

The Ichnofacies Paradigm: A Fifty-Year Retrospective

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SUMMARY: The ichnofacies paradigm endures as the elegant, unifying framework within which accurate ichnological observations and reliable environmental interpretations can be derived from the rock record. These temporally and geographically recurring, strongly facies-controlled groupings of trace fossils reflect specific combinations of organism behavior (ethology), and constitute the benchmark animal-sediment responses to optimum environmental conditions. Seilacherian ichnofacies are distinctive, archetypal associations of traces. Ichnofacies are part of the total aspect of the rock, and consist of primary biogenic structures imparted by organisms responding in predictable ways to variations in energy conditions, deposition rates, food resource types, substrate consistency, water salinity, oxygenation, subaerial exposure, substrate moisture, and temperature, among others. Like lithofacies, ichnofacies are subject to Walther's Law, have lateral continuity, display predictable vertical successions, and lead to mappable constructs. Like all facies analyses, interpretations of ichnofaunas are improved substantially when evaluated in the context of the host rocks and their sedimentologic and stratigraphic implications.

INTRODUCTION

Modern depositional systems are characterized by a complex interaction of numerous physical, biological, and chemical processes, including

wave energy, tidal flux, storm influence, fluvial-sediment input, subaqueous *vs.* subaerial exposure, salinity, temperature, substrate consistency, water turbidity, oxygenation, and other physico-chemical factors. These factors can be very difficult to discern and apply to paleoenvironmental interpretations of the rock record. Ichnology constitutes a valuable tool in diagnosing many of these physico-chemical parameters in ancient systems, particularly when integrated with sedimentological and stratigraphic analysis. Trace fossils are unique, in that they are not merely paleontologic entities but also biogenic sedimentary structures, and must be evaluated in this sense. They are strongly facies controlled, and generally temporally long ranging, making them ideal for facies analysis. Ichnofossils are also readily observable at both outcrop and subsurface core scales, making their identification and interpretation as routine as that of physical sedimentary structures. The integration of both sedimentological and ichnological data, therefore, constitutes a powerful tool in the interpretation of ancient depositional systems.

Ichnofacies consist of distinctive, recurring (both in space and time) ethological groupings of trace fossils, reflecting specific combinations of organism responses to environmental conditions. Interpretations of ichnofacies are enhanced when placed into the context of the original ichnocoenoses (temporally and genetically related trace fossils). It must be stressed that ichnofacies are *not* trace fossil

suites; rather, they are conceptual constructs based on numerous empirical observations, to which particular ichnocoenoses are attributable.

The ichnofacies paradigm offers critical information about the conditions operating during deposition (e.g., softground ichnofacies) or during colonization of stratigraphic discontinuities (e.g., substrate-controlled ichnofacies and palimpsest softground ichnofacies). One of the strengths of the ichnofacies concept lies in its ease of integration with classical physical sedimentologic facies analysis, and its adherence to Walther's Law (the basic tenet of sedimentary geology). The close ties of ichnofacies with lithofacies are further highlighted by the advent of genetic stratigraphic frameworks. Marine and marginal marine discontinuities are commonly demarcated by substrate-controlled trace fossil suites, and there is hardly an article published since 1995 dealing with such stratigraphic discontinuities that has not acknowledged the presence of omission suites attributable to the *Glossifungites*, *Teredolites*, and/or *Trypanites* ichnofacies.

Past misuse or misconception of 'ichnofacies' has led to considerable scrutiny and discussion of the concept (e.g., Ekdale, 1988; Frey et al., 1990; Bromley and Asgaard, 1991; Pickerill, 1992; Goldring, 1993; Savrda, 1995; Bromley, 1996). Some researchers have argued that if employed independently of lithofacies, the utility of ichnofacies may lead to limited resolution, and may yield grossly over-generalized results (Goldring, 1993; Savrda, 1995). Certainly, any interpretation that ignores the complete dataset is prone to inaccuracy or imprecision. Properly done, however, ichnofacies analysis is *fully* integrated with the sedimentology, paleontology, and stratigraphy of the succession, and emerges as a powerful tool for high-resolution reconstructions of depositional environments (e.g., Kern and Warme, 1974; Crimes et al., 1981; Wightman et al., 1987; Frey et al., 1990; MacEachern and Pemberton, 1992, 1994; MacEachern et al., 1992, 1999; Pemberton and MacEachern, 1995, 1997; Bromley, 1996; Gingras et al., 1998; Pemberton et al., 2001; Bann and Fielding, 2004; Bann et al., 2004; Fielding et al., 2006; MacEachern and Gingras, in press). Without the coherent underpinning of the ichnofacies concept, trace fossil identifications, ichnologic assemblages, and ichnofabric designations have no conceptual basis for interpretation. The ability to understand and therefore utilize ichnology in sedimentology and stratigraphy is contingent upon the unifying paradigm of ichnofacies.

THE RISE OF THE ICHNOFACIES CONCEPT

From the perspective of paleoenvironmental reconstruction of facies, nothing compares to the quantum leap in our comprehension of biogenically modified strata than that imparted by the development of the ichnofacies concept. This contribution cannot be overstated: the ichnofacies model elevated ichnology from the obscure concern with animal and plant 'scribbles' on rocks and disruptions in modern sediments, to a valuable facies analysis tool, superbly suited to outcrop and subsurface studies. As a conceptual framework, it forms the template within which ichnological data can be interpreted environmentally. The concept of ichnofacies was developed by Adolf Seilacher in the 1950s and 1960s (Seilacher, 1953a,b, 1967), originally based on the empirical observation that many of the parameters controlling the distribution of tracemakers tended to change progressively with increasing water depth (Fig. 4.1). In response to the potential geological value of this bathymetric relationship, the 'Seilacherian' ichnofacies framework soon came to be regarded almost exclusively (albeit erroneously) as a relative paleobathymeter (e.g., Weimer and Hoyt, 1964; Farrow, 1966). Though ichnofacies remain essential to environmental reconstructions, paleobathymetry is only one aspect of the modern concept. The principal controls on ichnofacies distributions tend to change progressively with bathymetry, and so ichnofacies are properly regarded to display a passive relationship to water depth (e.g., Ekdale et al., 1984; Ekdale, 1988; Frey et al., 1990). Organism behaviors, and their resulting biogenic structures are principally controlled by factors such as substrate consistency, energy near the bed, food resource types, water turbidity, water salinity, depositional rates, oxygenation, and temperature, among others (Fig. 4.1).

Seilacher (1967) defined six original ichnofacies, named for a characteristic ichnotaxon. These fall into four softground marine types (*Skolithos*, *Cruziana*, *Zoophycos*, and *Nereites*), one substrate-controlled type (*Glossifungites*), and a single softground continental type (*Scoyenia*). Frey and Seilacher (1980) added the *Trypanites* Ichnofacies to characterize borings associated with hardground substrates. Bromley et al. (1984) introduced the *Teredolites* Ichnofacies to encompass borings into xylic (woody) substrates. Frey and Pemberton (1987) proposed the *Psilonichnus* Ichnofacies for permanent vertical to inclined

Seilacher's Concept of Recurring Ichnofacies

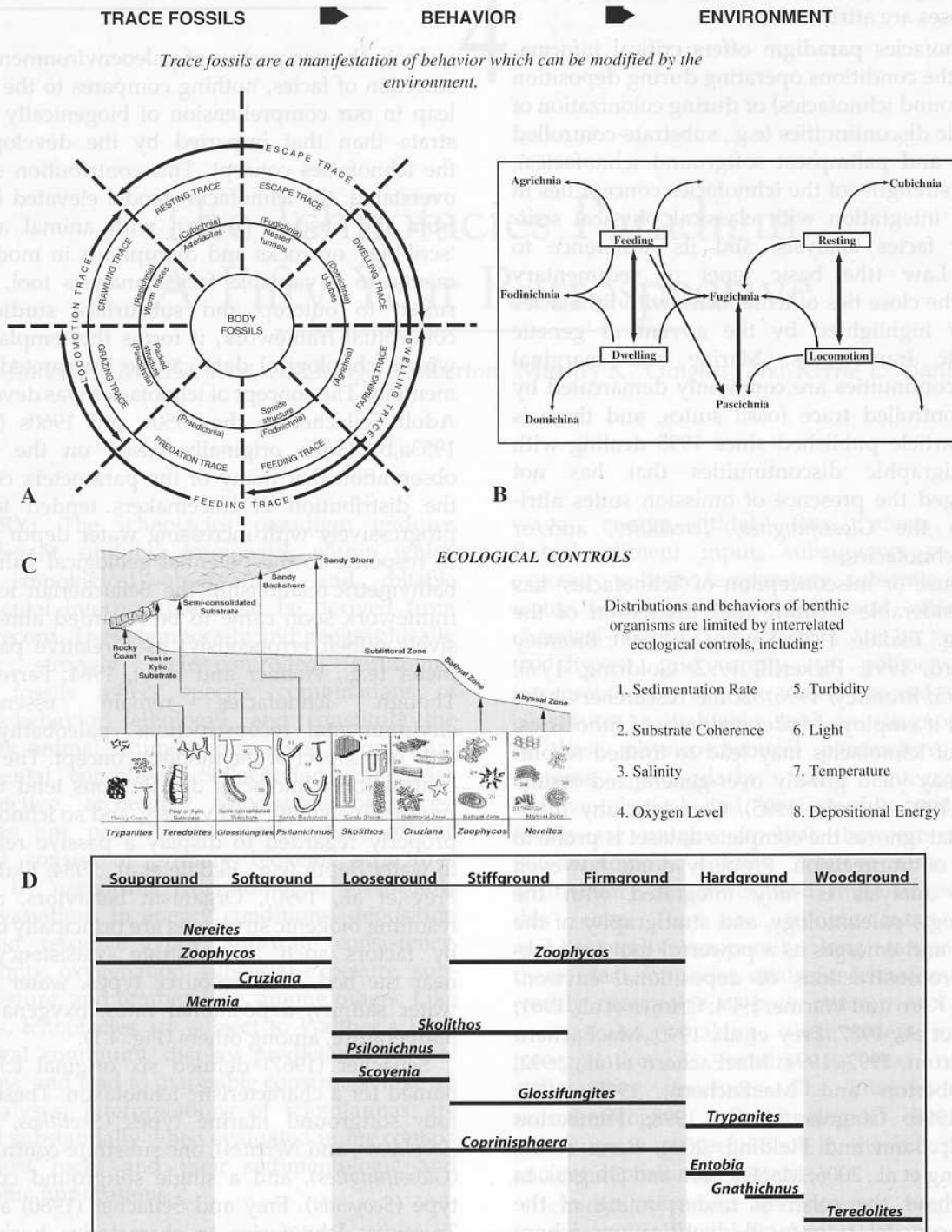


FIGURE 4.1 Seilacher's concept of recurring ichnofacies. (A) Ethological classification of trace fossils and their relationships with body fossils (Modified from Pemberton et al., 2001). (B) Behavioral classification of biogenic structures. With environmental fluctuations, virtually all traces are intergradational with the fugichnia (Modified from Pemberton et al., 2001). (C) Ecological controls that affect the distribution of trace-making organisms, many of which change predictably with relative water depth. (D) Relationship of substrate type and the distribution of the named ichnofacies.

dwelling in sand-prone substrates typical of high intertidal and supratidal coastal settings. These constitute the nine ichnofacies that have demonstrated recurrence both spatially and temporally. More recently, the hardground setting has been proposed to include two additional ichnofacies (*Gnathichnus* and *Entobia*) (Bromley and Asgaard, 1993). The continental setting has likewise seen some expansion, with the initial proposal of the *Termitichnus* Ichnofacies to address assemblages associated with paleosols (Smith et al., 1993) and *Mermia* Ichnofacies to reflect suites occupying lacustrine settings (Buatois and Mángano, 1995). Since then, the *Termitichnus* Ichnofacies has been discarded, in favor of the *Coprinisphaera* Ichnofacies (Genise et al., 2000).

CONTINENTAL ICHNOFACIES

There are currently three continental ichnofacies: *Scoyenia*, *Mermia*, and *Coprinisphaera* (Table 4.1). The systematic ichnological analysis of the continental realm has been a relatively recent development, with an ever increasing number of case studies being added to the developing models. Researchers have demonstrated that the continental regime is far more diverse and complex ichnologically than previously considered. Buatois and Mángano (2004) have recently summarized the *Mermia* and *Scoyenia* ichnofacies, typical of permanently to intermittently aquatic continental environments. Genise et al. (2000, 2004) have summarized many of the principal elements of the *Coprinisphaera* Ichnofacies, characteristic of more or less permanently terrestrial conditions, ranging from dry and cold to humid and warm climates. Donovan (1994) and Hasiotis (2002) have approached the study of continental ichnology from slightly different perspectives, yielding innovative insights into these regimes as well.

Scoyenia Ichnofacies

Frey et al. (1984) summarized and refined the original designation of Seilacher's (1967) *Scoyenia* Ichnofacies, and concluded that it remained a valid recurring grouping. Buatois and Mángano (1995) further refined the *Scoyenia* Ichnofacies, and placed it within a broader continental spectrum. The *Scoyenia* Ichnofacies (Fig. 4.2A, Table 4.1) is characteristic of low-energy continental settings characterized by periodically subaerial conditions. Most settings are inundated intermittently with freshwater. Common depositional environments include lake margins,

fluvial channel margins and overbanks, progressively desiccated crevasse splays, and wet interdune areas (e.g., Seilacher, 1967; Ekdale et al., 1984; Frey et al., 1984; Frey and Pemberton, 1987; Bromley and Asgaard, 1991; Buatois and Mángano, 1995, 2004).

The *Scoyenia* Ichnofacies encompasses trace fossil suites that consist of: (1) horizontal, meniscate (back-filled) structures made by mobile deposit-feeding organisms (e.g., *Scoyenia* (Fig. 4.2D), *Beaconites*, *Taenidium*, and adhesive meniscate burrows; Fig. 4.2E); (2) horizontal, mobile deposit-feeding structures (e.g., *Planolites*); locomotion traces, including tracks and trails (e.g., *Umfolozia*, *Hexapodichnus*, *Acripes*, and *Cochlichnus*); (3) fish fin markings (e.g., *Undichna*; Fig. 4.2F); (4) vertical dwelling structures (e.g., *Camborygma*, *Macanopsis*, *Skolithos*, and *Cylindricum*); (5) horizontal dwelling structures (e.g., *Palaeophycus*); (6) a mixture of invertebrate (predominantly arthropod) and vertebrate structures (dwelling structures and footprints); and (7) plant root traces. Suites tend to display low to moderate diversities, with localized high abundances. Ornamented structures and scratch marks (e.g., *Scoyenia*) are more typical of endobenthic activity during subaerial exposure and substrate desiccation. The *Scoyenia* Ichnofacies may comprise two distinct expressions: one characterized by meniscate, back-filled structures without ornamentation developed in a soft substrate, and the second characterized by striated traces developed in a firm substrate, which commonly cross-cut the former (Buatois and Mángano, 2004).

Mermia Ichnofacies

The *Mermia* Ichnofacies (Fig. 4.2B, Table 4.1) was proposed by Buatois and Mángano (1995) for freshwater assemblages associated with low energy, permanently subaqueous conditions, largely characterized by high degrees of environmental stability. Such suites probably record the highest preservation potential of all continental regimes (Buatois and Mángano, 2004). In recent years, a number of case studies identifying the *Mermia* Ichnofacies have been recorded. Buatois and Mángano (1995) included a table summarizing occurrences of the *Mermia* Ichnofacies from the Carboniferous to the Pleistocene. Suites attributable to the *Mermia* Ichnofacies are characterized by a dominance of horizontal to sub-horizontal grazing (e.g., *Mermia*, *Gordia*; Fig. 4.2G, *Cochlichnus*, and *Helminthoidichnites*) and feeding traces produced by mobile detritus and deposit feeders (e.g., *Planolites*, *Treptichnus*, and *Circulichnus*),

TABLE 4.1 Summary of Basic Features and Environmental Implications of Continental Ichnofacies. (Modified from Buatois and Mángano, 1995 and Pemberton et al., 2001)

Characteristic Trace Fossils	Typical Benthic Environment
<i>Scoyenia</i> Ichnofacies	
<p>Small, horizontal, lined, back-filled feeding burrows; curved to tortuous, unlined feeding burrows; crawling traces, vertical cylindrical to irregular shafts; tracks and trails. Invertebrates mostly deposit feeders and predators; vertebrates are grovellers, predators or herbivores. Invertebrate diversity typically low, yet some traces may be abundant. Vertebrate tracks may be diverse and abundant around water bodies; dung or coprolites occur locally. Trackways moderately diverse and dominant in Paleozoic examples. Arthropods comprise the most important invertebrate trace-maker. Typical components include <i>Scoyenia</i>, <i>Beaconites</i>, <i>Planolites</i>, <i>Skolithos</i>, <i>Cruziana</i>, <i>Rusophycus</i>, <i>Camborygma</i>, <i>Palaeophycus</i>, <i>Umfolozia</i>, <i>Acripes</i>, and vertebrate tracks.</p>	<p>Moist to wet, pliable, argillaceous to sandy sediment at low energy sites; either very slightly submerged lacustrine or fluvial deposits periodically becoming emergent, or water side subaerial deposits periodically or becoming submergent; semi-aquatic vegetation may be present. Intermediate between fully aquatic and non-aquatic, continental settings. Physical sedimentary structures may include desiccation cracks and allied features. Typical sedimentary environments: transitional alluvial lake zones, floodplains, ephemeral lakes, ponds, and wet interdunes.</p>
<i>Mermia</i> Ichnofacies	
<p>Small, horizontal to subhorizontal, simple, non-specialized grazing trails dominant; common feeding traces; rare locomotion traces. Tracemakers mostly mobile deposit feeders. Diversity moderate to high. Colonization suites are typically of low diversity. Producers may include annelids, arthropods, nematodes, nematomorphs, oligochaetes, bivalves, gastropods, and fishes. Trails are dominant in Paleozoic examples, whereas an increase in burrows is recorded in post-Paleozoic occurrences. Typical components include <i>Mermia</i>, <i>Gordia</i>, <i>Helminthoidichnites</i>, <i>Cochlichnus</i>, <i>Treptichnus</i>, <i>Undichna</i>, <i>Lockeia</i>, <i>Tuberculichnus</i>, <i>Maculichna</i>, and <i>Planolites</i>.</p>	<p>Non-cohesive, fine-grained sediment in well-oxygenated, low energy, permanently subaqueous zones; sedimentation rates are normally low, but punctuated episodic deposition (e.g., turbidity currents, density underflows) may occur. Physical sedimentary structures may include parallel lamination, ripple cross-lamination, normal grading, tool and flute marks, as well as soft-sediment deformation structures. Typical sedimentary environments include deep and shallow lakes, and fjord lakes.</p>
<i>Coprinisphaera</i> Ichnofacies	
<p>Large and small traces, mostly dwelling burrows (including breeding structures), less common feeding burrows, rhizoliths, tracks, coprolites, and bite traces in leaves. Termite, bee, and beetle nests are typical. Ichnodiversity is moderate to high. Tracemakers comprise a mixture of vertebrates (mainly mammals), invertebrates (particularly various types of arthropods, as well as oligochaetes and annelids), and plants. Typical components include <i>Coprinisphaera</i>, <i>Termitichnus</i>, <i>Edaphichnium</i>, <i>Scaphichnium</i>, <i>Celliforma</i>, <i>Macanopsis</i>, <i>Ichnogyrus</i>, <i>Attaichnus</i>, <i>Pallichnus</i>, <i>Daimonelix</i>, and <i>Uruguay</i>.</p>	<p>Soft to incipient cohesive muddy, silty, sandy and marly sediment, in low-energy terrestrial areas; associated plant growth is highly variable, from humid forest to open country. Associated inorganic sedimentary structures include parallel lamination, erosive surfaces, and a wide variety of paleosol and diagenetic features (e.g., concretions). Sedimentary environments include various types of mature and, more rarely, immature paleosols developed within alluvial plains, desiccated floodplains, abandoned fluvial bars, zones marginal to dune fields, and coastal plains.</p>

as well as subordinate occurrences of locomotion traces (e.g., *Undichna* and *Maculichna*). Assemblages generally lack striated or scratch-marked structures, and vertebrate trackways. Fish, amphibian, reptile, and possibly even mammal feeding structures may, however, be present. Suites display relatively high to moderate diversities and abundances, particularly for lacustrine settings that are hydrologically open. Restriction of the water body commonly leads to heightened salinities and oxygen reduction, and ichnogenera diversities decline markedly. Consequently, ephemeral lakes may be largely devoid of bioturbation.

Coprinisphaera Ichnofacies

The *Coprinisphaera* Ichnofacies (Fig. 4.2C, Table 4.1) was erected by Genise et al. (2000) to accommodate suites associated with more or less permanently subaerially exposed continental settings. Their analysis showed the recurrence of 28 suites derived from 58 paleosol intervals, reflecting a variety of geographic locations. Recurrence in time is less clearly extensive, with assemblages spanning the Paleocene to Holocene. Ethologically, the principal grouping is nesting/breeding (calichnia), but suites also include dwellings employed as refugia, aestivation, and ambush

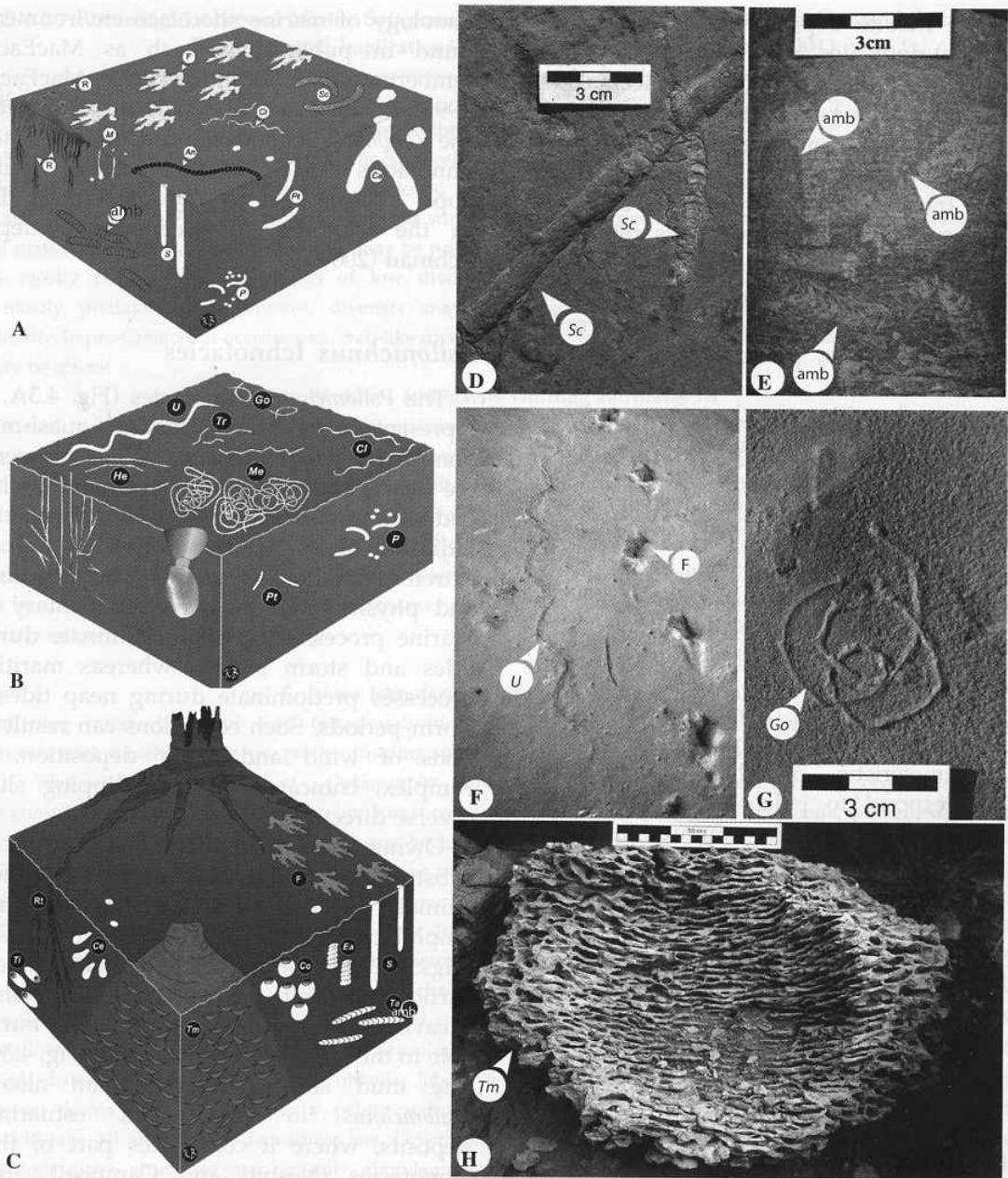


FIGURE 4.2 Schematic block diagrams of continental ichnofacies. (A) Diagram of the *Scoyenia* Ichnofacies. Traces include *Ancorichnus* (An), adhesive meniscate burrows (amb), *Camborygma* (Ca), *Cochlichnus* (Cl), tetrapod footprints (F), *Macanopsis* (M), *Palaeophycus tubularis* (Pt), *Planolites* (P), rhizoliths (R), *Scoyenia* (Sc), and *Skolithos* (S). (B) Diagram of the *Mermia* Ichnofacies. Traces include bivalve dwellings, *Cochlichnus* (Cl), *Gordia* (Go), *Helminthoidichnites* (He), *Mermia* (Me), *Planolites* (P), *Treptichnus* (Tr), *Palaeophycus tubularis* (Pt), and *Undichna* (U). (C) Diagram of the *Coprinisphaera* Ichnofacies. Traces include *Celliforma* (Ce), *Coprinisphaera* (Co), *Eatonichnus* (Ea), footprints (F), roots (Rt), *Skolithos* (S), adhesive meniscate burrows (amb), *Teisseirei* (Ti), and *Termitichnus* (Tm). (D) Scratch-marked expression of *Scoyenia* (Sc), with meniscate visible in the right-hand example, Triassic Tarkastad Subgroup, Karoo Basin, South Africa. (E) Adhesive meniscate burrows (amb), Lower Cretaceous Mannville, Group, Alberta, Canada. (F) Modern *Undichna* (U), formed by the pectoral fins of fish, and tetrapod footprints (F) in mud, Australia. (G) *Gordia* (Go), Upper Permian Balfour Formation, Karoo Basin, South Africa. (H) *Termitichnus* (Tm), Pleistocene of the Karoo Basin, South Africa. Photo (D) courtesy of Dr. Fiona J. Evans.

predation. Some mobile deposit-feeding structures, larger (vertebrate) domiciles, and rhizoliths may also be included in some suites. Predominant tracemakers include bees, ants, wasps, beetles, termites, and other unassigned insects. The ichnofacies namesake is for one of the most common structures; the nest structure of dung beetles. Trace fossil suites are prone to complex tiering patterns, particularly in mature soils, reflecting the variable depths of emplacement of hymenopterous, termite, and dung beetle nests. Suites show moderate to relatively high diversity, and generally high abundance of traces, particularly in mature paleosols.

The suites attributable to the *Coprinisphaera* Ichnofacies typically contain dung beetle nests (*Coprinisphaera*), bee traces (e.g., *Celliforma*, *Uruguay*, *Ellipsoideichnus*, *Palmiraichnus*, and *Rosellichnus*), wasp nests (e.g., *Chubutolithes*), ant traces (e.g., *Attaichus* and *Parowanichnus*), other beetle traces (e.g., *Monesichnus*, *Fontanai*, *Pallichnus*, *Eatonichnus*, and *Teisseirei*), and termite nests (e.g., *Termitichnus*; Fig. 4.2H, *Syntermesichnus*, and *Tacuruichnus*). Various larger mammal 'caves' may also be present, and the ichnofacies probably includes dwelling networks of rodents and other burrowing organisms.

Settings characteristic of the *Coprinisphaera* Ichnofacies correspond to paleosols developed in paleoecosystems of herbaceous communities. This may effectively limit the ichnofacies to units ranging from Late Cretaceous to the Holocene as there were no herbaceous communities earlier in Earth history. Climatically, settings range from arid and cold steppes (dominated by hymenopterous nests) to humid and hot subtropical savannas (dominated by termite nests). Paleosol settings occupy alluvial plains, desiccated floodplains, crevasse splays, levees, abandoned point bars, and vegetated eolian environments (Genise et al., 2000). These settings are strongly controlled by microclimates (e.g., temperature, radiation, humidity, and wind speed near the ground) associated with vegetation, topography, and overall climatic conditions (cf. Hasiotis, Chapter 16).

SOFTGROUND MARINE ICHNOFACIES

Softground ichnofacies tend to be differentiated from one another by variables that are typically depth related. The *Zoophycos* and *Nereites* ichnofacies are more characteristic of deeper-water environments, whereas the *Psilonichnus*, *Skolithos*, and *Cruziana* ichnofacies are represented in nearshore marine or coastal environments (Table 4.2). Summaries of the

ichnology of marine shoreface environments can be found in publications such as MacEachern and Pemberton (1992), Bromley (1996), MacEachern et al. (1999), Pemberton et al. (2001), and Bann et al. (2004). The *Zoophycos* Ichnofacies and especially the *Nereites* Ichnofacies tend to characterize outer shelf, slope, and bathyal to abyssal settings. For details on the ichnology of deep-marine deposits, see Uchman (2004).

Psilonichnus Ichnofacies

The *Psilonichnus* Ichnofacies (Fig. 4.3A, Table 4.2) represents a mixture of marine, quasi-marine, and non-marine conditions. Typical environments include the beach backshore, coastal dunes, washover fans, and supratidal flats. Frey and Pemberton (1987) indicated that such environments are subject to extreme variations in energy levels, sediment types, and physical and biogenic sedimentary structures. Marine processes generally dominate during spring tides and storm surges, whereas maritime eolian processes predominate during neap tides and non-storm periods. Such conditions can result in alternations of wind and water deposition, producing complex, truncated laminae dipping shallowly in diverse directions.

Owing to their topographic position, few such substrates are available to benthic marine animals. The only persistent, notable exceptions are amphibious crabs of the Family Ocypodidae (Figs. 4.3B,D), which include both scavengers and surficial deposit feeders; these animals typically excavate J-, Y-, or U-shaped dwelling burrows referable to the trace fossil *Psilonichnus* (Fig. 4.3C,E and F). The mud shrimp *Upogebia* can also construct *Psilonichnus* in subaqueous estuarine mouth deposits, where it constitutes part of the *Skolithos* Ichnofacies (Nesbitt and Campbell, 2002). Other biogenic structures are generated by essentially terrestrial organisms and include: (1) the vertical shafts of insects and spiders; (2) the horizontal tunnels of other insects and tetrapods; and (3) the ephemeral tracks, trails, and fecal pellets of insects, reptiles, birds, and mammals. The other major type of biogenic structure relates to plant-root penetrations. The types of plants able to exploit these substrates range from intertidal halophytes on the distal margins of some washover fans, to maritime or terrestrial grasses, weeds, vines, shrubs, bushes, and trees on backshore dunes.

To the extent that ocypodid crab burrows may occur in the uppermost foreshore or the upper part of

TABLE 4.2 Recurring Archetypal Marine Softground Trace Fossil Associations and their Common (but not exclusive) Environmental Implications (Adapted from Pemberton et al., 2001)

Characteristic Trace Fossils	Typical Benthic Environment
<i>Psilonichnus</i> Ichnofacies (shifting substrates I)	
<p>Predominantly vertical small shafts, some with bulbous basal cells, to larger, irregularly J-, Y-, or U-shaped dwelling burrows; local invertebrate and vertebrate crawling and foraging traces or surficial tunnels; algal mats, vertebrate tracks and coprolites may be present. Invertebrates mostly predators or scavengers of low diversity. Vertebrates mostly predators or herbivores; diversity may be appreciable locally. In pre-Cretaceous occurrences, crab-like dwelling structures may be absent.</p>	<p>Supralittoral to upper littoral, moderate to low-energy marine and/or eolian conditions subject to modification by torrential rains or storm surges. Associated with well-sorted, variably laminated to cross-stratified sands, to root- and burrow-mottled, poorly sorted sands or muddy sands. A common coastal setting, typically represented by the beach backshore and dunes, but also by washover fans and supratidal flats. Intergradational with the maritime terrestrial zone.</p>
<i>Skolithos</i> Ichnofacies (shifting substrates II)	
<p>Vertical, cylindrical or U-shaped dwelling burrows; protrusive and retrusive spreiten in some U-burrows, developed mainly in response to substrate aggradation or degradation (escape or equilibrium structures); forms of <i>Ophiomorpha</i> consisting predominantly of vertical or steeply inclined shafts. Animals are chiefly suspension feeders or passive (tubicolous) carnivores. Diversity is low, though given kinds of burrows may be abundant. Vertebrate biogenic structures may occur locally, especially in low-energy intertidal settings.</p>	<p>Lower littoral to infralittoral, moderate to relatively high-energy conditions most typical. Associated with slightly muddy to clean, well-sorted, shifting sediments subject to abrupt erosion or deposition. Higher energy increases physical reworking and obliterates biogenic sedimentary structures, leaving a preserved record of physical stratification. Generally corresponds to the beach foreshore and shoreface; but numerous other settings of comparable energy levels also may be represented, such as some estuarine point bars, tidal deltas, and deep-sea fans.</p>
<i>Cruziana</i> Ichnofacies (shifting to stable substrates)	
<p>Abundant crawling traces, both epi- and intrastratal; inclined U-shaped burrows with mostly protrusive spreiten (feeding swaths; soft-sediment <i>Rhizocorallium</i>); forms of <i>Ophiomorpha</i> and <i>Thalassinoides</i> consisting of irregularly inclined to horizontal components; scattered vertical cylindrical burrows (suspension feeders or passive carnivores). Animals may include mobile carnivores as well as various mixtures of suspension and deposit feeders. Diversity and abundance generally high, although crawling traces of limited diversity may predominate in certain Paleozoic nearshore settings.</p>	<p>In shallow marine settings, typically includes infralittoral to shallow circalittoral substrates below minimum but not maximum wave base, to somewhat quieter conditions offshore; moderate to relatively low energy; well-sorted silts and sands, to interbedded muddy and clean sands, moderately to intensely bioturbated; negligible to appreciable (though not necessarily rapid) sedimentation. A very common type of depositional environment, including not only shelves and epeiric embayments but also littoral to sub-littoral parts of certain estuaries, bays, lagoons, and tidal flats.</p>
<i>Zoophycos</i> Ichnofacies (oxygen-poor settings)	
<p>Relatively simple to moderately complex, efficiently executed grazing traces and shallow feeding structures; spreiten typically planar to gently inclined, distributed in delicate sheets, ribbons, lobes, or spirals (flattened forms of <i>Zoophycos</i> or, in pelitic sediments, <i>Phycosiphon</i>). Virtually all animals are deposit feeders. Diversity is very low, though given structures are typically abundant. The ichnogenus <i>Zoophycos</i> may also be abundant in the <i>Cruziana</i> and <i>Nereites</i> ichnofacies, under normal oxygen levels; occurrences of the ichnogenus thus do not necessarily constitute the ichnofacies.</p>	<p>Circalittoral to bathyal, quiet-water conditions, or protected intra-coastal to epeiric sites (silled basins, restricted lagoons) with muds or muddy sands rich in organic matter but more or less deficient in oxygen. Epeiric or coastal sites reflect somewhat stagnant waters. Offshore sites range from just below maximum wave base to fairly deep water, in areas free of turbidity flows or significant bottom currents. Where relict or palimpsest substrates are present, particularly if swept by shelf-edge or deeper water contour currents, this ichnofacies may be omitted in the transition from infralittoral to abyssal environments.</p>
<i>Nereites</i> Ichnofacies (turbidite-type settings)	
<p>Complex grazing traces and patterned feeding/dwelling structures, reflecting highly organized, efficient behavior; spreiten structures typically nearly planar, although <i>Zoophycos</i> forms are spiraled, multilobed, or otherwise very complex. Numerous crawling/grazing traces and sinuous fecal castings (<i>Helminthoidea</i>, <i>Cosmorhapha</i>), mostly intrastratal. Animals, chiefly deposit feeders or scavengers, although some may trap or farm microbes within essentially permanent, open domiciles (<i>Paleodictyon</i>, <i>Megagraption</i>). Diversity and abundance are generally significant.</p>	<p>Bathyal to abyssal, mostly quiet but oxygenated waters, in places interrupted by down-slope or down-canyon bottom currents or turbidity flows (flysch settings). Resident pelagic muds are typically bounded above and below by turbidites, some exhibiting complete Bouma cycles. In more distal regions, the sedimentary record is mainly one of continuous deposition and bioturbation; few physical or biogenic structures are preserved, unlike the <i>Nereites</i> Ichnofacies <i>sensu stricto</i>.</p>

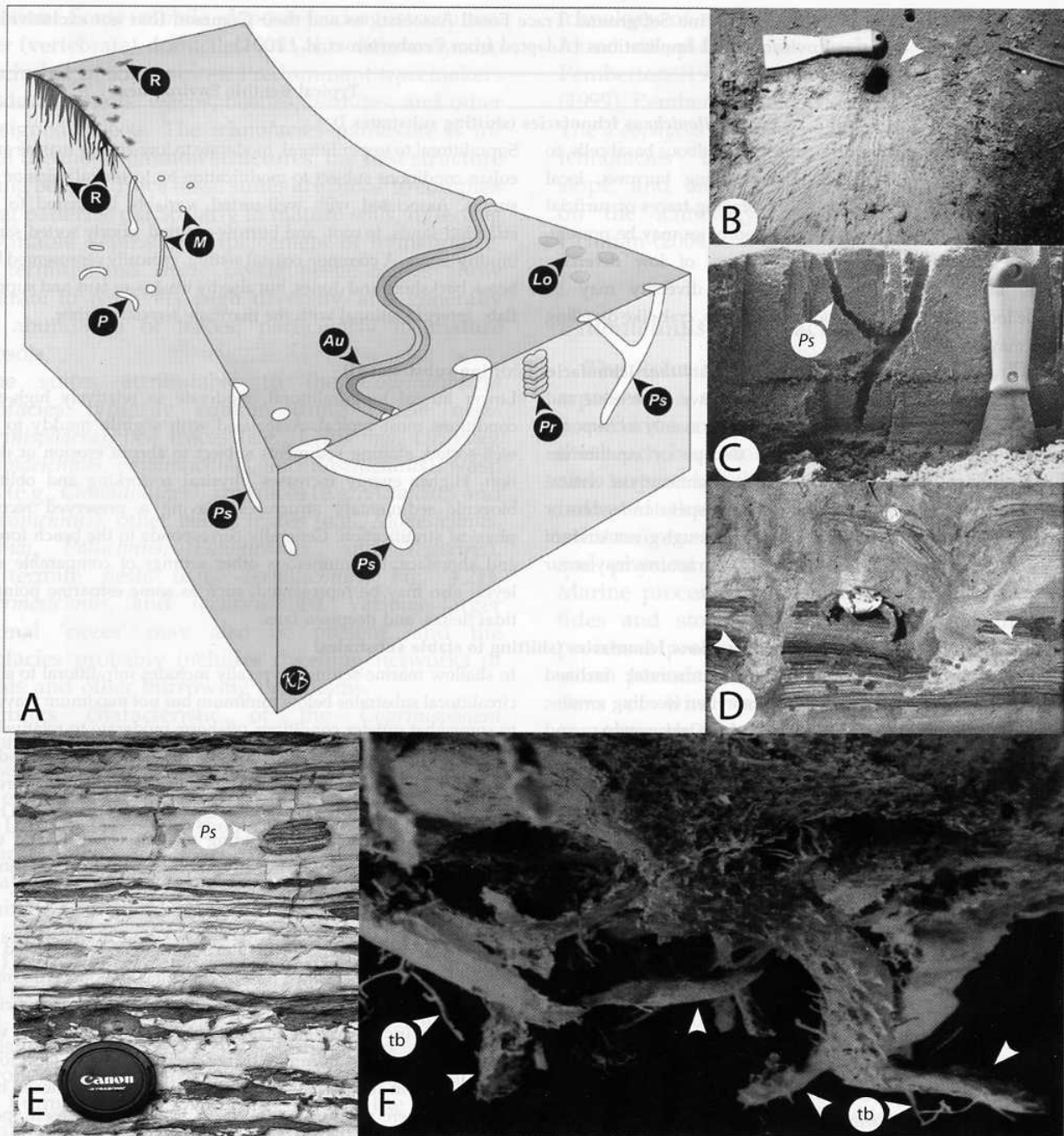


FIGURE 4.3 The *Pylonichnus* Ichnofacies. (A) Diagram of the *Pylonichnus* Ichnofacies developed in a back-barrier coastal dune setting. Traces include *Aulichmites* (Au), *Lockeia* (Lo), *Macanopsis* (M), *Planolites* (P), *Protovirgularia* (Pr), *Pylonichnus* (Ps), and rhizoliths (R). (B) Opening of modern *Ocypoda quadrata* in the backshore (arrow). (C) Y-shaped *Pylonichnus* (Ps) of the modern ghost crab in the backshore of Sapelo Island, Georgia, USA. (D) *Ocypoda quadrata* and the burrows that it makes (arrows) in the backshore, St. Catherines Island, Georgia, USA. (E) Outcrop photo of an inferred *Pylonichnus* (Ps), Pleistocene outcrop, Willapa Bay, Washington, USA. It is infilled with rhythmic (passive) laminations. (F) Resin cast of the burrows (unlabeled arrows) of *Hemigrapsus oregonensis* (shore crab) from the middle intertidal zone, Willapa Bay, Washington. Notable are the chelae impressions and (locally) commensal threadworm burrows (tb), likely of the capitellid polychaete *Heteromastus*.

estuarine point bars, the *Psilonichnus* Ichnofacies may slightly overlap the *Skolithos* Ichnofacies; however, the boundary between these two ichnofacies is normally distinct. In contrast, because of its potentially large numbers of terrestrial traces, the *Psilonichnus* Ichnofacies may be broadly intergradational with the continental *Scoyenia* and *Coprinisphaera* ichnofacies.

Skolithos Ichnofacies

The *Skolithos* Ichnofacies (Fig. 4.4A, Table 4.2) is indicative of relatively high levels of wave or current energy, and is typically developed in clean, well-sorted, loose or shifting particulate substrates. Abrupt changes in rates of deposition, erosion, and physical reworking of sediments are characteristic. Such conditions commonly occur on the shoreface and sheltered foreshores, but similar conditions may occur in a wide range of depositional environments (e.g., proximal wave-dominated delta fronts, sandy bars and spits, tidal channels and inlets, flood- and ebb -tidal deltas, sandy bay margins, low intertidal sand flats, estuary mouth complexes, and submarine fans). Associated stratification features typically consist of fine-scale, parallel to subparallel, gently seaward-dipping laminae (swash zone cross-strata) to large- and small-scale, multidirectional trough cross-stratification with current ripple cross-laminae. In strongly storm-dominated settings, low-angle, undulatory parallel lamination may be erosionally amalgamated into thick bedsets of swaley cross-stratification (SCS). In turbidites, beds may display massive, horizontal planar parallel, and current ripple cross-lamination (Bouma A, B, and C divisions). Settings characterized by tidal processes may show trough cross-beds and current ripples with cyclic development of mud drapes on foresets (i.e., tidal bundles), bidirectional orientations, and/or thin lenses of mud in the ripple troughs (i.e., flaser bedding).

As dictated by fundamental interrelationships of water agitation, sediment transport, and animal distribution, most tracemakers are suspension feeders. Substrates serve mainly as an anchoring medium. Infaunal organisms typically construct deeply penetrating, more or less permanent domiciles (Figs. 4.4B-I). Depth of burrowing in the intertidal zone is controlled, in part, by tidal range and height of the low-tide interstitial water column in the substrate. During low-tide, moist sediments at depth help to buffer organisms against desiccation and salinity or temperature shock, and also help to provide respiratory water. In both intertidal and high-energy

subtidal settings, deep burrowing is one means of escaping the instability of the ever-shifting substrate surface (Fig. 4.4).

The *Skolithos* Ichnofacies is characterized by: (1) predominantly vertical, cylindrical, or U-shaped burrows; (2) protrusive and retrusive spreiten in some U-burrows, which develop in response to substrate aggradation or degradation, respectively; (3) few horizontal structures; (4) few structures produced by mobile organisms; (5) low diversity suites, although individual forms may be abundant; (6) predominance of dwelling burrows constructed by suspension feeders or passive carnivores; and (7) vertebrate traces in some low-energy intertidal settings. Typical ichnogenera include *Skolithos* (Fig. 4.4I), *Diplocraterion* (Fig. 4.4H), *Ophiomorpha* (Fig. 4.4C,G and I), *Conichnus* (Fig. 4.4E,F), *Bergaueria*, *Lingulichnus*, *Piscichnus*, *Schaubcylindrichnus*, *Palaeophycus*, *Arenicolites* (Fig. 4.4B), and *Gyrolithes saxonicus*. Possible deposit-feeding structures that can be associated with the *Skolithos* Ichnofacies include *Taenidium*, *Siphonichnus*, *Macaronichnus*, *Cylindrichnus*, and *Rosselia* (Fig. 4.4D).

The *Skolithos* Ichnofacies ordinarily grades landward into supratidal or terrestrial zones and seaward into the *Cruziana* Ichnofacies. The landward boundary tends to be more abrupt than the latter. Finally, the *Skolithos* Ichnofacies may appear in slightly to substantially deeper-water deposits, wherever energy levels, food supplies, and/or hydrographic and substrate characteristics are suitable (Crimes et al., 1981). Potential examples include submarine canyons, deep-sea fans, and bathyal slopes swept by strong contour currents. Therefore, as emphasized previously, paleobathymetric interpretations cannot be based solely on checklists of trace fossil names: evaluation of associated physical sedimentary structures, stratigraphic position, and other facies evidence is essential, even in normal beach-to-offshore successions.

Cruziana Ichnofacies

The *Cruziana* Ichnofacies (Fig. 4.5A, Table 4.2) is most characteristic of permanently subtidal, poorly sorted, and unconsolidated cohesive (muddy) substrates in shallow marine settings typified by uniform salinity. Conditions typically range from moderate energy levels lying below fair-weather (minimum) wave base but above storm wave base, to lower energy levels in deeper, quieter waters. The most common settings correspond to the offshore extending to the very distal fringes of the lower shoreface. Variably impoverished

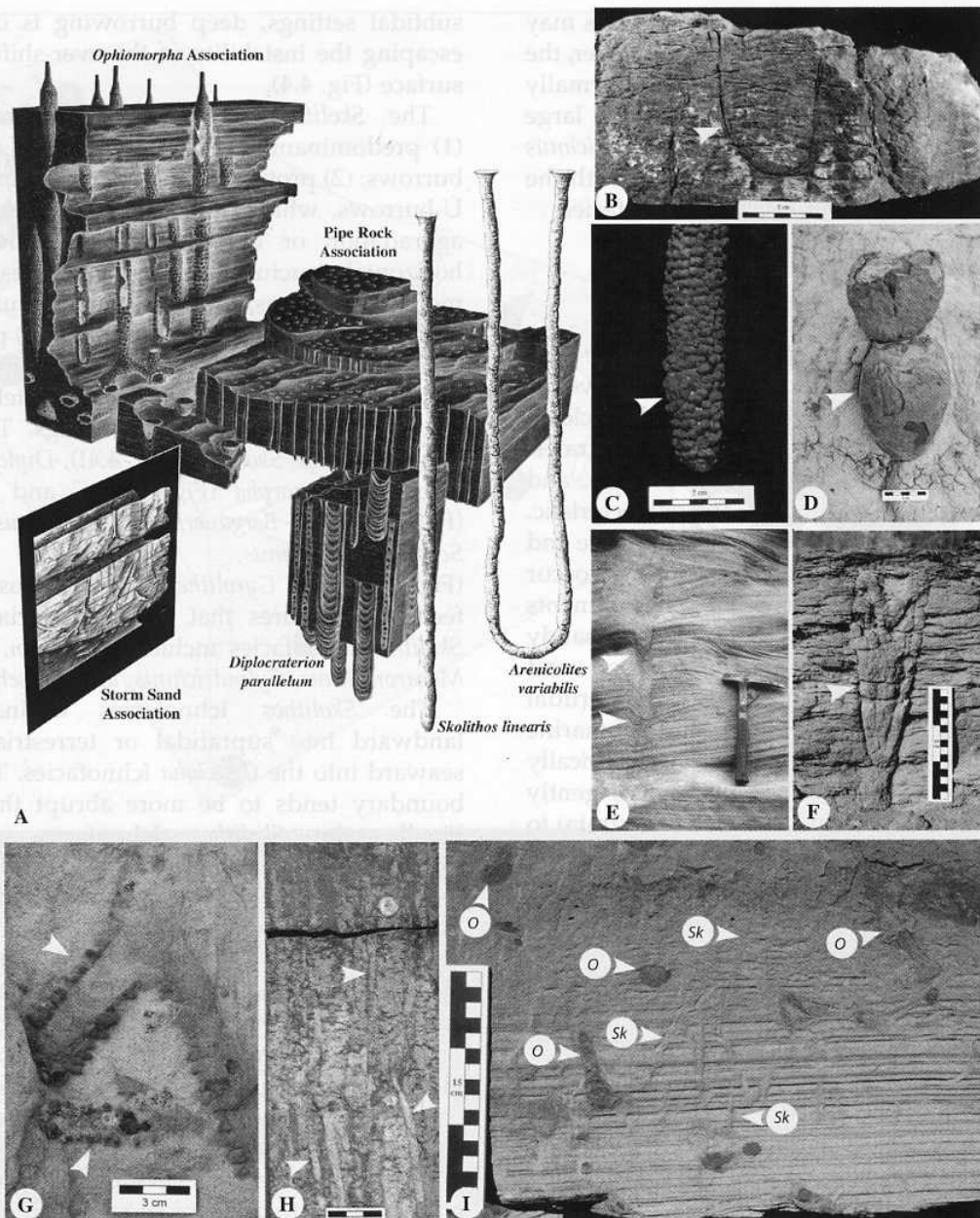


FIGURE 4.4 The *Skolithos* Ichnofacies. (A) Schematic block diagrams of the *Skolithos* Ichnofacies (artwork by Tom Saunders). (B) Sandstone with *Arenicolites* (arrow), Upper Cretaceous Horseshoe Canyon Formation, Alberta. (C) Siderite-cemented *Ophiomorpha borneensis* (arrow) from the Upper Cretaceous Appaloosa Sandstone, Drumheller, Alberta. (D) Vertically stacked (re-equilibrated), siderite-cemented *Rosselia socialis* (arrow), Upper Cretaceous Appaloosa Sandstone, Drumheller, Alberta. *Rosselia* is a common ichnogenus associated with the *Skolithos* Ichnofacies in storm-dominated successions, though it is a facies-crossing element of the *Cruziana* Ichnofacies. (E) *Conichnus conicus* (upper arrow) with associated escape/collapse structure (lower arrow) in upper shoreface deposits of the Upper Cretaceous Blackhawk Formation, Book Cliffs, Utah. (F) *Conichnus conicus* (arrow) from upper shoreface deposits of the Upper Cretaceous Appaloosa Sandstone, Drumheller, Alberta. (G) *Ophiomorpha nodosa* (arrow) with siderite-cemented pelleted margins, from the proximal lower shoreface deposits of the Upper Cretaceous Sego Sandstone, Utah. (H) Abundant *Diplocraterion habichi* (arrows), Middle Jurassic Fensfjord Formation, Northern North Sea, Norway. (I) Thick tempestite of the middle shoreface, with *Ophiomorpha nodosa* (O) and unlined *Skolithos linearis* (Sk), Upper Cretaceous Appaloosa Sandstone, Drumheller, Alberta.

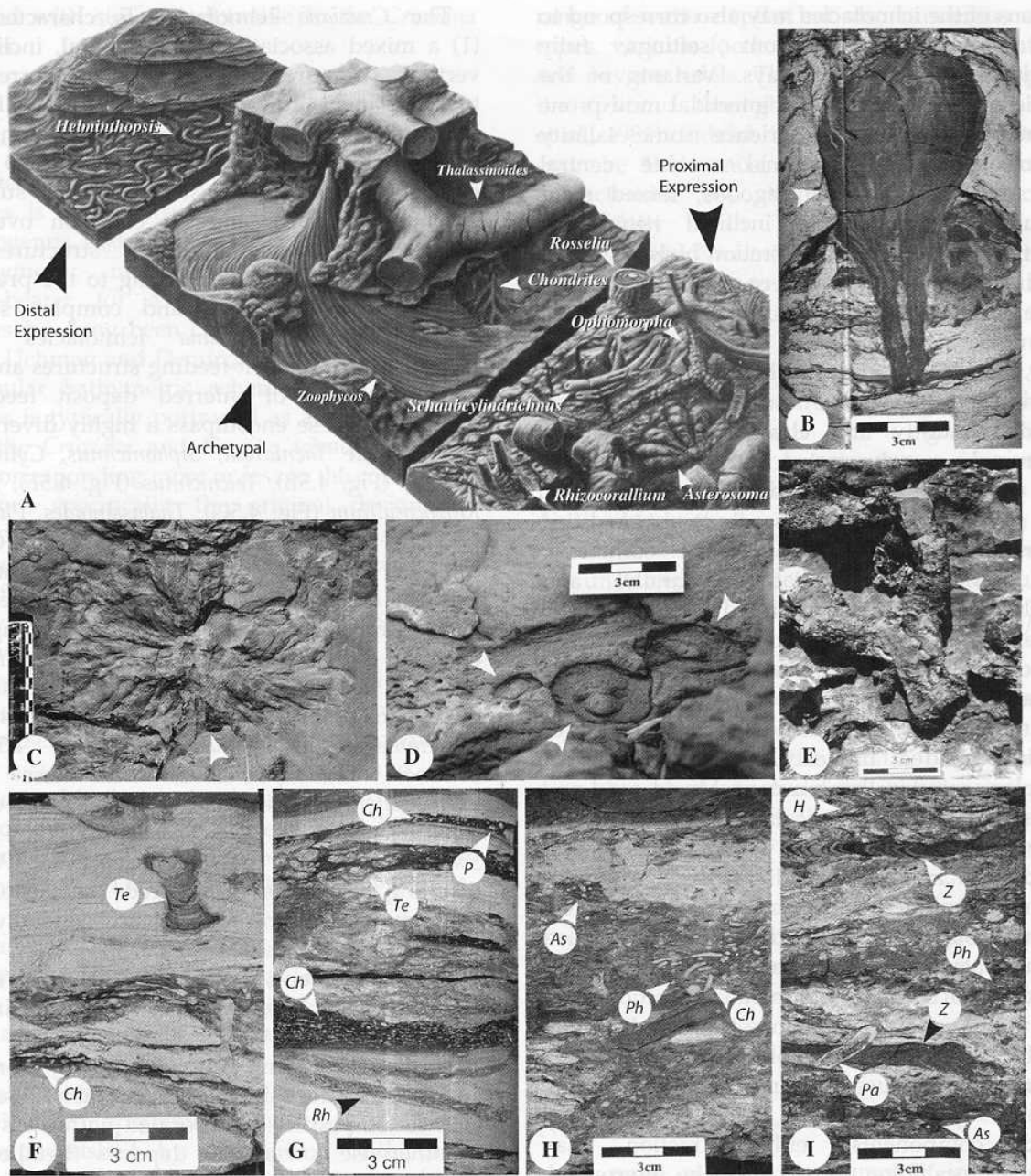


FIGURE 4.5 The *Cruziana* Ichnofacies. (A) Diagram of the *Cruziana* Ichnofacies showing the archetypal as well as distal and proximal expressions (artwork by Tom Saunders). (B) Siderite-cemented *Rosselia socialis* (arrow), Lower Cretaceous Viking Formation, Alberta. (C) Complete *Asterosoma* (arrow) exposed on bedding plane of outcrop, Upper Cretaceous Cardium Formation, Alberta. (D) *Asterosoma* lobes (arrows) in outcrop, Upper Cretaceous Blackhawk Formation, Book Cliffs, Utah. (E) Silicified *Thalassinoides* (arrow) showing Y-shaped branch, Mississippian Mount Head Formation, Mount Greenock, Jasper, Alberta. (F) Storm-bedded upper offshore deposits, with *Teichichnus* (*Te*) and *Chondrites* (*Ch*), Upper Cretaceous Cardium Formation, Alberta. (G) Heterolithic distal delta front deposits, with dense *Chondrites* (*Ch*), small *Teichichnus* (*Te*), *Planolites* (*P*), and *Rhizocorallium* (*Rh*), Lower Cretaceous Bow Island Formation, Alberta. (H) Upper offshore deposits with *Asterosoma* (*As*) (reburrowed with *Chondrites*), *Phycosiphon* (*Ph*), and robust *Chondrites* (*Ch*), Upper Cretaceous Cardium Formation, Alberta. (I) Upper offshore deposits with *Helminthopsis* (*H*), *Zoophycos* (*Z*), *Phycosiphon* (*Ph*), *Palaeophycus* (*Pa*), and *Asterosoma* (*As*), Upper Cretaceous Cardium Formation, Alberta.

expressions of the ichnofacies may also correspond to prodelta to distal delta-front settings, fully marine lagoons, and open bays. Variants of the ichnofacies occur in subtidal to intertidal mud-prone environments that may experience some salinity reductions, such as marginal marine central bays of estuaries, brackish lagoons, mixed sand and mud tidal flats, and inclined heterolithic stratification (IHS) in lateral accretion beds of tidally modified channels (MacEachern and Pemberton, 1994; MacEachern and Gingras, in press). Sediment textures and bedding styles exhibit considerable diversity, including thinly bedded, well-sorted silts and sands, discrete mud and shell layers, interbedded muddy and clean silts and sands, and extremely poorly sorted beds derived from any of the above, through intense bioturbation. Physical sedimentary structures, where not modified or destroyed by bioturbation, most commonly include low-angle, undulatory, parallel and subparallel lamination (interpreted as hummocky cross-stratification (HCS) and oscillation ripple laminated sand, alternating with silty or sandy mudstones. In restricted bays, estuarine central basins and lagoons, HCS is less common and/or more thinly bedded, but oscillation and combined flow ripples are typically abundant. Mixed sand and mud flats may display classical wavy, lenticular and pinstripe heterolithic bedding with current rippled sand beds, but in less markedly stressed examples such units may be pervasively bioturbated. Small-scale trough cross-bedded and current-rippled sands may also occur in some tidally generated lateral accretion bedding. Sediment deposition rates may be highly variable, and range from negligible to appreciable, though they are not normally rapid.

As a result of reduced but not negligible energy levels, food supplies consist of both suspended and deposited components; either fraction may predominate locally, or the two may be intermixed. Characteristic organisms, therefore, include suspension and deposit feeders, as well as mobile carnivores and scavengers. In response to lowered energy and cohesive substrates and an abundance of deposited food, tracemakers tend to construct their burrows horizontally rather than vertically, although scattered vertical or steeply inclined burrows occur locally. Profusions of burrows may be present at stable, low-energy sites. Trails of epibenthic and endobenthic foragers may also be common and reflect the abundance, diversity, and accessibility of food (Fig. 4.5). Surface grazing is also commonly associated but does not dominate the suites.

The *Cruziana* Ichnofacies is characterized by: (1) a mixed association of horizontal, inclined, and vertical structures, many of them corresponding to permanent to semi-permanent dwellings; (2) structures constructed by mobile organisms; (3) generally high diversity and abundance; (4) predominance of deposit-feeding structures with subordinate grazing structures; and (5) common overprinting of deep-tier over shallow-tier structures during continued burial, locally leading to the preservation of composite structures and complex structures. The dominant *Cruziana* Ichnofacies elements comprise both deposit-feeding structures and permanent dwellings of inferred deposit feeders (see Table 4.2). These encompass a highly diverse group, and include *Taenidium*, *Siphonichnus*, *Cylindrichnus*, *Rosselia* (Fig. 4.5B), *Teichichnus* (Fig. 4.5F), *Planolites*, *Rhizocorallium* (Fig. 4.5G), *Thalassinoides*, *Phoebichnus*, *Phycodes*, *Asterosoma* (Figs. 4.5C,D,I), *Chondrites* (Fig. 4.5F-H), and *Zoophycos* (Fig. 4.5I), though this list is by no means exhaustive. Resting structures and surface trails associated with deposit feeding are also common and include such structures as *Rusophycus*, *Cruziana*, *Lockeia*, *Gyrochorte*, and numerous others. Significant numbers of grazing structures such as *Helminthopsis* and *Phycosiphon* (Fig. 4.5H,I) are common and pervasive, with less common *Cosmorhapha* present locally. Passive carnivore structures such as *Palaeophycus* (Fig. 4.5I) and *Schaubcylindrichnus* may also be present. Permanent dwelling structures of inferred suspension-feeding and omnivorous tracemakers are generally uncommon, though in some successions they comprise significant elements to the suites. The main ichnogenera include *Ophiomorpha*, *Diplocraterion*, *Arenicolites*, and *Skolithos*.

In shallow waters, periodic scour by storm waves and renewed deposition following their cessation may lead to tempestites incorporated within a succession of otherwise low-energy deposits (Pemberton and MacEachern, 1997). Development of hummocky cross-stratification may involve the introduction of new sediment as well as the reworking of previously deposited sediment. Any of these conditions may yield burrow truncations and escape structures. Increased energy and allied parameters thus represent a temporary excursion of *Skolithos*-type conditions into an otherwise *Cruziana*-type setting. However, this overall bedding style differs from that of the main *Skolithos* Ichnofacies, in which stratification features, substrate scour, burrow truncations, and escape structures are contained entirely within discrete high-energy event beds, rather than persisting throughout the facies. Eventually, the storm beds are

overprinted with suites attributable to the *Cruziana* Ichnofacies.

Zoophycos Ichnofacies

Of all recurring marine ichnofacies, the *Zoophycos* Ichnofacies is most debated and least understood. The ichnogenus *Zoophycos* has an extremely broad paleobathymetric range; hence its designation as name-bearer for a supposedly depth-related ichnofacies has long been controversial (see Kotake, 1991; and Uchman and Demircan, 1999).

In popular bathymetric schemes, the *Zoophycos* Ichnofacies is typically portrayed as an intermediary between the *Cruziana* and *Nereites* ichnofacies, at a position corresponding more or less to the continental slope. More specifically, the original designation placed it in flysch-molasse areas below wave base and free of turbidites, within a broad depositional gradient (Seilacher, 1967).

As reevaluated (Seilacher, 1978; Frey and Seilacher, 1980), one of the major environmental controls represented by the ichnofacies is lowered oxygen levels, associated with organic debris accumulation in quiet-water settings. To some extent, these conditions do occur across the shelf-slope break, and thus the popularized bathymetric placement of the ichnofacies is commonly suitable. However, such reducing conditions replete with a dominance of *Zoophycos* are perhaps even better known in shallower water, epeiric deposits.

The *Zoophycos* Ichnofacies (Fig. 4.6A, Table 4.2) is characterized by suites that display: (1) low diversity, although individual traces may be abundant; (2) predominance of grazing structures and feeding structures produced by deposit feeders; (3) both shallow- and deep-tier structures; and (4) horizontal to gently inclined, spreiten-bearing structures. Suites appear impoverished by comparison with distal expressions of the *Cruziana* Ichnofacies, and are dominated by *Zoophycos* (Figs. 4.6B–D), *Helminthopsis* (Fig. 4.6C), *Phycosiphon* (Figs. 4.6E–G), *Cosmorhaphé* (Fig. 4.6C), and *Planolites* (Figs. 4.6B,G), with lesser *Chondrites*, *Thalassinoides* (Figs. 4.6F,G), *Scolicia* (Figs. 4.6F, G), and *Spirophyton* (Figs. 4.6F).

Considering the above characteristics of the ichnofacies, together with the widespread distribution of individual specimens of *Zoophycos* in both shallow- and deep-water deposits (Frey et al., 1990; Olivero and Gaillard, 1996; Uchman and Demircan, 1999), we speculate that *Zoophycos*-producing animals were simply broadly adapted in most ecologic respects. Some animals tolerated not only a considerable

range of water depths but also numerous substrate types, variable food resources, and different energy and oxygen levels. Their traces, therefore, appear in the *Cruziana* through *Nereites* ichnofacies (Crimes et al., 1981). Indeed, in final analysis, their tolerance may be their most distinguishing environmental characteristic. The animals were able to compete successfully with diverse tracemakers under *Cruziana*- and *Nereites*-type conditions, but few other animals were able to compete with them under the restricted conditions outlined above.

Due to its singular prominence in many restricted settings, the association seems to warrant its own ichnofacies designation. Conversely, the less restrictive the environment at a given site, the less distinctive the ichnofacies is as a separate entity. In numerous places, the ichnofacies is hardly discernible in the broad transition from the *Skolithos* or *Cruziana* to the *Nereites* ichnofacies, especially on unstable ancient slopes originally subject to turbidity flows, or swept by shelf-edge or contour currents.

Whatever the major environmental implications of the *Zoophycos* Ichnofacies and its variants, the final word is not yet in. The most important factors in the distribution of the animal, in addition to its own opportunism, evidently include water depth, depth of burrowing, sediment cohesiveness, and interstitial or bottom-water oxygen levels (Kotake, 1991; Olivero and Gaillard, 1996; Uchman and Demircan, 1999; and Olivero, 2003). Stressed quiet-water environments, particularly those exhibiting anoxia, seem to be the primary common denominator, even though the animal itself was cosmopolitan.

Nereites Ichnofacies

In most respects, bathymetric implications of the *Nereites* Ichnofacies (Fig. 4.7A, Table 4.2) are less equivocal than those of any other recurrent ichnofacies. Although numerous trace fossils otherwise typical of shallow-water deposits may range into deep-sea deposits, the reverse is not ordinarily true. In addition to water depth, turbidite deposition strongly influenced original environmental interpretations of the *Nereites* Ichnofacies. Despite this, depth- and energy-related variables appear to be of greater importance than turbidite deposition *per se* (Crimes et al., 1981; Leszczyński and Seilacher, 1991; Miller, 1993). For example, the ichnoenose persists today on distant abyssal plains essentially beyond the reach

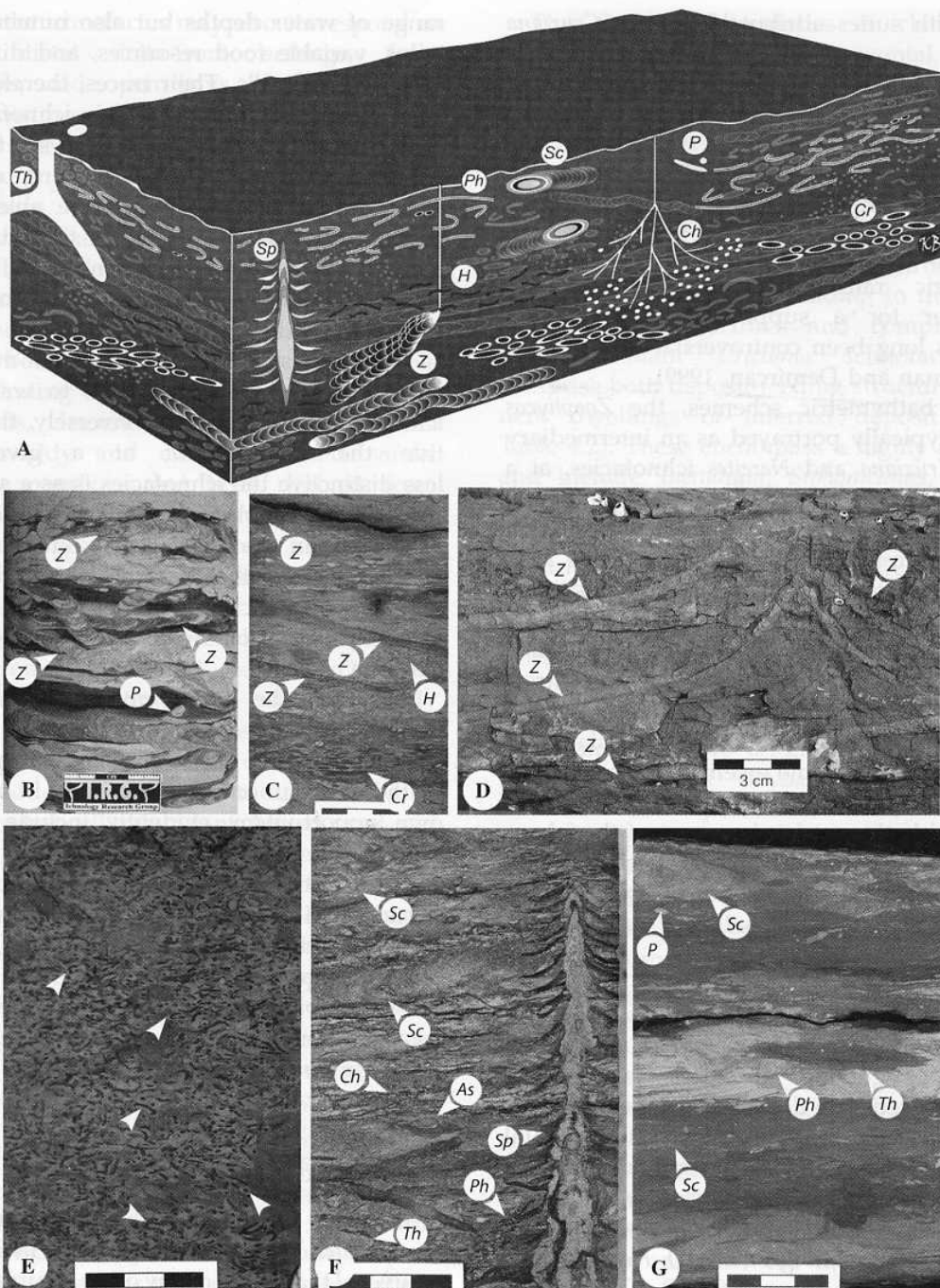


FIGURE 4.6 The *Zoophycos* Ichnofacies. (A) Diagram of the *Zoophycos* Ichnofacies. Traces include *Chondrites* (Ch), *Cosmorhaphis* (Cr), *Phycosiphon* (Ph), *Planolites* (P), *Scolicia* (Sc), *Spirophyton* (Sp), *Thalassinoides* (Th), and *Zoophycos* (Z). (B) Abundant *Zoophycos* (Z) and *Planolites* (P), Upper Cretaceous Doe Creek Formation, Alberta. (C) *Zoophycos* (Z), *Helminthopsis* (H), and *Cosmorhaphis* (Cr) in shelf deposits, Upper Cretaceous, Northern North Sea, Norway. (D) *Zoophycos* (Z) structure from slope deposits of the Upper Cretaceous Cedar District Formation, British Columbia. (E) Abundant *Phycosiphon* (arrows) in a shelf diatomite, Miocene Monterey Formation, San Joaquin Basin, California. (F) *Scolicia* (Sc), *Spirophyton* (Sp), *Chondrites* (Ch), *Phycosiphon* (Ph), *Thalassinoides* (Th), and diminutive *Asterosoma* (As) in shelf deposits of the Upper Cretaceous Northern North Sea, Norway. (G) *Scolicia* (Sc), *Planolites* (P), *Phycosiphon* (Ph), and *Thalassinoides* (Th) from shelf deposits of the Upper Cretaceous San Miguel Formation, Texas.

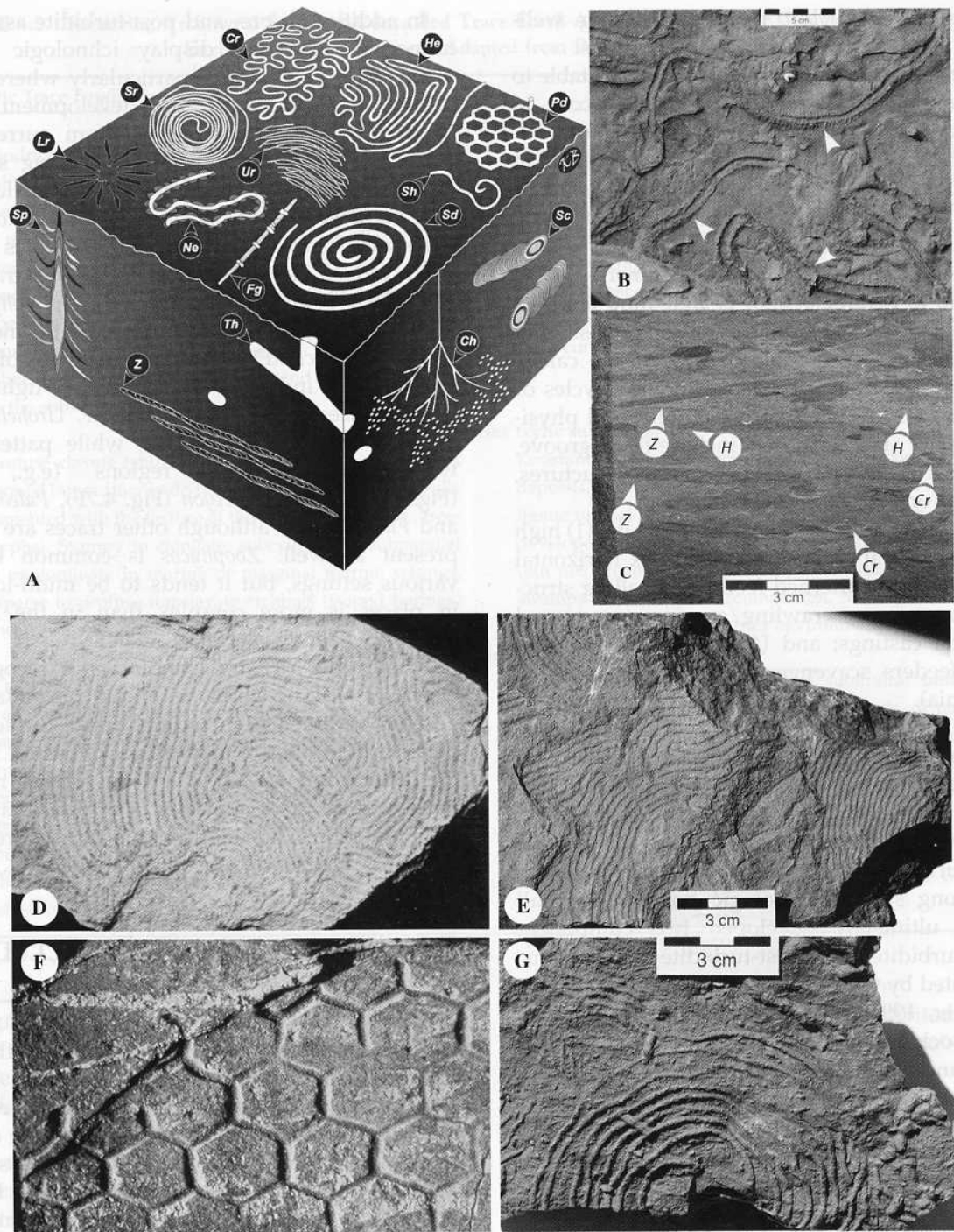


FIGURE 4.7 The *Nereites* Ichnofacies. (A) Diagram of the *Nereites* Ichnofacies. Traces include *Chondrites* (Ch), *Cosmorhaphes* (Cr), *Fustiglyphus* (Fg), *Helminthorhaphes* (He), *Lorenzina* (Lr), *Nereites* (Ne), *Paleodictyon* (Pd), *Planolites*, *Scolicia* (Sc), *Spirodesmos* (Sd), *Spirophycus* (Sh), *Spirophyton* (Sp), *Spirorhaphes* (Sr), *Thalassinoides* (Th), *Urohelminthoidea* (Ur), and *Zoophycos* (Z). (B) Bedding plane of *Scolicia* (arrows), Upper Cretaceous Nanaimo Group, British Columbia. (C) Thin, muddy *Zoophycos* (Z), with *Helminthopsis* (H), and *Cosmorhaphes* (Cr), Upper Cretaceous, North Slope of Alaska. (D) Bedding plane entirely covered with *Nereites*, Eocene Zumaya Flysch, Spain. (E) Bedding plane with abundant *Nereites*, Eocene, Austria. (F) *Paleodictyon* cast on the sole of a thin turbidite bed, Eocene Zumaya Flysch, Spain. (G) *Spirorhaphes* cast on the sole of a thin turbidite bed, Eocene, Austria.

of turbidity currents, but is absent among well-developed, shallow-water turbidite successions.

Nevertheless, most trace fossil suites attributable to the *Nereites* Ichnofacies studied to date occur in turbidite-rich successions, probably because the stratigraphic record of deep-water deposits examined in this context mainly represent subsiding basins or subduction zones, rather than the broad abyssal plain. Thus, associated sediments may consist of virtually any lithology, except that the ratio of sediment-gravity derived sand to hemipelagic or pelagic mud tends to diminish toward distal extremities of the deposit, and carbonates become increasingly scarce as the calcite compensation depth is approached. Bouma cycles or modified successions are common locally, and physical sedimentary structures may include flute, groove, and load casts as well as prod marks, flame structures, and linguoid or other current ripples.

The *Nereites* Ichnofacies is characterized by: (1) high diversity but low abundance; (2) complex horizontal grazing traces and patterned feeding/dwelling structures; (3) numerous crawling/grazing traces and sinuous fecal castings; and (4) structures produced by deposit feeders, scavengers, or possibly harvesters (i.e., *agrichnia*).

Animals exploiting lower bathyal to abyssal environments have two principal concerns: (1) scarcity of food, relative to more abundant supplies in shallower settings, and (2) periodic disruption by strong, down-canyon bottom currents or actual turbidity currents. In response to the latter factor, and over long spans of geologic time, the overall community ultimately developed two component parts: pre-turbidite and post-turbidite associations, as documented by their respective traces (Leszczyński and Seilacher, 1991; Miller, 1993). The pre-turbidite resident association is characteristic of quiet, normal conditions and is dominant wherever the substrate is free of the influence of turbidity currents. It tends to be overwhelmed or eliminated by severe erosion or turbulence, however, and is replaced by the post-turbidite association after cessation of the turbidity current. As conditions then revert to the normal, prevailing low-energy setting, the pre-turbidite association gradually reestablishes itself. Pre-turbidite animals thus comprise a stable, persistent community, well adapted to quiet conditions, derived mainly from original early-Paleozoic colonizers of the deep-sea floor. In contrast, post-turbidite animals represent a more opportunistic, less stable community better adapted to turbidite colonization, derived mainly from subsequent evolutionary immigrants from shallower waters (Frey and Seilacher, 1980).

In addition to pre- and post-turbidite associations, numerous turbidites display ichnologic gradients along depositional dips, particularly where they are related to submarine fan development (Crimes et al., 1981). Where strong bottom currents issue from submarine canyons or flow along submarine fan channels, components of the *Skolithos* Ichnofacies may be present (e.g., *Ophiomorpha* and *Diplocraterion*). Otherwise, proximal parts of turbidites may be characterized by rosetted or radiating traces (e.g., *Lorenzina*, *Spirorhapse* (Fig. 4.7G), *Spirophycus*, and *Zoophycos* (Fig. 4.7C)), as well as gently meandering forms of *Scolicia* (Fig. 4.7B). Medial areas of deep-sea fans may be indicated by spiraled or tightly meandering traces (e.g., *Helminthorhapse*, *Urohelminthoida*, and *Cosmorhapse* (Fig. 4.7C)), while patterned networks typify distal regions (e.g., *Nereites* (Figs. 4.7D,E), *Paleodictyon* (Fig. 4.7F), *Paleomeandron*, and *Fustiglyphus*) although other traces are generally present as well. *Zoophycos* is common locally in various settings, but it tends to be multi-lobed, and in places is more complex than in the *Zoophycos* Ichnofacies (cf. Savary et al., 2004).

Finally, the *Nereites* Ichnofacies is recognized in Deep Sea Drilling Cores, within unconsolidated, fine-grained sediments, including distal turbidites and pelagic rhythmites of modern ocean basins. However, the association *per se*, if present, tends not to be preserved on great expanses of abyssal plain, where sedimentation and bioturbation are more or less constant, rather than episodic (Scholle et al., 1983).

SUBSTRATE-CONTROLLED ICHOFAECIES

The ichnofacies paradigm recognizes three substrate-controlled ichnofacies: *Glossifungites*, *Teredolites* and *Trypanites* (Table 4.3). Each ichnofacies reflects different substrate consistencies at the time of colonization, and so, intuitively reflect palimpsest suites that typically cross-cut the original suites. In many examples, these ichnofacies are associated with erosionally exhumed discontinuities in the rock record, though scenarios favoring autocyclic development are also locally common (see MacEachern et al., Chapter 7). In the case of the *Glossifungites* Ichnofacies, firmground suites may be intergradational with palimpsest softground suites, particularly where substrates pass from muddy to sandy; burial compaction may lead to firm or stiff mud, but allow sands to retain their non-cohesive character. Likewise, trace suites attributable to the *Glossifungites* Ichnofacies may

TABLE 4.3 Recurring Archetypal Substrate-Controlled Trace Fossil Associations and their Common (but not exclusive) Environmental Implications (Adapted from Pemberton et al., 2001)

Characteristic Trace Fossils	Typical Benthic Environment
<i>Glossifungites</i> Ichnofacies (firm substrates)	
Vertical cylindrical, U-, or tear-shaped borings, or sparsely to densely ramified dwelling burrows, or various mixtures of burrows and borings. Protrusive spreiten in some U-shaped burrows, developed mostly through growth of animals (fan-shaped <i>Rhizocorallium</i> and <i>Diplocraterion</i> , formerly <i>Glossifungites</i>). Many intertidal species (e.g., crabs) leave the burrows to feed; others are mainly suspension feeders. Diversity is typically low, yet given kinds of structures may be abundant. Unlike ichnogenera of the <i>Trypanites</i> Ichnofacies, those of <i>Glossifungites</i> tend to avoid obstructions within the substrate.	Firm but unlithified marine littoral and sublittoral omission surfaces, especially semiconsolidated carbonate firmgrounds or stable, cohesive, partially dewatered muddy substrates either in protected, moderate-energy settings or in areas of somewhat higher energy where semiconsolidated micritic or siliciclastic substrates offer resistance to erosion. The final sedimentary record typically consists of a mixture of relict and palimpsest features, including cross-cutting ichnofaunas.
<i>Teredolites</i> Ichnofacies (xylic substrates)	
Sparse to profuse clavate (shipworm) borings. Dense excavations may be deformed but ordinarily do not interpenetrate. Boring walls may be ornamented with the texture of the host substrate (e.g., tree-ring xenoglyphs). Stumpy to elongate, subcylindrical, subparallel excavations predominate in marine or marginal marine settings. Shallower, sparse to profuse nonclavate etchings (isopod borings) typify freshwater ichnofaunas.	Resistant substrates consisting of driftwood pavements, peat deposits, or related xylic substances, many of which appear as lignite or coal in the rock record. May represent omission surfaces developed on matted wood clasts, log jams, or other xylic materials (but not single clasts or trunks), or slow deposition in marshy or swampy areas of peat accumulation. Most common in estuarine, deltaic, or various backbarrier environments.
<i>Trypanites</i> Ichnofacies (hard substrates)	
Cylindrical to vase-, tear-, or U-shaped to irregular domiciles of endoliths, oriented normal to the respective substrate surface, or shallow anastomosing systems of borings (sponges, bryozoans); excavated mainly by suspension feeders or passive carnivores. Raspings and gnawings of algal grazers and equivalent organisms (chitons, limpets, echinoids mainly). Diversity moderately low, although borings or scrapings of given kinds may be abundant. In particulate lithic substrates, margins of borings cut through grains or shells instead of skirting them.	Consolidated marine littoral and sublittoral omission surfaces (rocky coasts, beachrock, hardgrounds), reefs, or particulate strata formed of organic constituents (bone beds, shell beds, coquinities, but not individual bones, shells, or clasts). Bioerosion is as important as (and serves to accelerate), physical erosion of the substrate. Intergradational with the <i>Glossifungites</i> Ichnofacies; in sequential hardground development, suites of the <i>Trypanites</i> Ichnofacies may crosscut earlier suites of the <i>Glossifungites</i> or <i>Cruziana</i> ichnofacies.

be intergradational with hardground suites of the *Trypanites* Ichnofacies, where differential compaction and/or cementation occur (e.g., Bromley, 1975, 1996). The *Teredolites* Ichnofacies is somewhat more problematic in this grouping, as the consistency of the substrate may or may not fundamentally change prior to colonization. Some woodground suites correspond to the colonization of the xylic substrate prior to coalification, and this is particularly apparent in modern ichnocoenoses of Willapa Bay (Gingras et al., 2004). Some, however, are associated with erosional discontinuities that have 'bottomed-out' on a coal seam (presumably xylic material coalified prior to exhumation) (e.g., Bromley et al., 1984). The anomalous nature of a xylic medium for endobenthic colonization probably justifies its inclusion with these other 'substrate-controlled' ichnofacies, though it is somewhat distinct from the progressive change in

original substrate consistency exhibited from soft-ground through firmground and into hardground scenarios.

***Glossifungites* Ichnofacies**

The *Glossifungites* Ichnofacies (Fig. 4.8A, Table 4.3) is characteristic of firm but unlithified substrates, such as dewatered muds, though less commonly incipiently cemented sands may also host the firmground ichnogenera. In most siliciclastic settings, trace suites attributable to the *Glossifungites* Ichnofacies constitute the most widespread and pervasive expression of the substrate-specific suites. These demarcate a number of discontinuities of both sequence stratigraphic importance (e.g., sequence boundaries, transgressive surfaces of erosion, and amalgamated sequence

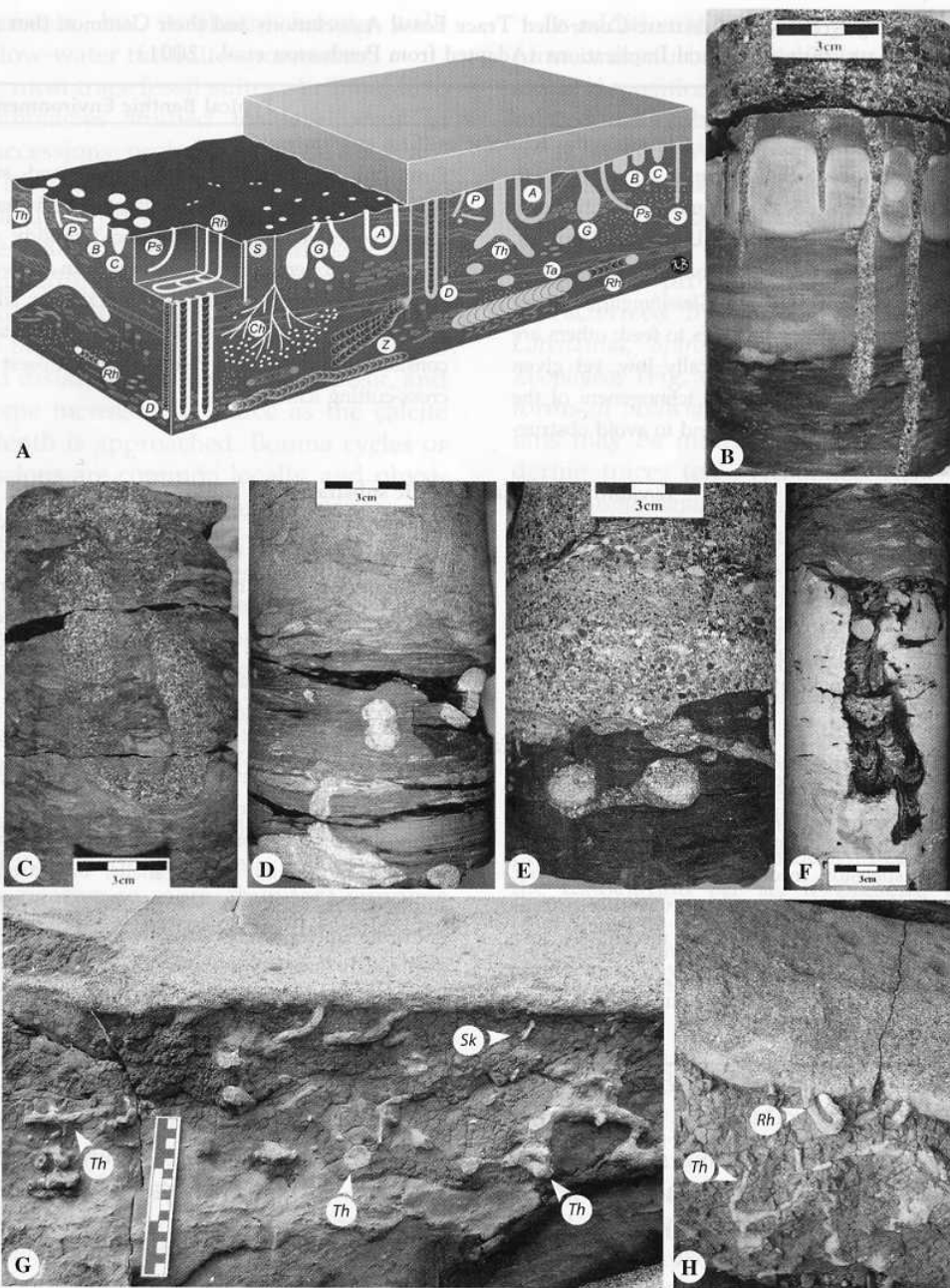


FIGURE 4.8 The *Glossifungites* Ichnofacies. (A) Diagram of the *Glossifungites* Ichnofacies. Firmground ichnogenes include *Skolithos* (S), *Gastrochaenolites* (G), *Arenicolites* (A), *Diplocraterion* (D), *Psilonichnus* (Ps), *Conichnus* (C), *Bergaueria* (B), *Palaeophycus* (P), *Taenidium* (Ta), *Rhizocorallium* (Rh), *Thalassinoides* (Th), *Chondrites* (Ch), and *Zoophycos* (Z). (B) Firmground *Skolithos* cross-cutting offshore mudstone and subtending from an amalgamated sequence boundary and flooding surface, Lower Cretaceous Viking Formation, Alberta. (C) Firmground *Arenicolites* filled with coarse-grained sandstone, associated with a transgressive surface of erosion, Lower Cretaceous Viking Formation, Alberta. (D) Firmground *Thalassinoides* subtending from an incised valley complex, Upper Cretaceous Dunvegan Formation, Alberta. (E) Firmground *Rhizocorallium* subtending from the base of an estuarine incised valley complex, Lower Cretaceous Viking Formation, Alberta. (F) Firmground *Diplocraterion* associated with a transgressive surface of erosion, Jurassic Gravelburg Formation, Saskatchewan. (G) Submarine canyon margin with a firmground suite of *Thalassinoides* (Th), and *Skolithos* (Sk), lower Miocene Nihotupu and Tirikohua formations, Northland, New Zealand. (H) Firmground *Rhizocorallium* (Rh) and *Thalassinoides* (Th) demarcating the same discontinuity as shown in (G).

boundaries and flooding surfaces) and autocyclic derivation (e.g., cut-bank margins of tidal channels, periodically exposed intertidal flats, etc.). The sequence stratigraphic significance of the *Glossifungites* Ichnofacies has been addressed by Savrda (1991a), MacEachern et al. (1992), Pemberton and MacEachern (1995, 2005), Pemberton et al. (2004) and MacEachern et al. (this volume).

Firmground ichnogenera are dominated by vertical to subvertical dwelling structures of suspension-feeding organisms (Figs. 4.8B–F). The most common structures correspond to the ichnogenera *Diplocraterion* (Fig. 4.8F), *Skolithos* (Figs. 4.8B,G), *Psilonichnus*, *Arenicolites* (Fig. 4.8C) *Conichnus*, *Bergaueria*, and firmground expressions of *Gastrochaenolites*. Dwelling structures of inferred deposit-feeding organisms are also constituents of the ichnofacies, and include firmground *Thalassinoides* (Figs. 4.8D,G,H), *Spongiomorpha*, *Taenidium*, *Palaeophycus*, *Chondrites*, and *Rhizocorallium* (Figs. 4.8E,H). More recently, *Zoophycos* has been recognized to occur within firmground suites (MacEachern and Burton, 2000). The presence of vertical shafts within shaly intervals is anomalous, as these structures are not capable of being maintained in soft muddy substrates. *Glossifungites* elements are typically robust, commonly penetrating 20–100 cm below the bed junction. Many shafts tend to be of large diameter (e.g., 0.5–1.5 cm), particularly *Diplocraterion habichi* and *Arenicolites*. This scale of burrowing contrasts markedly with the predominantly horizontal and diminutive trace fossils typical of shaly intervals. Firmground traces are also generally sharp-walled and unlined, locally with scratch-marked margins, reflecting the stiff, cohesive nature of the substrate at the time of colonization and burrow excavation. Further evidence of substrate stability, atypical of soft muddy beds, is the passive nature of burrow fill. This demonstrates that the structure remained open after the trace-maker vacated the domicile, thus allowing material from subsequent depositional events to be piped into the open burrow. The post-depositional origin of trace fossil suites attributable to the *Glossifungites* Ichnofacies is clearly demonstrated by the ubiquitous cross-cutting relationships with the previous softground assemblages. The final characteristic of the firmground suites is their tendency to demonstrate colonization in large numbers. In numerous examples, seven to fifteen firmground traces, most commonly *Diplocraterion habichi*, have been observed on the bedding plane of

a 9 cm (3.5 inch) diameter core, corresponding to a density between 1100 and 2300 shafts per m².

Teredolites Ichnofacies

The *Teredolites* Ichnofacies (Fig. 4.9A, Table 4.3) encompasses suites of borings excavated into xylic (woody or coaly) substrates (Bromley et al., 1984; Savrda, 1991b). It is critical to identify whether the woodground borings were excavated into an *in situ* xylic horizon (i.e., reflecting a substrate) or allochthonous (e.g., transported logs in coastal or marine environments). Savrda et al. (1993) applied the term 'log-grounds' to high concentrations of allochthonous wood strewn across a depositional surface. Only traces excavated into an *in situ* substrate, or bored into an allochthonous log-ground *after* log deposition constitute the *Teredolites* Ichnofacies (cf., Pemberton et al., 2001; MacEachern et al., Chapter 7). Isolated logs containing wood borings do not constitute the *Teredolites* Ichnofacies. Log-grounds consisting of logs bored prior to emplacement may form useful mappable horizons but do not constitute the ichnofacies, because the borings do not record colonization of a continuous substrate. Determining the timing of wood boring in such log-grounds may prove challenging.

The *Teredolites* Ichnofacies, as described from the rock record, is probably confined to marine and marginal marine settings. The principal namesake, *Teredolites*, reflects the borings of wood-boring bivalves (Fig. 4.9C), which in the present day only occur in fully marine to slightly salinity-reduced environments. The presence of the ichnogenera *Teredolites* (Figs. 4.9B–E,G), *Thalassinoides* (Fig. 4.9F), and *Diplocraterion* excavated into xylic material is taken, therefore, to indicate largely marine conditions. Non-marine wood borings do occur, but these are predominantly insect generated and lack marine ichnogenera. Hasiotis (2002) provides a good summary of the characteristics of terrestrial wood borings.

Most rock-record occurrences of woodgrounds display a low diversity of trace fossils (e.g., Bromley et al., 1984; Savrda, 1991b; Savrda et al., 1993). These low-diversity suites are dominated by penetrative borings attributable to *Teredolites longissimus* and *Teredolites clavatus*. Woodground trace suites are commonly monospecific, however, size-class variations have been observed in some of the boring assemblages (e.g., Bromley et al., 1984; Savrda et al., 1993). Modern wood-boring occurrences in the marine realm show higher diversities

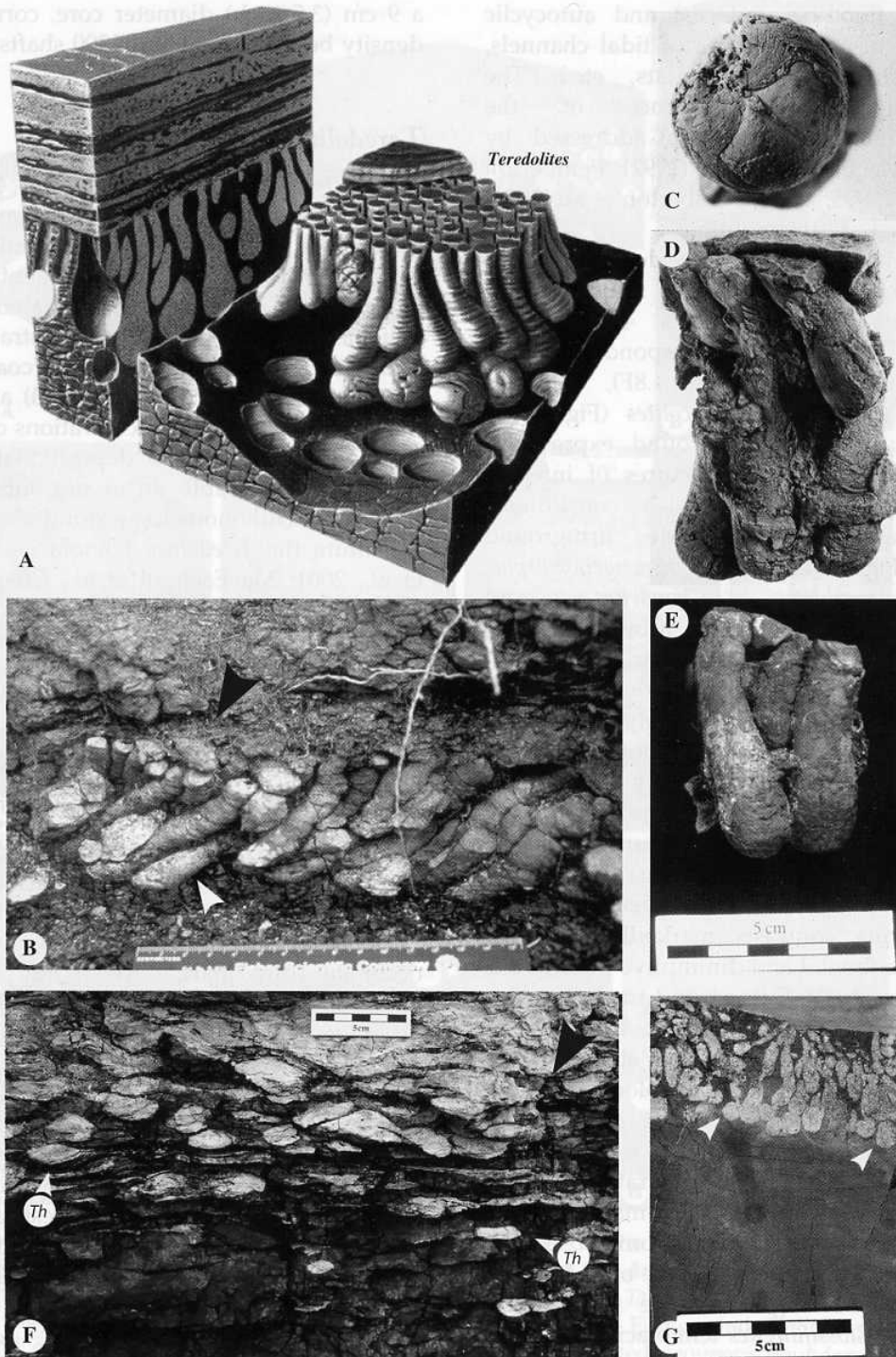


FIGURE 4.9 The *Teredolites* Ichnofacies. (A) Diagram of the *Teredolites* Ichnofacies (artwork by Tom Saunders). (B) *Teredolites clavatus* (white arrow) in peat horizon, truncated by mud-filled channel (black arrow), Upper Cretaceous Horseshoe Canyon Formation, Drumheller. (C) The wood-boring bivalve *Martesias* sp. at the base of the *Teredolites clavatus* depicted in (B) and (D). (D) *Teredolites clavatus* from the horizon depicted in (B) and (C). (E) Siderite-cemented *Teredolites clavatus*, Upper Cretaceous Horseshoe Canyon Formation, Drumheller. (F) Woodground *Thalassinoides* (*Th*), at the base of a tidal channel excavated into coal, Upper Cretaceous Ferron Sandstone, Utah. (G) *Teredolites* (arrows) excavated into lignitic coal, Lower Cretaceous Grand Rapids Formation, Alberta.

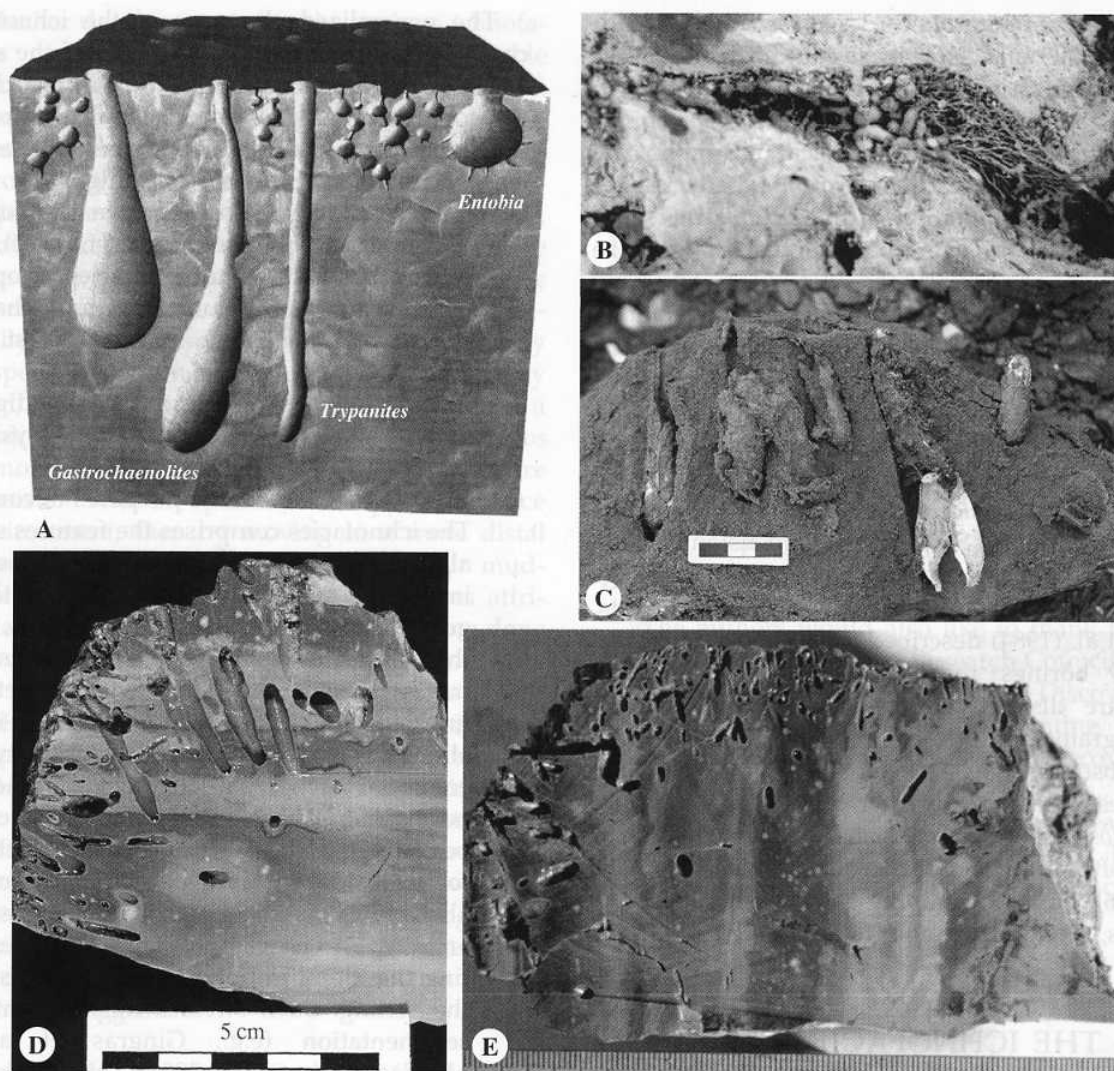


FIGURE 4.10 The *Trypanites* Ichnofacies. (A) Diagram of the *Trypanites* Ichnofacies (artwork by Tom Saunders). (B) *Entobia* in carbonate, Oligocene–Miocene Bluff Formation, Grand Cayman Island. (C) *Gastrochaenolites* with *in situ* bivalves (*Zirfaea pilsbyri*), excavated into Triassic sandstones along the margin of the Bay of Fundy, Economy, Nova Scotia. (D),(E) *Trypanites* excavated into carbonate hardground, marking the Silurian–Devonian disconformity, southern Ontario.

than generally recorded from the rock record (Gingras et al., 2004).

The *Trypanites* Ichnofacies

The *Trypanites* Ichnofacies (Fig. 4.10A, Table 4.3) is characteristic of fully lithified marine substrates such as reefs, hardgrounds, rocky coasts, beach rock, unconformities, and other omission surfaces. As in the case of the *Teredolites* Ichnofacies, the concept does not apply to borings in individual shells, bones, and

clasts. Bromley and Asgaard (1993) erected the '*Entobia* Ichnofacies' and the '*Gnathichnus* Ichnofacies' to either serve as subsets of the *Trypanites* Ichnofacies, or as its replacement. In reality, these new additions are closely associated with tiers. The '*Entobia* Ichnofacies' is broadly similar to the *Trypanites* Ichnofacies, in that it corresponds to long-term bioerosion of a lithified surface (typically carbonate), with little or no contemporaneous sedimentation, allowing deep-tier dwelling structures to be excavated and maintained, and superficial borings to be obliterated. The '*Gnathichnus* Ichnofacies'

encompasses ichnocoenoses associated with predominantly surficial bioerosion structures, but predominantly on isolated clasts, or skeletons. Such structures do not form continuous mappable surfaces, and do not correspond to the classical meaning of the word 'facies.' We suggest that *Trypanites* better serves as the ichnofacies while *Entobia* and *Gnathichmus* serve as expressions of the ichnocoenoses that characterize the ichnofacies as a whole.

Suites attributable to the *Trypanites* Ichnofacies consist of sharp-walled, unlined, cylindrical, vase- and tear-shaped domiciles (e.g., *Trypanites*, (Figs. 4.10D,E), *Gastrochaenolites* (Fig. 4.10C), and *Ubiglobites*), irregular dwellings (e.g., *Entobia*, Fig. 4.10B), irregular pits or borings formed by barnacles (e.g., *Rogerella*), shallow anastomose systems excavated by sponges, bryozoans, suspension feeders, or passive carnivores, and/or raspings and gnawings of algal grazers such as echinoids, chitons, or limpets. Golubic et al. (1984) described a number of microbial endolithic borings that may also be associated. Borings are distinctive, in that they cut through shells or grains, and are commonly oriented normal to the substrate. Suites attributable to the *Trypanites* Ichnofacies are commonly intergradational with those of the *Glossifungites* Ichnofacies, and may crosscut former softground and firmground suites (Bromley, 1975, 1996). Suites commonly show moderately low diversities, though trace abundances may be high.

USING THE ICHNOFACIES PARADIGM

We have asserted that ichnofacies serve as theoretical constructs, based on numerous case studies that demonstrate global and temporal recurrence. We have maintained that these formally defined ichnofacies record particular environmental conditions. As in formal, physically based facies models (e.g., Walker and James, 1992; Reading, 1996), the ichnofacies serve as models for evaluating discrete trace suites (MacEachern and Pemberton, 1992; Pemberton et al., 1992), a point echoed by Genise et al. (2000) in their analysis of the ichnofacies paradigm for the continental regime. In practice, the trace fossil suites are identified from the rock record and integrated with all aspects of the physical sedimentology, and with as many other lines of evidence as considered reasonable for the scope and limitations of the study. The trace suites are then evaluated in the context of various environmental factors and attributed to the relevant ichnofacies.

The generalized character of the ichnofacies, in contrast to the detailed information of the suite, has led many to erroneously conclude that the ichnofacies are too broad to yield precise paleoenvironmental interpretations. McIlroy (2004) has suggested that ichnofacies may serve as a starting point, but that otherwise, ichnology has outgrown the concept. In contrast, to turn a phrase of Walker (1992), it is the generality embodied by the ichnofacies, as opposed to the summary of one particular case study, that enables the ichnofacies concept to serve its most valuable functions.

Like facies models, the ichnofacies paradigm serves three main functions for ichnological analysis:

- (1) It acts as a norm for the purposes of comparison. The ichnofacies comprises the features shared by all suites attributable to the ichnofacies. Any individual suite need not contain all the ichnogenera characteristic of the ichnofacies, nor even the namesake element. Rather, it must contain traces that are consistent with the ethological grouping that defines the ichnofacies—it is what all suites, regardless of age and locality, have in common. Archetypal ichnofacies, by acting as a norm for comparison, allows new trace suites to be compared—does the new suite meet the criteria for inclusion within a particular ichnofacies? It also allows one to recognize departures from the archetypal expressions of the ichnofacies, permitting the identification of depositional stresses in the setting. Such stresses may indicate deltaic sedimentation (e.g., Gingras et al., 1998; MacEachern et al., 2005), or brackish-water accumulation (e.g., Beynon and Pemberton, 1992; MacEachern and Pemberton, 1994; Gingras et al., 1999; Bann et al., 2004; MacEachern and Gingras, in press). Without this norm for comparison, one cannot determine whether a new ichnocoenose contains any unusual or anomalous characteristics.
- (2) The ichnofacies concept acts as a framework or guide for future observations. Sand-prone marine successions tend to carry the *Skolithos* Ichnofacies. When the ichnologist is working in such units, mental search criteria are erected. The ichnologist working in sandy successions therefore knows that most elements of the suite tend to be vertical dwellings, branching dwellings, escape or equilibrium-adjustment structures, and lined horizontal dwellings, many of them exceedingly subtle in well-sorted sandstones.
- (3) The ichnofacies concept serves as a predictor in new situations. The paradigm erected by

Seilacher demonstrates that the various ichnofacies correspond to different but predictable combinations of environmental parameters. In a simple shoreline to basinal shoreline profile, these parameters tend to change progressively, according to a predictable distribution of ichnofacies. The *Skolithos* Ichnofacies, for example, corresponds to high-energy, shifting particulate substrates, generally in marine water. The *Cruziana* Ichnofacies records lower energy, generally more cohesive substrates, with mainly suspended sediment accumulation. We may then, reasonably, consider that if we have a locality with suites attributable to the *Skolithos* Ichnofacies, and the other facies indicators are consistent with an open marine, upper shoreface environment, then by moving in a more distal direction, we would expect to encounter mud-prone, open marine facies carrying suites attributable to the *Cruziana* Ichnofacies. Having done so, we can, with even greater confidence predict the presence of the *Zoophycos* Ichnofacies and of shelf-like conditions further basinward. Alternatively, should we move in what we believed to be the seaward direction, but encounter sand-prone environments with trace suites corresponding to the *Ptilonichnus* Ichnofacies, then we can predict that we have erred in our reconstruction of the paleogeography. In reality, the role of ichnofacies as a predictor is far more complex than this simple example suggests.

A physical facies model displays a fourth use: it may act as an integrated basis for interpretation of the system that it represents. Such a use is achieved once the model is fully mature, and is based on the combined features of many case studies. The turbidite model, for example, has reached this level: it has a hydrodynamic basis for interpretation of the event beds, based on many thousands of occurrences. The ichnofacies concept is starting to approach this use, owing to the continued clarification of the environmental parameters that constrain the faunal behaviors and the types and diversities of the resulting ichnogenera. Such process-based ichnofacies analyses are not far off (e.g., MacEachern et al., 2005). The *Skolithos* and *Cruziana* ichnofacies, for example, are particularly well poised to move into this arena, because of the great abundance of shallow marine successions that have been studied. Once a suite is identified to be attributable to a particular ichnofacies, a particular grouping of paleoenvironmental characteristics are indicated. A suite attributable to the

Skolithos Ichnofacies reflects persistent, high-energy deposition, shifting substrates, and clean (nonturbid) marine water. No matter what particular depositional environment is ultimately determined for the facies, it must embrace these physico-chemical parameters.

The ichnofacies paradigm comprises the unifying framework within which ichnological observations can be accurately interpreted in a depositional context. Rather than outgrowing the ichnofacies paradigm, it continues to operate as the solid underpinning of the entire science, and will continue to facilitate high-resolution paleoenvironmental interpretations of the rock record.

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