recent studies in the midcontinent of North America by Olszewski (1996) documented a striking ecologic segregation between articulate brachiopods and bivalves, and this

may indicate a higher tolerance of bivalves to unstable environments.

Mesozoic and Cenozoic tidal-flat ichnofaunas are quite different from their Paleozoic equivalents, but they share many similarities with Holocene examples. For example, Cretaceous tidal-flat deposits of the Dakota Group in Colorado contain an abundant ichnofauna represented by deep to relatively deep burrows (Chamberlain, 1980; Mángano and Buatois, unpublished observations). Cenozoic tidal-flat deposits of Patagonia are dominated by deep crustacean burrows (Buatois, unpublished observations). Preliminary information suggests the importance of crustaceans and polychaetes as dominant elements of post-Paleozoic tidal-flat ecosystems. This seems to be the case in most modern tidal flats, where these groups dominate (e.g., Howard and Dörjes, 1972). For example, Curran and Harris (1996) estimated that the callianasid *Glypturus acanthochirus* could move 118.6 kg of sediment/m^2/yr to the surface of a modern sand flat on San Salvador Island. Additionally, crustaceans and polychaetes produce large quantities of argillaceous fecal pellets, and they therefore are important agents of biosedimentation and modifiers of substrate properties (Pryor, 1975; Bromley, 1996). Establishment of crustacean communities in tidal-flat ecosystems may have played a significant role in the offshore expansion of bivalves during the Mesozoic.

Additionally, deep infaunal crustaceans are key bioturbators that commonly produce elite trace fossils (Bromley, 1990, 1996). Burrowing activities of crustaceans cause significant sediment reworking and obliteration of shallower tiers. Paleozoic tidal-flat ichnofaunas typically display a high diversity of shallow-tier trace fossils, and Mesozoic to Cenozoic ichnofaunas are biased towards deeper tiers and commonly exhibit only moderate levels of ichnodiversity. This trend likely represents a taphonomic artifact resulting from the dominance of deep infaunal crustaceans in post-Paleozoic tidal-flat ecosystems.

Concluding Remarks

Integrated stratigraphic, sedimentologic, and ichnologic analysis of the Waverly succession allows a detailed characterization of the sedimentary facies and associated trace fossils. Deposition occurred along a microtidal shoreline that was directly connected with the open sea. Paleogeographic information indicates an equatorial position.

Changes in diversity and abundance of trace fossils in the lower interval of the Waverly section reflect an overall shallowing-upward trend from lower-intertidal to fluvial facies. The highest ichnodiversity is recorded in the tidal-flat deposits, specifically in the sand-flat facies. A monospecific suite of myriapod trackways is present in the

fluvial deposits towards the upper part of the lower interval.

The Waverly tidal-flat is characterized by heterogeneous distribution of biogenic structures. At a larger scale, intertidal zonation of trace fossils is evident in sand-, mixed-, and mud-flat areas of the tidal flat. Trace fossils are diverse and abundant in the sand flat, recording the activity of a varied benthic community composed of animals that were able to deal with the stressful conditions of the intertidal realm, probably as a result of the predictability of such an environment. On the other hand, mixed- to mud-flat deposits contain a low diversity of biogenic structures, reflecting extremely high temperatures and

desiccation, as well as low-preservation potential due to lack of sandstone interbeds. At a smaller scale, spatial separation of species occurs within each zone of the tidal flat. Examples of ichnologic heterogeneity in Waverly include mounds characterized by dense aggregations of *Protovirgularia bidirectionalis* and small vertical burrows, and patchy distribution of *Psammichnites implexus*, which is commonly concentrated in ripple troughs.

The tidal-flat is a harsh environment where marine organisms are subjected to the extremes of terrestrial climate, heating, frost, and desiccation. Temperature, salinity, duration of exposure to subaerial conditions, energy, and substrate represent limiting factors in tidal-flat ecosystems. Changes in salinity and temperature, together with time of exposure, are extreme in the upper-intertidal zone and diminish toward the lower-intertidal zone. This gradient may have led to the increase in ichnodiversity in the sand-flat deposits at Waverly.

Ichnotaxonomic composition and dominance of horizontal structures of deposit feeders and grazers suggest a moderate- to low-energy coastal setting. However, sedimentologic and ichnologic evidence (e.g., deep gutter casts, truncation of vertical shafts) indicate occasional high-energy events that sculpted the tidal-flat surface. Substrate conditions also are highly variable, because tidal flats are regularly exposed and submerged by the tides, with concomitant fluctuations in pore-water content. Additionally, the physiography of the coast during low tide commonly is characterized by tide pools within an otherwise emergent area, which results in a range of substrate conditions along an isochronous surface. For example, morphologic variability of bivalve traces at Waverly was controlled in part by substrate fluidity. In the case of bivalve locomotion and escape structures, different morphotypes respond to the same style of motion, with substrate consistency playing a significant role in trace-fossil morphologic variability.

Analysis of Waverly tidal-flat deposits also reveals information on stratigraphic completeness. Amalgamated sandstones with preferential preservation of *Lockeia siliquaria* record a sequence of colonization events separated by erosional scouring and renewed deposition. Individual bedding planes represent time-averaged surfaces that record the work of successive communities of burrowing bivalves. Palimpsest surfaces are common in intertidal environments and provide evidence of complex depositional histories with considerable geologic time represented by units of relatively thin strata.

Analysis of crosscutting relationships, burrowing depth, wall sharpness, trophic types, and bauplan allows recognition of a tiering structure and ichnoguild model for the benthic fauna of the Waverly tidal flat. This tidal-flat community mainly occupied shallow tiers, with domiciles of bivalves and sea anemones being the deepest forms in the association.

Integrated ichnologic, sedimentologic, and sequence-stratigraphic information provides evidence of the deposi-tional history and role of sea level during accumulation of tidal-flat sediments. The sedimentary units of the lower interval of the Waverly succession form part of four fining-upward parasequences of tidal-flat progradation, separated by successive flooding surfaces. These four parasequences form a progradational parasequence set. A major transgres-sive surface separates the fluvial facies at the tops of the lower parasequence set from the subtidal orthomyalinid packstones and wackestones that, together with the Spring Branch Limestone Member, represent a retrogradational parasequence set. In the Stull Shale Member, this set is represented by the orthomyalinid packstone and wackestone parasequence. Paleosols developed during regressive maximums on top of tidal-flat parasequences, and they do not indicate sequence boundaries. Some of the transgressive surfaces contain a firmground suite regarded as an example of the *Glossifungites* ichnofacies.

Study of other outcrops of the Stull Shale Member in eastern Kansas shed light on the environmental signifi-cance of the Waverly trace-fossil site in a broader regional context. The Waverly ichnofauna developed in a tidal flat dominated by normal-marine salinity and connected directly to the open sea. This tidal flat was located outside of a northeast-southwest-oriented embayment that opened toward the southwest. Trace-fossil assemblages from coeval localities in the northeast indicate brackish-water conditions in a restricted, marginal-marine setting.

The Waverly assemblage clearly qualifies as an example of the *Cruziana* ichnofacies. Presence of the *Cruziana* ichnofacies in intertidal environments represents an occurrence in water shallower than expected according to standard ichnofacies models. The classic onshore-offshore ichnofacies replacement model should be applied only in wave-dominated systems, because the opposite gradient is observed in tide-dominated systems. In fact, many deposits that were interpreted as having been formed in subtidal environments based on the presence of the *Cruziana* ichnofacies probably should be revised.

Attributes of tidal-flat ecosystems, such as heteroge-neity, unrefined interactions, predictability, and high selective pressures, may have promoted evolutionary innovations. Comparative analysis of tidal-flat ichnofaunas through time supports this view. In the case of the Waverly ecosystem, the presence of *Wilkingia* and relatively deep bivalve burrows suggests incipient exploitation of the deep infaunal ecospace by bivalves, which occurred long before the Mesozoic revolution.

Acknowledgments

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Index

Acila, 57
Akinereites kannoiuraensis, 50
Alabama, 66
Alameda Avenue outcrop, 104
Altichnus, 52
amphipod, 70, 81, 82
Amphitrite ornata, 24
Amphorichnus, 29
Anadarko basin, 4
Anconichnus, 54, 55
Anconichnus horizontalis, 54
annelid, 33, 35, 52, 54, 59, 65, 68, 71, 72
anthoptiloid, 54
Anyao Formation, 43, 45
Appalachian basin, 89
Arborichnus, 51
Arenicola marina, 24, 81
Arenicolites, 24, 25, 32, 35, 68, 104, 106
Arenicolites carbonarius, 25
Arenicolites curvatus, 25
Arenicolites graptolithoformis, 25
Arenicolites isp., 18, 24, 25, 70, 80
Arenicolites stather, 25
Arenicolites variabilis, 25
Argentina, 103, 104, 107
Aristophycus, 19
Arkoma basin, 4
Arran, 35
Arthropleura, 21, 35, 80
arthropod, 2, 3, 4, 21, 38, 57, 59, 70, 72, 80, 81, 84, 92
Arthrophycus, 53, 58
Arthrophycus (?)dzulynskii, 58
Asteriacites, 4, 25, 52, 100
Asteriacites aberensis, 27
Asteriacites gugelhupf, 27, 52
Asteriacites lumbricalis, 16, 25, 26, 27, 28, 29, 30, 32, 33, 37, 38, 40, 42, 45, 47, 74, 76, 78, 80, 86, 88, 92
Asteriacites quinquefolis, 25, 27
Asteriacites stelliformis, 27
asteroid, 52
Asterophycus, 38
Asterosoma, 38
Asterosoma? isp., 80
asterozoans, 25
Astropecten aurantiacus, 25
Atchison County, 100, 101
Aulichnites, 100

Balanoglossus clavigerus, 24
Bay of Mont-Saint-Michel, 81
bedding, 2
    flaser, 2, 14, 18, 21, 22, 99, 100
    lenticular, 11, 13, 18, 21, 100
    wavy, 2, 11, 13, 14, 18, 21, 22, 99, 100
beetle, 84
Bergaueria, 74, 106
Biformites, 56, 57
bivalve, 4, 17, 19, 27, 40, 56, 57, 59, 62, 63, 66, 68, 74, 80, 82, 88, 89, 92, 97, 98, 100, 101, 107, 108, 109
Borneo, 32

brachiopod, 108
Brazil Formation, 97
British Columbia, 81, 104
Buildex quarry, 3, 4
burrow, 27, 52, 61, 73, 84, 87, 89, 92, 93, 98, 101, 107
    chip-shaped, 18, 73, 74, 75, 80
    cylindrical, 18, 25, 27, 54, 72, 76, 77, 80, 83
    U-shaped, 24, 62, 68, 69, 72, 73, 82, 88, 98
    vertical, 27, 29, 71, 72, 77, 78, 80, 82, 88, 103, 109

Caddo Creek Formation, 68
Cambrian, 24, 25, 27, 29, 30, 32, 33, 35, 38, 40, 43, 54, 65, 69, 70, 72, 73, 95, 103, 104, 108
Canada, 68, 103, 104, 105
    Arctic, 104
Carboniferous, 2, 29, 32, 33, 52, 65, 66, 71, 73, 89, 95, 104, 107
cast,
    gutter, 8, 9, 10, 11, 12, 13, 16, 93, 94, 100, 109
    load, 16, 17, 18, 94
    pot, 10, 12, 13
Caulostrepsis, 5
Cenozoic, 104, 108
Chaetopterus variopedatus, 24
Chautauqua County, 29, 71
Cherokee basin, 4
Chevronichnus, 56, 57, 63, 64, 87
China, 43
Chondrites, 27, 29, 54, 76, 100, 104
Chondrites? isp., 18, 28, 29, 79, 80
chonetid, 4
Cincinnati, 63, 70
Clay Creek Limestone Member, 4, 100, 102
Clinton Lake, 99
Clyde Estuary, 82
coal, 4, 5, 95, 100
Coal Measures, 66
Coffey County, 100
Colony Creek Shale Member, 68
Colorado, 104, 108
conchostracan, 40
Conichnus, 29
Conichnus conicus, 18, 25, 29, 30, 80, 92
Conichnus conosinus, 29
Conichnus papillatus, 29
Conostichus, 74
Conostichus broadheadi, 74
Corophiodes, 35
Corophium, 84
Corophium arenarium, 35
Corophium volutator, 35, 81, 82, 85
crab, 84
Cretaceous, 30, 104, 108
crinoid, 19, 52
Crossopodia, 58, 65, 68
Crossopodia dichotoma, 58
Crossopodia embletonia, 68
Crossopodia lata, 65
Crossopodia media, 68
Crossopodia scotica, 65
cross stratification, 22

crustacean, 24, 33, 38, 65, 69, 92, 98
Cruziana, 29, 58, 70, 103, 104, 105, 106, 108, 109
Cruziana balsa, 71
Cruziana carbonaria, 71
Cruziana isp., 31, 32, 80
Cruziana problematica, 10, 11, 16, 25, 26, 27, 29, 30, 31, 32, 33,
    34, 37, 38, 40, 41, 43, 44, 45, 47, 52, 53, 65, 66, 68, 69, 71,
    74, 75, 76, 78, 80, 84, 86, 92
Cruziana pudica, 71
Cruziana retroplana, 71
Cruziana rhenana, 71
Cruziana tenella, 32
Curvolithus, 32, 88
Curvolithus aequus, 32
Curvolithus annulatus, 32
Curvolithus davidis, 32
Curvolithus gregarius, 32
Curvolithus manitouensis, 32
Curvolithus multiplex, 16, 32, 33, 37, 76, 80
Curvolithus simplex, 16, 18, 25, 27, 28, 29, 30, 32, 33, 34, 37, 38,
    42, 50, 51, 52, 54, 66, 70, 72, 79, 80, 92
cyclothem, 2, 4, 5, 95, 98
    Cherokee, 95
    Kansas, 95
    Permian, 95
    Shawnee, 95
    Wabaunsee, 95
Cylindrichnus, 38, 69

Dakota Group, 104, 108
Deer Creek Limestone, 3
Delesserites, 43
Dendrotichnium hantzscheli, 76
Dendrotichnium llarenai, 76
Derbyia, 6
Desmoinesian, 4
dessication crack, 16, 17, 18, 19, 21
Devonian, 29, 57, 68
Dictyodora, 66, 68
Dictyodora scotica, 65, 66, 68
Didymaulichnus, 29, 32, 87
Didymaulichnus lyelli, 29
Diplichnites, 33
Diplichnites cuithensis, 21, 35, 36, 80
Diplocraterion, 24, 35, 37, 68, 72, 88, 100, 103, 104, 106
Diplocraterion isp., 98
Diplocraterion isp. A, 18, 33, 37, 38, 80
Diplocraterion isp. B, 18, 37, 38, 56, 80
Diplopodichnus biformis, 32
Doniphan Shale Member, 4
Douglas County, 99, 100, 101
Douglas Group, 3
Drilonereis longa, 98

echiuran, 65
Echiurus echiurus, 24
England, 105
Eocene, 105
Eurydice pulchra, 84
eurypterid, 35

Flathead Sandstone Formation, 104
Flexicalymene meeki, 70

fodinichnion, 27, 72, 73
Forest City basin, 4
Fraena tenella, 32
France, 81, 103
fugichnia, 25, 63
fusulinid, 4

Gajansar Beds, 32
gastropod, 65
Gemma gemma, 85
Georgia, 99
Germany, 42
glaebule, 19, 20
Glossifungites, 98, 99, 109
Glycera, 50
Glycera alba, 24
Glypturus acanthochirus, 108
Gondwana, 98
Gordia, 31
graphoglyptid, 52
graptolite, 56
Graham Formation, 68
Gyrochorte, 32, 57, 58
Gyrochorte obliterata, 58

halkieriid, 65
Halopoa, 38, 73
Halopoa annulata, 38
Halopoa imbricata, 38, 50, 73
Halopoa isp., 18, 25, 38, 39, 54, 73
Helminthoida irregularis, 43
Helminthopsis, 54, 55
Helminthopsis horizontalis, 54
Helminthorhaphe, 82
Hedista (Nereis) diversicolor, 72
Holocene, 24, 25, 27, 29, 35, 55, 59, 70, 71, 72, 108
holothurians, 24
Hunsrück Shale, 57
Hydrobia, 82

Ichnia spicea, 57
Ichnium problematicum, 30
Illinois, 104
Imbrichnus, 56, 57, 87
Imbrichnus wattonensis, 58
India, 32, 104
Indiana, 97
Ireland, 104
isopod, 4, 84
Isopodichnus, 70
Isopodichnus osbornei, 30

Jackson Park quarry, 100, 102
Jefferson County, 100, 101
Jurassic, 43, 78, 104

Kanwaka, 99, 100, 101
Kanwaka Shale, 2, 3, 4, 6, 103
Keckia, 58
Kentucky, 66, 104
Köningshafen, 82, 88
Kouphichnium, 79

lamination, 8
    cross, 8, 21
    parallel, 8
Lanice conchilega, 24, 88
Lansing Group, 3, 4
Lawrence Shale, 3
Lecompton Limestone, 4
Leptalosia, 6
Leptosynapta tenuis, 24
Lockeia, 38, 40, 56, 57, 58, 59, 63, 88, 89, 91, 100
Lockeia amygdaloides, 38
Lockeia avalonensis, 38, 40
Lockeia cordata, 38, 40
Lockeia czarnockii, 38
Lockeia elongata, 38
Lockeia hunanensis, 38, 40
Lockeia isp., 40, 63
Lockeia ornata, 16, 27, 29, 38, 40, 41, 42, 45, 63, 77, 80, 82, 83, 87, 88, 92
Lockeia siliquaria, 16, 17, 25, 27, 29, 30, 32, 38, 40, 41, 42, 43, 44, 51, 52, 64, 66, 68, 70, 72, 78, 80, 88, 89, 90, 92, 107, 109
Lockeia triangulichnus, 38, 40
Lockeia vagans, 58
Lyndon, 99, 100

Macaronichnus, 50, 55, 105
Macoma, 40
Macoma baltica, 68
Maldanidopsis, 43
Maldanidopsis meandriformis, 50
megacyclothem, 4, 5
    Oread, 4
Mesozoic, 25, 104, 105, 107, 108, 109
Microspherichnus linearis, 76
Miocene, 32, 38, 43, 52, 69, 70
Mississippian, 66, 104
Missourian, 3
Modern, 108
mollusk, 65, 66, 92, 108
Monocraterion, 32, 69, 71, 106
Monomorphichnus, 108
monuran insects, 4
Morrowan, 4
Morrow Sandstone, 4
mud drape, 21
Myrianites, 43
myriapod, 4, 33, 35, 80, 108

Namurian, 35
nematode, 81
nemertean, 98
Neonereites, 43
Neonereites biserialis, 43
Neonereites multiserialis, 43
Neonereites uniserialis, 43, 50
Nereis succinea, 98
Nereites, 32, 43, 45, 50, 88, 100
Nereites barrandei, 45
Nereites barroisi, 45
Nereites cambrensis, 16, 43, 45, 46, 80
Nereites castroi, 45
Nereites fengxianensis, 45

Nereites imbricata, 16, 30, 45, 47, 48, 52, 69, 80
Nereites irregularis, 43
Nereites isp., 43
Nereitis jacki, 43
Nereites jacksoni, 16, 43, 45, 46, 80
Nereites liebei, 45
Nereites lorioili, 45
Nereites macleayi, 43
Nereites marcoui, 45
Nereites missouriensis, 16, 25, 29, 39, 45, 49, 50, 55, 66, 72, 80, 92
Nereites murotoensis, 43
Nereites pugnus, 43
Nereites roemeri, 45
Nereites saltensis, 45
Nereites tosaensis, 43
Nereograpsus, 43
New Brunswick, 35
North America, 85, 98, 105
North Sea, 81, 88
Norway, 72
Notaculites toyomensis, 50
notostracan, 70
Nova Scotia, 33, 35
nuculanid, 42
Nuculopsis, 63

octocoral, 56
Oklahoma, 52
Olivellites, 65, 66
Olivellites grumula, 65
Olivellites plummeri, 66
Ophelia bicornis, 82
Ophiomorpha, 105, 106
Ophiura texturata, 25
ophiuroid, 25, 27, 52, 80, 88, 92
Ordovician, 40, 55, 59, 63, 70, 71, 103, 104, 108
Orthomyalina, 97
orthomyalinid, 4, 5, 97, 109
Osage County, 99, 100, 101
Osagia, 6
Ouachita Mountains, 4

Pakistan, 33
Palaeophycus, 50, 55, 73, 87, 98, 100, 101
Palaeophycus alternatus, 50
Palaeophycus annulatus, 50
Palaeophycus anulatus, 50
Palaeophycus canalis, 50
Palaeophycus crenulatus, 50
Palaeophycus ferrovittatus, 50
Palaeophycus heberti, 50
Palaeophycus imbricatus, 50
Palaeophycus serratus, 50
Palaeophycus striatus, 38, 50
Palaeophycus subornatus, 50
Palaeophycus sulcatus, 50
Palaeophycus tubularis, 11, 16, 18, 25, 40, 45, 50, 51, 52, 54, 68, 73, 80, 83, 87, 98
paleocurrent, 93
Paleogene, 57, 66
Paleohelminthoida, 43
Paleosceptrom, 57

paleosol, 19, 21, 94, 98, 99, 109
Paleozoic, 2, 4, 21, 25, 30, 42, 43, 50, 80, 92, 96, 98, 103, 104, 105, 107, 108
Parahaentzschelinia, 51, 52
Parahaentzschelinia ardelia, 18, 51, 52, 53, 54, 80
Parahaentzschelinia surlyki, 52
Paraonis, 82
Paraonis fulgens, 82
Patagonia, 108
pedogenic, 19
Pelecypodichnus, 38
Pelecypodichnus ornatus, 40
pelletoidal chain, 18, 74, 76, 80
pennatulacean, 54
Pennatulites, 57
Pennsylvanian, 2, 3, 4, 25, 40, 42, 66, 68, 71, 85, 95, 97, 99, 104
Pentichnus, 25, 52
Pentichnus gugelhupf, 27, 52
Pentichnus pratti, 18, 52, 54, 80
Permian, 2, 35, 65, 95, 97
Perry Lake, 100
Petit Chou Island, 99
Phestia, 42
pholadomid, 43
phoronid, 71
Phycodes, 53, 54, 55, 72, 106
Phycodes auduni, 53
Phycodes bromleyi, 54
Phycodes circinatus, 53
Phycodes coronatum, 53
Phycodes curvipalmatum, 53
Phycodes isp., 18, 54, 55, 80
Phycodes palmatus, 18, 53, 54, 55, 80
Phycodes pedum, 53, 54, 73
Phycodes reniforme, 53
Phycodes templus, 54
Phycodes ungulatus, 53
Phycodes wabanensis, 53
Phycodes yichangensis, 53, 54
Phycosiphon, 54, 55
Phycosiphon incertum, 18, 50, 54, 55, 56, 80, 92
Phyllodicites, 43
Phymatoderma, 27
Plagiogmus, 63, 65
Plagiogmus arcuatus, 63
Planolites, 32, 50, 55, 56, 87, 100, 101, 104
Planolites annularius, 55, 56
Planolites ballandus, 55
Planolites beverleyensis, 18, 55, 56, 57, 80
Planolites constriannulatus, 55, 56
Planolites montanus, 55, 56
Planolites nematus, 56
Planolites terraenovae, 55, 56
Pleistocene, 40, 56, 69
Poland, 32
polychaete, 24, 35, 50, 52, 55, 56, 69, 72, 78, 81, 82, 85, 88, 98, 99, 108
Polydora ?*websteri*, 99
Polypodichnus, 57
Polyupsilon, 35
Precambrian, 32, 40, 43, 56, 71, 103
Proterozoic, 13
Protovirgularia, 43, 50, 56, 57, 58, 59, 63, 68, 87, 100

Protovirgularia bidirectionalis, 16, 18, 23, 25, 27, 29, 30, 33, 34, 37, 38, 40, 45, 50, 51, 52, 53, 54, 55, 59, 60, 61, 62, 66, 68, 70, 72, 73, 76, 77, 78, 79, 80, 82, 83, 87, 88, 92, 109
Protovirgularia dichotoma, 56, 57, 58, 59, 63
Protovirgularia dzulynskii, 57, 58
Protovirgularia harknessi, 56
Protovirgularia longespicata, 43, 57, 58, 59
Protovirgularia mongraensis, 56
Protovirgularia nereitarum, 56
Protovirgularia obliterata, 57, 58
Protovirgularia pennatus, 58
Protovirgularia rugosa, 10, 16, 25, 27, 29, 30, 34, 40, 42, 57, 58, 59, 63, 64, 78, 80, 82, 86, 87, 88, 92
Protovirgularia rugosa var. *Chevronichnus*, 58, 63
Protovirgularia rugosa var. *Imbrichnus*, 58
Protovirgularia triangularis, 57, 58
Protovirgularia tuberculata, 57, 58, 59
Protovirgularia vagans, 57, 58
Psammichnites, 32, 63, 65, 66, 67, 68, 100
Psammichnites gigas, 63
Psammichnites grumula, 10, 30, 65, 66, 67, 68, 80
Psammichnites implexus, 16, 25, 65, 66, 67, 68, 80, 82, 92, 109
Psammichnites? isp, 16, 67, 68, 80, 86
Psammichnites plummeri, 16, 65, 66, 67, 68, 80
Psilonichnus, 105
Pustulichnus, 78
Pustulichnus gregarius, 78

Radionereites, 43
relict trough, 8, 11, 13, 14, 18, 80, 93, 94
Rhabdoglyphus, 58
Rhizocorallium, 35, 68, 73, 104, 106
Rhizocorallium irregulare, 52, 69, 80
Rhizocorallium isp., 18
Rhizocorallium jenense, 69
Rhizocorallium karaiensis, 69
Rhizocorallium kutchensis, 69
Rhizocorallium lixianensis, 69
Rhizocorallium mongraensis, 69
Rhizocorallium uliarense, 69
rib and furrow, 21
ripple, 11, 13, 14, 15, 16, 18, 19, 20, 21, 22, 34, 60, 62, 72, 73, 76, 79, 81, 81, 82, 84, 93, 94, 109
    flat-top, 2, 8, 13, 99, 100
    interference, 59
    wave, 2
Rituichnus, 50
Rock Bluff Limestone Member, 3
Rock Lake Shale Member, 3
rose diagram, 94
Rosselia, 38, 69, 70, 106
Rosselia chonoides, 69, 70
Rosselia isp., 25, 66
Rosellia rotatus, 69, 70
Rosselia socialis, 18, 24, 69, 70, 80
Rusophycus, 29, 70, 103, 108
Rusophycus carbonarius, 30, 71
Rusophycus isp., 16, 68, 70, 71, 80
Rusophycus pudicum, 70, 71

Sagittichnus, 38
Salina basin, 4
salinity, 84, 101, 103, 104, 109

sand volcano, 16, 19, 94
San Salvador Island, 108
Scalarituba, 43
Scalarituba? atoka, 50
Scalarituba darvaseana, 50
Scalarituba indica, 50
Scalarituba lungmaxiensis, 50
Scalarituba michlensis, 50
Scalarituba missouriensis, 43, 50
Scalarituba welleri, 50
scaphopod, 59
Scolecolepsis, 82
Scolecolepsis squamata, 82
Scolicia, 32, 66
Scolicia virgamontis, 66
scorpion, 35
Scotland, 35, 82
sea anemone, 74, 92, 109
Sedgwick basin, 4
sedimentologic log, 7
Sesarma reticulatum, 84
Shawnee Group, 2, 3, 4
Silurian, 65, 81, 104
Skolithos, 71, 88, 100, 103, 104, 105, 106
Skolithos annulatus, 71
Skolithos bulbus, 71
Skolithos gyratus, 71
Skolithos ingens, 71
Skolithos isp., 18, 69, 72, 80
Skolithos linearis, 71
Skolithos magnus, 71
Skolithos serratus, 71
Skolithos verticalis, 71
Solemyatuba, 24, 25, 59
Solemyatuba (Arenicolites) subcompressa, 25
Solemyatuba subcompressa, 25
Solemyatuba ypsilon, 25
South Bend Limestone, 3
South Korea, 81
Spain, 66, 103
Spring Branch Limestone Member, 4, 5, 97, 99, 100, 102, 109
Stanton Limestone, 3, 4
Stranger Formation, 3
Stull, 99, 100, 102
Stull Shale Member, 2, 3, 4, 5, 6, 7, 52, 66, 80, 84, 94, 96, 97, 98, 99, 100, 101, 102, 109
Sustergichnus, 56, 57
Sustergichnus lenadumbratus, 58
Sweden, 73

Taenidium, 50
Tecumseh Shale, 3, 45
Teichichnus, 61, 72, 74, 100, 104
Teichichnus ovillus, 73
Teichichnus pescaderoensis, 73
Teichichnus rectus, 18, 54, 72, 73, 80
Teichichnus repandus, 73
temperature, 85, 109
tempestite, 63
Tennessee, 104
Tertiary, 57
Texas, 65, 68
Thalassinoides, 32, 104, 106

Thalassotrechus barbarae, 84
Thyasira, 27
tidal flat, 2, 3, 4, 5, 7, 19, 24, 25, 27, 29, 30, 32, 35, 40, 50, 52, 54, 56, 59, 69, 70, 72, 73, 78, 80, 81, 82, 84, 85, 88, 92, 93, 95, 97, 99, 100, 101, 102, 103, 104, 105, 107, 108, 109
tiering, 89, 92, 108
Timberhill Siltstone Member, 4
Tonganoxichnus, 4
Tonganoxie Sandstone Member, 3, 4
Tournaisian, 104
track, 79
Treptichnus, 54, 73
Triassic, 40, 42, 104
Trichichnus, 99
Trichophycus, 54, 73
Trichophycus isp., 18, 38, 73, 74, 80
Trichophycus lanosus, 73
Trichophycus sulcatus, 73
Trichophycus thuringicum, 73
Trichophycus tripleurum, 73
Trichophycus venosus, 73
trilobite, 29, 70, 73, 103, 108
Trinidad, 57
Tuberculichnus, 58
Tuberculichus meandrinus, 58
Tuberculichnus vagans, 58

Uchirites, 57, 68, 87
Uchirites implexus, 66, 68
Uchirites (Protovirularia) triangularis, 59
Uchirites triangularis, 66, 68
Umbonichnus, 38
United Kingdom, 65
Urechis caupo, 24

Vagorichnus anyao, 45
Vendian, 40
Venezuela, 57, 66, 68
Vinland Shale Member, 3
Virgilian, 2, 3, 5, 45, 95, 96, 97
Virgularia presbytes, 57

Walcottia, 40, 56, 57, 87
Walcottia rugosa, 58
Waverly, 5, 72, 74, 78, 80, 82, 88, 89, 92, 93, 95, 96, 97, 98, 100, 101, 103, 107, 109
sequence/succession, 6, 81, 84, 85, 92, 94, 97, 99, 105, 107, 108, 109
Wayland Shale Member, 68
Western Interior Seaway, 105
Westphalian, 35
West Virginia, 104
Wichita Orogeny, 4
Wilkingia, 43, 107, 109
worm, 65, 72, 73, 78, 82, 88, 92
wrinkle mark, 2, 8, 13, 14, 72, 80
Wyoming, 104

Yellow River, 81

Zoophycos, 32, 105