Thalassinoides and the Enigma of Early Paleozoic Open-Framework Burrow Systems

PAUL M. MYROW

Department of Geology, The Colorado College, Colorado Springs, CO 80903

The trace fossil Thalassinoides, *a common constituent of the* Zoophycos *and* Glossifungites *ichnofacies, is abundant in post-Paleozoic rocks. Modern* Thalassinoides-*like burrows are constructed by a variety of marine organisms, most importantly decapod crustaceans such as thalassinid shrimp, in modern intertidal and shallow subtidal environments. Lower Paleozoic examples of* Thalassinoides *are poorly documented despite the abundance of Ordovician "burrow mottled" shelf limestone that is generally thought to represent dense populations of* Thalassinoides *burrows. The paleontological record of decapods begins only in the Devonian, and thus, a considerable time gap exists between the early occurrences of* Thalassinoides *burrows and the oldest fossils of organisms most commonly associated with their construction, particularly in post-Paleozoic forms.*

Specimens of a new ichnospecies of Thalassinoides *from the lower Paleozoic Manitou and Peerless formations of Colorado, herein defined as* Thalassinoides horizontalis, *consist of bedding-parallel polygonal networks of smooth-walled, unlined, horizontally branching burrows. Burrows form both Y- and T-junctions but contain no swellings at junctions or elsewhere. They consist of a narrow diameter tube or inner core (<4 mm) and a 3-4 mm outer wall, the latter representing a diagenetic halo formed around a mucus-impregnated burrow. Five styles of preservation relate to the presence or absence of burrow-fill and patterns of mineral replacement and weathering.*

The extremely small burrow diameters, lack of some features such as scratchings and swellings, absence of vertical shafts, and the common regularity of branching separates this new ichnospecies from other Thalassinoides *ichnospecies in either Paleozoic or post-Paleozoic strata.* Thalassinoides horizontalis *burrows were not made by large decapod crustaceans like those that made post-Paleozoic* Thalassinoides, *but by small crustaceans or, more likely, soft-bodied organisms that made semi-permanent to permanent tunnels within firmground sediment. The open-framework burrow systems may record the activities of some of the oldest vagile suspension feeders to colonize infaunal habitats.*

INTRODUCTION

The trace fossil *Thalassinoides,* an unlined, open-framework, branching burrow system, is common in Mesozoic and younger strata. It was not until the early 1980's that examples from the Paleozoic were recognized, particularly in Ordovician shelf carbonate deposits in which thick units of bioturbated strata are composed almost entirely of *Thalassinoides* burrows (Sheehan and Schiefelbein, 1984). The *Thalassinoides* trace fossil is formed in modern environments by a number of marine organisms, including cerianthis anemones, balanoglossan enteropneusts, and fish (Bromely, written communication, 1993), but most importantly by decapod crustaceans, primarily thalassinid shrimp. The paleontological record of these shrimp begins only during the Jurassic, although a few decapod fossils have been reported from Pennsylvanian and Devonian strata (Schram et al., 1978; Schram and Mapes, 1984). Therefore, a considerable time gap remains between the early occurrences of this trace fossil and the oldest fossil relatives of the organisms generally associated with the construction of the trace fossil, particularly in post-Paleozoic forms. There has been speculation (Miller, 1977; Bottjer et al., 1984; Sheehan and Schiefelbein, 1984; Miller and Knox, 1985) that either the early record of decapods is incomplete, or that other unidentified organisms, crustacean or otherwise, were responsible for the construction of the early Paleozoic burrows assigned to the ichnogenus *Thalassinoides.*

Outcrops of the Lower Ordovician Manitou Formation in the Manitou Springs area of Colorado (Fig. 1) contain abundant *Thalassinoides.* A generally less well preserved and more limited suite of similar fossils occurs in the underlying Late Cambrian Peerless Formation (Fig. 2). The specimens from the Manitou Formation are found within
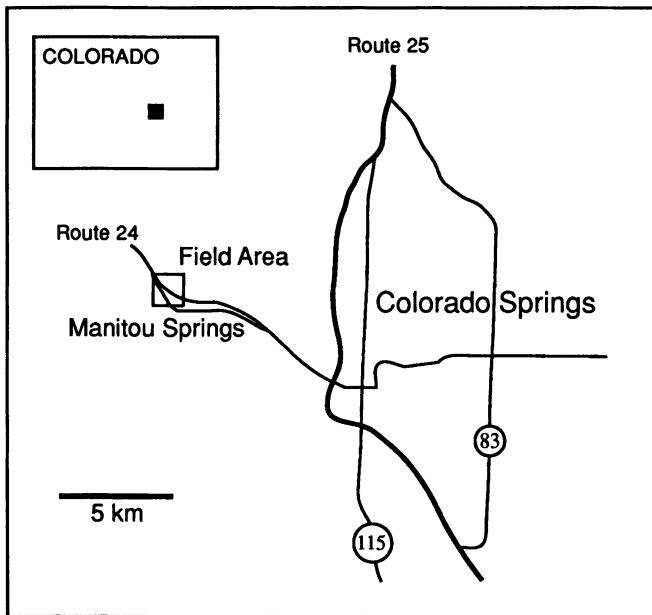
FIGURE 1—Location map of field area. Inset map shows location within Colorado.

a suite of facies that are, in part, arranged in meter-scale cycles interpreted as peritidal upward-shallowing cycles. The sedimentological aspects of these cycles, and the position of *Thalassinoides* within these cycles, indicate that the burrows were created in firm substrates in the incipient stages of hardground formation. A comparison of these Lower Paleozoic burrows from Colorado with burrows of a wide range of ages (Ordovician to Present) attributed to the ichnogenus *Thalassinoides* indicates considerable differences in size, overall geometry, and wall structure. A new ichnospecies of *Thalassinoides* lacks features common to burrows formed by decapods or other crustaceans and may have been formed by small crustaceans possibly ancestral to the decapods, or, more likely, by soft-bodied animals. In the first case, the similarities in burrow geometry and construction would reflect conservative behavioral traits, whereas the latter would indicate fortuitous similarity because of a strong environmental control on behavior.

This paper presents a brief review of the ichnogenus *Thalassinoides,* with emphasis on paleoenvironmental aspects of its occurrence. This review is followed by a description of the taphonomic variations in the ichnospecies *Thalassinoides horizontalis* (isp. nov.) and a subsequent discussion of the significance of this ichnospecies and other Ordovician *Thalassinoides* and *Thalassinoides*-like trace fossils.
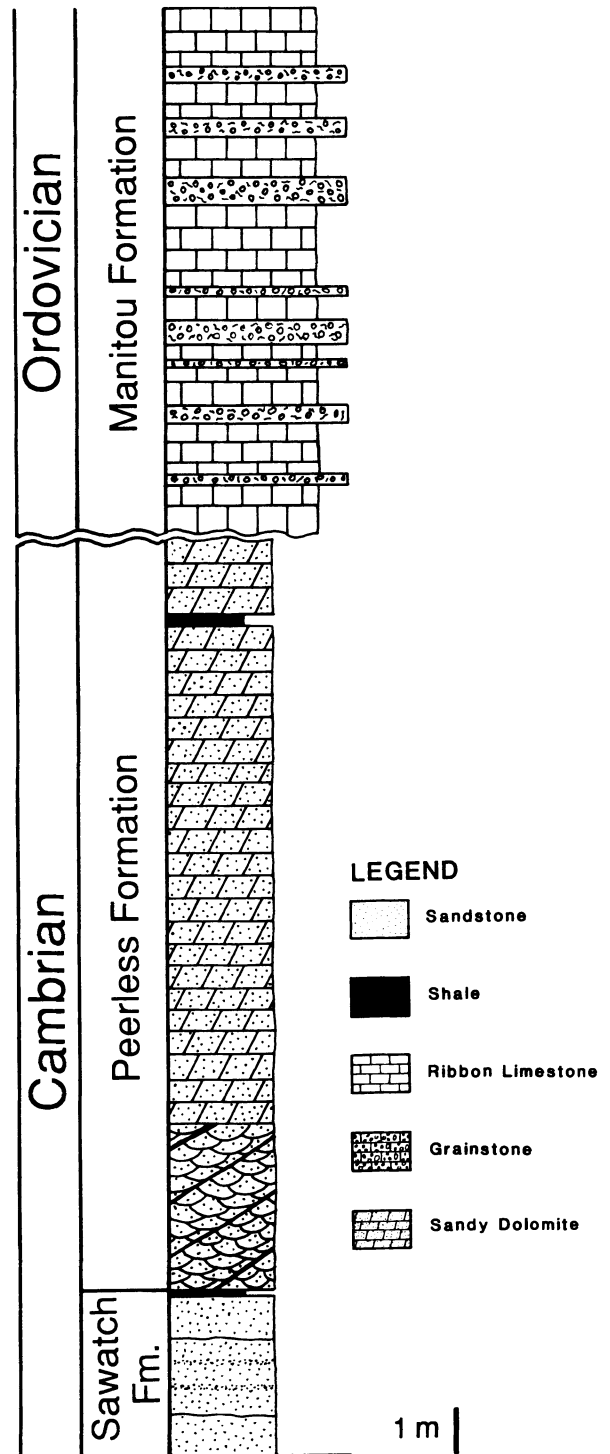
$\longrightarrow$

FIGURE 2—Generalized stratigraphic column of the lower Paleozoic units in central Colorado.

TABLE 1—Table of reported environments/paleoenvironments of thalassinid shrimp (T) and *Thalassinoides* burrows.

Author	Age	Environment/paleoenvironment
Ott et al. (1976)	Modern (T)	Variable: intertidal, shallow to deep subtidal; sandy beaches
Bromley (1990)	Modern (T)	Beach
Pryor (1975)	Modern (T)	Tidal Pools, Shores of Bays and Lagoons
Swinbanks and Luternauer (1987)	Modern (T)	Tidal Flat
Hertweck (1972)	Modern	Upper Shoreface (1.6–10 m depth)
Letzsch and Frey (1980)	Modern	Salt Marsh
Howard and Frey (1975)	Modern	Estuary
Curran and Frey (1977)/Belt et al. (1983)	Pleistocene	Estuary/Lagoon
Pedley (1992)	Oligo-Miocene	Outer Ramp
Crimes (1977)	Eocene	Deep-Sea Fan
Link and Bottjer (1982)	Upper Cretaceous	Deep-Sea Fan
Bromley and Ekdale (1984)	Upper Cretaceous–Lower Tertiary	Epicratonic Sea
Frey and Howard (1990)	Upper Cretaceous	Shoreface
Hattin (1971)	Upper Cretaceous	Epicontinental Offshore
Kamola (1984)	Upper Cretaceous	Marginal Marine: lagoon, channels, upper shoreface
Kamola and Chan (1988)	Permian	Marginal marine interfingered with eolian dunes
Heinberg and Birkelund (1984)	Middle Jurassic	Offshore
Miller and Knox (1985); Miller (1984)	Lower Pennsylvanian	Tidal Flat
Gutschick and Rodriguez (1977)	Late Devonian–Early Mississipian	Tidal Flat
Archer (1984)	Middle Mississipian	Shallow Lagoon
Stanistreet (1989)	Upper Ordovician	Offshore Epicontinental shelf
Miller (1977)	Middle/Upper Ordovician	Lower Shoreface
Sheehan and Schiefelbein (1984)	Upper Ordovician	Open Shelf

THE ICHNOGENUS *THALASSINOIDES*

The ichnogenus *Thalassinoides* Ehrenberg (1944) comprises cylindrical to elliptical burrows that form a three-dimensional to horizontal branching polygonal network with vertical shafts connected to the surface. Burrows show regular branching with Y- or T-shaped bifurcations, and in many specimens, swelling at branches and elsewhere, and superimposed tunnels. *Thalassinoides* burrows are common in Mesozoic and Cenozoic intertidal and shallow subtidal fine-grained lithofacies. They are particularly abundant in Cretaceous chalk deposits, where they are commonly found in association with hardground surfaces (Bromley, 1975; Bromley and Ekdale, 1984).

Thalassinoides is generally considered the dwelling structure of decapod crustaceans, most notably certain members of the superfamily Thalassinidea, including *Upogebia affinis* (Say) and some species of the ghost shrimp *Callianassa* (Swinbanks and Luternauer, 1987; Ott et al., 1976). There are numerous examples of modern thalassinid shrimp found within burrows having the characteristics of *Thalassinoides* (Ehrenberg, 1938; Glaessner, 1947; Beikirch and Feldmann, 1980). Other decapods are capable of making *Thalassinoides*-like burrow systems, including other shrimp (e.g., *Glyphaea*: Sellwood, 1971; Heinberg and Birkelund, 1984; Bromley and Asgaard, 1972; and *Alpheus*: Bromley and Frey, 1974), and both lobsters and

crabs (Rice and Chapman, 1971; Bromley and Frey, 1974; Jenkins, 1975; Richards, 1975; Frey et al., 1978; Letzsch and Frey, 1980). One geometrical difference between the structures made by shrimp or shrimp-like organisms and those of some other decapods is the enlargement of the burrow wall at junctions and elsewhere. These enlargements represent places where the shrimp turn around, an action that is unnecessary for those decapods capable of moving bidirectionally (Frey et al., 1984).

Some of the features associated with the ichnospecies of *Thalassinoides* are shared with other burrows made by crustaceans, namely the ichnogenera *Ophiomorpha* Lundgren (1891), *Spongeliomorpha* Saporta (1887), and *Gyrolithes* Saporta (1884). In fact, in certain specific instances, specimens of each of these ichnogenera have been shown to be gradational with *Thalassinoides* (Bromley and Frey, 1974, Table 1). Such gradation, even along individual burrows, led to Fürsich's (1973) suggestion to synonymize the pellet-lined burrow *Ophiomorpha* Lundgren (1891), *Spongeliomorpha,* a burrow with abundant wall stratchings, and *Thalassinoides* under the older name *Spongeliomorpha.* However, Bromely and Frey (1974) argued convincingly that the distinction between these ichnogenera is philosophically warranted and necessary on practical grounds (see discussion by Bromley, 1990), and subsequently most workers have followed that path.

Many of the differences between the various burrows

formed primarily by decapods result from behavioral patterns that are specific to particular taxa and from constraints imposed by the environment, and substrate in particular. For example, the thick pelletal lining of *Ophiomorpha,* a trace fossil almost exclusively found in sandy substrates, is necessary for stability of the burrow (Shinn, 1968; Frey et al., 1978). Sediment linings are unnecessary in muddy substrates (Hertweck, 1972; Bromley, 1990) and are generally absent in *Thalassinoides,* a trace fossil almost exclusively associated with fine-grained facies. Rare specimens of *Thalassinoides* contain linings, but they are very thin (Curran and Frey, 1977) and commonly consist of fish scales or shell fragments patchily distributed only on the top and bottom of the burrow (Bromley and Frey, 1974). The scratchings of *Spongeliomorpha,* which reflect the excavation process, are absent in *Thalassinoides* burrows, probably due to smoothing of the wall by the bodies of the inhabiting organisms (Bromley, 1967; Frey, 1970; Pickerill and Roulstone, 1977). Other aspects of burrow morphology and preservation are related to diagenetic processes, as described for different forms of *Thalassinoides horizontalis* (isp. nov.) in this paper.

Association with Firmgrounds/Hardgrounds

The association of *Thalassinoides* burrows with hardground surfaces is common in the rock record. *Thalassinoides* is found within the *Zoophycos* ichnofacies, a softground assemblage, and the *Glossifungites* ichnofacies (Frey and Seilacher, 1980), which includes trace fossils formed in "firm but unlithified marine littoral and sublittoral omission surfaces, or stable, coherent substrates . . ." (Pemberton and Frey, 1985, p. 238, Table 1).

Sediment consistency explains some variations in burrow geometry within the ichnogenus *Thalassinoides.* For instance, *Thalassinoides* from hardground beds in Cretaceous chalks are commonly more boxwork in geometry and have many cul-de-sacs and odd-shaped branches, but lack widenings at branches and elsewhere (Kennedy, 1970; Bromley, 1967). These geometric differences result, in part, from burrowing around growing nodules of chalk that are in the process of coalescing into a hardground (Kennedy, 1970, 1975; Bromley, 1967). In studies of omission surfaces in Cretaceous European Chalk deposits, Bromley (1967, 1968, 1975) illustrated the typical development of *Thalassinoides* burrows prior to, during, and after hardground formation. *Thalassinoides suevicus* burrows, the typical form in softgrounds, formed early and were cut by burrows of *Thalassinoides paradoxicus* created in the ensuing firmground conditions. *Thalassinoides* burrows lack sediment linings, and in the case of the dominantly horizontal *T. suevicus* burrows, they would have likely been maintained entirely by mucus linings (Bromley, written communication, 1993). The more vertical and irregularly-branching *T. paradoxicus* firmground burrows probably required firm, at least semiconsolidated, substrates to keep the burrow from collapsing.

Despite the fact that *Thalassinoides* burrows form in a range of sediment consistencies, they are extremely common in ancient hardgrounds (Kennedy, 1975), and likely represent the early and middle stages of hardground development. Examples of *Thalassinoides* hardgrounds are particularly common in Jurassic to early Tertiary chalk sequences in northwest Europe (Voigt, 1959; Bromley, 1967, 1968, 1975; Rasmussen, 1971; Kennedy and Juignet, 1974; Kazmierczak and Pszczolkowski, 1969; Bromley and Ekdale, 1984).

Environmental and Paleoenvironmental Distribution of *Thalassinoides*

Modern *Thalassinoides*-like burrows are common in both intertidal flats and other marginal marine environments such as salt marshes (Howard and Frey, 1975; Letzsch and Frey, 1980; Table 1). Swinbanks and Luternauer (1987), in a study of the Fraser Delta in British Columbia, found that the ghost shrimp *Callianassa californiensis,* which make *Thalassinoides*-type burrows, is capable of tolerating reduced salinity and oxygen, and as a result inhabits a wide range of environments and substrate grain sizes within the intertidal flats of the delta. Similar conclusions were reached by Ott et al. (1976) for modern tidal flat and marsh areas along the coast of Yugoslavia. The distribution of *Thalassinoides* in shelf and deep-water facies is not well known because of the inherent logistical problems of working in these environments.

The paleoenvironmental distribution of *Thalassinoides* is quite varied, ranging from tidal flats (Curran and Frey, 1977; Belt et al., 1983; Gutschick and Rodriguez, 1977; Miller and Knox, 1985) and both shoreline settings (Kamola, 1984; Ekdale et al., 1984), to outer shelf facies (Ekdale and Bromley, 1984), and even deep sea fan deposits (Crimes, 1977; Link and Bottjer, 1982) (Table 1). In shallow marine deposits, sandy sediment, such as carbonate beach and shoal facies typically contain *Ophiomorpha* burrows, whereas muddy intertidal and subtidal deposits commonly contain *Thalassinoides, Chondrites,* and other traces (Kennedy, 1975). Ancient examples of extensive fine-grained carbonate shelves have abundant *Thalassinoides.* The trace fossil is ubiquitous in a variety of facies in the Cretaceous chalks of Western Europe from ancient ocean depths from 50–300 m, but rapidly decreases in abundance below these depths (Ekdale and Bromley, 1984). Massive bioturbated outer shelf carbonate mudstone deposits of Ordovician age are comprised of dense masses of *Thalassinoides* burrows (see discussion below).

Thalassinoides and the Decapod Crustacean Fossil Record

As noted earlier, decapod crustaceans, most notably thalassinidean shrimp, create modern *Thalassinoides* burrows, and have been associated with the construction of similar ancient burrows. The record of thalassinidean shrimp extends only to the Jurassic (Glaessner, 1969). Decapods were not common until the Permo-Triassic (Glaessner, 1969), but there are fossil examples from Pennsylvanian (Schram and Mapes, 1984) and Devonian (Schram
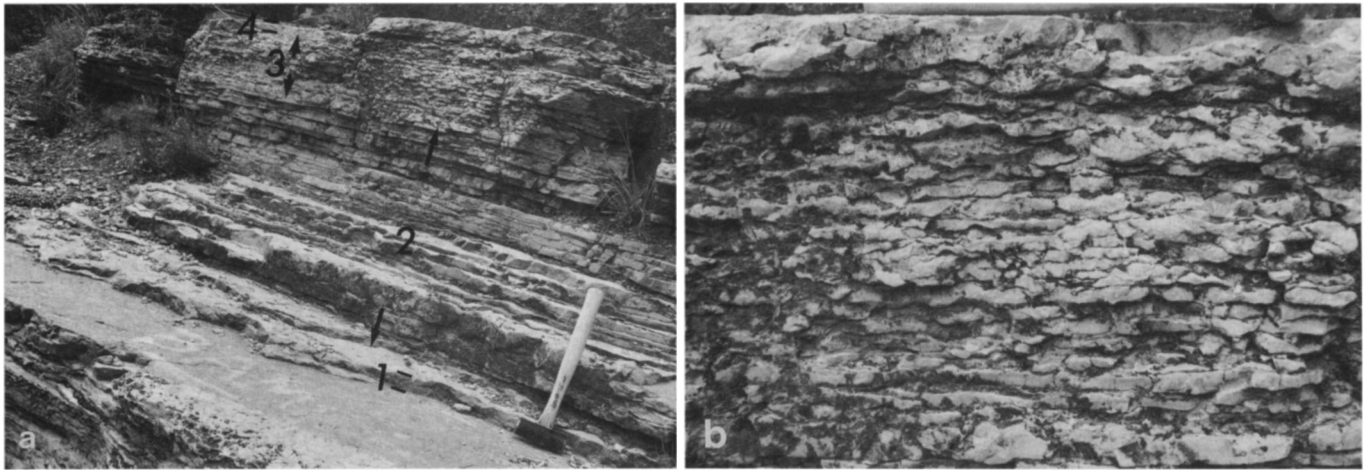
FIGURE 3—a) Shoaling cycle in lower Manitou Formation. Hammer rests on flat hardground surface which is overlain by: (1) a grainstone bed—next to hammer head, (2) upward-thinning beds of ribbon bedding, (3) nodular bedding, (4) thin bioturbated bed, and (5) a second hardground surface (at top of "4"). b) Nodular bedded limestone overlain by thin massive-weathering bioturbated bed and a flat hardground surface, on which the hammer rests. Hammer is 38 cm long.

et al., 1978) strata. Stomatopods—mantis shrimps—have also been associated with the construction of *Thalassinoides* burrows (Frey and Howard, 1969; Hertweck, 1972; Braithwaite and Talbot, 1972), but their record does not extend beyond the earliest Mississippian (Tasch, 1973, Fig. 11.29). The fossil record of shrimp-like crustaceans of the Superorder Eocarida (Schram et al., 1978) dates back to the Late Devonian, and these organisms may also have been capable of burrowing (Carney, 1981).

The record of *Thalassinoides* trace fossils—which begins in the late Cambrian (Miller and Byers, 1984), and shows great abundance in the Ordovician—therefore extends more than 150 m.y. beyond the oldest known body fossils of organisms either: (1) known to make morphologically similar burrow systems in modern environments, or (2) associated with *Thalassinoides* in mid-Paleozoic and younger deposits. Previous workers have hypothesized that this gap is due to either poor preservation of the organisms' exoskeletons relative to their burrows, or construction by different crustaceans that were either not preserved or simply not involved in the construction of such burrows (Miller and Knox, 1985; Miller, 1977; Bottjer et al., 1984; Sheehan and Schiefelbein, 1984). Specimens of the Lower Paleozoic *Thalassinoides horizontalis* (isp. nov.) described in this study have features indicative of formation not by decapods or their ancestors, but by soft-bodied organisms.

THALASSINOIDES HORIZONTALIS (ISP. NOV.) FROM THE CAMBRO-ORDOVICIAN OF CENTRAL COLORADO

The trace fossil *Thalassinoides horizontalis* generally consists of smooth-walled, unlined, horizontally branching burrows that form polygonal networks. The bedding-parallel frameworks contain both Y- and T-junctions. The burrows are even in diameter, lacking swellings at junctions or elsewhere, and have inner diameters of 3–4 mm (Appendix A).

Specimens of this ichnospecies occur within the Lower Ordovician Manitou Formation and the disconformably underlying Upper Cambrian Peerless Formation, which are cliff-forming units exposed along the fronts range of the Rocky Mountains in the vicinity of the city of Manitou Springs (Fig. 1) and elsewhere. In the Manitou Springs region, the Peerless Formation consists of approximately 15 m of red, glauconite- and quartz-rich dolostone of shallow-marine origin (Fig. 2). The basal part of the Manitou Formation contains a series of meter-scale upward-shoaling carbonate cycles that contain abundant *Thalassinoides horizontalis* burrows. A description of these depositional cycles is given below.

Sedimentological Context

The lowermost Manitou Formation in the Manitou Springs region consists of a number of limestone and dolostone lithofacies arranged in meter-scale, upward-shoaling cycles (Figs. 3a, 4). Cycles consist of, in ascending order, (1) a basal wave-rippled grainstone; (2) thin, ribbon-bedded micrite; (3) very thin to thin, nodular-bedded micrite; (4) bioturbated micrite; and (5) a planar hardground surface. The shoaling nature of these cycles is reflected in the transition from coarse-grained grainstone to micrite, an upward thinning of bedding both within the ribbon-beds and between the ribbon and nodular beds, and evidence for subaerial exposure—microkarst and pseudomorphs of evaporite minerals—in the burrowed intervals below hardground surfaces.

Specimens of *Thalassinoides* occur in the ribbon-bedded micrite, but are most abundant in the nodular-bedded and bioturbated sub-hardground micritic lithofacies in the
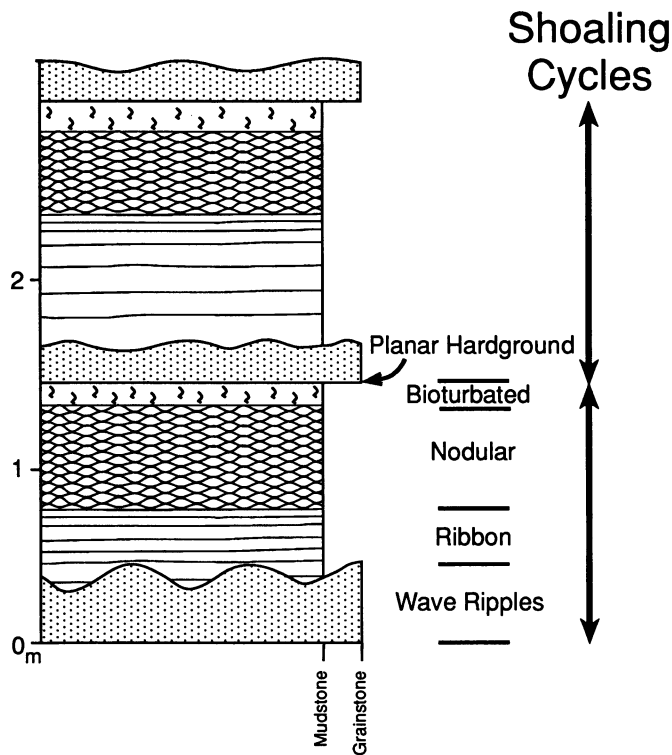
Shoaling Cycles

FIGURE 4—Generalized shoaling cycles in lower Manitou Formation. Each cycle consists (from base to top) of: (1) a rippled grainstone bed, (2) ribbon-bedded micrite, (3) nodular bedded micrite, and (4) a bioturbated bed that is capped with a planar hardground surface. Dolomitized *Thalassinoides horizontalis* burrows occur only within the upper bioturbated unit.

FIGURE 5—Four styles of preservation of *Thalassinoides horizontalis*. Inner cores represent the diameter of the burrows and the walls shown in A–C are diagenetic micritic halos. A) Burrows are filled with similar micrite to surrounding sediment. B) Same as "A" except inner core has been eroded away. C) Burrow filled with geopetal structure that includes micritic sediment and late-stage blocky calcite. D) Dolomitized inner core that weathers in full relief.

upper parts of these cycles (Fig. 3b). This lithofacies specificity may reflect the control of sediment consistency on the distribution of burrowing organisms at the time of deposition. The nodular-bedded micrite represent an arrested transition from soft sediment to hardground, namely firmground conditions. Such nodular fabrics result from initial lithification of the sediment into nodules and concomitant burrowing (Bromley, 1967).

Although the depositional processes responsible for these fine-grained, nodular beds are not readily apparent, the evidence for subaerial exposure at the top of some cycles shows that these cycles are likely peritidal, and the nodular facies are partially or totally intertidal in origin. Sediments of the nodular facies would therefore have been subjected to short periods of subaerial exposure and thereby drained of water for some portion of the tidal cycle. This exposure would have resulted in consolidation of the substrate through dewatering and presumably allowed for the construction and maintenance of open burrow structures within the sediment. Crustacean dwelling structures are abundant in modern intertidal and supratidal environments because of such sediment consistency (Pemberton and Frey, 1985). The paucity of burrows in the underlying, deeper-water facies of these cycles would suggest unsuitable substrate consistency at the time of deposition, such as soft-

ground conditions. Unconsolidated conditions would have been more common in subtidal or lowermost intertidal environments in which early compaction and dewatering would have been minimized.

TAPHONOMY OF
THALASSINOIDES HORIZONTALIS
BURROWS

Five styles of preservation are associated with the *Thalassinoides horizontalis* burrows, each transitional with the other, sometimes along the length of one burrow (Fig. 5). These styles relate to the presence or absence of burrow infilling sediment and/or cement, type and degree of mineral replacement, and the differential weathering of bur-

TABLE 2—Average size data (in mm) for specimens of *Thalassinoides horizontalis*. Standard deviations are given in parentheses.

	Inner diameter	Outer diameter	Diameter of outer wall (outer–inner diameter/2)
Solid Calcite Traces (n = 11)	—	9.9 (1.9)	—
Open Tube/No Fill (n = 6)	2.8 (0.8)	9.7 (1.2)	3.4 (0.8)
White Calcite Fill (n = 4)	2.5 (0.6)	9.8 (0.5)	3.6 (1.0)
Red Calcite Cement Fill (n = 10)	4.8 (1.9)	10.6 (1.8)	2.9 (1.6)
Brown Dolomite at H-Grnd (n = 21)	3.0 (1.4)	—	—
Total means	3.4 (n = 4)	10.0 (n = 31)	3.2 (n = 21)

row parts and surrounding sediment. Size data for the five preservational styles of the burrows is given in Table 2.

The first preservational style (Fig. 5A) consists of a thick wall of white calcite and a central core with a small-diameter inner fill of brown dolomite or tan calcite. In many cases the outer surface of the burrow walls stand out in positive relief (Fig. 6a) and the inner fill is not exposed. The outer diameters of these specimens average about 1.0 cm. In other specimens the central core has been exposed because of weathering and stands out in positive relief around the clearly-defined but more weathered wall (Fig. 6b). The diameters of the central core in these specimens average 2.5 mm.

A second preservational style has the burrows preserved as horizontal sections through thick white calcite walls (Fig. 5B), as described above, with open central cavities of similar diameter to the sediment cores described above (2.8 mm average) (Fig. 6c). This style of preservation reveals the smooth interior surface of these burrows.

A third style of preservation (Fig. 5C), is much rarer and is best preserved on one extraordinary slab (Fig. 7a, b). The burrows consist of a wall of white calcite with an inner core of bright red calcite cement. Petrographic analysis revealed that the cement consists of crystals of blocky calcite up to 1.3 mm in diameter, and that many of the burrows have a layer of geopetal sediment at their base (Fig. 7c). The burrow system exposed on the one large slab is anomalously large (outer diameters average 10.6 mm) and has calcite burrow walls that are slightly thinner than normal (average = 2.9 mm). On the other hand, a sample from the Peerless Formation (Fig. 7d) has a very thin red calcite inner core (1.5 mm) and a thick calcite wall (4.8 mm).
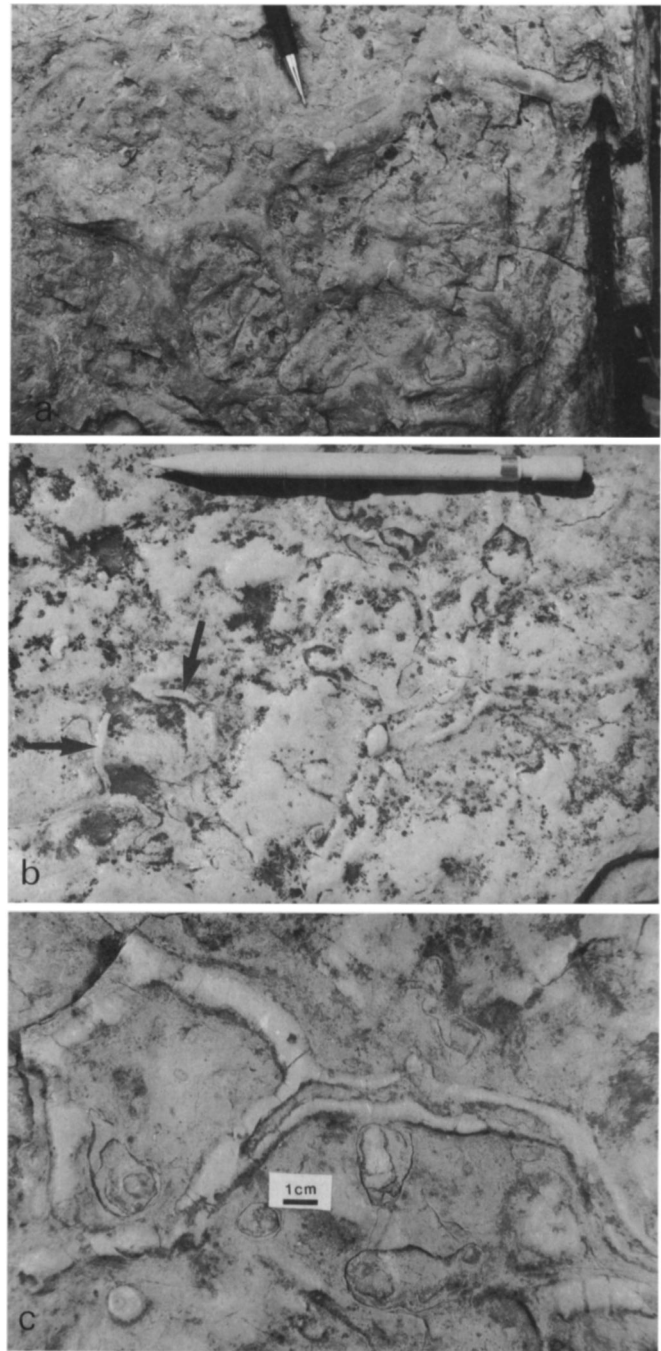

FIGURE 6—a) Bedding plane view of polygonal branching pattern of solid calcite preservation of *Thalassinoides horizontalis*. Silver tip of pencil is 2 cm long. b) Branching open tubes with isolated segments of calcitic inner cores (arrowed). Pencil is 14 cm long. c) Polygonal branching solid calcite and open tube styles of preservation (Fig. 5A, B).
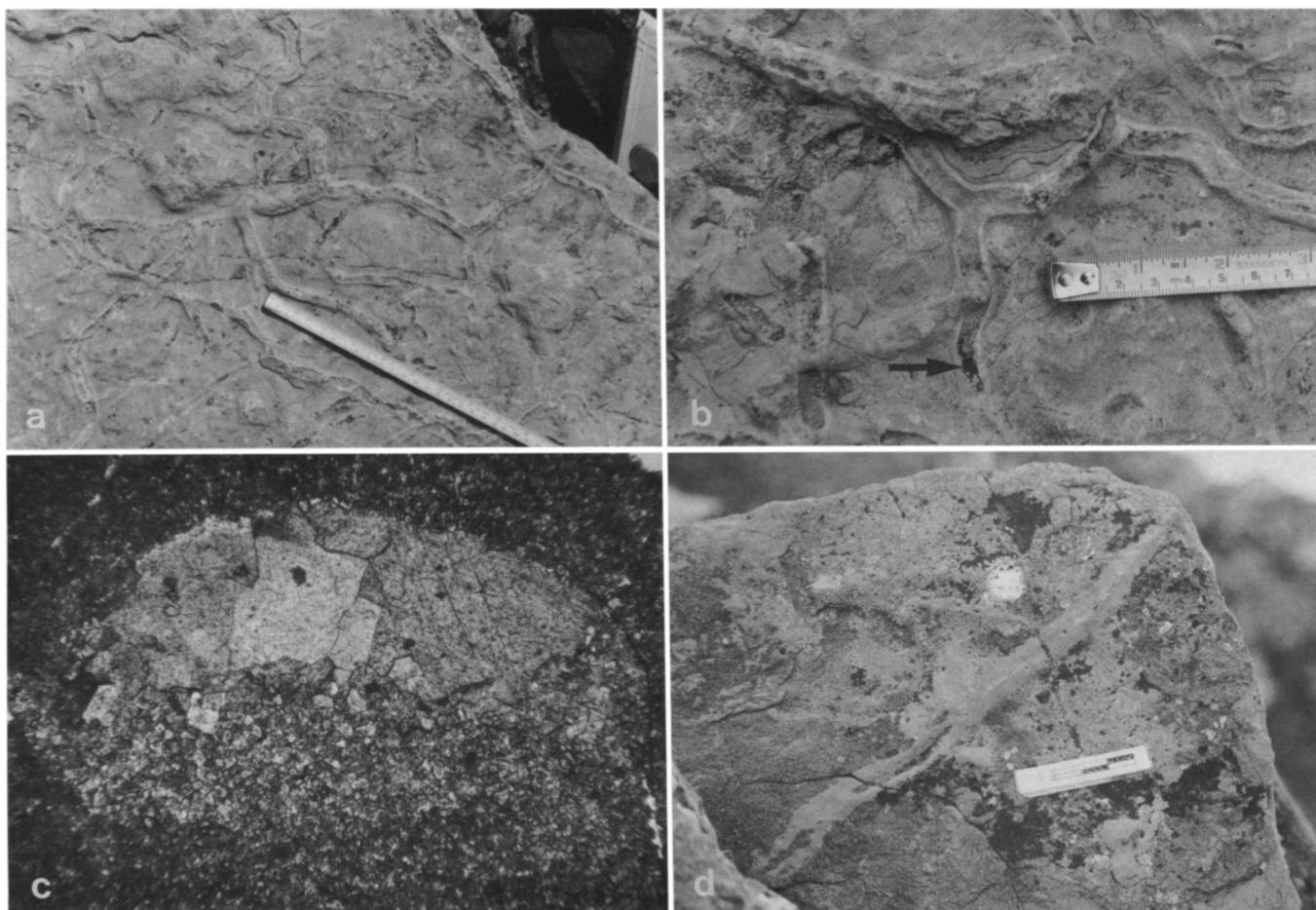
FIGURE 7—a) Slab with polygonal branching burrows of *Thalassinoides horizontalis* with geopetal filling style of preservation (Fig. 5C), showing both T- and Y-branching. b) Close-up of slab showing Y-branching and prominent red calcite cement filling (arrowed). Scale is in cm and inches. c) Photomicrograph of geopetal burrow fill with crystalline dolomitic sediment at base and blocky, red calcite fill at the top. Width of photograph is 6.8 mm. d) Specimen of *Thalassinoides horizontalis* from Upper Cambrian Peerless Formation with thin central inner core filled with red calcite cement (Fig. 5C). Scale is in cm.

In each of the three styles of preservation described above the interior surface of the calcite "walls" is sharp. The exterior surface appears sharp in the field but is very diffuse and commonly difficult to discern in thin section.

The fourth style of burrow preservation (Fig. 5D) is consistently associated with highly burrowed layers directly below hardground surfaces. Here the burrows consist of thin, tubular, brown, dolomite ridges that weather out in near-full relief (Fig. 8a). The geometry is slightly more three-dimensional than those burrows described above. The diameters of these dolomitic burrows range from 1 to 7 mm, with 90% between 1 and 4 mm. The average diameter is 3.0 mm, which is similar to the average diameter of the inner core of the first two burrow types described above. In thin section, the dolomitic cores are distinct, well-defined, light colored finely-crystalline masses of dolomite crystals with sharply gradational boundaries (Fig. 8b).

A fifth style of burrow preservation, found within the upper chert-rich units of the Manitou Formation, consists of brown-weathering, irregular, bedding-parallel, siliceous burrow tubes. These range from thin 1–3 mm diameter burrows, that form 1–3 cm polygons (Fig. 9), to 1–1.5 cm burrows that coalesce into irregular masses up to 6 cm across. Even the thinnest and most distinct of these silica-replaced burrows show irregular thickening and thinning. Extreme cases of silica replacement result in bedding parallel siliceous masses up to 30 × 50 cm across.

Comments on Burrow Walls

The burrows described above represent smooth-walled, branching burrow systems. The geopetal structures with blocky calcite cement (Fig. 5C) clearly prove that these were open burrows (e.g., Fillion, 1989). The diameter of the open burrows, and presumably of the organisms themselves, was equal to the diameter of the inner core of those traces with calcite walls (Fig. 5A–C), or the full diameter

FIGURE 9—Silica-replaced burrows of *Thalassinoides horizontalis* from the upper Manitou Formation. All gradations exist from fairly-well preserved polygonal patterns to solid masses of silica. Pencil is 14 cm long.
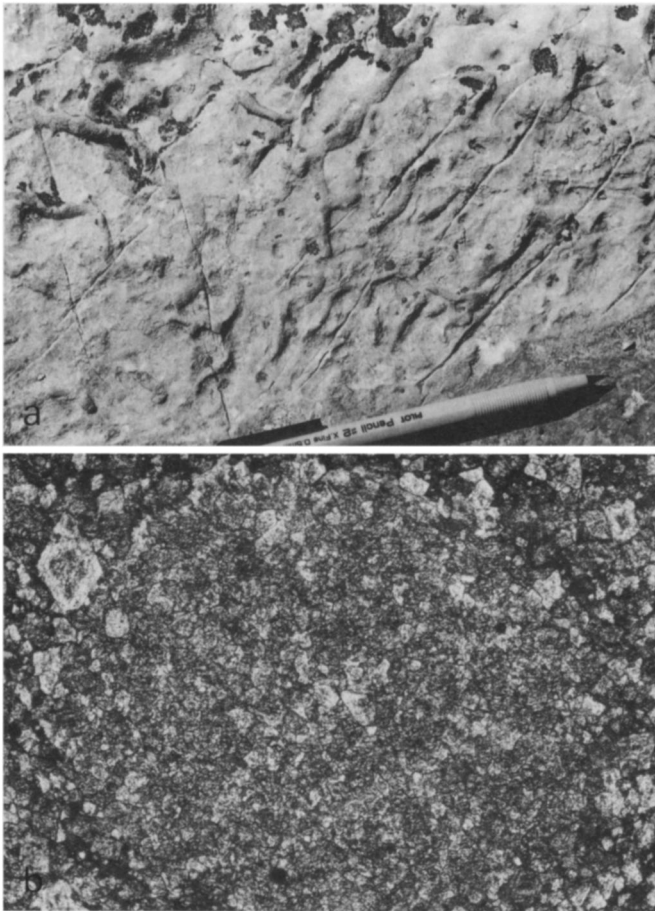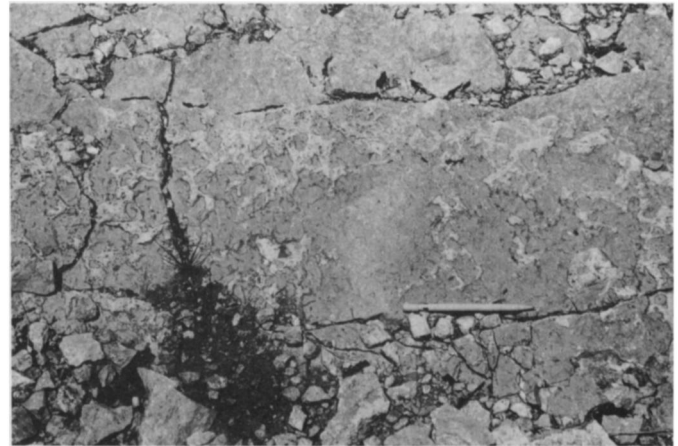
FIGURE 8—a) Brown, dolomitized inner core sediment infills of *Thalassinoides horizontalis* from sub-hardground bed. Pencil is 8 mm in width. b) Photomicrograph of core of dolomitized burrow with sharply gradational boundary. Width of photograph is 5.3 mm.

of the thin dolomitic traces (Fig. 5D) below the hardground surfaces (see Table 2). The burrow "walls" of white calcite described previously are considered diagenetic halos (see Fillion, 1989, Fig. h), probably representing a zone of mucus-impregnated sediment around the original burrow. This interpretation is supported by the sharp interior surface and the diffuse outer surfaces, of the "walls", as viewed in thin section. The sharpness of the inner surface is a reflection of the work done by the organism in the production and upkeep of the open burrow system. The outer surface marks the distal position of calcite cementation of sediment surrounding the burrow. This boundary is diffuse because the concentration gradient in microchemical conditions that favored the precipitation of calcite—possibly set up by mucus impregnation of the sediment around the burrow—was gradual in its outer limits. A modern analog of a microchemical concentration gradient around burrows was given by Ott et al. (1976) who described the dwelling burrows of the thalassinid *Upogebia litoralis,* a major former of modern *Thalassinoides*-like burrows worldwide.

These have a surrounding layer approximately 10 mm thick which is characterized by elevated Eh values, the result of higher concentration of organic matter. Burrows in sediment undergoing cementation into nodules and hardgrounds would be preferentially disposed towards precipitation of diagenetic halos because of the introduction of organic material during burrowing.

The calcitic halos might initially be mistaken for a thick burrow lining. However, the walls lack concentric lamination which would reflect a lining origin. Additionally, the outer diameter of the calcitic walls are 2–4 times greater than the organisms' maximum body diameters, which would require organisms generally less than 3 mm in diameter (represented by the burrow cores) to excavate tunnels roughly 10 mm in diameter (outer wall diameters) and then make 3–4 mm thick linings (wall widths) with near perfectly centrally located burrow tubes (see Table 2 for data). Even if such construction were possible, horizontal, open burrow systems in fine-grained sediment, such as *Thalassinoides,* are generally unlined. As Crimes (1975) pointed out, the factors for stability of burrows are those outlined in geotechnical studies for sediment stability: sediment grain size, cohesion forces, pore-fluid pressure and degree of sediment consolidation. In mud, sediment linings are generally unnecessary (Bromley, 1967; Shinn, 1968) because these sediment parameters are usually such that the sediment is sufficiently cohesive to support open burrows with nothing more than a mucus lining.

An alternative interpretation for the open-cored burrows described herein would involve a second stage of open tunnel burrowing by organisms that followed along previous burrow-fills. Kendall (1977) describes dolomitic *Thalassinoides* burrows (mottles) that are cored by tubular cavities filled with either calcite or dolomite. He considers these central cores to be smaller burrows that postdated the earlier burrow-fill. Such an explanation is unlikely for the burrows in the Manitou Formation because

the central cores are consistently centered relative to the calcite walls, even along the Y- and T-branches.

Interpretation of Preservational Styles

The five styles of burrow preservation described previously all stem from the open and branching burrows. The first style of preservation of these burrows (Fig. 5A) involves the infilling of the burrow tube with sediment of the same grain size as the surrounding sediment. In this case, the sediment both outside and inside of the original burrow wall either underwent similar diagenetic changes or the infilled sediment was preferentially dolomitized. In some cases, the inner wall of the burrow is represented in thin section by a dark line of insoluble residue.

In the second style of preservation (Fig. 5B), the central core is missing because of a combination of weathering and erosional processes. In some instances these open burrows may have never experienced sediment infilling or cementation during diagenesis; however, in many cases the open tubes can be traced along their length into sediment-cored burrows.

The third style of preservation (Fig. 5C) result from partial infilling of sediment and later occlusion of the burrow tube by precipitation of calcite cement. The nonfibrous texture of this blocky cement indicates that it precipitated as low-Mg calcite and is of either late-stage burial or early meteoric origin. It should be noted that Upper Ordovician Thalassinoides burrows of the Bighorn Dolomite, described by Zenger (1984), also contain cement-fills, in this case chalcedonic quartz.

The fourth style of preservation, associated with hardground surfaces, results from preferential dolomitization of the sediment-fill (burrow cores), as indicated by the size data in Table 2. This dolostone is more resistant to weathering than the surrounding sediment, including the diagenetic halo, and therefore stands out in positive relief. Partial or complete enhancement or loss of burrows commonly results from surface weathering phenomena (Archer, 1984). A similar style of preservation is illustrated by Savoy (1992, Fig. 6b) in Devonian strata. In the Manitou Formation, grainstone—which in nearly all cases overlies the hardground surfaces—is never found within the underlying dolomitized burrows. This indicates that lithification and formation of hardgrounds followed infilling of burrows with soft ambient sediment. Burrow systems may not have been maintained up to and including the time of full lithification as described by Bromley (1967) and Bromley and Ekdale (1984).

Examples of preferentially dolomitized burrows are common in Phanerozoic rocks (Wallace, 1913; Beales, 1953; Kendall, 1977; Jones et al., 1979). Upper Ordovician examples of Thalassinoides are common in partially-dolomitized carbonate mudstone, and are generally preserved by preferential dolomite replacement of burrow infills (Zenger, 1984; Morrow, 1978; Kendall, 1977; Delgado, 1983; Sheehan and Schiefelbein, 1984). Sediment infills of burrows are preferentially dolomitized because the porosity and permeability, and therefore the rates of diffusion of Mg-rich seawater, are higher in the burrow fills than in the surrounding sediment (Morrow, 1978; Pickerill et al., 1984).

Selective diagenetic replacement by chert, the fifth style of preservation described before, is common in Thalassinoides from Late Cretaceous European chalk deposits (Bromley, 1967; Kennedy and Juignet, 1974: Bromley and Ekdale, 1984; Ekdale et al., 1984). Silica replacement is attributed by Bromley and Ekdale (1984, p. 309) in part to elevated levels of organic matter: "the history of occupation of Thalassinoides would ensure both a high organic content of the burrow (due to wall impregnation, long occupation, detritus entering with pumped sea water, etc.) and high permeability of the fill (passive or uncompacted fill at some depth below the sea floor)." Thalassinoides burrows with well-preserved microcoprolites have been documented from Triassic rocks (Senowbari-Daryan and Stanley, 1986) and present-day burrows of the thalassinid shrimp Callianassa stebbingi are infilled with sediment having high concentrations of organic matter and, as a result, low values of Eh (Ott et al., 1976). The chemical composition—e.g., dolomite or silica—associated with preferential replacement of the microchemically predisposed burrow-fill would reflect the spatial- and time-dependent history of diagenetic conditions within the burrow-fill and surrounding sediment.

PALEOZOIC THALASSINOIDES AND THALASSINOIDES-LIKE TRACE FOSSILS

Paleozoic Thalassinoides and Thalassinoides-like trace fossils are poorly documented in comparison with Mesozoic and Tertiary examples, or other Lower Paleozoic traces (see Sheehan and Schiefelbein, 1984, Table 1). Except for the study of Sheehan and Schiefelbein (1984), the bulk of the literature on Lower Paleozoic burrows is found in meeting abstracts (e.g., Bottjer et al., 1984; Zenger, 1984, 1988) and guidebooks (Delgado, 1983; Johnson and Worsely, 1982), or as short parts of papers that focus on other aspects of the strata (e.g., Johnson et al., 1988).

Maze (primarily two-dimensional) burrow networks are reported from Lower Cambrian rocks by Droser and Bottjer (1988); these may represent the oldest reported examples of Thalassinoides. Mottled and "tubular-burrowed deposits" of Middle to Late Cambrian age throughout the Great Basin (Brady and Rowell, 1976; Kepper, 1981; Sheehan and Schiefelbein, 1984; Droser and Bottjer, 1988) are thought to represent sediment that was disrupted by Thalassinoides burrow systems. Burrow-mottled fabrics are also abundant in subtidal Ordovician carbonate of the Great Basin and elsewhere (e.g., Morrow, 1978; Sheehan and Schiefelbein, 1984), and have been interpreted to represent densely packed Thalassinoides burrows (Bottjer et al., 1984). The recognition of burrows in these deposits is best in strata affected by partial dolomitization (Morrow, 1978; Zenger, 1984, 1988). The most thorough description of such burrows, by Sheehan and Schiefelbein (1984), indicates that they are strongly three-dimensional branching structures that extended to more than 1 meter in depth. This

is in striking contrast to specimens of *Thalassinoides hor-izontalis* which are composed of solely bedding-parallel, open-framework structures. It should be noted that, according to Droser and Bottjer (1989), *Thalassinoides* from Lower and Middle Ordovician strata are characterized by more two-dimensional and discrete networks, in comparison to Upper Ordovician specimens. Few, if any, detailed descriptions of these Lower Ordovician burrows exist, and thus many burrows of this age, described as *Thalassinoides*, may have close affinity to the trace fossil *Thalassinoides horizontalis* described herein. One note of interest in this regard is the author's observation of *Thalassinoides* burrows with three-dimensional geometry, typical of Upper Ordovician *Thalassinoides* (Sheehan and Schiefelbein, 1984), in outcrops of the Lower Ordovician Manitou Formation in north-central Colorado.

The ichnofabric indices (Droser and Bottjer, 1986) of subtidal Cambrian and Ordovician *Thalassinoides*-burrowed deposits is typically in the range of 3–5 (Kepper, 1981, Fig. 7; Sheehan and Schiefelbein, 1984, Figs. 2, 3; Droser and Bottjer, 1988, Fig. 1; Droser and Bottjer, 1989). The ichnofabric index is difficult to apply to the strata in this study because much of the bedding in which the trace fossil *Thalassinoides horizontalis* occurs is highly nodular because of early diagenetic processes, including early cementation of nodules and compaction. However, these two-dimensional burrows do not markedly disrupt bedding: a visual estimate of bedding disruption is less than 10%, corresponding to an ichnofabric index of 2. The hardground occurrences of *Thalassinoides horizontalis,* however, have ichnofabric indices of 5 (100% disruption).

One of the most intriguing aspects of the Paleozoic trace fossil record is that, according to Bottjer et al. (1984), the abundance of *Thalassinoides*-bioturbated rocks drops off after the end of the Ordovician. They speculate about a possible extinction of *Thalassinoides* trace-markers at that time. Several workers have postulated about the identity of the burrowing organisms responsible for lower Paleozoic *Thalassinoides* traces (Miller, 1977; Bottjer et al., 1984; Sheehan and Schiefelbein, 1984; Droser and Bottjer, 1989), but little has been resolved given the poor record of decapod crustacean fossils.

DISCUSSION

Trace fossils from the Cambro-Ordovician deposits of Colorado represent a new ichnospecies *Thalassinoides horizontalis* (see Appendix A). These trace fossils are characterized by a complete absence of features that would indicate construction by crustaceans (e.g., scratch marks, burrow swellings at junctions and elsewhere, three-dimensional branching systems, etc.). The inner core diameters of these burrows, generally less than 3 mm in diameter, argue strongly against a taxonomic affinity with either Paleozoic or post-Paleozoic forms of *Thalassinoides* or construction by decapod crustaceans like those that have been linked to most, but not all, examples of post-Paleozoic *Thalassinoides.*

The sediment-fill of *Thalassinoides* burrows is normally of different texture from the surrounding matrix and represents backfill spreite or sediment introduced from overlying beds during storms (Bromley and Ekdale, 1984; Sheehan and Schiefelbein, 1984; Wanless et al., 1988). Variable grain sizes in *Thalassinoides* burrows may also be ascribed to biogenic sorting. Modern thalassinids, such as the ghost shrimp *Callianassa,* are very effective sediment sorters, sifting through mixed sediment, ingesting the finer organic-rich material, and removing coarse sediment, which is carried to the surface (Meglitsch, 1972; Tudhope and Scoffin, 1984). The burrows of *Thalassinoides horizontalis* are both composed of and set in sediment of extremely uniform grain size (micrite that has recrystalized to microspar or micro-dolomite). Thus, there is no evidence of physical introduction of different-sized sediment or biological segregation like that described for modern shrimp burrowers.

Based on primary and diagenetic features of the trace fossil, and various field relationships, the organisms that constructed the trace fossil *Thalassinoides horizontalis* made semi-permanent to permanent tunnels with firm-ground sediment. These organisms were most likely either very small, primitive crustaceans or soft-bodied organisms.

A decapod crustacean origin for lower Paleozoic *Thalassinoides* must be reconciled with a poor Paleozoic record and a pre-Devonian record that is devoid of decapods. One can hypothesize that the poor fossil record resulted from preservational effects: crustaceans commonly leave their burrows prior to death (Schäfer, 1972), and their poorly calcified integument is a taphonomic liability against preservation (Pickerill and Roulstone, 1977). However, Plotnick (1986) concludes from a modern taphonomic study that the preservation potential of arthropods may have declined since the Paleozoic. If one assumes that the burrowers were marine crustaceans, the most likely candidates would have been the phyllocarids, the most primitive members of the Class Malacostraca. Phyllocarids are small crustaceans that generally have bivalved carapaces with a distinctive moveable plate at the front (Tasch, 1973). The fossil record of phyllocarids ranges from the Cambrian to the present (Rolfe, 1969) and several examples are known from Ordovician strata (Moberg and Segerberg, 1906; Van Straelen and Schmitz, 1934; Rolfe, 1969; Dzik, 1980; Basset and Berg-Madsen, 1993). Fossil specimens vary considerably in size, but in many cases the carapace is less than 1 cm in length and only a few mm in diameter (e.g., Moberg and Segerberg, 1906). Modern phyllocarids (e.g., *Nebalia*), however, live in soft fluid mud (Russell-Hunter, 1979), not firmground mud, and do not make semi-permanent tunnel systems.

A non-crustacean origin for lower Paleozoic *Thalassinoides,* and for *Thalassinoides horizontalis* in particular, would reconcile the problems with the crustacean fossil record, but it must also explain the similarity in geometry of these burrows with younger Paleozoic to modern forms. If these older burrows were formed by phyllocarids or some other early crustaceans that were ancestral to the decapods, the polygonal geometry of the burrows could reflect a conservative behavioral trait that was passed on to a host of decapods that produced such burrows right up to the

present (e.g., shrimp, lobsters, crabs). However, polygonal, open-tunnel systems such as *Paleodictyon,* albeit smaller and more regular in geometry, are constructed by soft-bodied organisms (Webby, 1969). In a similar manner, burrows formed by acorn worms (hemichordates of the Class Enteropneusta) have very similar geometries—cylindrical with vertical-branching (Hymen, 1959; Barnes, 1980; Chamberlain, 1977, Fig. 2x)—to Mesozoic and Cenozoic examples of *Thalassinoides* that were clearly formed by large decapod crustaceans. Although the enteropneusts create larger, differently-shaped burrows than *Thalassinoides horizontalis,* the similarity of their burrows with other *Thalassinoides* burrows clearly indicates the potential for soft-bodied forms to closely mimic the geometry of burrows known to be of decapod origin.

In addition to the gross similarity in geometry between *Thalassinoides horizontalis* and some other *Thalassinoides* burrows, there is a shared affinity with peritidal paleoenvironments and a common association with hardgrounds. These affinities may indicate that instead of a long-term evolutionary control, a similarity in the geometry of these burrows may be due entirely to strong environmental and substrate controls. Unlined horizontal burrows are common in softground and firmground sediment, and such substrates are in turn common in nearshore and shoreline environments. Therefore the lack of linings, and possibly even the polygonal geometries, of both *Thalassinoides horizontalis* and other *Thalassinoides* burrows may be simply an ethological response to sediment consistency. The abundance of both Ordovician and middle to late Cenozoic *Thalassinoides* burrows is notable given the abundance of hardgrounds in rocks of this age (e.g., Wilson et al., 1992). These intervals coincide with times of depressed aragonite saturation or "calcite-sea" conditions (Mackenzie and Pigott, 1981; Sandberg, 1983) during which times the inorganic precipitation of carbonate—as mud, allochems, and cements—was exclusively as calcite (Folk, 1974; Wilkinson et al., 1982).

By comparison with some modern crustaceans that make open-framework burrows in firmground settings (e.g., *Callianassa*), it is possible that *Thalassinoides horizontalis* burrows represent conduits through which water was pumped during filter-feeding. The organisms would have exploited an infaunal suspension-feeding life habit, and thereby would represent some of the oldest known organisms to take up this model of life. Equally plausible is an interpretation that *Thalassinoides horizontalis* represents a feeding structure, in particular an agrichnia burrow. In this case, the mucous-lined walls of these open-framework burrows would have been colonized by microbes, thus providing a food source for the deposit-feeding organisms. The lack of burrow ornamentation or other irregularities makes more detailed ethological interpretations unlikely.

According to Thayer (1979), benthic communities in the lower Paleozoic were dominated by immobile epifaunal suspension feeders, and infaunal suspension feeders, which strongly disrupt sediment, diversified later in the Phanerozoic as the epifaunal groups declined. Regardless of the interpretation of *Thalassinoides horizontalis* as suspension or deposit-feeding burrows, the abundance of *Thalassinoides*-burrowed Cambrian and Ordovician carbonate deposits indicates that infaunal burrowers destroyed the primary fabrics of sediments to substantial depths during the early Paleozoic. It may be that Late Ordovician extinctions of organisms responsible for *Thalassinoides* and *Thalassinoides*-like burrows are in part responsible for the paucity of infaunal suspension feeders during the middle Paleozoic, and as a result, the limited degree of bioturbation of marine sediment at that time (Bottjer et al., 1984).

The extraordinary preservation of the Manitou samples of *Thalassinoides horizontalis* that has allowed for clear differentiation of this ichnospecies from other *Thalassinoides* ichnospecies is not found in most other Paleozoic *Thalassinoides* and *Thalassinoides*-like burrows. The complex taphonomic modes of preservation of the trace fossil *Thalassinoides horizontalis* also include those that are highly fabric-destructive (e.g., silicification). The gross similarity of this trace fossil to abundant Ordovician trace fossils ascribed to the ichnogenus *Thalassinoides* underlines the need for a comprehensive and detailed comparative study of lower Paleozoic *Thalassinoides*-like trace fossils.

ACKNOWLEDGMENTS

REFERENCES

ARCHER, A.W., 1984, Preservational control of trace-fossil assemblages: Middle Mississippian carbonates of south-central Indiana: Journal of Paleontology, v. 58, p. 285–297.

BARNES, R.S.K., 1980, Invertebrate Zoology, 4th ed.: Saunders College/Holt, Rinehart and Winston, Philadelphia, Pennsylvania, 1089 p.

BASSET, M.G., and BERG-MADSEN, V., 1993, *Protocimex:* A phyllocarid crustacean, not an Ordovician insect: Journal of Paleontology, v. 67, p. 144–147.

BEALES, F.W., 1953, Dolomitic mottling in Palliser (Devonian) Limestone, Banff and Jasper National Parks, Alberta: American Association of Petroleum Geology Bulletin, v.37, p. 2281–2293.

BEIKIRCH, D.W., and FELDMANN, R.M., 1980, Decapods crustaceans from the Pflugerville Member, Austin Formation (Late Cretaceous: Campanian) of Texas: Journal of Paleontology, v. 54, p. 309–324.

BELT, E.S., FREY, R.W., and WELCH, J.S., 1983, Pleistocene coastal marine and estuarine sequences, Lee Creek phosphate mine, eastern North Carolina: *in* RAY, C.E., ed., The Geology and Paleontology of the Lee Creek Mine, North Carolina: Smithsonian Contributions to Paleobiology, no. 53, p. 229–263.

BOTTJER, D.J., SHEEHAN, P.M., MILLER, M.F., BYERS, C.W., and HICKS, D.O., 1984, *Thalassinoides* in the Paleozoic: Geological Society of America Bulletin, Abstracts with Programs, v. 16, no. 6, p. 451.

BRADY, M.J., and ROWELL, A.J., 1976, Upper Cambrian subtidal blan-

ket carbonate of the miogeocline, eastern Great Basin: *in* ROBISON, R.A., and ROWELL, A.J., eds., Brigham Young University Geology Studies, v. 23, p. 153–163.

BRAITHWAITE, C.J.R., and TALBOT, M.R., 1972, Crustacean burrows in the Seychelles, Indian Ocean: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 11, p. 265–285.

BROMLEY, R.G., 1967, Some observations on burrows of thalassinidean Crustacea in Chalk hardgrounds: Quarterly of Geological Society of London, v. 123, p. 157–182.

BROMLEY, R.G., 1968, Burrows and borings in hardgrounds: Dansk Geologisk Forening Meddelelser, v. 18, p. 247–250.

BROMLEY, R.G., 1975, Trace fossils at omission surfaces: *in* FREY, R.W., ed., The Study of Trace Fossils: New York, Springer-Verlag, p. 399–428.

BROMLEY, R.G., 1990, Trace Fossils, Biology and Taphonomy: Special Topics in Paleontology, Unwin Hyman, Ltd., London, 280 p.

BROMLEY, R.G., and ASGAARD, U., 1972, Notes on Greenland trace fossils. II. The burrows and microcoprolites of *Glyphea resenkrantzi*, a Lower Jurassic palinuran crustacean from Jameson Land, East Greenland: Geological Survey of Greenland, Report 49, p. 15–21.

BROMLEY, R.G., and EKDALE, A.A., 1984, Trace fossil preservation in flint in the European chalk: Journal of Paleontology, v. 58, no. 2, p. 298–311.

BROMLEY, R.G., and FREY, R.W., 1974, Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides, Ophiomorpha* and *Spongeliomorpha*: Bulletin Geological Society of Denmark, v. 23, p. 311–335.

CARNEY, R.S., 1981, Bioturbation and biodeposition: *in* BOUCOT, A.J., ed., Principles of Benthic Marine Paleoecology: Academic Press Inc., New York, p. 357–407.

CHAMBERLAIN, C.K., 1977, Ordovician and Devonian trace fossils from Nevada: Nevada Bureau of Mines and Geology, Bulletin 90, 24 p.

CRIMES, T.P., 1975, The production and preservation of trilobite resting and furrow traces: Lethaia, v. 8, p. 35–48.

CRIMES, T.P., 1977, Trace fossils of an Eocene deep-sea sand fan, northern Spain: *in* CRIMES, T.P., and HARPER, J.C., eds., Trace Fossils 2: Geological Journal Special Issue 9, Liverpool, Seel House Press, p. 71–90.

CURRAN, H.A., and FREY, R.W., 1977, Pleistocene trace fossils from North Carolina (U.S.A.), and their Holocene analogues: *in* CRIMES, T.P., and HARPER, J.C., eds., Trace Fossils 2: Geological Journal Special Issue 9, Liverpool, Seel House Press, p. 71–90.

DELGADO, D.J., 1983, The Ordovician Galena Group in south central Wisconsin: *in* BYERS, C.W., et al., eds., Sedimentology of Ordovician Carbonates and Sandstones in Southeastern Wisconsin: Field trip guidebook, 17th annual meeting North Central Section Geological Society of America, p. 17–22.

DROSER, M.L., and BOTTJER, D.J., 1986, A semiquantitative field classification of ichnofabric: Journal of Sedimentary Petrology, v. 56, p. 558–559.

DROSER, M.L., and BOTTJER, D.J., 1988, Trends in depth and extent of bioturbation in Cambrian carbonate marine environments, western United States: Geology, v. 17, p. 233–236.

DROSER, M.L., and BOTTJER, D.J., 1989, Ordovician increase in extent and depth of bioturbation: Implications for understanding early Paleozoic ecospace utilization: Geology, v. 17, p. 850–852.

DZIK, J., 1980, Isolated mandibles of early Paleozoic phyllocarid Crustacea: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, p. 87–106.

EHRENBERG, K., 1938, Bauten von Decapoden (*Callianassa* sp.) aus dem Miozän (Burdigal) bei Eggenburg im Gau Nieder-Donau (Niederösterreich): Paläontologische Zeitschrift, Berlin, v. 20, p. 263–284.

EHRENBERG, K., 1944, Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleintz beschriebenen Gangkeren und Bauten dekapoder Krebse: Paläeontologische Zietschrift, Berlin, v. 23, p. 354–359.

EKDALE, A.A., and BROMLEY, R.G., 1984, Comparative ichnology of shelf-sea and deep-sea chalk: Journal of Paleontology, v. 58, p. 322–332.

EKDALE, A.A., BROMLEY, R.G., and PEMBERTON, S.G., 1984, Ichnology: The use of trace fossils in sedimentology and stratigraphy: Society of Economic Paleontologists and Mineralogists Short Course 15, 317 p.

FILLION, D., 1989, Les critéres discriminants a l'intérieur du triptyque *Palaeophycus—Planolites—Macaronichnus*. Essai de synthése d'un usage critique: C. R. Académie des Sciences Paris, t. 309, Serie II, p. 169–172.

FOLK, R.L., 1974, The natural history of crystalline calcium carbonate: effects of magnesium content and salinity: Journal of Sedimentary Petrology, v. 44, p. 40–53.

FREY, R.W., 1970, Trace fossils of Fort Hays Limestone Member of Niobrara Chalk (Upper Cretaceous), west-central Kansas: Paleontology Contributions of the University of Kansas, Article 53, 41 p.

FREY, R.W., CURRAN, H.A., and PEMBERTON, S.G., 1984, Tracemaking activities of crabs and their environmental significance: the Ichnogenus *Psilonichnus*: Journal of Paleontology, v. 58, no. 2, p. 333–350.

FREY, R.W., and HOWARD, J.D., 1969, A profile of biogenic sedimentary structures in a Holocene barrier island-salt marsh complex, Georgia: Gulf Coast Association of Geologist Societies Transactions, v. 19, p. 427–444.

FREY, R.W., and HOWARD, J.D., 1970, Comparison of Upper Cretaceous ichnofaunas from siliceous sandstones and chalk, Western Interior Region, U.S.A.: *in* CRIMES, T.P., and HARPER, J.C., eds., Trace Fossils: Geological Special Issue 3, Liverpool, Seel House Press, p. 141–166.

FREY, R.W., and HOWARD, J.D., 1985, Trace fossils from the Panther Member, Star Point Formation (Upper Cretaceous), Coal Creek Canyon, Utah: Journal of Paleontology, v. 59, p. 370–404.

FREY, R.W., and HOWARD, J.D., 1990, Trace fossils and depositional sequences in a clastic shelf setting, Upper Cretaceous of Utah: Journal of Paleontology, v. 64, p. 803–820.

FREY, R.W., HOWARD, J.D., and PRYOR, W.A., 1978, Ophiomorpha: Its morphological, taxonomic, and environmental significance: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 23, p. 511–528.

FREY, R.W., and SEILACHER, A., 1980, Uniformity in marine invertebrate ichnology: Lethaia, v. 13, p. 183–207.

FÜRSICH, F.T., 1973, A revision of the trace fossils *Spongeliomorpha, Ophiomorpha*, and *Thalassinoides*: Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, p. 719–735.

GLAESSNER, M.F., 1947, Decapod Crustacea (*Callianassidae*) from the Eocene of Victoria: Proceedings Royal Society of Victoria, Melbourne, v. 59, p. 1–7.

GLAESSNER, M.F., 1969, Decapoda: *in* MOORE, R.C., ed., Treatise on Invertebrate Paleontology, Part R, Arthropoda: Geological Society of America and University of Kansas Press, p. 399–651.

GUTSCHICK, R.C., and RODRIGUEZ, J., 1977, Late Devonian–Early Mississippian trace fossils and environments along the Cordilleran Miogeocline, western United States: *in* CRIMES, T.P., and HARPER, J.C., eds., Trace Fossils 2: Geological Journal Special Issue 9, Liverpool, Seel House Press, p. 195–208.

HÄNTZSCHEL, W., 1964, Spurenfossilien und Problematika im Campan von Beckum (Westf.): Fortschritte in der Geologie von Rheinland und Westfalen, Krefeld, v. 7, p. 295–308.

HÄNTZSCHEL, W., 1975, Trace fossils and problematica: *in* TEICHERT, C., ed., Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 1: Geological Society of America and University of Kansas Press, Lawrence, Kansas.

HATTIN, D.E., 1971, Widespread, synchronously deposited, burrow-mottled limestone beds in Greenhorn Limestone (Upper Cretaceous) of Kansas and southeastern Colorado: American Association of Petroleum Geology Bulletin, v. 55, p. 412–431.

HEINBERG, C., and BIRKELUND, T., 1984, Trace-fossil assemblages and basin evolution of the Vardekløft Formation (Middle Jurassic,

central east Greenland): Journal of Paleontology, v. 58, p. 362–397.

HERTWECK, G., 1972, Georgia coastal region, Sapelo Island, U.S.A.: Sedimentology and biology: V. Distribution and environmental significance of lebensspuren and in-situ skeletal remains: Senckenbergiana Maritima, v. 4, p. 125–167.

HOWARD, J.D., and FREY, R.W., 1975, Estuaries of the Georgia coast, U.S.A.: Sedimentology and Biology, II. Regional animal-sediment characteristics of Georgia estuaries: Senckenbergiana Maritima, v. 7, p. 237–256.

HOWARD, J.D., and FREY, R.W., 1984, Characteristic trace fossils in nearshore to offshore sequences, Upper Cretaceous of east-central Utah: Canadian Journal of Earth Sciences, v. 21, p. 200–219.

HYMAN, H.L., 1959, The Invertebrates, Vol. 5, Smaller Coelomate Groups: McGraw-Hill, New York, 783 p.

JENKINS, R.J.F., 1975, The fossil crab *Ommatocarinus corioensis* (Cresswell) and a review of related Australian species: Memoirs, National Museum of Victoria, v. 36, p. 33–62.

JOHNSON, M.E., SKINNER, D.F., and MACLEOD, K.G., 1988, Ecological zonation during the carbonate transgression of a Late Ordovician rocky shore (northeastern Manitoba, Hudson Bay, Canada): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 65, p. 93–114.

JOHNSON M.E., and WORSELY, D., 1982, Chronology and depositional environments of Early Silurian sequences in the Oslo region: *in* WORSELY, D., ed., IUGS Subcommission on Silurian Stratigraphy, Field Trip Meeting, Oslo Region: Paleontological Contributions from the University of Oslo, no. 278.

JONES, B., OLDERSHAW, A.E., and NARBONNE, G.M., 1979, Nature and origin of rubbly limestone in the upper Silurian Read Bay Formation of Arctic Canada: Sedimentary Geology, v. 24, p. 227–252.

KAMOLA, D.L., 1984, Trace fossils from marginal-marine facies of the Spring Canyon Member, Blackhawk Formation, (Upper Cretaceous), east-central Utah: Journal of Paleontology, v. 58, no. 2, p. 529–541.

KAMOLA, D.L., and CHAN, M.A., 1988, Coastal dune facies, Permian Cutler Formation (White Rim Sandstone), Capital Reef National Park area, southern Utah: Sedimentary Geology, v. 56, p. 341–356.

KAZMIERCZAK, J., and PSZCZOLKOWSKI, A., 1969, Burrows of Enteropneusta in Muschelkalk (Middle Triassic) of the Holy Cross Mountains, Poland: Acta Palaeont. Polonica, v. 14, p. 299–324.

KENDALL, A.C., 1977, Origin of dolomite mottling in Ordovician limestones from Saskatchewan and Manitoba: Bulletin of Canadian Petroleum Geologists, v. 25, p. 480–505.

KENNEDY, W.J., 1967, Burrows and surface traces from the Lower Chalk of southern England: Bulletin British Museum of Natural History, Geology, v. 15, p. 127–167.

KENNEDY, W.J., 1970, Trace fossils in the Chalk environment: *in* CRIMES, T.P., and HARPER, J.C., eds., Trace Fossils: Geological Journal Special Issue 3, Liverpool, Seel House Press, p. 263–282.

KENNEDY, W.J., 1975, Trace fossils in carbonate rocks: *in* FREY, T.W., ed., The Study of Trace Fossils: New York, Springer-Verlag, p. 377–398.

KENNEDY, W.J., and JUIGNET, P., 1974, Carbonate banks and slump beds in the Upper Cretaceous (Upper Turonian—Santonian) of Haute Normandie, France: Sedimentology, v. 21, p. 1–42.

KEPPER, J.C., 1981, Sedimentology of a Middle Cambrian outer shelf margin with evidence for syndepositional faulting, eastern California and western Nevada: Journal of Sedimentary Petrology, v. 51, no. 3, p. 807–821.

KERN, J.P., and WARME, J.E., 1974, Trace fossils and bathymetry of the Upper Cretaceous Point Loma Formation, San Diego, California: Geological Society of America Bulletin, v. 85, p. 893–900.

LETZSCH, W.S., and FREY, R.W., 1980, Deposition and erosion in a Holocene salt marsh, Sapelo Island, Georgia: Journal of Sedimentary Petrology, v. 50, p. 529–542.

LINDSTRÖM, M., 1979, Diagenesis of Lower Ordovician hardgrounds in Sweden: Geologica et Palaeontologica, v. 13, p. 9–30.

LINK, M.H., and BOTTJER, D.J., 1982, Turbidites and slope facies association, Upper Cretaceous Holz Shale Member of the Ladd Formation, Santa Ana Mountains, California: *in* BOTTJER, D.J., COLBURN, I.P., and COOPER, J.D., eds., Late Cretaceous Depositional Environments and Paleogeography, Santa Ana Mountains, Southern California: Pacific Section Society of Economic Paleontologists and Mineralogists Guidebook, p. 91–96.

LUNDGREN, B., 1891, Studier öfver fossilförande lösa block: Geologiska Föereningensi i Stockholm Förhandlingar, v. 13, p. 111–121.

MACKENZIE, F.T., and PIGOTT, J.D., 1981, Tectonic controls of Phanerozoic sedimentary rock cycling: Journal of Geological Society, v. 138, p. 183–196.

MEGLITSCH, P.A., 1972, Invertebrate Zoology: Oxford University Press, New York, 2nd ed., 834 p.

MILLER, M.F., 1977, Middle and Upper Ordovician biogenic structures and paleoenvironments, southern Nevada: Journal of Sedimentary Petrology, v. 47, no. 3, p. 1328–1338.

MILLER, M.F., 1984, Abundant and diverse early Paleozoic infauna indicated by the stratigraphic record: Geology, v. 12, p. 40–43.

MILLER, M.F., and BYERS, C.W., 1984, Abundant and diverse early Paleozoic infauna indicated by the stratigraphic record: Geology, v. 12, p. 40–43.

MILLER, M.F., and KNOX, L.W., 1985, Biogenic structures and depositional environments of a Lower Pennsylvanian coal-bearing sequence, northern Cumberland Plateau, Tennessee, U.S.A.: *in* CURRAN, H.A., ed., Biogenic Structures: Their Use in Interpreting Depositional Environments: Society of Economic Paleontologists and Mineralogists Special Publication 35, p. 67–97.

MOBERG, J.C., and SEGERBERG, C.O., 1906, Bidrag till kännedomen om Ceratopygeregionen med särskild hänsyn till dess utveckling i Fogelsångstrakten: Meddelande från Lunds Geologiska Fältklubb, Series B, v. 2, p. 1–116.

MORROW, D.W., 1978, Dolomitization of lower Paleozoic burrow-fillings: Journal of Sedimentary Petrology, v. 48, no. 1, p. 295–306.

OTT, J.A., FUCHS, B., FUCHS, R., and MALASEK, A., 1976, Observations on the biology of *Callianassa stebbingi* Borrodaille and *Upogebia litoralis* Risso and their effect upon the sediment: Senckenbergiana Maritima, v. 8, p. 61–79.

PEDLEY, M., 1992, Bio-retexturing: early diagenetic fabric modifications in outer-ramp settings—A case study from the Oligo-Miocene of the Central Mediterranean: Sedimentary Geology, v. 79, p. 173–188.

PEMBERTON, S.G., AND FREY, R.W., 1985, the *Glossifungites* ichnofacies: modern examples from the Georgia coast, U.S.A.: *in* CURRAN, H.A., ed., Biogenic Structures: Their Use in Interpreting Depositional Environments: Society of Economic Paleontologists and Mineralogists Special Publication 35, p. 237–259.

PICKERILL, R.K., FILLION, D., and HARLANDS, T.L., 1984, Middle Ordovician trace fossils in carbonates of the Trenton Group between Montreal and Quebec City, St. Lawrence Lowland, Eastern Canada: Journal of Sedimentary Petrology, v. 58, p. 416–439.

PICKERILL, R.K., and ROULSTONE, B.V., 1977, Enigmatic trace fossils from the Silurian Chaleurs Group of the southeastern Gaspé Peninsula, Quebec: Canadian Journal of Earth Sciences, v. 14, p. 2729–2736.

PLOTNIK, R.E., 1986, Taphonomy of a modern shrimp: Implications for the arthropod fossil record: PALAIOS, v. 1, p. 286–293.

PRYOR, W.A., 1975, Biogenic sedimentation and alteration of argillaceous sediments in shallow marine environments: Geological Society of America Bulletin, v. 86, p. 1244–1254.

RASMUSSEN, H.W., 1971, Echinoid and crustacean burrows and their diagenetic significance in the Maastrichtian-Danian of Stevns Klint, Denmark: Lethaia, v. 4, p. 191–216.

RICE, A.L., and CHAPMAN, C.J., 1971, Observations on the burrows and burrowing behavior of two mud-dwelling decapod crustaceans, *Nephrops norvegicus* and Goneplax rhomboides: Marine Biology, v. 10, p. 330–342.

RICHARDS, B.C., 1975, *Longusoris cuniculosus*: a new genus and species of Upper Cretaceous crab; with comments on spray formation

at Shelter Point, Vancouver Island, British Columbia: Canadian Journal of Earth Sciences, v. 12, p. 1850–1863.

RIETH, A., 1932, Neue Funde spongeliomorpher Fucoiden aus dem Jura Scwabens: Geologische und Paläontologishe Abhandlungen, new se., v. 19, p. 257–294.

ROLFE, W.D.I., 1969, Phyllocarida: *in* MOORE, R.C., and TEICHERT, C., eds., Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 1: Geological Society of America and University of Kansas Press, Lawrence, Kansas.

RUSSELL-HUNTER, W.D., 1979, A Life of Invertebrates: Macmillan Publishing Co., Inc., New York, New York, 650 p.

SANDBERG, P.A., 1983, An oscillating trend in Phanerozoic non-skeletal carbonate mineralogy: Nature, v. 305, p. 19–22.

SAPORTA, G. DE. 1884, Les orgnismes problématiques des anciennes mers: Paris, Masson, 102 p.

SAPORTA, G. DE. 1887, Nouveaux documents relatifs aux organismes problématiques les anciennes mers: Bulletin de la Societe Géologique de France, v. 15, p. 286–302.

SAVOY, L.E., 1992, Environmental record of Devonian–Mississippian carbonate and low-oxygen facies transitions, southernmost Canadian Rocky Mountains and northwestern Montana: Geological Society of America Bulletin, v. 104, p. 1412–1432.

SAVRDA, C.E., and BOTTJER, D.J., 1989, Trace-fossil model for reconstructing oxygenation histories of ancient marine bottom waters: Application to Upper Cretaceous Niobrara Formation, Colorado: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 74, p. 49–74.

SCHÄFER, W., 1972, Ecology and Palaeoecology of Marine Environments: University of Chicago Press, Chicago, Illinois, 568 p.

SCHRAM, F.R., FELDMANN, R. M., and COPELAND, M.J., 1978, The Late Devonian Palaeopalaemonidae and the earliest decapod crustaceans: Journal of Paleontology, v. 52, p. 1375–1387.

SCHRAM, F.R., and MAPES, R.H., 1984, *Imocaris tuberculata*, n. gen., n. sp., (Crustacea Decapoda) from the upper Mississippian Imo Formation, Arkansas: Transactions of San Diego Natural History Museum, v. 20, p. 165–168.

SEILACHER, A., 1955, Spuren und Leenweise der Trilobiten: Spuren und Fazies im Unterkambrium: *in* SCHINDEWOLF, O.H., and SEILACHER, A., eds., Beiträge Zur Kenntnis des Kambriums in der Salt Range (Pakistan): Akademie der Wissenschraften und der Literatur, Mainz, Abhandlungen der Mathematisch—Naturwissenschraftlichen Klasse, v. 10, p. 86–143.

SELLWOOD, B.W., 1971, A *Thalassinoides* burrow containing the crustacean *Glyphaea udressieri* (Meyer) from the Bathonian of Oxfordshire: Paleontology, v. 14, p. 589–591.

SENOWBARI-DARYAN, B., and STANLEY, G.D., JR., 1986, Thalassinid anamuran microcoprolites from Upper Triassic carbonate rocks of central Peru: Lethaia, v. 19, p. 343–354.

SHEEHAN, P.M., and SCHIEFELBEIN, D.R.J., 1984, The trace fossil *Thalassinoides* from the Upper Ordovician of the eastern Great Basin: Deep burrowing in the early Paleozoic: Journal of Paleontology, v. 58, p. 440–447.

SHINN, E.A., 1968, Burrowing in recent lime sediments of Florida and Bahamas: Journal of Paleontology, v. 42, p. 879–894.

STANISTREET, I.G., 1989, Trace fossil associations related to facies of an upper Ordovician low wave energy shoreface and shelf, Oslo-Asker district, Norway: Lethaia, v. 22, p. 345–357.

SWINBANKS, D.D., and LUTERNAUER, J.L., 1987, Burrow distribution of thalassinidean shrimp on a Fraser Delta tidal flat, British Columbia: Journal of Paleontology, v. 61, no. 2, p. 315–332.

TASCH, P., 1973, Paleobiology of the Invertebrates: Data retrieval from the fossil record: John Wiley and Sons, New York, 975 p.

THAYER, C.W., 1979, Biological bulldozers and the evolution of marine benthic communities: Science, v. 203, p. 458–461.

TUDHOPE, A.W., and SCOFFIN, T.P., 1984, The effects of *Callianassa* bioturbation on the preservation of carbonate grains in Davies Reef lagoon, Great Barrier Reef, Australia: Journal of Sedimentary Petrology, v. 54, no. 4, p. 1091–1096.

VOIGT, E., 1959, Die ökologische Bedeutung der Hartgründe ("Hard-

grounds") in de oberen Kreide: Paläeontologische Zeitschrift, v. 33, p. 129–147.

VAN STRAELEN, V., and SCHMIDT, G., 1934, Crustacea Phyllocarida (=Archaeostraca): *in* QUENSTEDT, W., ed., Fossilium Catalogus, 1: Animalia, W. Junk, Berlin, Pars 64, p. 1–246.

WALLACE, R.C., 1913, Pseudobrecciation in Ordovician limestones in Manitoba: Journal of Geology, v. 21, p. 402–421.

WANLESS, H.R., TEDESCO, L.P., and TYRELL, K.M., 1988, Production of subtidal tubular and surficial tempestites by Hurricane Kate, Caicos platform, British West Indies: Journal of Sedimentary Petrology, v. 58, p. 739–750.

WEBBY, B.D., 1969, Trace fossils (Paschichnia) from the Silurian of New South Wales, Australia: Paläeontologische Zeitschrift, v. 43, p. 81–94.

WILKINSON, B.H., JANECKE, S.U., and BRETT, C.E., 1982, Low-magnesium calcite marine cement in Middle Ordovician hardgrounds from Kirkfield, Ontario: Journal of Sedimentary Petrology, v. 52, p. 47–57.

WILSON, M.A., PALMER, T.J., GUENSBURG, T.E., FINTON, C.D., and KAUFMAN, L.E., 1992, The development of an Early Ordovician hardground community in response to rapid sea-floor calcite precipitation: Lethaia, v. 25, p. 19–34.

ZENGER, D.H., 1984, Dolomitization patterns in subtidal Bighorn Dolomite (Upper Ordovician), southeastern Wind River Range, Wyoming: American Association of Petroleum Geology Bulletin, Abstracts with Programs, v. 68, no. 4, p. 542–543.

ZENGER, D.H., 1988, Stratigraphy, petrology and dolomitization, Bighorn Dolomite (Upper Ordovician), northwest Wyoming: Geological Society of America Bulletin, Abstracts with Programs, Rocky Mountain Section, v. 20, p. 476.

APPENDIX A

SYSTEMATIC ICHNOLOGY

Ichnogenus Thalassinoides Ehrenberg, 1944
Thalassinoides horizontalis n. ichnosp.
Figures 6–9

Thalassinoides galleries Savoy, 1992, p. 1414–1415, fig. 6B.

Origin of name: Species name *horizontalis* reflects the bedding-plane orientation of the polygonal arrangement of burrows.

Type locality: Type specimens were taken from exposures of the Cambrian Peerless Formation and Ordovician Manitou Formation at the western end of Manitou Springs, Colorado along Fountain Creek and Route 24 (Fig. 1).

Repository: Type material has been placed in the Paleontological Collections of the Department of Geology, Colorado College. Specimen numbers: holotype, #4645: paratype, #4646.

Diagnosis: Branching framework of smooth-walled, unlined burrows with diameters (inner tube) of less than 5 mm (3–3.5 mm on average; Table 2). The diagnosis also rests on the combination of the following characteristics: (1) an entirely bedding-parallel orientation; (2) absence of vertically oriented offshoots from polygonal frameworks, and (3) diameters of both inner and outer burrow walls is consistent within specimens, including a notable lack of constrictions or swellings at both junctions and inter-junction segments.

Description of specimens in the type area: Polygonal network of smooth-walled, unlined, branching burrows. Burrows form both Y- and T-junctions defining a bedding parallel framework. The plan-view geometries range from irregularly-shaped rectilinear networks to pseudo-polygonal mazes, the latter of which in cases form near-equant, five-sided polygons. Burrow segments are generally linear, but may show minor changes in orientation. Burrows occur as endichnia in bioturbated sub-hardground micrite beds and on bedding planes in nodular and ribbon bedded micrite with hyporelief of approximately half a burrow diameter. Outer wall diameters of the

TABLE 3—Reported diameters of *Thalassinoides* burrows.

Author	Age	Diameter
Ott et al. (1976)	Modern	7–9 mm; turnarounds 12–15 mm
Hertweck (1972)	Modern	4–10 mm
Häntzschel (1975) [Treatise]	Triassic–Tertiary	10–200 mm (typically 10–15 mm)
Curran and Frey (1977)	Pleistocene	10–25 mm; branches enlarged at Y junctions (30–50 mm)
Bromley and Ekdale (1984)	Upper Cretaceous–Lower Tertiary	20–50 mm (determined from photographs)
Bromley (1967)	Upper Cretaceous	10–50 mm
Frey and Howard (1970)	Upper Cretaceous	*T. paradoxica* = 8 to >50 mm; *T.* sp. = 5–20 mm
Frey and Howard (1990)	Upper Cretaceous	7–15 mm; ave. 11 mm
Hattin (1971)	Upper Cretaceous	9–15 mm
Frey (1970)	Upper Cretaceous	5–20 mm
Beikirch and Feldmann (1980)	Upper Cretaceous	11 mm flattened cyclinder; 7 mm or > before compaction
Häntzschel (1964)	Upper Cretaceous	18–28 mm
Kern and Warme (1974)	Upper Cretaceous	burrow dia. 3–35 mm
Kamola (1984)	Upper Cretaceous	5–30 mm
Savrda and Bottjer (1989)	Upper Cretaceous	7–15 mm max.
Kennedy (1975)	Cretaceous	20–200 mm
Seilacher (1955)	Lower Jurassic	18–24 mm
Miller and Knox (1985)	Lower Pennsylvanian	7–12 mm
Gutschick and Rodriguez (1977)	Late Devonian–Lower Mississipian	Flattened tubes 10 mm max.
Archer (1984)	Middle Mississipian	7–9 mm
Pickerill and Roulston (1977)	Silurian	5 mm min.; Max. 30 mm at turnarounds
Chamberlain (1977)	Ordovician and Devonian	5–10 mm
Miller (1977)	Middle/Upper Ordovician	30–60 mm
Sheehan and Schiefelbein (1984)	Upper Ordovician	10–20 mm; turnarounds = 40 mm

burrows show little variation and average 10 mm (Table 2). Five transitional styles of preservation are associated with these burrows (see text and Fig. 5), and these relate to the presence or absence of burrow-filling sediment and/or cement, type and degree of mineral replacement, and the differential weathering of burrow parts and surrounding sediment. Size data for the different preservational styles of the burrows are given in Table 2.

Discussion: The systematics of the ichnogenus *Thalassinoides* are complex (see Kennedy, 1967; Frey, 1970; Bromley and Frey, 1974; Häntzschel, 1975; Frey and Howard, 1985, 1990). The most common ichnospecies include: *T. saxonicus* (Geinitz), a large form with tunnels 5–20 cm in diameter (Kennedy, 1967, Pl. 1, Fig. 1; Pl. 5, Figs. 2, 3; Pl. 6, Figs. 3, 4); *T. ornatus* (Kennedy), smaller ovate (8 × 16 mm to 10 × 22 mm; Kennedy, 1967) horizontal to gently inclined burrows with swellings (Kennedy, 1967, Pl. 6, Fig. 4; Pl. 7, Fig. 6); *T. paradoxicus* (Woodard), branching, boxwork burrows that are highly irregular in size and geometry (Kennedy, 1967, Pl. 3; Pl. 4; Pl. 8, Fig. 5; Pl. 9, Fig. 2; Frey, 1970, Pl. 5, Fig. 5; Pl. 6, Figs. 2, 3, 9; Bromley and Ekdale, 1984, Fig. 5); and *T. suevicus* (Rieth, 1932) a predominantly horizontal form that may contain enlargements at Y-shaped bifurcations (Kamola, 1984, Figs. 13, 14: Bromley and Ekdale, 1984, Figs. 6, 11; Frey and Howard, 1985, Figs. 5.8, 10.13, 16.3c, 16.4, 19.1a, 24.1, 24.2; Frey and Howard, 1990, Fig. 28).

There are important geometric and size differences between *Thalassinoides horizontalis* and the other ichnospecies of *Thalassinoides*. The most similar ichnospecies is *T. suevicus* (Rieth, 1932) which is a dominantly horizontal, smooth-walled form. Kennedy (1967, p. 140) describes *T. suevicus* burrows with 2–5 cm diameters which he states are comparable in size to the type material of Rieth. In fact, in the type collections of *T. suevicus* described by Rieth (1932, p. 275, under name *Spongites suevicus quendstedti*), the burrow segments between enlarged Y-junctions average 2–3 cm in diameter (range = 0.3 cm to

4 cm). *Thalassinoides horizontalis* burrows are therefore considerably thinner (inner diameter data in Table 2; mean = 3.4 mm) than Rieth's (1932) type material of *T. suevicus*. In fact, burrows of *T. horizontalis* are thinner than most reported examples of *Thalassinoides* by at least a factor of two (Table 3: mean of *minimum* diameters = 4.6 mm; mean of average/mid-range diameters = 15.9 mm) and, importantly, anywhere from 50% to more than an order of magnitude smaller than the diameter of reported examples of *T. suevicus* (e.g., 18–24 mm, Seilacher, 1955, Fig. 5; 2–5 cm, Kennedy, 1967; 9–15 mm, Howard and Frey, 1984; 2.5–4 cm, Bromley and Ekdale, 1984, Fig. 11; 11 mm, Frey and Howard, 1990). In addition, the length of the relatively straight burrow segments between junctions is also generally smaller (Fig. 6a, c) than the 15 cm average for Rieth's (1932) type material. One example of consistently thin (2–6 mm diameter) *Thalassinoides*-like burrows was described by Lidström (1979), but these contain numerous vertical offshoots. The geometry of *T. horizontalis* is more regularly polygonal than many other described examples of *T. suevicus* (e.g., Howard and Frey, 1984, Fig. 24; Bromley and Ekdale, 1984, Fig. 6; Frey and Howard, 1990, Fig. 28), but is similar to the type material of *T. suevicus* (Rieth, 1932, Pl. 13a, b, under name *Cylindrites suevicus* Quenstedt).

The burrows of *Thalassinoides horizontalis* are devoid of meniscate fillings, which are frequently found in Mesozoic and Tertiary examples of *Thalassinoides* (Kern and Warme, 1974; Kamola, 1984; Bromley and Ekdale, 1984), including *T. suevicus* (Frey and Howard, 1990). Such fillings are usually absent from Paleozoic *Thalassinoides* specimens (Gutschick and Rodriguez, 1977; Kennedy, 1975) with rare exceptions (see Miller and Knox, 1985). Specimens of *Thalassinoides horizontalis* also lack burrow offshoots and other geometric irregularities. In addition, they lack burrow enlargements that are found at Y- and T-junctions or the ends of burrow offshoots, which have been described from some examples of *Thalassinoides* ranging from

Ordovician to the Modern (Gutschick and Rodriguez, 1977; Curran and Frey, 1977; Frey et al., 1984; Sheehan and Schiefelbein, 1984; Swinbanks and Luternauer, 1987).

In summary, the distinction between *Thalassinoides horizontalis* burrows and other ichnospecies of *Thalassinoides,* including *T. suevicus* rests primarily on the burrow diameter which is almost exclusively less than 5 mm, but also on the combination of the following features: strictly bedding-parallel orientation, lack of vertical or inclined offshoots, and extremely regular burrow diameter. As described in the text, *T. horizontalis* burrows represent open-framework burrow systems that lack evidence for creation by decapod crustaceans, and were therefore most likely created by small-diameter soft-bodied suspension- or deposit-feeding organisms.