SELECTED STUDIES IN LOWER PALEOZOIC ICHNOLOGY

By

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Abstract

Despite the attention recently given to ichnology, intensive investigations have been mounted in only a limited number of critical areas. These include the zoological affinities of, and the paleobathymetric significance of soft-sediment ichnofossils. Such areas as establishing a workable nomenclatural system, the significance of Lower Paleozoic macroborings, and quantitative methods in ichnology, although important, have received considerably less mention. In order to examine these lesser known facets an integrated study of selected Lower Paleozoic ichnofossils was conducted.

Part one involves the identification and significance of an extensive ichnofossil suite, comprising 27 different ichnogenera from the Middle Silurian Thorold Sandstone of southeastern Ontario and New York. These ichnofossils are indicative of the shallow-water, nearshore Skolithos and Cruziana ichnofacies, and can be divided into four distinctive assemblages. As well as providing information on the interpretation of the paleoenvironments, lateral variations in ethological categories prove valuable in delineating ancient storm deposits.

Part two comprises a collection of individual investigations of significant Lower Paleozoic

ichnofossil occurrences with particular attention paid to quantitative methods.

1). Since ichnofossils are used not only by ichnologists but by vertebrate and invertebrate paleontologists, paleobotanists, stratigraphers, and sedimentologists, it is impertive to have a workable nomenclatural system. One of the most abundant and important groups of ichnofossils are single-entranced, vertical burrows, which currently include many ill-defined and poorly understood forms. Through the examination of type specimens and an analysis of pertinent morphological characteristics, this diverse group can be referrable to only four distinct ichnogenera: *Cylindrichnus*, *Monocraterion*, *Skolithos*, and *Stipsellus*.

2). Ichnology also encompasses structures produced biogenically in hard substrates. Such ichnofossils, although well studied in post-Paleozoic deposits, have received considerably less attention in Lower Paleozoic strata. The Silurian-Devonian disconformity in southern Ontario exhibits well-preserved macroborings of the ichnogenus *Trypanites*. Quantification of borings using shape parameters shows that boring morphology can be described accurately. Comparison with borings made by recent sipunculids indicates a high degree of similarity, suggesting that these examples of *Trypanites* were probably produced by sipunculids.

3) A specimen of the ichnospecies Lingulichnus verticalis was recovered from the Lower Cambrian Bradore Formation of southern Labrador. The sample represents the only known Cambrian example of an in situ lingulid, and sheds light on the evolution of their ethology. Prior to this, it was assumed that Cambrian lingulids maintained a non-burrowing mode of life.

4) Ichnology has progressed beyond the stage of mere description and it may now be possible to try to apply some quantitative concepts. Modern ecological methods to measure and interpret spatial distributions were applied to selected Lower Paleozoic vertical ichnofossils. Such analyses may prove valuable in interpreting a host of biotic interactions among ichnofossil assemblages.

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In as much as a study of this magnitude is the work of one man, it also reflects those around him: to all my friends and colleagues a hearty thank you!

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CHAPTER 1

Introductory Remarks

1-1. Purpose and Scope

The study of ichnology encompasses a wide array of complex animal-sediment interactions in both ancient and recent deposits. Although quite slow in its development, ichnology has recently received widespread acceptance since many of these interactions are dependent on both the morphology of the trace maker and the physical properties of the sedimentological environment. As such, these structures provide pertienent information in the interpretation of paleoenvironments and sedimentological regimes. This increased awareness of the usefulness of trace fossils is in part a result of a number of recently published works which have focused attention on them (see Crimes and Harper, 1970, 1977; Osgood, 1970; Frey, 1971, 1973, 1975; and Basan, 1978).

In spite of this attention, intensive investigatons have been mounted in only a limited number of critical areas in ichnology. These include the zoological affinities of, and the paleobathymetric significance of, soft sediment ichnofossils, as well as descriptive work on the distribution of trace fossils within specific geological formations. Such areas as establishing a workable nomenclatural system, the significance of Lower Paleozoic macroborings, and quantitative methods in ichnology, although important, have received considerably less mention.

The purpose of this study is to examine a number of these lesser known facets of ichnology, as well as examining the more traditional approaches. As a result, the study is divisible into two major sections. Section one concerns the identification and paleoenvironmental significance of the ichnofossils from a Lower Paleozoic clastic unit. An extensive suite of trace fossils was recognized from the Middle Silurian Thorold Formation of southeastern Ontario and northwestern New York State (Chapters 2 and 3). The trace fossils of this otherwise unfossiliferous unit seem to be the only clue to its original biologic component (Chapter 3), and their distribution and lateral variations are used to interpret the depositional history (Chapter 4).

In the past, trace fossils were viewed as unique depth indicators. This concept, although responsible for the rapid growth and acceptance of ichnology, has also proven to be one of its major curses. More often than not trace fossils were cited as the sole criteria for establishing paleobathymetrys. Recent investigations, however, have revealed that such a simplistic view is not entirely accurate (see Chapter 4). Although ichnofossils are extremely valuable in delineating facies they should not be viewed as separate entities, but instead must be utilized in context with the entire spectrum of physical and biological characteristics. In this regard the present study (Section 1) will report on what ichnofossils are present in the Thorold as well as their paleoenvironmental significance. It should therefore be stressed that this is by no means a definitive answer but represents merely one line of evidence. The final solution can be postulated only when both the sedimentological and ichnological data are incorporated

Section two is a collection of separate investigations which are referable to some of the lesser known approaches in ichnology and include:

i). Since trace fossils are used not only by ichnologists but by invertebrate and vertebrate paleontologists, paleobotanists, stratigraphers, and sedimentologists, it is imperative to have a workable nomenclatural system. Unfortunately, this is not the case and Chapter 5 is an attempt to illustrate the nomenclatural problems presently facing geologists. In this regard, single-entranced, vertical ichnofossils were chosen for study. Through the examination of type specimens (where possible) and an analysis of pertinent morphological characteristics a revised nomenclatural classification for these most useful and abundant forms is proposed.

ii). Ichnology does not restrict itself to structures generated solely in soft sediment but also encompasses structures produced biogenically in hard substrates. Such ichnofossils, although well-studied in post-Paleozoic rocks, have received considerably less attention in Lower Paleozoic strata. Exceptionally well-preserved macroborings were studied from the Silurian-Devonian disconformity in southern Ontario (see Chapter 6). By employing a quantification of the morphology of the macroborings using shape parameters and a comparison to boring of modern endoliths, the establishment of the zoological affinities of these structures may be possible.

iii). It is a common misconception that trace fossils are the result of the activities of soft-bodied organisms exclusively. Such a generalization, however, is not accurate since many shelled organisms are known to create a variety of ichnological structures. A rather spectacular example from the Lower Cambrian Bradore Formation of southern Labrador is reported in Chapter 7. The structure, a dwelling burrow of a Lingulid brachiopod, is described and its significance on the evolution of the ethology of linguloid brachiopods is examined.

iv). The study of trace fossils has recently progressed beyond the stage of mere description and it may now be possible to try to apply some rudimentary quantitative concepts. Chapter 8 is an attempt to implement modern ecological methodology to measure and interpret the spatial distribution of some selected vertical ichnofossils. Such analyses may ultimately reveal a host of biotic interactions which were once thought to be restricted to the study of recent animal structures. In addition, a discussion of the limitations of such a measurement is also included.

Frey (1971, p. 121) concluded that "Ichnology is undoubtedly on a firm footing; certain areas need considerably more study, but mostly the science needs only the continuous refinement necessary in all earth sciences." Such a diverse format ultimately serves not only to integrate some of the more important approaches currently being advanced in ichnology, but also to explore the possibilities of others.

CHAPTER 2

The Thorold Sandstone: Stratigraphy, Sedimentology, and Ichnology

2-1. Introduction

The Thorold Sandstone (Silurian, Niagaran) is believed to have been deposited in a shallow, nearshore environment (see Martini, 1966, for details), and contains a wealth of trace fossils. Ichnofossils have often been used as paleobathymetric indicators for nearshore environments (Seilacher, 1967a). Recent studies, however, suggest that ichnofossils may not be as reliable as previously thought for such depth determinations (see Osgood and Szmuc, 1972; Hayward, 1976; Crimes, 1977; among others). It was therefore thought advisable to investigate the distribution of the ichnofossil suite found in the Thorold Sandstone and compare it to the sedimentological model of deposition proposed by Martini (1966, 1971, 1974). The major objectives of this section of the present study can be summarized as follows:

1). To report on the extensive (and previously unreported) ichnofossil suite found in the Thorold Sandstone.

2). To trace the distribution and density of the ichnofauna, as they occur along the outcrop belt.

3). To investigate the variation in densities and distributions of feeding types.

2-2. The Thorold Sandstone

A). Definition

The Thorold Sandstone was first defined by Grabau (1913) for a greyish sandstone bed which capped the Medina Formation in the vicinity of Thorold, Ontario. Since that time, the actual positioning of the unit has been the center of considerable controversy. Some subsequent investigators placed it as the lowermost member of the Clinton Group, thus implying a Middle Silurian age (Chadwick, 1918; Gillette, 1940, 1947; and Bolten, 1957; among others); while others view it as the final deposit of the Medina Group, thus implying a Lower Silurian age (Williams, 1919; Ulrich and Bassler, 1923; Sanford, 1936; Caley, 1940; Fisher, 1954; Martini, 1965, 1971b, 1972, 1974; and Kilgour, 1972; among others). In order to resolve some of the problems, Fisher (1954) postulated that the Thorold was an eastward, transgressive unit, crossing time lines and becoming progressively younger towards the east. This satisfies a number of field observations, in that the Thorold is clearly the uppermost member of the Medina Group in northwestern New York and southwestern Ontario (Martini, 1966) and is the lowermost member of the Clinton Group in central New York (Gillette, 1947). Fisher's time-transgressive theory has met with favourable response from a number of subsequent workers (Bolton, 1957; Martini, 1966, 1971b, 1972, 1974; Kilgour, 1972).

An earlier attempt to rectify this problem of age difference resulted in the erection of a new formation. Chadwick (1918) proposed the Kodak Sandstone as the stratigraphic equivalent of the Thorold in the Genesse Gorge section of Rochester, New York, and placed it as the lowermost deposit of the Clinton Group. The Thorold was thought to be absent east of Dickersonville, New York (about 11 km east of Lewiston, New York) and its position was occupied by the Kodak Sandstone at the Medina section (Oak Orchard Creek) eastwards to Rochester and Fulton, New York (see Chadwick, 1918; Kilgour, 1972). Examination of the outcrops at Medina and Rochester, however, have led subsequent investigators to question the validity of the term Kodak. Gillette (1947) and Martini (1966) state that the Thorold is indeed found at these sections. Similar observations were also made during the present study and the term Kodak Sandstone should be abandoned.

The Thorold is a light grey quartzose sandstone with shale and siltstone interbeds locally well developed. The lower contact with the mottled red and white Grimsby Sandstone is gradational and based primarily on a distinctive colour change. The upper contact of the Thorold with the Reynales Formation (in the Hamilton area), the Neahga Shale (from Grimsby, Ontario, east to Lockport, New York), and the Maplewood Shale (in the Rochester area) is disconformable. The Thorold Sandstone is laterally transitional with the Oneida Conglomerate to the east (Gillette, 1947) and the Cabot Head Shale to the west.

B). Study area

The Thorold Sandstone crops out along the Niagara Escarpment from Dundas, Ontario in the west, to Fulton, New York in the east (fig. 2-1). Along the belt a total of 25 outcrops were examined (Table 2-1), all of which were previously described and measured by Martini (1966) and others (see Martini, 1966, Table 1-2 and contained references). Recorded observations and measurements all correspond with the previous work of Martini (1966), except at the Town Line Road section in New York (section 0, of Martini, 1966). At this secton, Martini observed a thin (3 in.) layer of Thorold which was not observed in this present study (probably overgrown vegetation). Similar alterations

Fig. 2-1. Index map showing the locations of the sections used in studying the ichnofossils of the Thorold. For specific outcrop locations, see Martini (1966).

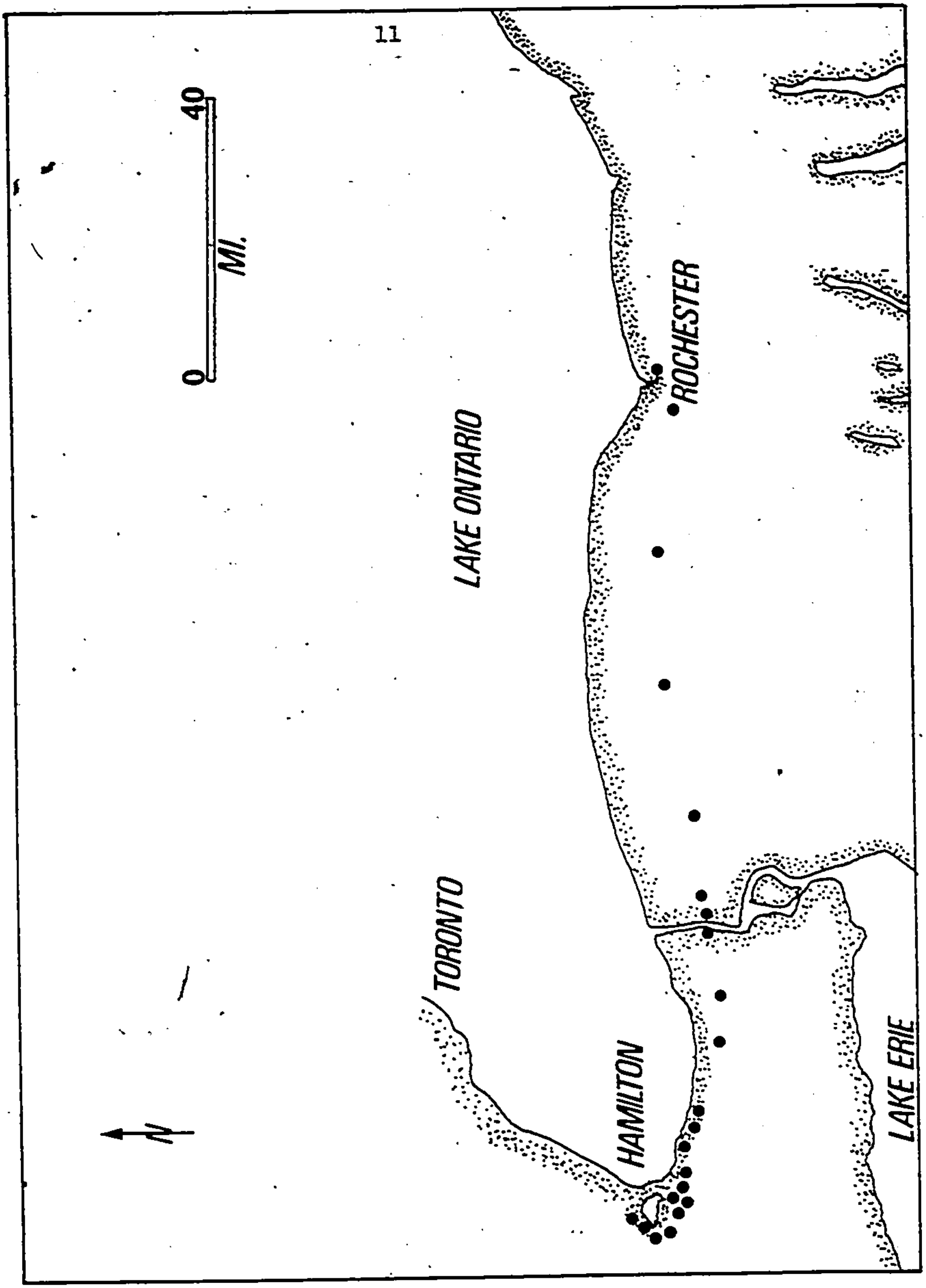
0
40
MI.
LAKE ONTARIO
ROCHESTER
TORONTO
HAMILTON
LAKE ERIE
N

Table 2-1. Thorold outcrops investigated, sediment thickness after Martini (1966).

Section	Thorold Thickness	Section Designation
Glen Edith	4' 6"	X
Genesee Gorge	5' 4"	G
Medina	10' 2"	U
Lockport	2' 6"	K
Town Line Road	3"	Q
Niagara Gorge	9' 11"	R
Niagara Glenn	7' 5"	NG
DeCew Falls	10' 7"	A
Rockway	10'	RC
Balls Falls	10'	BF
Grimsby Beach	6' 9"	GB
Woolverton Road	10' 9"	WR
Vinemount	9'	Vn
Fruitland Road	12' 8"	FC
Stoney Creek	7' 6"	SC
Highway 20	6'	20
Albion Falls	10' 2"	AF
Flock Road	15' 3"	FR
Mountain Bld.	14' 5"	MB
Jolley Cut	14' 10"	JC

Table 2-1 continued.

Highway 403	14' 11"	403
Webster's Falls	11' 4"	WF
Sydenham Road	11' 7"	SR
Rock Chapel Falls	14' 11"	RF
Clappisons Corners	14' 11"	CC

of outcrops were noticed at the Highway 403 section (outcrop P1, of Martini, 1966) which is a new road cut and the Clappison Corner section (outcrop CC of Martini, 1966), which also has considerable overgrowth. In an effort to avoid confusion the present study will retain (where appropriate) the same outcrop designations employed by Martini (1966).

C). Regional geological framework

In order to understand fully the interpreted depositional history of the Thorold a brief review of the regional sequence of events is necessary (after Martini, 1966, 1971b):

1). Commencing during the Late Ordovician a series of clastic deposits (the Bald Eagle, Juniata and Queenston Formations) were lain down westward from the rising Taconic Mountains. These sediments comprise deltaic complexes and cover the east-central section of North America (Grabau, 1908; Yeakel, 1959, 1962).

2). The reworking of the clastic deposits of the Bald Eagle and Juniata Formations provided the sediments which formed the Medina complex during the early Silurian. In the Great Lakes area the complex consists of littoral sands (the Whirlpool), deltaic and littoral to sublittoral sands and muds (the Grimsby and Thorold) which covered northwestern New York and the Niagara Peninsula. More distal from the Appalachian clastic sources, sublittoral, open marine, muds and carbonates (The Cabot Head and Manitoulin) were deposited in the Niagara-Manitoulin Island area (Fisher, 1954; Bolten, 1951; Martini, 1966). Swartz, *et al.* (1942) points out that the Medina Group correlates with the clastic Tuscarora Sandstone of the Appalachians and with the Manitoulin and Mayville Dolomites towards the Michigan area.

3). The low-lying Taconic Hills supplied little clastic material to the Great Lakes area during the Middle Silurian time. Following the clastic deposition of the Thorold, the carbonate, minor evaporates, and minor quantities of mud of the Clinton were deposited.

2-3. Martini's Depositional Model

Over a period of eight years, Martini (1966, 1971a, 1971b, 1972, 1974) developed a depositional model for the Medina Formation (including the Thorold Sandstone). This interpretation is employed as the starting point for the present study, to test the validity of ichnofossils as reliable paleobathymetric indicators in shallow, near-shore environments. In order to avoid repetition, all statements made in this section (unless specifically indicated) are after Martini (1966, 1971b). This synopsis will be limited only to those details specifically related to the Thorold Sandstone.

The Medina Formation displays lateral and vertical variations of textures, fabrics, sedimentary structures and faunal assemblages which are indicative of a deltaic to shallow marine origin. Specifically, the Thorold Sandstone records the destructive phase of the Medina delta complex in Ontario, in which the sediments were reworked and dispersed in uniform thickness over an area of at least 255 km. The formation of the Thorold was possible due to the slow subsidence of the Medina basin, a change in the power of sediment reworking for a relatively long period of time, and a reduced availability of clastics carried into the exposed portion of the Medina basin.

Extensive analysis of a number of parameters enables Martini (1971a) to identify two major paleocurrent systems in the Thorold. These two systems can be separated geographically:

1). The first system trends northwest and is recorded in the azimuths of crossbeds and in grain orientations measured in crossbeds in the New York region east of Model City (section M). Martini (1971a) suggested that the unimodal distribution and the low measured variability is indicative of a channelized paleocurrent displaying fluviatile characteristics.

Such a system also indicates the paleoslope, hence Martini states that the source of the Medina sediments was from the Appalachian region.

2). A second paleocurrent system trending northeast-southwest is recorded in the azimuths of cross-beds and in grain orientations measured in crossbeds of the Niagara-Ontario region west of Model City. Martini (1971a) suggested that the tendency of the azimuths of crossbeds to have bimodal distributions with modes 180° apart is indicative of a marine longshore and/or tidal paleocurrents.

Although Martini (1971a) states that the two systems are found partially interstratified, the Model City section can be taken as an arbitrary cut-off between the predominantly channelized (deltaic) paleocurrent of parts of the New York sections, and the marine paleocurrent of the Niagara-Ontario sections.

Martini's proposed model suggests that there exists three sources for the sediments that comprise the Thorold:

1). The Niagara-DeCew Falls region, since eastward and westward from this area is a distinct increase in the shaly content of the Thorold.

2). The Oneida Conglomerate, which is laterally transitional to the Thorold in the Clyde quadrangle (Gillette, 1947).

3). Reworking of the upper beds of the Grimsby (as indicated by the channelized contact between the Grimsby and Thorold at certain outcrops).

Analysis of the paleocurrent systems, sediment source areas, sedimentary structures, and lithologic variations enabled Martini to differentiate certain depositional trends within the Thorold Sandstone. The easternmost sections exposed at Rochester (section G), Medina (section U), and Lockport (section K) were interpreted as being deposited in a tidal flat or interdistributory environments. These outcrops display characteristics indicative of deposition at varying distances from the clastic input areas and under low wave energy conditions. The Town Line Road section (0) was deposited in a similar environment but Martini noted that it represented the westernmost expression of low energy conditions in the Thorold.

The area encompassing the outcrops at Niagara and DeCew Falls (sections R, N.G, and A) record the uppermost expression of the destructive phase of the Medina delta complex. The Thorold was interpreted as resulting from the reworking of deltaic sediments in a sublittoral environment. At the Niagara Glenn section (N.G.) the entire Thorold has been considered to represent a long-shore bar deposited under high wave energy. Westwards from Niagara the Thorold takes on decidedly marine characteristics, and the shale content increases indicating a greater distance from the clastic input area as well as the weakening of long-shore currents. Martini suggests that in this area sublittoral environments dominate but also notes the presence of periodic littoral conditions.

In the Hamilton area, the Thorold represents the spreading out of the course clastics of the Medina delta and is characterized by alternating quartz sandstones, siltstones and shale interbeds. The high siltstone and shale content indicates a greater distance from the sediment source area. This trend continues west of Hamilton, at the Webster's Falls (WF) and Clappison Corners (CC) sections progressively more finer-grained sediments were observed.

2-4. Ichnogenera Recognized

Ichnofossils have long been known from rocks assigned to the Medina Group. Unfortunately early investigators did not differentiate between forms located in the different formations of the Medina and thus it is often impossible to ascertain if a partilar form was associated with the Thorold Sandstone. Hall (1852) defined the ichnogenus Arthrophycus from abundant specimens found in Medina rocks at Rochester. In addition, he described forms which he placed in the ichnogenera Skolithus and Paleophycus. Ringueberg

(1884) described a trace fossil from the Medina at Lockport, New York, under the name Spirophyton (which was subsequently shown to be referrable to the ichnogenus Daedalus). Sarle (1906) observed that Arthrophycus and Daedalus were abundant in the Medina strata of western New York.

More recently, a host of trace fossils have been described from the Thorold Sandstone. Martini (1966, 1971b) described both Arthrophycus and Daedalus as common elements of the Thorold. In the Hamilton, Ontario area, Thorold outcrops have yielded a number of different forms. Langille (1970) observed the ichnogenera Arenicolites, Arthrophycus, Daedalus, and Diplocraterion, as well as trilobite feeding tracks. Risk (1973) described forms which he compared to modern echiuroid traces; and Risk and Szczuzko (1977) illustrate forms of the ichnogenera Chondrites, Cruziana, Diplocraterion, and Skolithos from the Thorold strata of the Hamilton area.

The present study recognizes 22 different ichnogenera, 4 miscellaneous forms and one unidentified form (the probable echiuroid trace of Risk, 1973). Although the majority of these are restricted to the Hamilton area, ichnofossils were discerned at virtually every Thorold outcrop. Table 2-2 lists the ichnogenera and subdivides them using simple morphological criteria.

Table 2-2. Purely morphological classification of ichnofossils encountered in the Thorold.

Rank IV	Rank III	Rank II	Rank I	
Trail-like trace on bedding plane	Freely winding	Simple trail	No Ornamentation	? *Gordia*
		Bilobed trail	Transverse Ornamentation	*Cruziana*
		Trilobed trail	Transverse Ornamentation	? *Scolicia*
Tunnels and shafts	Of uniform diameter	Vertical	Circular cross-section	*Skolithos*
			Elliptical cross-section	*Lingulichnus*
		Horizontal	Transverse annulations	*Arthrophycus*
			Longitudinal striations	*Fucusopsis*
			Infill similar to matrix	*Palaeophycus*
			Infill not similar to matrix	*Planolites*

Table 2-2 -- Continued

		Paired branches	*Caprionichnus*
	U-shaped	Horizontal basal connection	*Bifungites*
		Curved basal connection	*Arenicolites*
		Longitudinal striations	? *Trichophycus*
	Regularly branching		*Chondrites*
Variable diameter	Horizontal	Cup-like expansions	*Rhabdoglyphus*
		Transverse annulations	*Scalarituba*
		Regularly branching	*Lobichnus*
	Vertical		*Dolopichnus*

Table 2-2 -- Continued

Forms having a spreite		Inclined		*Polycylindrichnus*
		U-shaped		*Diplocraterion*
		J-shaped		*Daedalus*
		Fan-shaped		Echiuroid traces
		Vertical		*Teichichnus*
Pouch-shaped		Transverse ornamentation		*Rusophycus*
Track-like trace on bedding plane	Paired	Pods or scratches all alike	Uniform diameter	*Incisifex*
			Not uniform in diameter	*Diplichnites*
	Not paired			*Monomorphichnus*

CHAPTER 3

Ichnofossil Descriptions

3-1. Introduction

A). Classification

In conventional paleontology invertebrate body fossils are classified and named using strictly morphological criteria. Ichnofossils, on the other hand, express animal-sediment interactions. As such, aspects of both the physiological characteristics of the producer and the physical properties of the sediment have a controlling influence on the resultant morphology. Therefore, ichnofossils are unique in that they may be classified in a number of different ways, ranging from a purely sedimentological system to a purely morphological system. Each system, although different, contributes to the overall understanding of both the ichnofossil and the enclosing sedimentary unit. The present study will employ three basic classificational schemes which have previously been applied to ichnofossils.

i). Preservational classification

A number of different classificational schemes based on the mode of preservation of the ichnofossil have been devised (see Hallam, 1975; Simpson, 1975; for complete details). Such schemes analyze ichnofossils from a sedimentological point of view, since it has been shown that trace fossils are normally preserved as interfacial elements. In this regard, the present study has adapted the system proposed by Seilacher (1953a, 1964a, 1964b) and later modified by Webby (1969). This system (fig. 3-1) recognizes two main classes of traces: 1). semireliefs, which are sculptures at an interface found on either the top or bottom of a bed; and 2). full-reliefs, which are discrete bodies occurring within beds or at bed junctions.

ii). Ethological classification

A classification of ichnofossils according to ethological principles was first proposed by Seilacher (1953a). This scheme (fig. 3-2) was based on the fact that morphologically dissimilar organisms displaying similar life habits will produce identical traces. Originally Seilacher (1953a) recognized five basic groups: domichnia (dwelling burrows), fodinichnia (feeding burrows), pascichnia (grazing traces), cubichnia (resting traces), and repichnia (crawling traces). Although many other different groups have been proposed to expand this system (see Häntzschel, 1975; Simpson, 1975; for details) only one other category, the fugichnia (escape structures) has been deemed distinct enough for inclusion (Simpson, 1975; Frey and Seilacher, in press).

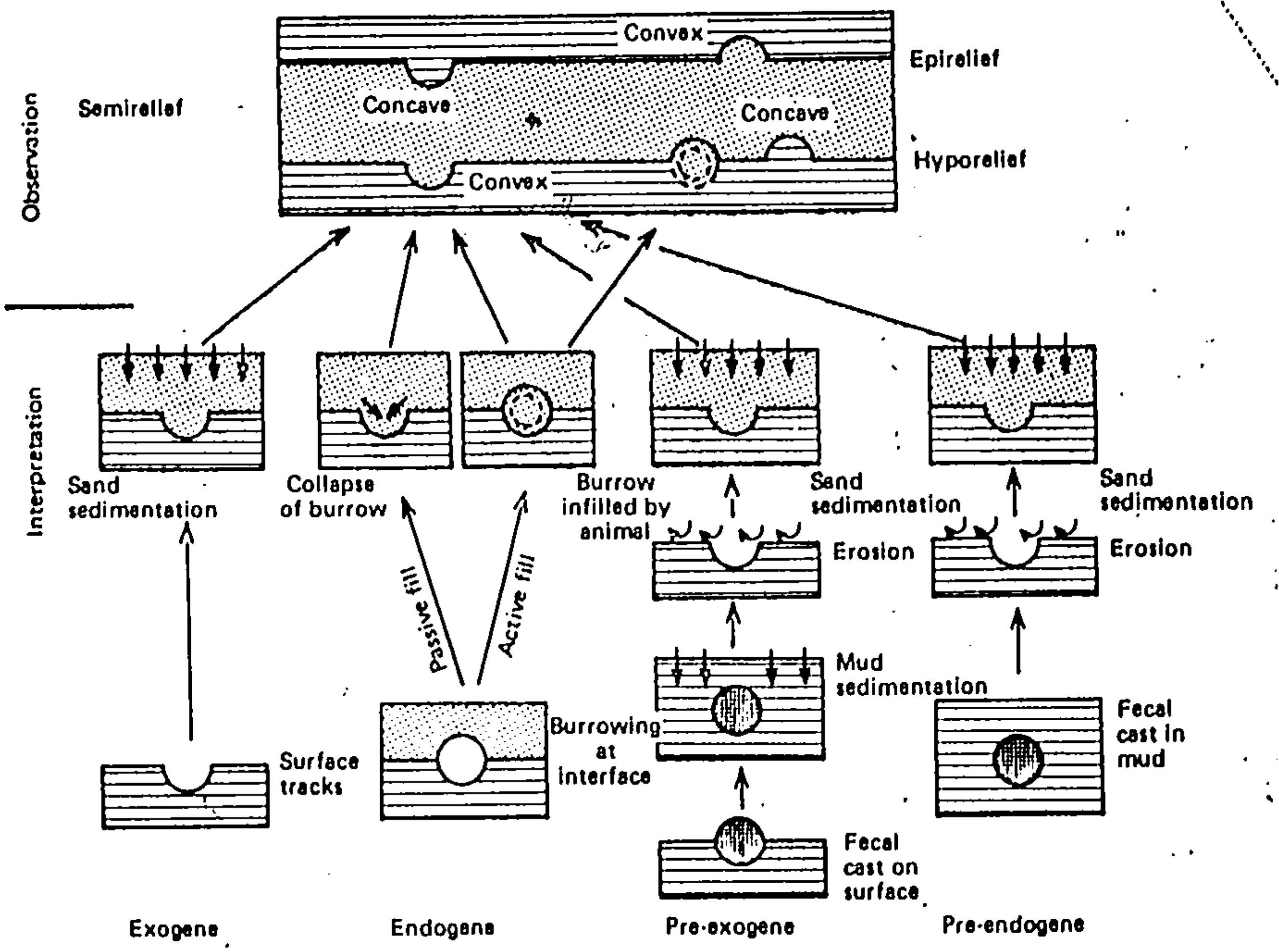

Fig. 3-1. Seilacher's classification of trace fossil preservation types, and their interpretation (after Hallam, 1975).

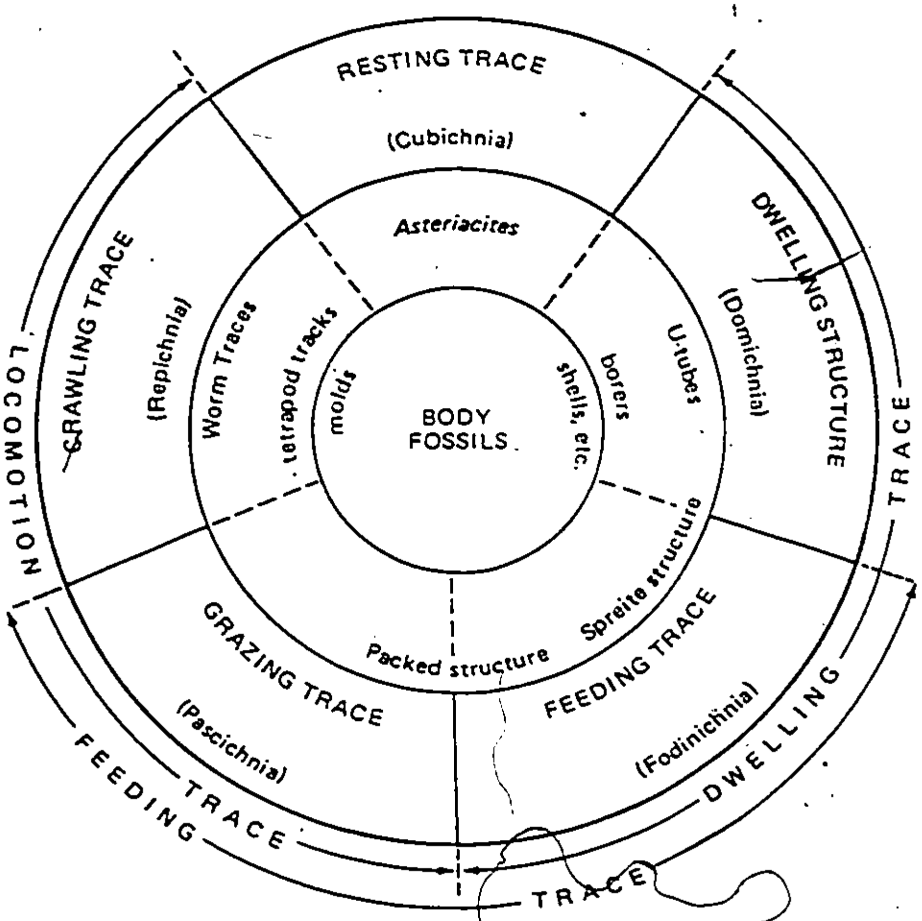

Fig. 3-2. Ethological classification of ichnofossils. Diagram shows five main behavioural categories and their relations to one another and to body fossils. Escape structures (Fugichnia), which overlap with several other categories, are not shown (from Osgood, 1970, after Seilacher, 1953a).

iii). Taxonomic classification

This scheme is based on the fact that ichnofossils are the product of particular organisms which are related to one another by natural descent (Seilacher, 1953a). Therefore, it infers a taxonomic element, in which the ichnofossil is related to a specific producer. Although, in most cases, this is a very tenuous system, it may provide some additional information.

B). Nomenclature

[For a more complete analysis of the problems associated with the nomenclature of ichnofossils, refer to Chapter 5.]

Simpson (1975) has re-emphasized that a nomenclature is a system of rules and conventions for labeling the elements of a classification, and its main purpose is to facilitate communication. As such, it is possible to devise as many different nomenclatures as we can classifications. Since trace fossils are not governed by any formal international code of rules, nomenclatural difficulties often arise.

Since ichnofossil morphology is dictated not only by the producers' characteristics but also by sedimentary properties, many acute problems can arise in a binary nomenclatural system. This is evident by the large numbers of ill-defined ichnogenera and ichnospecies which are found in the literature. As early as the late 1800's James (in Häntzschel, 1975, p. W15) warned that "when every turn made by a worm or shell, and every print left by the claw of a Crustacean is described as a new addition to science, it is time to call halt and eliminate some of the old before making any more new species." With this in mind and in the absence of any formal nomenclatural code, the present study will regard the ichnogenus as the basic unit of nomenclature.

In describing the ichnogenera found in the Thorold Sandstone an attempt was made to compile as complete a synonym list as possible. In this regard, I have utilized a number of detailed source materials which include Bassler (1915), Andrews (1955, 1970), Häntzschel (1962, 1965, 1975), and Osgood (1970). In addition, a number of recent studies on the ichnogenera Cruziana (Alpert, 1976), Diplocraterion (Fursich, 1974b), Planolites (Alpert, 1975), and Skolithos (Alpert, 1974b) proved invaluable.

3-2. Systematic Ichnology

A). Ichnogenus Arenicolites Salter, 1857

Arenicola carbonaria Binney, 1852, p. 192.

non Arenicola diclyma Salter, 1856, p. 248 [= Cruziana, Seilacher, 1955, p.]

Arenicolites Salter, 1857, p. 204; Nicholson, 1873,

p. 310; Nicholson, 1879, p. 318; Nathorst, 1881, p. 49; Whitfield, 1882, p. 177; Miller, 1889, p. 517; Bassler, 1915, p. 67; Richter, 1924, p. 137; Richter, 1926, p. 212; Bather, 1925, p. 188; Trusheim, 1934, p. 408-412; Peneau, 1946, p. 90; Häntzschel, 1962, p. W183-W184; Häntzschel, 1965, p. 9; Howard, 1966, p. 47; Frey and Howard, 1970, p. 162; Chamberlain, 1971b, p. 219-220; Frey and Chowns, 1972, p. 29; Häntzschel, 1975, p. W38; Hakes, 1976, p. 20; Pickerill, 1977, p. 7-8; Crimes, *et al*., 1977, p. 111; Ireland, *et al*., 1978, p. 416.

Arenicolithes Hildebrane, 1924, p. 27 (misspelling)

Type species - *Arenicola carbonaria* Binney, 1852, p. 192; subsequent designation by Richter, 1924, p. 137.

i). *Description*

Simple U-tubes without spreite, oriented perpendicular to the bedding plane. Great variations in tube diameter, distance between limbs, and depth of penetration. The limbs are never branched and sometimes display a funnel-shaped aperture. The walls are commonly smooth, but may occasionally be lined or sculptured.

ii). Discussion

The ichnogenus Arenicolites was established by Salter (1857) for simple, U-shaped burrows that display no spreite between the limbs. The ichnogenus was thought to be analogous to the burrow of the modern lugworm Arenicola; hence the derivation of the name. There does exist an inherent difficulty in the recognition of Arenicolites, and as a result it may be more abundant than previously thought. On bedding plane views a simple U-tube, lacking spreite, appears as two circular openings which could be mistaken for two Skolithos burrows. This problem can be solved by sectioning the rock to see if the paired openings join. In connection with this, Risk and Szczuczko (1977) have developed a staining procedure (using a PAS stain) which accentuates burrow outlines and aids in the differentiation and identification of specific ichnogenera. Arenicolites has been identified in rocks ranging in age from Cambrian to Cretaceous (Häntzschel, 1975).

It is generally conceded that Arenicolites represents the dwelling burrow (domichnia) of a filter-feeding worm or worm-like organism (see Ireland, et al., 1978). This interpretation is consistent with the known data on its distribution, since it is frequently associated with the shallow water, intertidal environments of the Skolithos ichnofacies and the slightly deeper water Cruziana ichnofacies. These environments provide sufficient organic material and water turbulence to enable filter-feeding organisms to survive (Seilacher, 1964a, 1967a; Farrow, 1967; Hakes, 1976). There is, however, new data which tend to question the bathymetric importance of this form. Crimes, et al., (1974) have found Arenicolites associated with Ordovician deep-water turbidites in Northern Spain. Jansa (1974) discovered Arenicolites in the Cambro-Ordovician Cow Head Group of Newfoundland and suggested that the burrows may have been formed at depths greater than 200 meters. Finally, a recent study by Crimes (1977) showed that Arenicolites (and other presumed shallow-water ichnofossils) were found in a deep-sea fan environment of Eocene age in Northern Spain. The consequences of these and other studies will be discussed in the next chapter.

iii). Thorold specimens

Arenicolites sp.

(Pl. 3-2, fig. 1)

a). Description

Simple U-shaped burrow without spreite, oriented perpendicular to the bedding plane. Tube diameter varies from 3 to 6 mm; distance between limbs variable but commonly 15 mm. Burrow length is difficult to ascertain since complete specimens are rare; however, several intact samples (Pl. 3-2, fig. 1) indicate that depths of at least 7 cm were attained. Individual tubes are usually unornamented; however, some do show a faint annulation. Horizontal expression of burrow consists of small paired tubes, circular in cross-section and displaying no funnels or subsidence cones.

b). Occurrence

Specimens of Arenicolites were recovered from the Mountain Boulevard and Jolley Cut sections. In addition, samples which may be referrable to Arenicolites were observed in the Balls Falls and Highway 20 sections. Generally found in quartz sandstone.

B). Ichnogenus Arthrophycus Hall, 1852

Fucoides Brongniart, 1823 (partim), p. 308.

Fucoides allegheniensis Harlan, 1831, p. 289, Pl. 15; Taylor, 1834, p. 5; Harlan, 1835, p. 393.

Fucoides harlani Conrad, 1838, p. 113; Vanuxem, 1842, p. 71, fig. 10; Hall, 1843, p. 46; Owen, 1845, p. 299, figs. 1, 2; Hall, 1852, p. 5, Pl. 1, fig. 1; Pl. 2, fig. 1a-c.

Arthrophycus Hall, 1852, p. 4-5; Dawson, 1864, p. 366; Nathorst, 1881, p. 32, 86; J. F. James, 1894, p. 172; Grabau, 1901a, p. 247; Grabau, 1901b, p. 132; Sarle, 1906, p. 203-210; Grabau and Shimer, 1910, p. 247; Bassler, 1915, p. 70; Schiller, 1930, p. 145-151; Abel, 1935, p. 476; Shimer and Shrock, 1944, p. 719; Wilckens, 1947, p. 47; Becker and Donn, 1952, p. 214-215; Andrews, 1955, p. 111; Häntzschel, 1962, p. W184; Häntzschel, 1965, p. 10-11; Howard, 1966, p. 41-42; Borrello, 1966, p. 10-11; Frey and Howard, 1970, p. 159, 162; Ksiazkiewics, 1970, p. 285; Andrews, 1970, p. 27; Mayberry, 1971, p. 11-12; Alpert, 1974a, p. 50-51; Häntzschel, 1975, p. W38-W39; Baldwin, 1977a, p. 26.

Arthropicus Hernandez-Pacheco, 1908, p. 83 (misspelling).

Harlania Goeppert, 1852, p. 98; Roemer, 1880, p. 135; Nathorst, 1886, p. 32; J. F. James, 1893, p. 85; Kilian, 1931, p. 1742; Picard, 1942, p. 14-17; Andrews, 1955, p. 167; Häntzschel, 1965, p. 43; Andrews, 1970, p. 100.

Raufella palmipes Ulrich, 1889, p. 235.

Arthrichnites (author and date unknown) Dawson, 1890, p. 596; Häntzschel, 1965, p. 10.

Phymatoderma Brongniart, Fuchs, 1805 (*partim*), p. 448, Pl. 9, fig. 2.

Phycodes Richter, Seilacher, 1955 (*partim*), p. 386.

Type species - *Arthrophicus harlani* Hall, 1852, p. 5, by monotypy.

i). Description

Bundles of annulated curved burrows that can be simple or branched and display a subquadrate cross-section. Diameter is variable, usually from 1 to 2 cm, with lengths up to 60 cm. The burrow is commonly bilobate with a medial longitudinal depression. The surface exhibits regularly spaced transverse ridges.

ii). Discussion

Arthrophycus is a relatively little known horizontal, annulated burrow system erected by Hall (1852) for samples found in the Medina Formation of western New York. Although somewhat distinctive, Seilacher (1955) suggested that it should be considered as a junior synonym of Phycodes. Even though there does exist an apparent similarity in gross morphology, Arthrophycus exhibits a number of diagnostic characteristics (prominent transverse ridges, bilobate branches, and large size) which warrants its recognition as a separate ichnogenus (Häntzschel, 1962, 1965; Osgood, 1970).

Arthrophycus has been reported from a number of lower Paleozoic deposits ranging in age from Cambrian to Silurian (Häntzschel, 1975, Baldwin, 1977a). In addition, forms similar to Arthrophycus have been reported from Cretaceous strata of the American midcontinent (Howard, 1966; Frey and Howard, 1970). For details of the early occurrences of Arthrophycus see James (1893). Since relatively few specimens have been reported, not much is known about its facies-relationships. Alpert (1974a) reported samples of Arthrophycus from the Skolithos ichnofacies of the Lower Cambrian Campito Formation of California. Seilacher (1969a) indicated that it is abundant in the Cruziana ichnofacies of Silurian strata in Libya. Sarle (1906), on the other hand, suggests that Arthrophycus is indicative of very shallow water environments, perhaps even estuarine in origin.

As is the case with many ichnofossils, Arthrophycus was originally interpreted as the stems of seaweeds (Hall, 1852; Dawson, 1864. This interpretation has persisted even as late as Becker and Donn (1952). Nathorst (1881) first suggested that Arthrophycus was an ichnofossil and attributed it to the activity of polychaetes or arthropods. James (1893) reinforced the ichnofossil interpretation with a number of direct observations on Hall's type material. Detailed analysis of well-preserved specimens from the Lower Silurian Medina Formation of New York led Sarle (1906) to postulate that Arthrophycus was the feeding burrow of a sedentary polychaete. The bundled structure of the burrow was interpreted as a response to sedimentation, the organism being forced to raise the level of the burrow as sediment repeatedly buried the aperture (Sarle, 1906). Despite the detailed work of Sarle, a number of subsequent interpretations, varying from an inorganic origin (Schiller, 1932) to the casts of worm tubes thrown together during a storm (Abel, 1935), have been postulated. These interpretations have been dismissed by latter workers and it is now generally accepted that *Arthrophycus* represents a feeding (fodinichnia) or dwelling (dominichnia) burrow of an infaunal polychaete (see Osgood, 1970; Häntzschel, 1975).

iii). Thorold specimens

Arthrophycus sp.

a). Description

Bundles of predominantly horizontal, curved burrows displaying a subquadrate cross-section. Burrow diameters vary from 4 to 12 mm and are not constant throughout the length of the burrow system. Burrow lengths were almost impossible to determine, since observed samples covered the entire length of the rock slabs and no complete specimens were discerned. Burrows display a faint longitudinal depression (Pl. 3-1, fig. 1) and are marked by prominent transverse annulations (Pl. 3-1, fig. 2). The spacing of the annulations varies from .8 to 2.8 mm, and seems to bear a direct relationship to the diameter of the individual traces (diameter:annulation spacing ratio is approximately 3.9: 1). Burrow systems commonly branch (Pl. 3-1, fig. 3; Pl. 3-2, fig. 6) and bifurcation angles vary from 3 to 40 degrees (no consistant branching pattern was detected). Individual burrow systems commonly cross-over and interpenetrate (Pl. 3-1, fig. 2). Since most specimens were found in densely packed associations, it was virtually impossible to discern individual systems, thus hindering any further investigations. Preserved in convex hyporelief.

b). Remarks

The Thorold samples of Arthrophycus, apart from being very profuse, are exceptionally well-preserved and allow for detailed morphological examination. Apart from the early work done by Sarle (1906) on these same Medina samples, very little work has been conducted on Arthrophycus. In the Thorold, Arthrophycus is commonly preserved in hyporelief, on the underside of sandstone beds which directly overlie thin shale partings. Sarle (1906) and Ksiazkiewicz (1970) both concluded that Arthrophycus was a post-depositional ichnogenus, that is, it was an active burrower after the deposition of the sandstone unit in which it is contained. Based on this conclusion and the fact that the burrow does not diplay any collapse features, Sarle (1906) postulated that it seemed likely that the burrow walls were reinforced with some kind of quick-hardening mucus. An S.E.M. micrograph (Pl. 3-1, fig. 4) revealed a sheath-like object (possibly enrolled) along the burrow wall which may possibly be a remnant of the original burrow lining. Such linings are commonly associated with infaunal burrow-dwelling organisms (Schäfer, 1972). The nature of the burrow infill indicates that the animal was probably foraging in the underlying shale partings; distinct aggregates of clay are clearly visible in the burrow cross-section (Pl. 3-1, fig. 4). The significance and composition of these burrow linings are presently under investigation.

c). Occurrence

Specimens of Arthrophycus were common to abundant in all the New York sections (except the Niagara Glen outcrop). In Ontario, numerous samples of Arthrophycus were discerned in the De Cew Falls, Rockway, Balls Falls, Woolverton Road, and Vinemount sections. Problematical structures which may or may not be referrable to Arthrophycus were observed in the Flock Road and Jolly Cut sections.

C). Ichnogenus Bifungites Desio, 1940

? Buthotrophis impudica Hall, 1852, p. 20

Bifungites Desio, 1940, p. 78-79; Seilacher, 1955, p. 382; Gutschick, *et al.*, 1962, p. 79-89;

Häntzschel, 1962, p. W186; Dubois and Lessertisseur, 1964, p. 626-634; Häntzschel, 1965, p. 16; Osgood, 1970, p. 314-325; Rodriguez and Gutschick, 1970, p. 418-419; Knox, 1973, p. 142; Fursich, 1974b, p. 957, 959-960; Häntzschel, 1975, p. W46; Gutschick and Lamborn, 1975, p. 200-202.

Corophioides Smith, Osgood, 1970 (_partim_), p. 323.

Diplocraterion Torell, Fursich, 1974b (_partim_), p. 959-960.

Type Species - _Bifungites_ _fezzanensis_, Desio, 1940, by monotypy.

i). _Description_

Vertical tubes with a horizontal basal connection with lateral diverging cul-de-sac expansions or chambers. The latter are arrow-head or dumb-bell shaped. Convex casts of the shafts are most common on the top and bottom of bedding surfaces. The paired tubes lack spreiten and are commonly not preserved.

ii). _Discussion_

The ichnogenus _Bifungites_ was erected by Desio (1940) for dumbell-shaped traces exposed on bedding planes. The fact that the outer tubes were connected led Seilacher (1955) to postulate that the burrow was in fact U-shaped. Later investigators may have mistaken the horizontal connection for spreite since

Bifungites was placed in questionable synonymy with several spreiten-bearing, U-shaped ichnogenera, such as Corophiodes (by Osgood, 1970; and Knox, 1973) and Diplocraterion (by Furisch, 1974b). This, however, is not the case. In an excellent review of Bifungites, Gutschick and Lamborn (1975) recently discovered some complete specimens (see Gutschick and Lamborn, 1975, Pl. 1, figs. 1, 4), which do not show any sign of spreite.

Bifungites has been recorded from a variety of beds ranging in age from Lower Cambrian to Mississippian (Häntzschel, 1975), but it is particularly abundant in strata from the Lower Devonian (Desio, 1940; Gutschick, et al., 1962; Rodriguez and Gutschick, 1970; Gutschick, and Lamborn, 1975).

The origin of the ichnogenus Bifungites has been speculated upon by a number of investigators. Desio (1940) initially interpreted it as an algae or a colonial organism. Dubois and Lessertisseur (1965) later interpreted it as the filling of the top of a U-shaped burrow, perhaps inhabited by a small trilobite. Seilacher (1955) noted that it may represent a special type of preservation of a protrusive, vertical, U-tube representing a feeding burrow. The latest interpretation (based on the entire burrow) indicates that it may in fact be the dwelling burrow of a filter-feeding organism, such as an amphipod, a polychaete, or a hemichordate

(Gutschick and Lamborn, 1975). An alternate hypothesis was presented by Karcz, et al. (1974), who claimed to have produced a Bifungites-like structure in hydrodynamic-sedimentary experiments on a mud surface, and suggested an inorganic origin. Gutschick and Lamborn (1975) after comparative work on these experimental impressions and actual fossil types rejected this hypothesis.

Little is known on the environmental distribution of Bifungites, but Gutschick and Lamborn (1975) consider it to be representative of shallow, nearshore, environments (tidal flats, delta and bar margins, and very shallow basinal areas). Similarily, Seilacher (1969a) found abundant samples in the Skolithos ichnofacies from Devonian rocks in Libya.

iii). Thorold Specimens

Bifungites sp.

(Pl. 3-2, fig. 2)

a). Description

A number of poorly preserved burrows have been tentatively assigned to the ichnogenus Bifungites. These burrows are similar in form to the closely related ichnogenus Diplocraterion. The burrow consists of two tubes (approximately 6 mm in diameter) and a horizontal basal connection with lateral diverging expansions which appear to be arrow-shaped. It is this horizontal basal segment which is preserved on the tops of fine-grained sandstone units. Such preservation makes them indistinguishable from Diplocraterion; however, on further examination, very faint tube outlines could be discerned in the overlying shale unit. These tubes were not joined by spreite. Based on this observation, the trace seems to be similar to ones assigned to Bifungites by Gutschick and Lamborn (1975).

b). Occurrence

Rare specimens of Bifungites were recovered from the Jolley Cut section. Observed on the top of a sandstone unit directly underlying a shale unit.

D). Ichnogenus Chondrites Sternberg, 1883

Fucoides Brongniart, 1823 (partim), p. 308.

Chondrites Sternberg, 1833, p. 25 [non M'Coy, 1848]; Salter, 1856, p. 246; Nathorst, 1886, p. 74; Miller, 1889, p. 114; Rauff, 1891, p. 701; Fuchs, 1895, p. 407-410; Rothpletz, 1896, p. 857-859; Reis, 1910, p. 615-638; Bassler, 1915, p. 217; Richter, 1928, p. 216-219; Richter, 1931, p. 301-308; Solle, 1938, p. 168; Wilickens, 1947, p. 45-46; Tauber, 1949, p. 141-145; Andrews, 1955, p. 130; Lessertisseur, 1955, p. 20; Simpson, 1957, p. 475-500; Häntzschel, 1962, p. W187-W188; Ferguson, 1965, p. 79-82; Häntzschel, 1965,

p. 21; Howard, 1966, p. 43; Kennedy, 1967, p. 148; Bandel, 1967, p. 4-5; Gregory, 1969, p. 7-8; Andrews, 1970, p. 52; Frey and Howard, 1970, p. 160, 163; Kennedy, 1970, p. 270; Kslazkiewicz, 1970, p. 288; Frey, 1970, p. 14-15; Chamberlain, 1971b, p. 234; Frey and Chowns, 1972, p. 30-32; Young, 1972, p. 10; Kern and Warme, 1974, p. 897; Semeniuk, 1975, p. 132-133; Chamberlain, 1975a, p. 1081-1082; Häntzschek, 1975, p. W49-W52; Hakes, 1976, p. 34; Shourd and Levin, 1976, p. 261-262; Pickerill, et al., 1977, p. 241; Gutschick and Rodriguez, 1977, p. 200-201; Ekdale, 1977, p. 165; Ekdale, 1978, p. 821-822; Ekdale and Berger, 1978, p. 132-133.

Caulerpites Sternberg, 1833 (partim), p. 20; Andrews, 1955, p. 127; Häntzschel, 1965, p. 20; Andrews, 1970, p. 48.

Sphaerococcites Sternberg, 1833 (partim), p. 28; Schimper, 1969, p. 163; Heer, 1877, p. 110; Solle, 1938, p. 168; Andrews, 1955, p. 240; Häntzschel, 1965, p. 86; Andrews, 1970, p. 200.

Buthotrephis Hall, 1847, p. 8; Goeppert, 1860, p. 452; Billings, 1865, p. 99; Geinitz, 1867, p. 15; Lesquereux, 1869, p. 321; Nathorst, 1873, p. 46; Grote and Pitt, 1876, p. 88; Miller, 1878, p. 26; Nathorst, 1883, p. 34; J. F. James, 1885,

p. 159; Dawson, 1890, p. 613; White, 1901, p. 270; Basseler, 1915, p. 143; Andrews, 1955, p. 121; Häntzschel, 1965, p. 18; Andrews, 1970, p. 40.

Bythotrephis Eichwald, 1860, p. 56 (misspelling); Roemer, 1880, p. 123; Miller, 1889, p. 109; Whiteaves, 1897, p. 139; Graubau, 1901a, p. 130; Graubau, 1901b, p. 130; Andrews, 1955, p. 121; Andrews, 1970, p. 40.

Phymatoderma Brongniant, 1848 (*partim*), p. 59; Fuchs, 1895 (*partim*), p. 448, Pl. 9, fig. 1; Rothpletz, 1896, p. 905-907; Andrews, 1955, p. 211; Häntzschel, 1965, p. 71; Andrews, 1970, p. 182.

? *Trevisania* Zigno, 1856, p. 64; Andrews, 1955, p. 252; Häntzschel, 1965, p. 94; Andrews, 1970, p. 217.

Nulliporites Heer, 1865, p. 140; Heer, 1877, p. 111; Schimper, 1879, p. 65, Andrews, 1955, p. 196; Häntzschel, 1965, p. 62; Andrews, 1970, p. 143.

Leptochondrites Schimper, 1869, p. 171; Häntzschel, 1965, p. 52.

Palaeophycus gracilis Lesquereux, 1875, p. 137-138, Pl. 1, figs. 4, 5.

Theobaldia Heer, 1877 (*partim*), p. 114; Andrews, 1955, p. 250; Häntzschel, 1965, p. 92; Andrews, 1970, p. 214.

Palaeochondrites de Saporta, 1882, p. 35; Nathorst, 1886, p. 37; Häntzschel, 1965, p. 64.

Dendrograptus Hall, J. F. James, 1885 (partim), p. 159-161.

Chondropogom Squinabol, 1890, p. 180; Fuchs, 1895, p. 425.

Planolites Nicholson, J. F. James, 1891 (partim), p. 17.

Prochondrites Fritsch, 1918, p. 22; Andrews, 1955, p. 218; Häntzschel, 1965, p. 74; Andrews, 1970, p. 170;

? Labyrinthochorda Weissenbach, 1931, p. 76; Prantl, 1944, p. 15; Häntzschel, 1965, p. 50.

Clematischnia Wilson, 1948, p. 10.

? Chondritoides Borrello, 1966, p. 15.

? Isawaites Hatai and Noda, 1971, p. 5.

Type species - Fucoides lycopodiodes Brongniart, 1828, p. 72; subsequent designation by Andrews, 1955, p. 127.

i). Description

Dendritic patterns of small cylindrical subcylindrical ramifying tunnel systems. The individual branches may or may not cross over and interpenetrate. A small number of master shafts open to the surface, with the branches trending downward across the bedding and lying parallel to the bedding planes (at the distal end). The branching pattern is highly variable and may be regular or irregular. The branches may be arranged in pinnate or radial patterns or form compact groups. Branch diameters are commonly from .5 to 5 mm, and remain constant within the entire tunnel system.

ii). Discussion

The ichnogenus Chondrites is regarded as one of the most prolific trace fossils in the rock record and is the essence of the "form-genus" concept. As a result, a vast array of forms have been recognized, and frequently new ichnogeneric names have been proposed. Häntzschel (1975) placed over 20 ichnogenera in synonym with Chondrites, and Chamberlain (1971b) stated that over 120 separate ichnospecies have been erected. Simpson (1957) noted that most differences at the ichnospecific level involved only slight changes in the orientation and size of individual tunnels in the entire system and he concluded that these differences were not sufficient to warrant separation. Details of the history of Chondrites, as well as discussions on its confused nomenclature, are found in Simpson (1957), Häntzschel (1962, 1965, 1975), and Osgood (1970).

It is now generally accepted that Chondrites represents the feeding structure (fodinichnia) of a sediment-eating organism (Richter, 1927; Seilacher, 1955; Osgood, 1970). Early investigators, however, believed that Chondrites was a marine plant, because of its branching pattern (see Sternberg, 1833; Hall, 1857; Salter, 1856; and Billings, 1865; among others). This "fucoidal origin" was first questioned by Nathorst (1881), who suggested that Chondrites was a trace fossil produced by worm-like organism. This was based on the fact that Chondrites contained no organic material, was found in rocks believed to have been deposited in deep water, and was contained in sediment types that displayed no firm foundations for the attachment of plants. Subsequent studies were divided on the question of the origin of Chondrites; Fuchs (1895) conducted chemical analyses and substantiated Nathorst's non-algal interpretation, while Rothpletz (1896) concluded (also from chemical studies) that it was in fact an algae or a sponge. A sponge-affinity was also maintained by Walther (1904). The trace fossil nature of Chondrites was convincingly proven by Richter (1927a, 1928, 1931). Detailed analysis of the branching patterns exhibited by Chondrites led Richter (1927a) to conclude that they were affected by phobotaxis and hence were a product of animal activity. Despite the work of Richter, old theories die slow deaths, and an algal-origin was still being postulated by some workers as late as Wilson (1948).

Although Richter (1927a, 1931) proved an animal origin, controversy still persisted concerning the type of animal producing the Chrondrites burrow. Since Richter believed that the branching pattern was the result of phobotaxis (or chemical sensing) he interpreted it as the feeding structure of a sediment-eating animal, mining a layer of sediment. Conversely, Tauber (1949) stated that the fillings of the branches were composed of fecal material and collapsed linings, and hence were the product of a filter-feeding animal in which the tiers were merely a response by the animal to keep up with sedimentation. This dilemma was finally resolved by Simpson (1957), who undertook an exhaustive study of a multitude of different types of Chondrites burrows. He maintained that the system was the result of a deposit-feeder, and the branching pattern resulted from the probing of an extensible proboscis.

Differences in burrow orientation have been related to food abundances. Planar systems indicate that food was concentrated on bedding planes within the sediment; and oblique systems indicate that the food was evenly dispersed throughout the sediment (Osgood, 1970; Ekdale, 1977). Therefore, it is now accepted that Chondrites represents the feeding structure (fodinichnia) of a sediment-eating organism. Possible creators include worms or worm-like organisms (Simpson, 1957;

Ferguson, 1965; Osgood, 1970), an organism with numerous tentacles working simultaneously in the sediment (Taylor, 1967), or tiny arthropods (Ekdale, 1977).

Chondrites is known to be a facies-crossing form (see Seilacher, 1955, fig. 5; Simpson, 1937; Seilacher and Meischner, 1964) and is thus not restricted to any one environment. Crimes (1973) illustrated the lack of facies control of Chondrites in the Paleocene-Eocene flysch of northern Spain. Chamberlain (1971b), however, proposed a Chondrites ichnofacies in the Ouachita Geosyncline of Oklahoma, which was positioned between the Zoophycos and Nereites ichnofacies, and was indicative of relatively deep water. Frey and Chowns (1972) questioned such an ichnofacies since Chondrites is also well-known from numerous shallow-water deposits. In addition, Ekdale (1977, 1978) has recently described Chondrites from deep water (greater than 3,000 meters) cores, ranging in age from Upper Cretaceous to Pliocene. Chondrites, therefore, has limited value as a facies or bathymetric indicator; it has, however, not yet been found in non-marine deposits (Seilacher, 1955, 1963, 1967a; Bromley and Asgaard, 1972; Stanley and Fagerstrom, 1974).

iii). Thorold Specimens

Chondrites sp.

(Pl. 3-3, fig. 1)

a). Description

Dendritic branching structures, usually oriented parallel to bedding surfaces. Branch diameters are consistent throughout the length of each individual burrow and range from 1 to 4 mm; burrow length is highly variable, but commonly 4 cm. The branches of the burrows never intersect or cross one another. No evidence of vertical expression was found to be associated with these structures. No regular pattern in the angle of branching was detected. Structures preserved in convex hyporelief and convex epirelief; commonly associated with siltstones.

b). Occurrence

Chondrites burrows were recorded from the Medina, Woolverton Road, Dewitt Road, Highway 20, Albion Falls, Flock Road, Mountain Boulevard, Jolley Cut, 403, Webster Falls, Sydenham Road, Rock Chapel Falls, and Clappison Corners sections.

E). Ichnogenus Cruziana d'Orbigny, 1842

Cruziana d'Orbigny, 1842, p. 30 (non viso); Salter, 1861, p. 70; Salter, 1866, p. 291; Trombelin and Lebesconte, 1876, p. 626; Salter, 1881, p. 482; Lebesconte, 1883, p. 466-472; Lebesconte, 1887, p. 810-811; Miller, 1889, p. 115; Walcott, 1890a, p. 35-36; Walcott, 1890b (partim),

p. 604; Fritel, 1925, p. 34-35; Yin, 1932, p. 75-80, Picard, 1942, p. 9; Sampelayo, 1950, p. 151-168; Seilacher, 1953c (*partim*), p. 107-108; Lessertisseur, 1955, p. 44-47; Andrews, 1955, p. 138; Häntzschel, 1962, p. W189; Radwanski and Roniewics, 1963, p. 267-269; Häntzschel, 1965, p. 27-28; Gubler, 1966, p. 153; Crimes, 1970a, p. 49; Crimes, 1970b, p. 111-112, 119-124; Seilacher, 1970 (*partim*), p. 454-456; Andrews, 1970, p. 62; Birkenmajer and Bruton, 1971, p. 303-310, 313-318; *non* Bromley and Asgaard, 1972, p. 7-13; Frey and Chowns, 1972, p. 35; Häntzschel, 1975, p. W55; Osgood and Drennen, 1975, p. 317; Hakes, 1976, p. 24-25; Bergstrom, 1976, p. 1619-1623; Alpert, 1976, p. 226-227; Baldwin, 1977a, p. 17-23; Gutschick and Rodrigues, 1977, p. 201-202; Crimes, *et al*.., 1977, p. 97; Pickerill, p. 2-3; Drennen, 1975, p. 317; Crimes, 1975a, p. 36-37; Crimes, 1975b, p. 34-39; Hakes, 1976, p. 24-25; Bergstrom, 1976, p. 1619-1623; Alpert, 1976, p. 226-227; Baldwin, 1977a, p. 17-23; Gutschick and Rodriguez, 1977, p. 201-202; Crimes, *et al*., 1977, p. 97; Pickerill, 1977, p. 2-3.

Cryziana Giebel, 1851, p. 115 (misspelling).

Crusiana Dawson, 1880, p. 46 (misspelling).

Cruciana Sampelayo, 1915, p. 279 (misspelling).

Crucianas Sampelayo, 1915, p. 279 (misspelling).

Cruzianas Sampelayo, 1950, p. 148, 149 (misspelling).

Fraena Rouault, 1850 (partim), p. 729.

Bilobichnium Krejci-Graf, 1932, p. 31.

Type species - Cruziana furcifera d'Orbigny, 1842, p. 30, subsequent designation by Seilacher, 1953b, p. 107.

i). Description

Elongate, band-like, furrows generally preserved as hypichnial casts. The cast consists of two parallel ridges with transverse, oblique, or longitudinal striations (or scratch marks). A medial groove is present that bisects the furrow longitudinally. There exists great variability in size and sculpture of the ichnogenus; widths vary from .5 to 8 cm; and lengths up to 1 m are known. Expodal, genal and plural markings may or may not be present.

ii). Discussion

Cruziana is perhaps one of the best known lower Paleozoic ichnofossils and numerous studies have been conducted on its morphology, distribution, ethological implications, and nomenclature. The reader is referred to Seilacher (1953c, p. 107) for a more complete synonymy list of forms erected prior to 1842. The nomenclatural history of Cruziana closely parallels that of

Rusophycus (a related form), and early workers often regarded them as synonyms (for a more detailed discussion, see Osgood, 1970, p. 303). Later workers, however, have separated them, restricting Rusophycus to short, bilobate, resting traces (Lessertisseur, 1955, p. 45; Seilacher, 1955, p. 366; Osgood, 1970, p. 303). In somewhat of a turn around, Seilacher (1970) later grouped all resting trails and burrows, previously described as Rusophycus, in with Cruziana. This designation, however, did not gain much support and a number of subsequent investigators called for the separation of the two and hence the retention of Rusophycus (Orlowski, et al., 1971; Birkenmajer and Bruton, 1971; Bergstrom, 1973; Crimes, 1975a, 1975b; Crimes, et al., 1977).

Cruziana has been recognized in rocks ranging in age from Upper Pre-Cambrian to Devonian (Häntzschel, 1975). Additional forms which may be referrable to Cruziana have also been recorded from the Upper Pennsylvanian of Kansas (Hakes, 1976); the Carboniferous of Bolivia (Helwig, 1972); and the Triassic of East Greenland (Bromley and Asgaard, 1972).

Cruziana is the dominant element in the Cruziana ichnofacies, and is generally associated with shallow subtidal environments (Seilacher, 1967). In addition, Cruziana is also known to occur in the Skolithos and shallow Zoophycos ichnofacies (see Osgood, 1970;

Crimes, 1970b). Although usually regarded as strictly a marine ichnofossil, Cruziana-like forms have also been described from fresh-water deposits by Bromley and Asgaard (1972) and Helwig (1972).

Originally Cruziana was interpreted as a fossil plant or sponge (Lebesconte, 1883; Delgado, 1885; de Saporta, 1884). Nathorst (1881) first suggested that Cruziana was in fact an ichnofossil, and attributed it to the activities of benthic organisms. The modern interpretation attributes Cruziana to the furrowing, burrowing, or shoveling activities of trilobites or other trilobite-like arthropods (see Crimes, 1970a, 1970b, 1975a, 1975b, for details). The fresh-water type cruzianids, previously mentioned, have been attributed to the activity of notostracan branchiopods (Bromley and Asgaard, 1973; Hakes, 1976). (For a more detailed treatment of the interpretation, origin and significance of Cruziana, refer to Crimes, 1970a, 1970b, 1975a, 1975b; Osgood, 1970; Seilacher, 1970; Osgood and Drennen, 1975; Alpert, 1976, and Baldwin, 1977b).

iii). Thorold Specimens

Cruziana sp.

(Pl. 3-2, figs. 3-5).

a). Description

Small, indistinct structures straight to slightly curved up to 4.5 cm in length (generally 3-4 cm) and 1 cm in width. Medial groove is rather pronounced with numerous transverse striations spaced approximately .8 to 1 mm apart. No specimens were found that displayed any additional ornamentation such as exopodal, genal or pleural markings. The ichnofossil is consistantly preserved in convex hyporelief.

b). Remarks

The figured specimens are similar to another ichnogenus Isopodichnus (see Schindewolf, 1928, p. 27). Considerable debate has been generated concerning the relationship of Isopodichnus to Cruziana (Osgood, 1970; Seilacher, 1970; Hakes, 1976). Although Isopodichnus is generally much smaller than Cruziana, considerable morphological overlap does exist at the extremes of the size ranges. Hakes (1976) insists that large specimens of Isopodichnus (several millimeters in width) exhibit vague transverse striations (claw markings) similar to those associated with typical Cruziana specimens. Additionally, Seilacher (1970) points out that small Cruziana specimens (generally less than 2 m in width) do not exhibit the distinct transverse striations typically associated with other larger cruzianids, but instead display a faint ornamentation which could be mistaken for an exceptionally large Isopodichnus. This taxonomic problem becomes acute when applying known environmental relationships to these ichnogenera. Cruziana is generally considered to be exclusively marine (Seilacher, 1970), while Isopodichnus has been used as a non-marine to brackish water indicator (Linck, 1942; Seilacher, 1970; Hakes, 1976).

Based primarily on size considerations, as well as its associ~~ations~~ with the other typically trilobite related ichnogenera, Diplichnites, Monomorphichnus and Rusophycus, the Thorold specimens are considered to be small cruzianids.

c). Occurrence

Small, poorly preserved specimens of Cruziana were recorded from the Flock Road, Jolley Cut, 403, Websters Falls, Sydenham Road, Rock Chapel Falls, and Clappison Corners outcrops. Generally associated with fine-grained sandstones and siltstones.

F). Ichnogenus Daedalus Rouault, 1850

Daedalus Rouault, 1850, p. 736-737; Salter, 1864a, p. 10-11; Salter, 1864b, p. 288; Lebesconte, 1883, p. 45-57; Sarle, 1906, p. 203; Grabau and Shimer, 1910, p. 247; Bassler, 1915, p. 375; Andrews, 1955, p. 143; Häntzschel, 1962, p. W191; Häntzschel, 1965, p. 29; Martini, 1966, p. 314-316; Andrews, 1970, p. 69; Lessertisseur, 1971, p. 39-46; Häntzschel, 1975, p. W58.

<u>Daldalus</u> Schäfer, 1972, p. 361, 550 (misspelling).

<u>Humulis</u> Rouault, 1850, p. 788; Tromelin and Lebesconte, 1876, p. 628; Lessertisseur, 1955, p. 74; Andrews, 1955, p. 170; Häntzschel, 1965, p. 47; Andrews, 1970, p. 105.

<u>Vexillum</u> Rouault, 1850, p. 738; [<u>non</u> Bolten, 1798]; Salter, 1864a, p. 10-11; Salter, 1864b, p. 288; Lebesconte, 1883, p. 467; de Saporta, 1884, p. 43; Peneau, 1946 (<u>partim</u>), p. 81-82; Andrews, 1955, p. 257; Häntzschel, 1965, p. 97; Andrews, 1970, p. 224.

<u>Arthrophycus</u> sp. Hall, 1852, p. 6

<u>Spirophyton</u> <u>archimedes</u> Ringueberg, 1884, p. 144, Pl. 2, fig. 1

<u>Taonurus</u> <u>archimedes</u> Miller, 1889, p. 146.

<u>Type species</u> - <u>Vexilium</u> <u>desglandi</u> Rouault, 1850, p. 733; subsequent designation by Häntzschel, 1962, p. W191.

i). <u>Description</u>

Vertically penetrating J-shaped burrow, associated with complex spreiten structures that are spirally twisted. The spreiten surface may cut through itself. The entire burrow structure is up to 35 cm long and up to 10 cm wide. The cylindrical J-shaped burrow tube extends downwards and around the base of the spreiten structure.

ii). Discussion

Daedalus is a little-known ichnofossil that is almost exclusively restricted to deposits ranging in age from Cambrian to Silurian (Häntzschel, 1975). For a complete discussion of the description and nomenclatural history of *Daedalus*, refer to Lessertisseur (1971). Sarle (1906) was the first to attempt a detailed analysis of the complex morphology of *Daedalus*. He recognized a number of different forms, which were related to sedimentation rates:

1). A rapid vertical descent form associated with eroding sediments. In such a case the resultant spreite should be protrusive in nature (Pemberton and Risk, 1978);

2). Less rapid vertical descent form associated with slowly depositing sediments. In this case the resultant spreite should be retrusive in nature (Pemberton and Risk, 1978).

The spreiten-structure was attributed to the packing of sediment which had sifted into the burrow. The final burrow configuration consists of a series of "rugose plates which may be flat, vertical or U-shaped in outline" (Sarle, 1906, p. 203), which are arranged around a J-shaped burrow. The morphological analysis led Sarle (1906) to conclude that *Daedalus* was the result of the activities of infaunal sedentary polychaetes.

Additional investigations by Seilacher (1957) led him to postulate that the spreiten structure of Daedalus was related to waste storage activities and the final J-shaped burrow was a dwelling (domichnia) burrow. Schäfer (1972) pointed out that such waste storage systems were due to external conditions affecting the producer. He suggested that they were caused by more sediment penetrating the dwelling burrow than could be removed. Seilacher (1957) inferred that the recent polychaete Nereis diversicolor may be a producer of such a system. In addition, Schäfer (1972) concluded that similar structures were constructed by the polychaetes Heteromastus filiformis and Arenicola marina, and the sea urchin Echinocardium cordatum. Of particular interest is the morphology of Arenicola burrows; in sandy sediments the burrow takes on a J-shaped configuration, while in muddy sediments it is U-shaped (Schäfer, 1972). The burrow of Arenicola may be a likely analogue for Daedalus.

Daedalus has been observed to be associated with shallow, marine environments of the Skolithos and Cruziana ichnofacies (Lessertisseur, 1971). More specifically, Sarle (1906) and Martini (1966) suggest a tidal-flat habitat for specimens from the Middle Silurian Medina Formation of New York and Ontario, while Crimes (1977) lists its distribution as being from intertidal to shoreface.

iii). Thorold Specimens

Daedalus sp.

(Pl. 3-4, figs. 1-4)

a). Description

Extremely complex, vertical penetrating burrow system. The basic plan of the burrow suggests a J-shaped tube surrounded by an array of spreite structures (see Sarle, 1966, fig. 2, p. 205). The J-shaped burrow (Pl. 3-4, fig. 1) varies from 6 to 12 mm in diameter and is up to 32 cm in length. It descends vertically and then curves upward and gradually terminates (Pl. 3-4, fig. 2). Tubes may or may not display faint annulations (Pl. 3-4, fig. 2). The spreite structures are highly variable and well-defined and are usually retrusive in nature (Pl. 3-4, fig. 3). They are commonly up to 12 cm in width, of variable length, and are connected to the J-shaped tube (Pl. 3-4, fig. 4). In some units, the spreite structures are much more evident than the J-shaped tubes, which makes final identification difficult. Structures preserved in full relief.

b). Occurrence

Well-preserved specimens of Daedalus were observed at the Glen Edith, Genesee Gorge, Medina, Lockport, Niagara Gorge, DeCew Falls, Rockway, and Balls Falls sections. Samples possibly referrable to Daedalus were recorded from the Flock Road, Mountain Boulevard, and Jolley Cut sections. Generally associated with fine-grained sandstones.

G). <u>Ichnogenus Diplichnites Dawson, 1873</u>

<u>Diplichnites</u> Dawson, 1873, p. 19-20; Miller, 1889, p. 554; Seilacher, 1955, p. 343; Häntzschel, 1962, p. W191-W192; Radwanski and Roniewicz, 1963, p. 269; Häntzschel, 1965, p. 32; Glassener, 1969, p. 383; Crimes, 1970a, p. 56-57; Crimes, 1970b, p. 119-124; Young, 1972, p. 13; Häntzschel, 1975, p. W61; Osgood and Drennen, 1975, p. 323-324; Alpert, 1976, p. 234; Crimes, <u>et al</u>., 1977, p. 102-103; Baldwin, 1977a, p. 24.

<u>Acripte</u> Matthew, 1910, p. 122; Häntzschel, 1965, p. 6.

<u>Type species</u> - <u>Diplichnites</u> <u>aenignia</u> Dawson, 1873, p. 19-20; by monotypy.

i). <u>Description</u>

Morphologically simple, biserial tracks, consisting of two parallel series of fine ridges. The individual ridges are elongated obliquely to the track axis and occassionally are found in pairs. The width of the trackway varies from 1 to 2 cm and the individual ridges are commonly 1.5 mm long.

ii). Discussion

Diplichnites was originally interpreted by Dawson (1873) to be the trace of large worms or crustaceans or the imprints of the pectoral spines of fish. This was later revised to include the tracks of amphibians (Dawson, 1884). Detailed studies by Seilacher (1955) led him to believe that Diplichnites represented the trackways (repichnia) of trilobites. Crimes (1970b) observed a transition from Diplichnites (trackway) to Cruziana (crawling trace) in a single rock slab.

Diplichnites occurs in rocks ranging in age from Lower Cambrian to Permian (Häntzschel, 1975), and is usually associated with other trilobite ichnofossils in the Cruziana ichnofacies (Crimes, 1970a, 1970b).

iii). Thorold Specimens

Diplichnites sp.

a). Description

Simple biserial tracks comprising of two parallel series of fine ridges. The ridges are situated obliquely to the track axis and vary from .8 to 1.2 cm in length. Total width of the trackway varies from 1.2 to 1.6 cm.

b). Occurrence

Common to rare samples of Diplichnites were recorded from the Jolley Cut, 403, Sydenham Road and

Clappison Corners outcrops. Abundant specimens were observed on the upper surface of siltstone layers at the 403 section.

H). Ichnogenus Diplocraterion Torell, 1870

Diplocraterion Torell, 1870, p.13. Andrée, 1927, p. 127; Westergard, 1931, p. 3-11; Abel, 1935, p. 456-457; Howell, 1945, p. 36-38; Häntzschel, 1962, p. W193; Goldring, 1962, p. 235-245; Seilacher, 1963, p. 86; Goldring, 1964, p. 137-140; Häntzschel, 1965, p. 32; Seilacher, 1967a, p. 419-420; Osgood, 1970, p. 316; Heinberg, 1970, p. 232; Goldring, 1971, p. 709; Knox, 1973, p. 134-135; Fleming, 1973, p. 416; Fursich, 1974b, p. 952-962; Häntzschel, 1975, p. W62; Hakes, 1976, p. 26; Bergstrom, 1976, p. 1630; Pickerill, 1977, p. 7; Crimes, et al., 1977, p. 118; Pickerill, et al., 1977, p. 241-242; Ireland, et al., 1978, p. 414-416.

?Arthreria Billings, 1872, p. 467.

Artharia Billings, Miller, 1875, p. 54; Häntzschel.

Arenicolites Matthew, 1890, p. 159; Kolesch, 1922, p. 344-364; Coysh, 1931, p. 15 [non Salter, 1857].

Corophioides Smith, 1893, p. 282; Richter, 1924, p. 128-140; Blanckenhorn, 1925, p. 269-278; Richter, 1926, p. 200-219; Schindewolf, 1928,

p. 40-42; Opik, 1929, p. 30-42; Mägdefrau, 1930, p. 291-292; Westergard, 1931, p. 3-9; Mägdefrau, 1932, p. 229-232; Abel, 1935, p. 452-456; Rose, 1936, p. 58; Dahmer, 1937, p. 533-535; Seilacher, 1955, p. 377; Howell, 1957, p. 150; Lohmann, 1960, p. 76-78; Häntzschel, 1962, p. W189; Seilacher, 1963, p. 86-87; Häntzschel, 1965, p. 26; Deiderich, 1967, p. 232-234; Osgood, 1970, p. 314-325; Heinberg, 1970, p. 232; Knox, 1973, p. 133-146.

Tigillites Lisson, 1904, p. 31-43; Douvillé, 1908, p. 362; [*non* Rouault, 1850 = *Skolithos*].

Arenicoloides Blanckenhorn, 1916, p. 36-40; Schindewolf, 1921, p. 40-44; Schindewolf, 1923, p. 662-670; Sorgel, 1923, p. 510-549; Prell, 1926, p. 325-396; Andréé, 1927, p. 125; Strigel, 1929, p. 362-366.

Rhizocorallium Hosius, 1893, p. 34-53; Kraus, 1930, p. 172-174; [*non* Zenker, 1836].

Polyupsilon Howell, 1957, p. 151-152; Häntzschel, 1965, p. 73; Häntzschel, 1966, p. 15.

? *Corophioides* Smith, Miller, 1967, p. 1063-1067.

Diplocraterion ? Torell, Fischer and Paulus, 1969, p. 86-88.

Diplocration Goldring, 1964, p. 137 (misspelling).

Type species - *Diplocraterion parallelum* Torell, 1870, p. 13; subsequent designation by Richter, 1926, p. 213.

i). Description

Vertical U-shaped burrows with spreiten. Limbs of the U are parallel and both limbs of each successive U-tube are confluent with the limbs of the preceeding U-tube. Dimensions variable, tube diameters commonly from 5 to 15 mm, distance between limbs from 1 to 7 cm, and depth of burrows from 2 to 15 cm. The apertures of the tubes are commonly funnel-shaped. Spreiten are usually protrusive but retrusive forms are also known. Commonly preserved as a horizontal dumbell-shaped cross-section on bedding planes.

ii). Discussion

Diplocraterion and other related vertical, U-shaped, spreiten-bearing ichnofossils have received considerable attention (see Richter, 1926; Seilacher, 1967a; Osgood, 1970; Knox, 1973; Fursich, 1974b). Torell (1870) erected the ichnogenus Diplocraterion to encompass vertical, U-shaped, spreiten-bearing burrows but unfortunately the description was vague, lacked photographs, and was not widely distributed. As a result, some confusion existed as to the designation of the name. Smith (1893) erected another ichnogenus Corophioides to encompass U-shaped forms with laterally displaced spreiten. These two forms were additionally confused with an earlier designated form of horizontal, U-shaped, spreiten-bearing burrow, Rhizocorallium (erected by Zenker, 1836).

This confusion prompted Richter (1926) to attempt a revision of these three ichnogenera. Working solely from the literature, he proposed two classes of U-shaped burrows: the Rhizocorallidae - to encompass all streiten-bearing U-tubes; and the Arenicollidae - to encompass all non-spreiten-bearing U-tubes. Unfortunately, Richter included in the Arenicollidae forms of Diplocraterion, which he concluded did not bear spreite. This misnomer was discovered by Westergard (1931), who redefined Torell's original description (as well as re-examining Torell's type specimens) and stressed that Diplocraterion did indeed bear spreite.

Two recent studies have attempted to rectify the present nomenclatural difficulties. Knox (1973) distinguishes Corophioides and Diplocraterion on the basis of the differing spreite: Corophioides is the product of the lateral displacement of successive migrating U-tubes; and Diplocraterion is produced by the vertical migration of successive U-tubes. Furisch (1974b), on the other hand, recognizes only Diplocraterion (with Corophioides considered a junior synonym) and concludes that variation in spreiten development should not be used to separate ichnogenera. Subsequent studies have tended to favour the proposal by Knox to retain both ichnogenus names and to separate them on spreiten development (Häntzschel, 1975; Hakes, 1976). In addition, Rhizocorallium is distinguished from the other two, based on orientation; it is primarily horizontal in attitude, but does include oblique forms (Furisch, 1974a).

Diplocraterion has a reported range from Cambrian to Cretaceous (Häntzschel, 1975). It is generally accepted that it represents the dwelling burrow (domichnia) of a suspension-feeing worm or worm-like organism that inhabits a zone of high wave activity (Sorgel, 1923; Richter, 1928; Goldring, 1962; and Seilacher, 1964a, 1967a).

iii). Thorold Specimens

Diplocraterion sp.
(Pl. 3-3, figs. 2-4)

a). Description

U-shaped burrow with spreite, oriented perpendicular to the bedding. These burrows, in the Thorold, are normally only seen on the tops of sandstone units where they are dumbell-shaped traces consisting of paired circular openings joined by a horizontal band of reworked sediment which corresponds to the spreite.

Measured burrow width ranges from 1.7 to 4.2 cm (mean of 2.2 cm); individual tube diameter ranges from 4 to 8 mm (mean of 5.4 mm); burrow depth could not be ascertained. There exists no distinction in size or ornamentation between the individual openings of a single burrow. Although found in dense numbers along certain bedding planes, no preferred orientation was detected.

b). Occurrence

Specimens referrable to Diplocraterion were recorded from the Flock Road, Mountain Boulevard, Jolley Cut, and Clappison Corners sections. Generally associated with fine-grained sandstone beds.

I). Ichnogenus Dolopichnus Alpert, 1975

Cyclozoon Wurm, 1912 (partim), p. 127-129.

Laevicyclus Quenstedt, Häntzschel, 1962 (partim), p. W201, fig. 123:3a (non 3b); Häntzschel, 1965, p. 51; Häntzschel, 1975 (partim), p. W77-W78, fig. 47:5b (non 5a).

Dolopichnus Alpert and Moore, 1975, p. 228-229.

i). Description

Large vertical burrows with a cylindrical to conical outline. Diameters range from 2 to 5 cm, with lengths up to 20 cm observed. A central, vertical, internal cylinder about 10 mm in diameter and up to 120 mm in height occurs in some samples. The distal portion of the burrow may or may not display a flattened hemispherical depression.

ii). Discussion

Dolophichnus is a little known form that has only been recorded from the Lower Cambrian (Alpert and Moore, 1975; Pemberton, et al., 1978). Alpert and Moore (1975) interpreted it as the dwelling (domichnia) burrow of sea anemones. He cites such features as the radial symmetry, the cylindrical to conical shape, and the hemispherical termination as being features possessed by other ichnogenera generally attributed to sea anemones: Conostichus Lesquereux (Chamberlain, 1971b); Bergaueria Prantl (Alpert, 1973); Kulindrichnus Hallam (1960); Cylindrichnus Toots (Chamberlain and Clark, 1973, p. 677, as Anemonichnus). In addition, he cites the size and the presence of a central sub-cylindrical core as also being indicative of a sea anemone origin. These last two characteristics will be examined later.

Dolopichnus is a common element of a shallow-water Skolithos-dominated ichnofossil suite in the Lower Cambrian Poleta Formation of California (Alpert and Moore, 1975), as well as the Lower Cambrian Bradore Formation of Labrador (Pemberton, et al., 1978). Alpert and Moore (1975) indicated that it was perhaps found in high energy sand environments which were subject to fluctuating sedimentation rates.

iii). Thorold Specimens

Dolopichnus sp. A

(Pl. 3-5, fig. 4)

a). Description

Vertical, cylindrical burrows, which display a central cylindrical core. Outer diameters up to 23 mm on upper bedding surfaces which taper downwards gradually to approximately 12 mm. Central core is up to 12 mm in diameter and is isodiametric throughout its length. Maximum depth of penetration observed was 33 mm. Burrow walls rather indistinct and sediment infill homogenous with a similar composition to the surrounding matrix.

iv). Dolopichnus Sp. B

(Pl. 3-5, figs. 1-3)

a). Description

Large cylindrical, vertical burrows with a central core. Burrow openings rather irregular in shape and up to 7 cm in diameter, taper distally to approximately 4 cm in diameter. Burrow terminates in a semi-hemispherical expansion up to 5 cm in diameter (Pl. 3-5, fig. 2). Lengths are highly variable, up to 20 cm maximum. Burrow walls rather indistinct, and sediment infill is homogenous. The central core [illegible] these larger specimens is difficult to discern, but was commonly found to be one-half the maximum diameter of the entire structure. Found in rather large densities along a single bedding surface.

b). Remarks

Two rather distinctive structures have been placed in the same ichnogenus since both display similar broad characteristics. Species A is almost identical to the specimen figured in Alpert and Moore (1975; fig. 4c). Although somewhat larger, Species B is also similar to a specimen figured in the same publication (fig. 6). Both Thorold species can therefore be assigned to this ichnogenus.

One rather confusing note, regarding the origin of the central core, was noticed in the Alpert and Moore paper. They attribute this to the preservation of the coelenteron, which was filled in with sediment. Arai (personal communication, 1978), however, indicates that anemones (both actinians and cerianthids) close the coelenteron very effectively and could not foresee how such an object would hold its shape during the decomposition of the organism. Perhaps a more realistic interpretation centers on the vertical movements observed in modern anemones (Ansell and Trueman, 1968; Shinn, 1968; Mangum, 1970). During initial burrowing and in response to sediment influxes, the animal employes peristaltic contractions to migrate

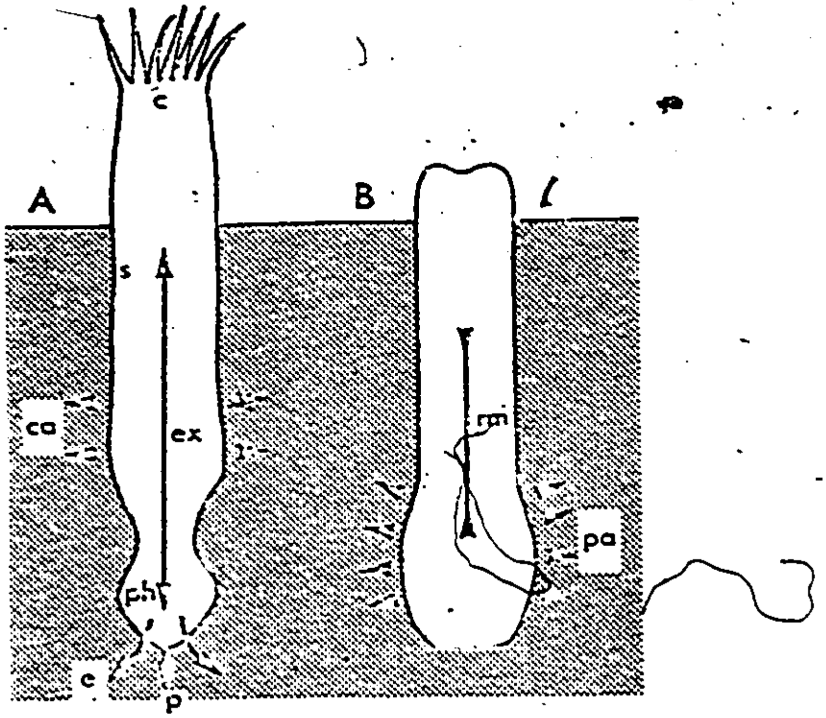

Fig. 3-3. Diagram of the two principal stages of burrowing in Peachia. A. eversion of physa (e) with displacement of sand (arrows) and further penetration of the subtratum (p); the anemone is held in the sand by the column anchor (ca, arrowheads) as extension (ex) follows retraction in B; c, capitulum; s, scapus; ph, physa; B, tentacles infolded, physa swollen to form anchor (pa, arrowheads), which allows retractor muscles (rm) to pull anemone into the sand (after Ansell, and Trueman, 1968).

upward and downward in its burrow; this results in a lateral displacement of sediment grains along the burrow walls (Ansell and Truemann, 1968). A series of such movements would ultimately end in a multi-lined burrow wall which consists of a zone of displaced sediment and a central living chamber. The terminal expansion observed in the Thorold specimens would represent the position of the physa which is used to anchor the organism in its burrow.

c). Occurrence

Dolopichnus sp. A was observed at the Jolley Cut section. Restricted to a single fine-grained sandstone unit.

Dolopichnus sp. B was recovered from the DeCew Falls section. Restricted to a single fine-grained sandstone unit. Similar structures may also be present at the Balls Falls section.

J). Ichnogenus FucusopsisPalibin, in Vassoevich, 1932

Trichophycus Miller and Dyer, 1878 (partim), p. 4.

Fucusopsis Palibin, in Vassoevich, 1932, p. 51. Seilacher, 1959, p. 1070, Table 2, fig. 3; Häntzschel, 1962, p. W194; Häntzschel, 1965, p. 37; Ksiazkiewicz, 1970, p. 286-287; Osgood, 1970, p. 380; Hakes, 1976, p. 27; Häntzschel, 1976, p. W64.

non *Fucusopsis angulatus* Birkenmajer, 1959, p. 229
[= *Planolites*].
Fucopsis Grossheim, 1946, p. 115 (misspelling).
Fuccusopsis Osgood, 1970, p. 440 (misspelling).
? *Gyrochorda fraeniformis* Farrés, 1963, p. 116.
Type species - *Fucusopsis angulatus* Palibin, in
Vassoevich, 1932, by monotypy.

i). Description

Stretched tubiform burrows, straight to curved and commonly from 2 to 10 mm in diameter. Branches, cross-overs and interpenetrations occur and the burrow exhibits typical thread-like ridges or sculptures.

ii). Discussion

Fucusopsis is a little known ichnofossil first described by Palibin (in Vassoevich, 1932) for horizontal tubes, which he originally interpreted as being either algal or inorganic in origin. Detailed analysis by Seilacher (1959) led him to conclude that *Fucusopsis* represented a burrow created by an infaunal organism. The thread-like sculpturing on the surface resulted from tension faulting in the host rock, brought on by the pressure of the organism's body (Seilacher, 1959; Osgood, 1970). This indicates that the host sediment was cohesive enough to fault rather than flow, and hence the presence of *Fucusopsis* may shed light on the physical properties of the sediment (Osgood, 1970). Hakes (1976) compared Fucusopsis to the ichnogenera Halopora (Torell, 1870) and Scoyenia (White, 1929) and concluded that they could be distinguished by the shape and distribution of their external sculptured ridges.

Fucusopsis is a well-known facies-crossing ichnofossil and displays no bathymetric control. It has been recorded from the Cruziana to the Nereites ichnofacies (Seilacher, 1959, 1964a; Osgood, 1970; Ksaizkiewicz, 1970; Hakes, 1976). Samples have been recorded from the Upper Ordovician (Osgood, 1970), the Upper Pennsylvanian (Hakes, 1976) and from the Cretaceous to the Lower Tertiary (Palibin, in Vassoevich, 1932; Seilacher, 1959; Ksiazkiewicz, 1970).

iii). Thorold Specimens

Fucusopsis sp.

(Pl. 3-3, fig. 5)

a). Description

Straight, horizontal tubiform burrows, 6 to 10 mm in width and with lengths of up to 16 cm. External ornamentation consists of several slender, ill-defined, thread-like ridges which may or may not run the entire length of the structure. Thorold specimens display considerable cross-overs, but do not branch or interpenetrate. Fucusopsis preserved in convex hyporelief.

b). Occurrence

Rare samples of Fucusopsis were observed at the Jolley Cut and 403 sections. Burrows associated with fine-grained sandstones and siltstones.

K). Ichnogenus Incisifex, Dahmer, 1937

Incisifex Dhamer, 1937, p. 525; Häntzschel, 1975,

Type species - Incisifex rhenanus, by monotypy.

i). Description

Trace consisting of two parallel rows of obliquely arranged notches. The sediment between and outside the row is smooth.

ii). Discussion

A little known ichnofossil described from the Lower Devonian of Germany (Dahmer, 1937), and attributed to the activity of arthropods.

iii). Thorold Specimens

Incisifex sp.

(Pl. 3-7, fig. 1)

a). Description

Morphologically simple trail consisting of 2 parallel rows of notches. The entire trail varies from 9 to 12 mm in length and is generally arcuate (Pl. 3-7, fig. 1). The individual notches are oriented obliquely to the longitudinal axis of the trail and are generally 1 to 2 mm in length. The two rows were consistantly observed to be 5 to 6 mm apart and the sediment between and adjacent to the rows was generally smooth.

b). Occurrence

Rare samples of Incisifex were recorded from the Jolley Cut and 403 sections. Associated with fine-grained siltstones and shales.

L). Ichnogenus Lingulichnus Hakes, 1976

For details on systematics, description and discussion of the ichnogenus, see Chapter 7.

Type species - Lingulichnus verticalis, by monotypy, Hakes, 1976, p. 28-29.

i). Thorold Specimens

Lingulichnus sp.

(Pl. 3-7, fig. 4).

a). Description

Vertical to inclined ichnofossil displaying an elliptical cross-section. Commonly preserved only as a horizontal projection on the top of fine-grained sandstone beds. Burrow displays a 2-fold symmetry with lengths up to 18 mm and widths up to 8 mm. Preserved convex epireliefs, no specimens in full relief were recovered.

b). Remarks

The figured specimen (Pl. 3-7, fig. 4) is similar to the material described by Hakes (1976, Pl. 7, fig. 1a) and Szmuc, et al. (1976, fig. 1). Although no vertical expression could be determined, it should be noted that immediately overlying the Lingulichnus burrows a well-developed siltstone containing numerous unbroken shells of Lingula clintoni (Pl. 3-7, fig. 3) was observed. In this bed, numerous vertical shells (presumably in the in situ burrowing position) were found (Pl. 3-7, fig. 2). This may suggest that the lingulids were actively burrowing in the overlying siltstone and that the observed Lingulichnus burrows formed when the lingulids periodically intersected the underlying sandstone. In addition, the elliptical outline has been postulated to be a diagnostic characteristic of the ichnogenus. Hakes (1976) correctly pointed out that lingulids display two planes of symmetry; most other shelled infauna such as bivalves display only one plane of symmetry.

The Thorold specimens have therefore been assigned to the ichnogenus Lingulichnus based on their elliptical outline, their association with in situ lingulid shells, and the fact that the burrows and shells are of a comparable size.

c). Occurrence

Rare specimens of Lingulichnus were observed only at the Jolley Cut section.

M). Ichnogenus Lobichnus Kemper, 1968

Lobichnus Kemper, 1968, p. 72; Häntzschel, 1975, p. W78.

Type species - Lobichnus variabilis, by monotypy.

i). Description

Small scooped-out hollows which form an irregular main stem with unilateral pectinate branches, comprised of small leaf-shaped hollows which are similarly arranged unilaterally. The systems are highly variable with many transitions between forms.

ii). Discussion

Lobichnus has been described only once, that being the original designation by Kemper (1968). He found it preserved exclusively in the troughs of ripple marks and believed that it was an indicator of shallow-water environments in the Lower Cretaceous Bentheimer Sandstein of Germany.

iii). Thorold Specimens

Lobichnus sp.

(Pl. 3-6, figs. 1-3)

a). Description

Problematical trace consisting of a small hollow with a radiating network of dendritic branches. The entire structure is approximately 2 cm in length with branch diameters being highly variable. Sometimes associated with a faint vertical opening (as in Pl. 3-6, fig. 2), from which larger main shafts radiate. Preserved as a convex or concave epirelief.

b). Remarks

The designation of these structures as ichnofossils is tenuous since a non-organic origin could be easily postulated. Morphologically, they do resemble rill marks. However, the presence of a faint vertical opening, the fact that the secondary branches are of a uniform thickness and never cross over, and their existence as convex epireliefs indicate that they may have an organic origin. Somewhat identical observations were made by Osgood (1970) in explaining a very similar ichnogenus Aristophycus (which differs from Lobichnus in being somewhat larger and more complex). Specimens always found in the troughs of ripple marks where abundant organic matter often collects.

c): Occurrence

Specimens of Lobichnus were observed in the Balls Falls, Woolverton Road and Jolley Cut sections. Consistently found in the troughs of small-scale ripple marks on the top of fine-grained sandstone units.

N). Ichnogenus Monomorphichnus Crimes, 1970

Monomorphichnus Crimes, 1970a, p. 57; Häntzschel, 1975, p. W84; Alpert, 1976, p. 234; Crimes, et al., 1977, p. 103; Baldwin, 1977a, p. 25.

Type species - Monomorphichnus bilineatus Crimes, 1970a, p. 57-58; by monotypy.

i). Description

Series of straight or slightly sigmoidal ridges associated in pairs. One ridge of each pair is usually more prominent than the other. The ridges are commonly 2 to 4 cm long and are sometimes repeated laterally.

ii). Discussion

Monomorphichnus resembles Dimorphichnus (Seilacher, 1965), but does not display any blunt markings or any other markings that suggest sideways progression (Häntzschel, 1975). Crimes (1970b) erected the ichnogenus for markings which he felt were produced by trilobites caught up in a current and raking the sediment surface at intervals with their endopodite claws. The ichnofossil, therefore, represents a locomotion trace (repichnia).

To date, Monomorphichnus has only been described from rocks of Cambrian to Ordovician in age (Crimes, 1970b; Alpert, 1976; Baldwin, 1977a; Crimes, et al., 1977). Because of its trilobite (or arthropod) affinities, it is commonly associated with other trilobite ichnofossils in the Cruziana ichnofacies.

iii). Thorold Specimens

Monomorphichnus sp.

(Pl. 3-7, fig. 5).

a). Description

Five to seven parallel, slightly curved scratch marks up to 18 mm in length and 10 mm in width. Individual scratch marks vary from .5 to 1 mm in width with the larger ones positioned centrally. Preserved in convex hyporelief.

b). Occurrence

Monomorphichnus tracks were observed in the Jolley Cut, 403, Sydenham Road, and Clappison Corners sections. Generally associated with fine-grained sandstones and siltstones.

O). Ichnogenus Palaeophycus Hall, 1847

Palaeophycus Hall, 1847, p. 7; Hall, 1852, p. 6, 22; Billings, 1864, p. 2-3; Lesquereux, 1869, p. 321; Nathorst, 1873, p. 46; Lesquereux, 1875, p. 135-136; James, 1879, p. 17-24; Roemer, 1880, p. 131; Nathorst, 1881, p. 38, 90; J. F. James, 1885, p. 157; Hinde, 1887, p. 228; Miller, 1889, p. 130; Bassler, 1915, p. 939; Fenton, 1928, p. 126-127; Häntzschel, 1965, p. 65; Hallam, 1970, p. 195-197; Andrews, 1970, p. 150; Ksiazkiewicz, 1970, p. 303; Osgood, 1970, p. 373-376; Frey and Chowns, 1972, p. 32-33; Häntzschel, 1975, p. W88-W89.

Paleophycus J. F. James, 1879, p. 19 (misspelling).

non *Palaeophycus kochi* Ludwig, 1869, p. 10 [= *Belorhaphe*].

non *Palaeophycus gracilis* Lesquereux, 1875, p. 137-138, Pl. 1, figs. 4, 5 [= *Chondrites*].

non *Palaeophycus flexuosus* J. F. James, 1879, p. 19 [= inorganic].

Palaeospongia d'Orbigny, 1948 (*partim*).

Palaeospongia prisca Bornemann, 1886, p. 21; Hinde, 1887, p. 228; Rauff, 1891, p. 92-100; Bornemann, 1891, p. 492.

Aulacophycus Massalongo in Massalongo and Scarbella, 1859 (*partim*), p. 92.

Phymatoderma Bronigniant, Dawson, 1890, p. 602.

Planolites Nicholson, J.F. James, 1891 (*partim*) p.47.

Type species - Palaeophycus tubularis Hall, 1847, p. 7; subsequent designation by Bassler, 1915, p. 939.

i). Description

Ichnogenus showing a wide range of morphology. Burrow is usually cylindrical to sub-cylindrical and varies from straight to sinuous. Oriented more or less obliquely to the bedding. The surface of the walls are smooth but may display faint longitudinal striae. Dimensions are highly variable, with lengths up to 20 cm or more and diameters ranging from 30 to 15 mm. The burrows can be branched and commonly intersect one another.

ii). Discussion

Palaeophycus is another well-known form-ichnogenus, in that a multitude of different morphologies are included in it. In general, Palaeophycus is a horizontal burrow system that sometimes displays branches and intersections (Hall, 1847). Osgood (1970) pointed out the inherent difficulties in differentiating Palaeophycus from the other well-known horizontal burrow Planolites. Since both ichnogenera are horizontal, possess distinct, lined walls, display similar ornamentations, and frequently show intersections, a number of different methods have been proposed to separate them. Frey and Chowns (1972) have correctly pointed out that Palaeophycus occasionally displays subcollapsed structures, which are evident from their subcylindrical cross-section, and Planolites never exhibits such a feature. Alpert (1975) points out that Planolites never branches, while Palaeophycus does. There exist a number of problems with this designation, since it does not conform to the original description of the ichnogenus. Nicholson (1873) erected the ichnogenus Planolites to encompass forms that were actively filled by the inhabitant of the burrow, and indicated that the burrow infill was distinct from the surrounding rock matrix. This difference in lithology was attributed to the fact that the sediment infill has passed through the alimentary system of the burrower. Häntzschel (1975) has indicated that many samples of Palaeophycus do not branch. Thus, these specimens would be placed in Planolites by Alpert (1975), even though they do not exhibit a distinct burrow infilling. Conversely, Häntzschel (1975) also points out that while Planolites does not exhibit true branching, intersections are common, which could be misinterpreted as branches.

The differentiation of these two forms must lie with the differences in the burrow infilling. Planolites, being actively infilled, displays an infilling distinctive from the rock matrix; Palaeophycus, being passively infilled, does not display a distinct infilling. This difference also allows differentiation on purely ethological grounds: Planolites represents a feeding burrow (fodinichnia); and Palaeophycus represents the locomotion trace (repichnia) of an infaunal organism.

Palaeophycus has been reported from strata ranging in age from Pre-Cambrian to Recent (Häntzschel, 1975), and is commonly associated with the Cruziana ichnofacies (Seilacher, 1967).

Originally, Palaeophycus was interpreted as the stems of fucoids (Hall, 1847; Billings, 1862), an interpretation which was in fact still advocated as late as Wilson (1948). James (1885) was the first to recognize that it was in fact the burrow of a sediment-dwelling organism, and even compared them to recent annelid trails. An alternate interpretation was given by Wilckens (1947), who suggested that they may represent fragments of worm tubes that were uprooted during storms. Osgood (1970) reviews the history of the ichnogenus and interprets it as the unorganized pathways of infaunal errant organisms moving through the sediment. He goes on to suggest that possible recent counterparts may include predaceous polychaetes (e.g., Glycera), gastropods (e.g., Polynices), or certain pelecypods.

iii) Thorold Specimens

Palaeophycus sp.

(Pl. 3-9, figs. 1-3)

a). Description

Straight to gently arcuate, horizontal burrows, that can be branched (Pl. 3-9, fig. 1) or unbranched (Pl. 3-9, fig. 2). Diameters range from 3 to 4 mm and lengths of up to 25 cm were observed. Although distinct burrow margins could be discerned, the walls appeared to be very irregular. Many specimens displayed an elliptical cross-section which suggests that perhaps the burrows had collapsed. Sediment infill was similar to the surrounding matrix. No distinctive ornamentation was discernible. Commonly preserved in convex hyporelief.

b). Occurrence

Specimens of Palaeophycus are widespread in the Thorold Sandstone. They were recorded from virtually all the outcrops investigated with the exception of the sections at the Genesee Gorge, Lockport, Town Line Road, Niagara Gorge, Niagara Glenn and DeCew Falls. Generally associated with fine-grained sandstones and siltstones.

P). Ichnogenus Planolites Nicholson, 1873

Palaeophycus Hall, 1847 (partim), p. 7; Osgood, 1970 (partim), p. 373-376;

Chondrites sp. Salter, 1856, p. 246; Salter, 1866, p. 243, Text - fig. 1; Salter, 1881, p. 336, Text - fig. 1.

? Scolites ~~Salter~~, 1857 (partim), p. 204; Salter, 1866, p. 292, Pl. 12, fig. 2; Salter, 1881, p. 485, Pl. 12, fig. 2; Häntzschel, 1965, p. 83.

Scoleicites Salter, 1873, p. 2, 10; Häntzschel, 1965, p. 82.

Planolites Nicholson, 1873, p. 289; Nicholson and Hinde, 1875, p. 138-139; Nicholson, 1875, p. 41-42; Nicholson, 1879, p. 319-320; Nicholson, 1885, p. 122-123; Nicholson and Lydekker, 1889, p. 482-484; Miller, 1889, p. 520; Walcott, 1890, p. 34; Bassler, 1915, p. 982; Howell, 1943, p. 17-18; Häntzschel, 1962, p. W210; Gekker and Ushakov, 1962, p. 72; Häntzschel, 1965, p. 72; Gregory, 1969, p. 6; Frey, 1970, p. 16; Heinberg, 1970, p. 230-231; Osgood, 1970 (partim), p. 375-377; Chamberlain, 1971b, p. 226; Young, 1972, p. 14; Frey and Chowns, 1972, p. 32-33; Chamberlain and Clark, 1973, p. 679; Alpert, 1975, p. 512; Chamberlain, 1975, p. 1082; Häntzschel, 1975, p. W97-W97; Hakes, 1976, p. 32; Pickerill, 1977, p. 6-7; Curran and Frey, 1977, p. 145-148; Crimes, et al., 1977, p. 124; Roniewicz and Pienkowski, 1977, p. 277; Ekdale, 1977, p. 169; Pickerill, et al., 1977, p. 244; Baldwin, 1977a, p. 27; Ekdale, 1978, p. 822; Ekdale and Berger, 1978, p. 273; Ireland, et al., 1978, p. 418.

Planulites Dawson, 1892, p. 29 (misspelling).

Planotites J. F. James, 1894, p. 135 (misspelling).

Planilites Dawson, 1897, Text - fig. 11, p. 53 (misspelling).

? Montfortia Lebseconte, 1887, p. 782 [non Recluz, 1843].

Type species - Planolites vulgaris Nicholson, 1873, p. 289, by original description.

i). Description.

Unilobate, cylindrical or sub-cylindrical infilled burrows that are straight to gently curved and never branch. Usually more or less horizontal or oblique to bedding planes. Dimensions highly variable, diameters range up to 15 mm and lengths up to 5 cm.

ii). Discussion

Nicholson (1873) erected the ichnogenus Planolites to encompass unilobate, horizontal burrows which were filled with sediment that had passed through the animal's alimentary canal. For a discussion of its relation to Palaeophycus, see the preceeding section. The presence of a definite mucous wall lining, altered infilled sediment, and features indicative of an active filling process have led Frey (1970) and Häntzschel (1975) to conclude that it represents a feeding burrow (fodinichnia). Burrows of this nature have been recorded in rocks ranging in age from Pre-Cambrian to Recent (Häntzschel, 1975).

Planolites is a well-known facies-crossing ichnofossil and has been recorded in sediments associated with the Skolithos to Nereites ichnofacies (Crimes, 1970b). In addition, Richter (1937) erected an ichnospecies (Planolites montamus) which is restricted to non-marine deposits. Recently, Ekdale (1977, 1978) and Ekdale and Berger (1978) have recognized Planolites in deep-sea cores ranging in age from Lower Cretaceous to Pliocene, some of which were recovered from depths in excess of 4,440 m. As a result, Planolites has very little value in paleobathymetric determinations.

Although it is now widely accepted that Planolites represents the feeding burrows (fodinichnia) of vermiform organisms (see Häntzschel, 1975), very little has been done to pinpoint probable producers. Curran and Frey (1977) suggest that Pleistocene samples from North Carolina were probably produced by a number of foraging polychaetes, such as Marphysa sanguinea and

Nereis succinea, in a wide range of sediment types and habitats (coherent sands, muddy sands, sandy or shelly offshore muds; protected beaches, tidal flats, shoals, and point bars). Ekdale (1977) offers an alternate interpretation for deepsea samples and suggests that probable producers may include infaunal, deposit-feeding polychaetes or holothurians. It should suffice, however, to indicate that a number of different organisms are capable of producing ichnofossils similar to Planolites.

iii). Thorold Specimens

Planolites sp.

(Pl. 3-8, figs. 1-2; Pl. 3-9, fig. 4)

a). Description

Straight to sinuous unilobate burrows, oriented parallel to bedding planes. Diameters range from 3 to 5 mm and are constant throughout the entire length of the burrow. Lengths variable but structures up to 7 cm in length were observed. No true branching was noticed; however, frequent cross-overs have been recognized (Pl. 3-8, fig. 1). Display circular cross-sections and distinct burrow walls. Sediment infill, although structureless, differs noticeably from surrounding matrix. Aside from faint longitudinal striations on some specimens, no ornamentation was observed. Preserved most commonly in convex hyporelief but also in concave epirelief and rarely in full relief.

b). Occurrence

Specimens of Planolites have been recorded from all Thorold outcrops, with the exception of the Niagara Glen section. In sections east of the Balls Falls area, however, these horizontal burrows are not common. Prolific burrows were observed in most outcrops of the Hamilton area. Generally associated with fine-grained sandstone and siltstone beds.

Q). Ichnogenus Polycylindrichnus Risk, Pemberton and Fournier, 1979

(P. 3-10, figs. 1-3)

Type species - Polycylindrichnus concentricnus; monotypic. The generic name is derived from its similar appearance to the ichnogenus Cylindrichnus, its budding nature, and the internal structure of the burrow infilling.

i). Diagnosis

A branching network of conical elements, which appear to bud from one another (Pl. 3-10, fig. 2). The individual elements (Pl. 3-10, fig. 3) are conical to subconical, curved and oriented from nearly vertical to inclined to nearly horizontal to the bedding. Apertures are circular to oval in cross-section

(Pl. 3-10, fig. 1) and vary from 6 to 15 mm in diameter. In transverse section, the individual elements are composed of concentric bands (Pl. 3-10, fig. 1), with a central core from 1 to 4 mm in diameter. The sediment infill is much finer-grained than the host rock and exhibits concentric lamination. The burrow network is intrastratal and preserved in full-relief.

ii). Distinguishing Characteristics

The systematic budding pattern illustrated in Plate 3-10, figure 2 is the single most diagnostic feature. Specimens in which this feature is lacking could very easily be confused with the ichnogenus *Cylindrichnus*.

iii). Similarity to Other Forms

Although the burrow complex is readily differentiated from any other known form, it could be confused with certain samples of the ichnogenera *Teichichnus* Seilacher, 1955 (see Martinson, 1965, fig. 2, p. 212) and *Trichophycus* Miller and Dyer, 1878 (see Seilacher and Meischner, 1964, fig. 11, p. 614; and Osgood, 1970, fig. 16, p. 349).

The name *Teichichnus* is applied to a wide range of trace fossils, from straight retrusive septa to sinuous and U-shaped forms, some of which lie obliquely in the sediment (Chisholm, 1970). It is generally conceded that Teichichnus represents the feeding burrows of various deposit-feeding organisms (Seilacher, 1955). Polycylindrichnus differs from Teichichnus in that it does not possess the characteristic septate structures that are associated with all teichichnid forms (Seilacher, 1955; Chisholm, 1970). In addition, teichichnids never show any form of true branching (Martinson, 1965).

Trichophycus venosum is a cylindrical gently U-shaped burrow with a small number of vertically directed secondary branches (Häntzschel, 1975). Seilacher and Crimes (1969) have interpreted it as a feeding burrow probably made by small trilobites. It differs from Polycylindrichnus in that the branches do not taper but remain isodiametric, and display striae radiating from the midline on the ventral surface (Osgood, 1970). In addition, the secondary branches of Trichophycus remain bundled to the main cylinder for some distance beyond the actual point of bifurcation (see Osgood, 1970, Pl. 68, fig. 1), in contrast to the branching pattern exhibited by Polycylindrichnus.

As stated previously, the individual elements bear a close resemblance to the ichnogenus Cylindrichnus (Toots, in Howard, 1966), and if encountered in hand samples as a discrete element, it would be impossible to distinguish between them. Cylindrichnus is an uncommon form originally described by Toots in Howard (1966) from the Upper Cretaceous Mesaverde Formation of Wyoming. Subsequently, the name Cylindrichnus was used by Bandel (1967) for another unrelated trace fossil. This led to some degree of confusion and later investigators proposed new names for this form. Frey (1970) described Cylindrichnus from the Upper Cretaceous Fort Hays Limestone of Kansas and considered it to be a form of the ichnogenus Asterasoma. Chamberlain and Clark (1973) proposed the name Anemonichnus for similar forms from the Lower Pennsylvanian Manning Canyon Shale of Utah. Ksiazkiewicz (1970) described a rather large form from the Upper Eocene of the Polish Carpethians. In order to clear up some of the confusion, Bandel (1973) later renamed his Cylindrichnus form Margaritichnus and in the revised Treatise Häntzschel (1975) reestablished the name Cylindrichnus for the form described by Toots in Howard (1966), and placed Anemonichnus in synonymy with it.

Cylindrichnus is a subconical to conical form, weakly curved and circular to oval in cross-section, with diameters of 10 to 20 mm. It possesses a central core and the exterior wall is composed of concentric layers. Orientation is from nearly horizontal to vertical. Howard (1966) considered it to be a dwelling burrow of a filter-feeding organism, while Chamberlain and Clark (1973) considered it to be a dwelling burrow of an anemone. Polycylindrichnus varies from Cylindrichnus in having the elements budding off from one another (Pl. 3-10, figs. 2).

iv). Occurrence

Rare specimens of Polycylindrichnus were recorded from the Jolley Cut road section. Associated with fine-grained sandstones and siltstones.

R). Ichnogenus Rhabdoglyphus Vassoevich, 1951

Rhabdoglyphus Vassoevich, 1951, p. 61; Boucek and Elias, 1962 (partim), p. 146; Ksiazkiewicz, 1970, p. 285-286; Vyalov, 1971, p. 90; Häntzschel, 1975, p. W99-W101.

non Rhabdoglyphus Vassoevich, Boucek and Elias, 1962 (partim), p. 46; Häntzschel, 1965, p. 75; Häntzschel, 1966, p. 15; Osgood, 1970, p. 369 [= Fustiglyphus, Vyalov, 1971, p. 90].

"Rhabdoglyphen" Fuchs, 1895, p. 391.

Type species - Rhabdoglyphus grossheimi, by monotypy, Vassecvich, 1951, p. 61.

i). Description

Cylindrical tubes with periodic well-defined swellings, that are not regularly spaced. Structure may or may not branch.

ii). Discussion

Rhabdoglyphus, although a rare form, has a complex nomenclatural history which has recently been outlined by Häntzschel (1975). The form is closely related to the ichnogenus Fustiglyphus (Vyalov, 1971). It is known only from Cretaceous to Tertiary flysch deposits (Vassoevich, 1951, Boucek and Elias, 1962; Ksiazkiewicz, 1970, Vyalov, 1971); however, similar forms (Fustiglyphus) are known from the Ordovician (Osgood, 1970).

Boucek and Elias (1962) postulated that forms similar to Rhabdoglyphus may represent the activities of a number of different organisms and compared it to traces made by amphipods, gastropods (e.g., Bulla), and holothurians (e.g., Leptosynapta). Osgood (1970) pointed out, however, that no reasons were given for such an interpretation. He considered the trace to be a feeding burrow (fodinichnia) of an organism that burrowed into a clay layer and then moved horizontally along a clay-silt interface; the periodic knobs were interpreted as responses to either peristaltic constrictions and expansions, or the result of the eversion of the proboscis. Ksiazkiewicz (1970) postulated a similar post-depositional origin for the ichnogenus, and considered it as a feeding burrow mining at the clay-sand interface.

iii). Thorold Specimens

Rhabdoglyphus sp.

(Pl. 3-8, fig. 5)

a). Description

A single specimen was found and tentatively assigned to the little-known ichnogenus Rhabdoglyphus. It consists of a relatively long (up to 20 cm) horizontal burrow which displays a cylindrical cross-section and regularly-spaced, invaginated "calyces." An uniform width of 8 mm was displayed along the entire width of the burrow. The individual swellings (which numbered 13) were spaced at an interval of 1.5 cm; this measurement was found to be relatively constant. Although the figured specimen (Pl. 3-8, fig. 5) gives the impression of branching, it could not be determined if this represents true branching or is merely a cross-over phenomenon. Preserved in convex hyporelief.

b). Remarks

The Thorold specimen, although quite a bit larger, is essentially similar to forms assigned to the ichnogenus Rhabdoglyphus by Ksiezkiewicz (1970, fig. 1,i) and Häntzschel (1975, fig. 61-3).

c). Occurrence

One specimen was recovered from the Jolley Cut section, which was associated with a fine-grained sandstone.

S). Ichnogenus Rusophycus Hall, 1852

Rusophycus Hall, 1852 (*partim*), p. 23; Dawson, 1864, p. 363-367; Nathorst, 1881, p. 33; J. F. James, 1885 (*partim*), p. 153-155; Miller, 1889, p. 138; Dawson, 1890, p. 599; Bassler, 1915, p. 1132; Andrews, 1955, p. 230; Seilacher, 1959, p. 292-293; Häntzschel, 1962, p. W212-W214; Radwanski and Roniewicz, 1963, p. 265-267; Häntzschel, 1965, p. 80; Kegel, 1965, p. 1-11; Osgood, 1970, p. 301-305; Crimes, 1970a, p. 53-57; Crimes, 1970b, p. 114-116, 119-124; Andrews, 1970, p. 187; Bergstrom, 1970, p. 37-40; Scintos and Campanha, 1970, p. 742; Birkenmajer and Brunton, 1971, p. 303-313, 318; Young, 1972, p. 14; Häntzschel, 1975, p. W101-W102; Osgood and Drennan, 1975, p. 311-312; Crimes, 1975a, p. 37-41; Crimes, 1975b, p. 34-35; Hakes, 1976, p. 32-33; Bergstrom, 1976, p. 1623-1624; Alpert, 1976, p. 227-233; Pickerill, 1977, p. 3-4; Crimes, *et al.*, 1977, p. 105; Gutschick and Rodriguez, 1977, p. 203;

Baldwin, 1977a, p. 25-26; Martino and Zapecza, 1978, p. 185-188.

Rhysophycus Eichwald, 1880, p. 54 (non viso); Linnersson, 1869, p. 403-405; Schimper and Schenk, 1885, p. 54; Lessertisseur, 1955, p. 44-47; Häntzschel, 1965, p. 79; Gubler, 1966, p. 155.

Rhyssophycus Goeppert, 1860, p. 434; Häntzschel, 1965, p. 79; Andrews, 1970, p. 186.

Rusichnites Dawson, 1864, p. 367; Dawson, 1873, p. 18; Miller, 1889, p. 566; Dawson, 1890, p. 595-596; Häntzschel, 1965, p. 80.

Russichnites Bonney, 1903, p. 290 (misspelling).

Rysophycus Tromelin and Lebesconte, 1876, p. 627; Lebesconte, 1883, p. 466-472; Häntzschel, 1965, p. 81.

Rhizophycus Peneau, 1946, p. 88; Häntzschel, 1965, p. 79.

Cruziana d'Orbigny, J. F. James, 1885 (partim), p. 154-157; Seilacher, 1970 (partim), p. 454-456.

Type species - Rusophycus clavatus Hall, 1852, p. 23; subsequent designation by S. A. Miller, 1889, p. 138.

i). Description

Short, bilobate forms, resembling the shape of coffee beans and exhibiting an elliptical outline. The lobes are transversely wrinkled by anterolaterally directed coarse to fine straiae; and a medial furrow is present. Dimensions are highly variable but generally the width is equal to one-half to two-thirds the length.

ii). Discussion

Osgood (1970) regards Rusophycus as perhaps the most famous of all ichnofossils. Its relatiionship with Cruziana has previously been discussed. Rusophycus has been interpreted as a resting trace (cubichnia) of trilobites or other trilobite-like arthropods (Osgood, 1970). Seilacher (1960), however, points out that not all short, bilobate, Rusophycus-like traces are the result of trilobite activities. He suggests that organisms such as the modern polychaete Aphrodite and some gastropods (e.g., Bullia) are capable of producing similar traces.

iii). Thorold Specimens

Rusophycus sp.

(Pl. 3-8, figs. 3-4)

a). Description

Bilobate traces in which individual lobes are separated by a shallow groove and are ornamented with transverse to oblique striations (or scratch marks). Entire trace varies from 3 to 5 mm in width and from 1 to 2.5 cm in length; striations are spaced approximately 1 mm apart. The lobes taper posteriorly and display an elliptical cross-section. The trace was consistently preserved in convex hyporelief.

b). Occurrence

Specimens of Rusophycus were recorded from the Flock Road, Jolley Cut, 403, Webster Falls, Sydenham Road, Rock Chapel Falls and Clappison Corners sections. Generally associated with fine-grained sandstones and siltstones.

T). Ichnogenus Scalarituba Weller, 1899

Scalarituba Weller, 1899, p. 12; Branson, 1938, p. 14-15; Henbest, 1960, p. 383; Häntzschel, 1962, p. W215; Häntzschel, 1965, p. 82; Branson, 1966, p. 236; Conkin and Conkin, 1968, p. 3-4; Rodriguez and Gutschick, 1970, p. 419-420; Chamberlain, 1971b, p. 228-229; Chamberlain and Clark, 1972, p. 678; Häntzschel, 1975, p. W103-W106; Hakes, 1976, p. 83; Pickerill, et al., 1977, p. 244-246.

Type species - Scalarituba missouriensis, Weller, 1899, p. 12, by monotypy.

i). Description

Sub-cylindrical, sinuous burrows usually oriented parallel or oblique to a bedding plane. Commonly from 2 to 10 mm in width and with lengths of up to 15 cm. Marked by transverse scalariform ridges that are situated at average distances of 2 to 3 mm.

ii). Discussion

Scalarituba is a horizontal ichnogenus that has been interpreted as the feeding burrow (fodinchnia) of a sediment-eating worm or worm-like organism (Henbest, 1960; Conkin and Conkin, 1968; Chamberlain, 1971b). The transverse partitions results from the organism episodically back-filling the burrow (Seilacher and Meischner, 1965; Conkin and Conkin, 1968). The ichnogenus has been recorded in rocks ranging in age from Ordovician to Permian (Häntzschel, 1975).

Scarlarituba displays a wide range of facies tolerances and has been reported from the Cruziana, Zoophycos and Nereites ichnofacies by Seilacher (1964); the Zoophycos ichnofacies by Seilacher and Meischner (1964) and Chamberlain (1971b); as well as from tidal flat to shallow subtidal environments by Henbest (1960), Conkin and Conkin (1968) and Hakes (1976).

iii). Thorold Specimens

Scalarituba sp. (Pl. 3-11, fig. 4)

a). Description

Sinuous, horizontal burrows varying from 4 to 6 mm in width and displaying variable lengths. The magnitude and direction of the curving is not constant in any one specimen. The burrow displays transverse scalariform ridges that are spaced approximately 1 to 1.5 mm apart. These ridges, although not conspicuous, may be detected by their slightly different colour, which Weller (1899) attributed to the reducing conditions which existed in the digestive tract of the worm during life. Preserved in concave epirelief.

b). Occurrence

Specimens of Scalarituba were recorded from the 403, Sydenham Road and Clappison Corners sections. Generally associated with shales and siltstones.

U). Ichnogenus Skolithos Haldemann, 1840

For complete details on the nomenclature, description, and discussion of the ichnogenus Skolithos, see Chapter 5.

i). Thorold Specimens

Skolithos sp.

(Pl. 3-9, figs. 5-6; Pl. 3-10, figs. 4-5)

a). Description

Simple vertical burrow which displays a circular cross-section. Diameters are quite variable, ranging from 1 to 5 mm. In most samples, the depth of penetration was difficult to discern, but some specimens were up to 3 cm long. Burrow orientation was from vertical (Pl. 3-9, figs. 5, 6) to inclined (Pl. 3-10, fig. 5). No ornamentation on the outer burrow wall was observed and no internal structures could be discerned. Although commonly preserved in full-relief, many samples were found in convex epirelief.

b). Remarks

Detailed examinations of S.E.M. micrographs indicate that a preserved burrow lining may be present (Pl. 3-10, fig. 4). The structure is somewhat enrolled, linear, and situated along the burrow margin. Modern soft bodied organisms utilize organic linings to strengthen the burrow wall (see Schäfer, 1972) and there exist numerous accounts of wall linings associated with different ichnogenera including Skolithos (Frey, 1971; Goodwin and Anderson, 1974; among others). Well-preserved linings, however, are rare and as a result very little is known about their characteristics.

In most cases, modern organisms use organic compounds (mainly mucro-proteins) in constructing burrow linings. When such organic compounds are incorporated into a sediment, microbes immediately begin to utilize them as a source of carbon and energy (Kononova, 1966; Martin and Haider, 1971). In modern sediments, microbial populations are most abundant along the sediment-water interface corresponding to high concentrations of incorporated organic matter (Zobell, 1946; Oppenheimer, 1960). The bacterial decomposition of these organic substances results in a number of refactory compounds which include various humic and fulvic acids (Zhukova and Fedosov, 1963; Kononova, 1966; Martin and Haider, 1971); polysaccharides (Parsons and Tinsley, 1961); amino acids (Rittenburg, et al., 1963; Degens, et al., 1964; Emery, et al., 1964); and guinone groups (Flaig, 1960, 1966); among others. Such groups are known to react with certain di- and tri-valent metals which results in rendering insoluble metals soluble (for complete details, see Rashid, 1969, 1971, 1972a, b, c; and Rashid and King, 1969, 1970). These complexes can then be mobilized and subsequently reprecipitated, creating zones of enrichment. In modern undisturbed sediments, however, these groups generally decrease in abundance with increasing sediment depth (Rittenberg, et al., 1963). This may be related to the similar distribution pattern exhibited by marine bacteria (Zhukova and Fedosov, 1963).

In most cases, open burrow systems represent an extension of the sediment-water interface and thus serve to increase the reaction surface available for microbial decomposition (Aller and Yingst, 1978).

Organic wall linings would therefore be subjected to the same decomposition processes. In a recent study Aller and Yingst (1978) investigated the geochemistry of the wall lining of the burrowing terebellid polychaete Amphitrite ornata. They found that these linings displayed high concentrations of Mn, Zn and Fe, which they attributed to the intense decomposition processes in the burrow wall which mobilized and concentrated them along the inner burrow wall.

Preliminary studies on the well-preserved burrow linings of the Thorold Skolithos specimens indicate a similar reaction. Samples of Skolithos which displayed well-preserved burrow linings were subjected to a Kevex X-ray energy dispersive analyzer in order to gain some information on the contained elemental distribution. Although by no means absolute, the Kevex does give reliable indications of relative abundances. A spot analysis was conducted outside the burrow wall, at the burrow wall, and inside the burrow wall. It was found that two tri-valent metals, Fe and Al, seemed to be greatly enriched along the burrow wall (Table 3-1). More detailed research on the distribution of metals in relation to these burrow linings is presently underway.

Table 3-1. Preliminary results of elemental abundances in relation to burrow linings in Skolithos sp. burrows from the Jolley Cut section of the Thorold Sandstone (O = outside burrow; L = burrow lining).

Burrow Number	Station	Centroid[1]	Area[2]	Element
74-124	O_1	1.45	262.79	Al
		3.32	162.58	K
		5.92	31.49	Mn
		6.39	257.65	Fe
74-124	L_1	1.48	1984.01	Al
		3.32	1889.47	K
		5.78	390.42	Mn
		6.40	1507.02	Fe
75-39	O_5	1.42	905.5	Al
		3.43	266.41	K
		6.42	21.75	Fe
75-39	L_5	1.47	4359.77	Al
		3.31	7673.97	K
		6.40	871.25	Fe

[1] Centroid: number on energy spectrum chart which indicates the particular element.

[2] Area: total number of counts within the peak limits.

c). Occurrence

Abundant specimens of Skolithos were observed at all outcrops west of and including DeCew Falls. No samples were recorded from the New York sections. Generally associated with fine-grained sandstones.

V). Ichnogenus Teichichnus Seilacher, 1955

Teichichnus Seilacher, 1955, p. 378; Seilacher, 1956, p. 164; Seilacher, 1957, p. 203-204; Muller, 1959, p. 244; Häntzschel, 1962, p. W218; Häntzschel, 1965, p. 91-92; Martinsson, 1965, p. 211-219; Doughty, 1965, p. 147-148; Howard, 1966, p. 41; Frey, 1970, p. 17-18; Heinberg, 1970, p. 231-232; Chisholm, 1970, p. 32-47; Warme, et al., 1973, p. 815; Chamberlain, 1975a, p. 1084; Häntzschel, 1975, p. W114; Hakes, 1976, p. 34; Bergstrom, 1976, p. 1630; Pickerill, 1977, p. 7; Crimes, et al., 1977, p. 126; Ekdale, 1977, p. 170; Baldwin, 1977a, p. 29-30; Ekdale and Berger, 1978, p. 275.

? Teichichnus sp. Frey, 1970, p. 1748; Frey and Howard, 1970, p. 160.

Type species - Teichichnus rectus, Seilacher, 1955, p. 378; by monotypy.

i). Description

Blade-like spreiten structures, formed by a series of long horizontal burrows stacked vertical to the bedding. The wall-shaped laminar body is straight to slightly sinuous and does not generally branch. Spreite commonly retrusive but can also be protrusive. Dimensions variable, commonly up to 50 cm long and 10 cm or more high.

ii). Discussion

Teichichnus is a well-known ichnofossil erected by Seilacher (1955) to encompass blade-like spreiten structures. Martinsson (1965) pointed out that the system was the result of a digging action in the sediment and the resulting spreiten could be either protrusive or retrusive in form. *Teichichnus* has been observed to be related to a number of other ichnogenera resulting in some confusion regarding its identity. Chisholm (1970) observed *Teichichnus* grading into *Rhizocorallium*, in the Lower Carboniferous of Scotland. Similar observations were reported by Sellwood (1970), who stated that a limb of a vertically retrusive *Rhizocorallium* could be mistaken for *Teichichnus*. Hestor and Pryor (1972) observed tunnels of *Ophiomorpha* grading into *Teichichnus*-like structures. *Teichichnus* is also often confused with the ichnogenus *Phycodes*, another spreiten-bearing ichnofossil (for details, see Häntzschel and Reineck, 1968, p. 26).

Although *Teichichnus* has been recorded in rocks ranging in age from Lower Cambrian to Tertiary

(Häntzschel, 1975), it is probably even more prolific. The nature of Teichichnus makes it a hard ichnofossil to identify. There is usually no tube associated with the spreiten-structure, except in areas where the burrow branches upwards and intersects a bedding plane, resulting in a circular burrow opening. Therefore, in many cases, the burrow is reflected as merely an alteration of sediment grains and not as a distinct structure.

Teichichnus is a well-known facies-crossing ichnofossil and has been found in the Cruziana, Zoophycos, and Nereites ichnofacies (Ekdale, 1977). In fact, Ekdale and Berger (1978) have observed Teichichnus in deep-sea cores from depths in excess of 1,500 m. As a result, it has little value as a paleobathymetric indicator. It is, however, almost always associated with finer-grained sediments, such as siltstones and shales (Seilacher, 1955).

The characteristics of Teichichnus led Seilacher (1957) to suggest that it probably represents a feeding burrow (fodinichnia) produced by a number of different organism groups. Seilacher (1957) pointed out that comparable structures were produced by the recent polychaete Nereis diversicolor. Martinsson (1965) observed that the base of many teichichnids displays a noticeable bilateral symmetry, which led him to postulate an arthropod origin for them. Ekdale (1977), studying deep-sea samples, suggested that Teichichnus was a shallow burrow that migrated upwards in response to increased sedimentation. The spreiten-structure resulted from the organism repeatedly moving back and forth in the same vertical plane, probing the sediment for food. These observations led him to interpret it as a dwelling-feeding burrow, perhaps of annelid or crustacean origin.

iii). Thorold specimens

Teichichnus sp. /

(Pl. 3-11, figs. 1-3)

a). Description

A rather indistinct form of Teichichnus was discerned in the siltstone beds of the Thorold. It consists of an unbranched, blade-like structure formed by the vertical upward migration of the burrow. This upward displacement is expressed by a retrusive spreite orientation. The entire structure is 10 to 15 mm in width and up to 6 cm in height. The length could not be determined because of sedimentary overburden. One slabed section (courtsey of D. Craig) displays the horizontal projection of the spreite-layers.

b). Occurrence

Rare samples of *Teichichnus* were recorded from the Jolley Cut, 403, Sydenham Road and Clappison Corners outcrops. Specimens generally associated with fine-grained siltstones.

W). Problematical Forms

i). *Gordia* sp.

(Pl. 3-12, fig. 5)

a). Description

Long, thin, horizontal burrows, straight to arcuate to sinuous. Diameters are very small, less than 1 mm, but appear to remain constant in any one specimen. Although difficult to discern, it does not appear that the burrows branch; however, they frequently cross one another. Preserved in convex hyporelief.

b). Remarks

Originally described by Emmons (1844, p. 24), *Gordia* is also frequently referred to by its synonomy *Palaeochorda*. The Thorold specimens are similar to the ones figures by Häntzschel (1975, fig. 39, 1a, 1b). Since the preservation is poor, an exact determination could not be made.

Gordia has been interpreted as a feeding structure (fodinichnia) of a worm-like organism

(Häntzschel, 1975). Emmons (1844) remarked on its close resemblance to the structures produced by the modern hair-worm, Gordius, hence the ichnogeneric derivation. Specimens range in age from the Pre-Cambrian to the recent and no ichnofacies restrictions have been noted (Häntzschel, 1975).

c). Occurrence

Rare specimens of ? Gordia were recorded from the Jolley Cut, Websters Falls and Sydenham Road sections. Generally associated with fine-grained sandstones and siltstones.

ii). ? Caprionichnus sp.
(Pl. 3-12, fig. 3)

a). Description

Horizontal burrow system consisting of divergent pairs of burrows arranged in a linear chevron-like pattern joined to a central, common linear burrow. The entire structure is 7.6 cm in length and 5.4 cm in width. The central burrow is 5 mm wide, side branches are 3 to 4 mm in width and up to 4 cm in length. The angle between the paired burrows was approximately 64 degrees. The Thorold sample displayed 3 paired burrows and was preserved in concave epirelief.

b). Remarks

Caprionichnus is a newly described ichnogenus from the Ordovician of southern Norway (Harland, 1978). Although the poor preservation of the Thorold structure limits an exact identification, it does resemble Caprionichnus.

Harland (1978) attributes Caprionichnus to the feeding activities of an infaunal organism (similar in nature to the producer of a Chondrites burrow system). The animal inhabited the central shaft and the paired branched structures represent feeding probes. Although Harland (1978) does not give any paleoenvironmental information on the rocks containing Caprionichnus, it was found in a silty mudstone bed which was part of a transgressive sequence.

c). Occurrence

A single specimen of ? Caprionichnus was recovered from the Sydenham Road section, associated with a siltstone layer.

iii). Form C: ? Scolicia sp.

(Pl. 3-6, fig. 4)

a). Description

Rather indistinctive horizontal ribbon-like trail approximately 5 cm in length. Trail consists of a medial depression 1 mm in length surrounded by a zone of disturbance which exhibits transverse striations. The entire trail is 3.5 to 4 mm in width. Preserved as a concave epirelief.

b). Remarks

A single specimen was located which is similar to the form-ichnogenus Scolicia. Häntzschel (1975) states that the ichnogenus ranges in age from Cambrian to Recent and shows a wide facies range (commonly found in the Nereites and Cruziana ichnofacies). Although Scolicia encompasses a wide range of morphological variations, it is considered to be the feeding trail of burrowing gastropods (Häntzschel, 1975).

c). Occurrence

A single sample of ? Scolicia was recovered from the Sydenham Road section, associated with a siltstone layer.

iv). Form D: ? Trichophycus
(Pl. 3-12, fig. 4)

a). Description

Straight to gently curved horizontal burrows ornamented with distinct longitudinal striations (Pl. 3-12, fig. 4). Specimens vary from 3 to 4 mm in diameter and display infrequent branching and a circular cross-section. The diameter of the branches is more or less equal to that of the main burrow. Burrow terminations are upturned, giving the impression that the burrow continues diagonally into the substrate. Some specimens display irregularly spaced transverse constrictions. Preserved as convex hyporelief.

b). Remarks

The Thorold specimens are very similar to forms assigned to the ichnogenus Trichophycus by Frey and Chowns (1972, Species A, Pl. 3, C, D, G; Pl. 5I) from the Silurian Red Mountain Formation of Georgia. They point out that although similar, the trace does not closely resemble any previously known species of Tricophycus, hence the tentative assignment.

Trichophycus has been interpreted to be a dwelling or a combined feeding-dwelling burrow of an arthropod, possibly a trilobite (Seilacher and Crimes, 1969) or a polychaete (Osgood, 1970). Häntzschel (1975) states that Trichophycus seems to be restricted to Ordovician strata; however, Silurian samples are known (Frey and Chowns, 1972). Since many samples have been associated with other trilobite ichnogenera, Trichophycus is commonly found in the Cruziana ichnofacies (Frey and Chowns, 1972).

c). Occurrence

A number of fragmentary samples of ?. Trichophycus were recovered from the Jolley Cut, 403, and Sydenham Road sections. Generally associated with fine-grained sandstones and siltstones.

v). Echiuroid Traces

(Pl. 3-12, fig. 1)

a). Description

A number of enigmatic ichnofossils were described by Risk (1973) from the Thorold Sandstone. They are fan-shaped (Pl. 3-12, fig. 1), occurring in an imbricated series radiating from a focal area, in which there is a depression possibly representing a vertical burrow. The resulting fan can be either narrow or full circle, and in places symmetry is developed on either side of the focus (Risk, 1973). The ichnofossils average 5 cm in length and 3 cm in width. X-ray radiography by Risk (1973) revealed definite burrow structures continuing downward from the focus of the fan and penetrations in excess of 6 cm were observed.

b). Remarks

Risk (1973) attributed these ichnofossils to the grazing activities of echiuroids and, if correct, this interpretation would represent the first description of fossil echiuroid feeding traces, and the oldest occurrence of echiuroids in the fossil record. Actual body fossils of echiuroids have now been recently described from the Middle Pennsylvanian Francis Creek Shale, of northeastern Illinois (Jones and Thompson, 1977). The downward trending burrow, at the focus, represents the dwelling (domichnia) burrow of the organism; and the fan-shaped traces represent grazing trails (passichnia) left by a protrusible element (Risk, 1973). This protrusible element was interpreted by Risk (1973) to be a single, unbranched organ, most likely a palp or proboscis. Comparative work pointed out the similarity of the trace to those left by the modern echiuroid Listriolobus pelodes.

Of particular interest is the environmental implication of this ichnofossil, if it is indeed the result of the activities of echiuroids. Although modern echiuroids are found in a wide depth range (intertidal to depths in excess of 10,000 meters), they are exclusively marine organisms which are stenohaline (see Risk, 1973). As such, they are not frequently found in shallow water environments that are subject to periodic freshwater influxes (see Risk, 1973).

c). Occurrence

Several samples of this enigmatic ichnofossil were recorded from the 403, Sydenham Road, and Clappison Corners sections.

Explanation of Plate 3-1

Fig. 1. <u>Arthrophycus</u> sp. from Balls Falls section, scale bar equals 2 cm.

Fig. 2. <u>Arthrophycus</u> sp. from Balls Falls section, displaying distinct interpenetrations and cross-overs. Scale bar equals 1 cm.

Fig. 3. <u>Arthrophycus</u> sp. from Balls Falls section, displaying distinct branching. Note faint longitudinal depression running along the length of some specimens. Scale bar equals 1 cm.

Fig. 4. <u>Arthrophycus</u> sp. S.E.M. micrograph showing distinct lining situated at the burrow wall. Material at the top right of the photograph is found in the burrow, X220.

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2

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4

Explanation of Plate 3-2

Fig. 1. Arenicolites sp. from the Jolley Cut section. Scale bar equals 1 cm.

Fig. 2. Bifungites sp. from the Jolley Cut section. Note similarity to Diplocraterion.

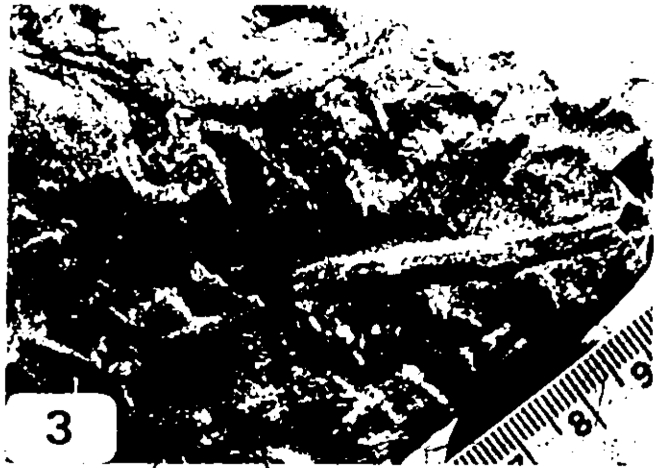
Fig. 3. Cruziana sp. from the 403 section, centimeter scale.

Fig. 4. Cruziana sp. from the 403 section, centimeter scale.

Fig. 5. Cruziana sp. from the Jolley Cut section. Scale bar equals 1 cm.

Fig. 6. Arthrophycus sp. S.E.M. micrograph showing the distinct branching pattern. X50.


1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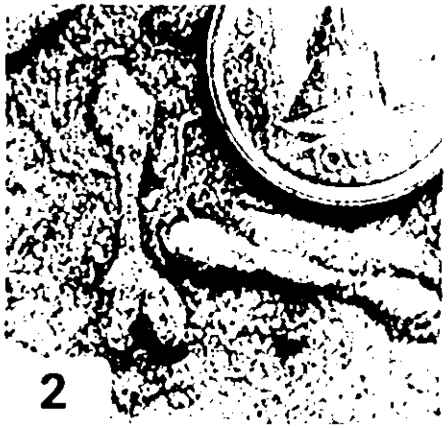
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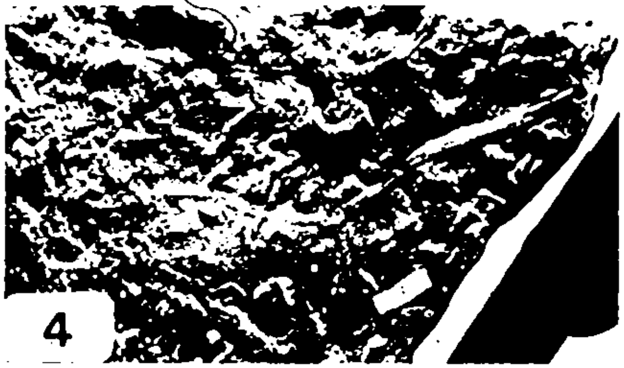
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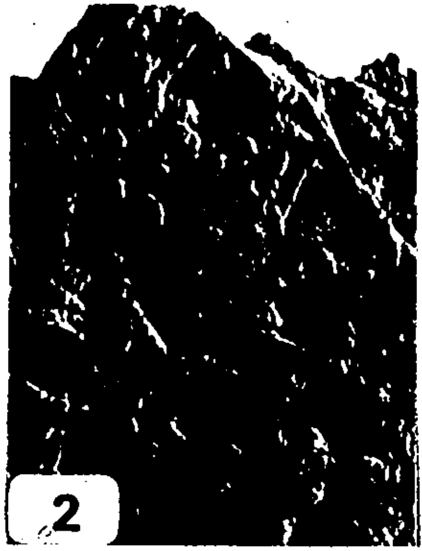
Explanation of Plate 3-3

Fig. 1. Chondrites sp. from the Sydenham Road section, X1.

Figs. 2-4. Diplocraterion sp. (2) from the Jolley Cut section, typical preservation, X1; (3) large burrow termination from the DeCew Falls section, scale bar equals ½ cm; (4) specimens from the Jolley Cut section, note that the specimens display no preferred orientation; scale bar equals 1 cm.

Fig. 5. Fucusopsis sp. from the Jolley Cut section, note distinct longitudinal striations, X2.


1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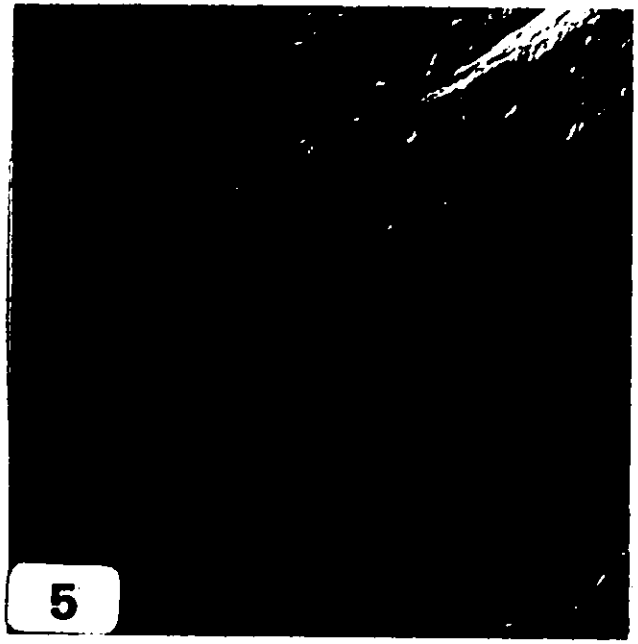
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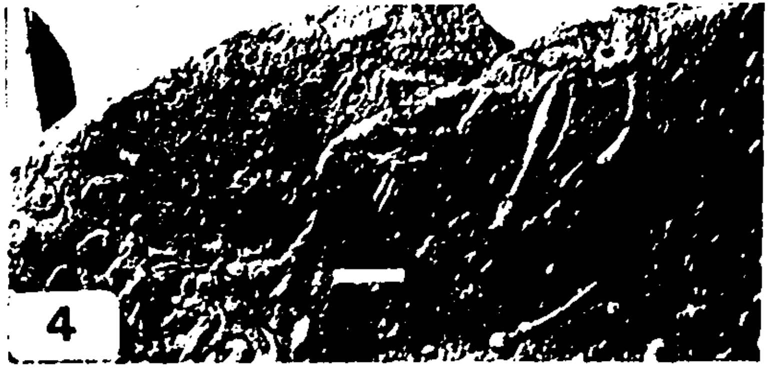
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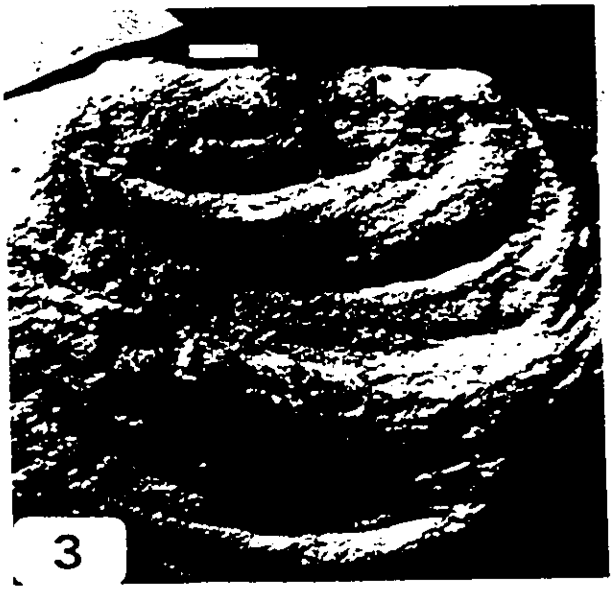
Explanation of Plate 3-4

Figs. 1-4. Daedalus sp. (1) full relief burrow system from the Genesee Gorge section, which represents the final dwelling structure of the organism, x 1; (2) termination of the J-shaped dwelling burrow, from the Genessee Gorge section, x 1; (3) complex blade of spreiten which radiates from the main dwelling burrow, note similarity to Diplocraterion, scale bar equals 1 cm; (4) stacked arrangement of spreiten, from the Medina section, pen for scale.


1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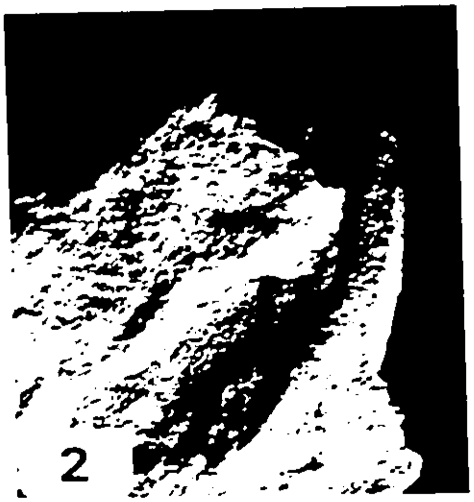
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Explanation of Plate 3-5

Figs. 1-3. <u>Dolopichnus</u> sp. B (1) longitudinal section of two burrows from the DeCew Falls outcrop, lens cap for scale; (2) longitudinal section of burrow from DeCew Falls, note semi-circular termination, lens cap for scale; (3) transverse section of burrows shown in fig. 2, lens cap for scale.

Fig. 4. <u>Dolopichnus</u> sp. A. Transverse section of burrows from the Jolley Cut outcrop, arrow points to central living chamber, scale bar equals 1 cm.


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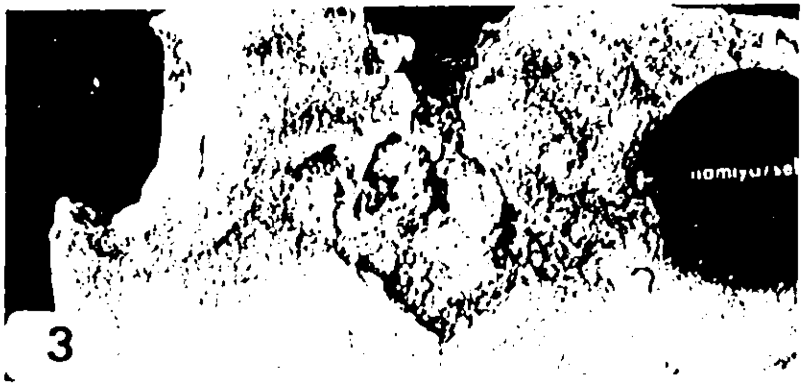
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Explanation of Plate 3-6

Figs. 1-3. *Lobichnus* sp. (1) from the Jolley cut section, note similarity to inorganic rill marks, scale bar equals 1 cm; (2) from the Jolley Cut section, note large central shaft which seems to terminate at what appears to be a vertical opening, scale bar equals ½ cm; (3) plan view of burrow system which may be inorganic, scale bar equals ½ cm.

Fig. 4. ? *Scolicia* sp. horizontal, trilobed trail from the Sydenham Road section, scale bar equals ½ cm.


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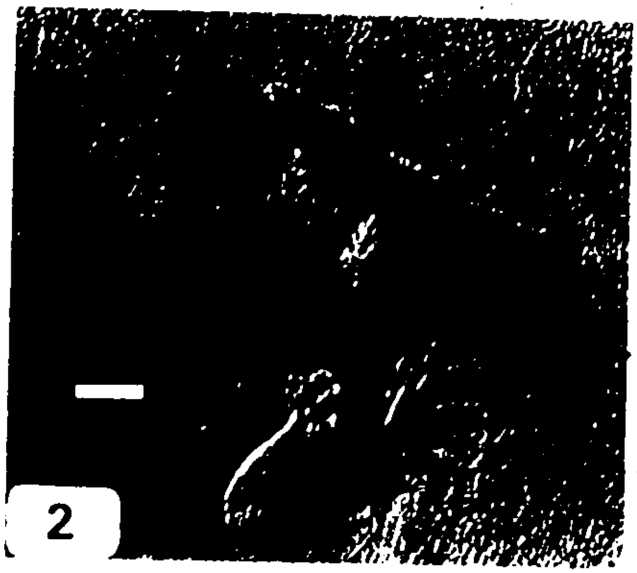
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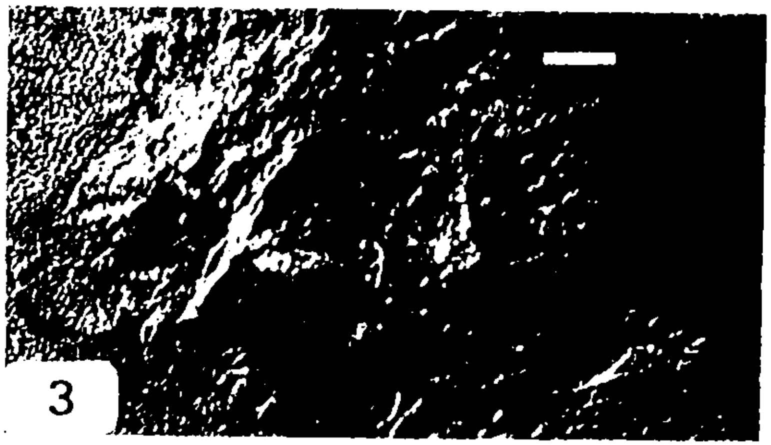
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Explanation of Plate 3-7

Fig. 1. *Incisifex* sp. long horizontal trackway from the 403 section, scale bar equals 2 cm.

Figs. 2-3. *Lingula clintoni*. (2) *in situ* specimen of *L. clintoni* from the Jolley Cut section, scale bar equals ½ cm; (3) numerous shells of *L. clintoni* from the Jolley Cut section, note that the shells are well-preserved and intact, scale bar equals 1 cm.

Fig. 4. *Lingulichnus* sp. from the Jolley Cut section, note the distinctive bi-symmetrical shape of the burrow, transverse view, X 1 .

Fig. 5. *Monomorphichnus* sp. from the 403 section, X 1.


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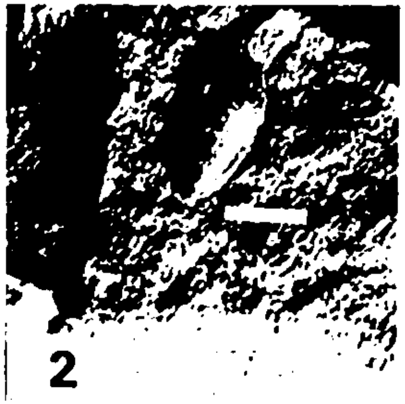
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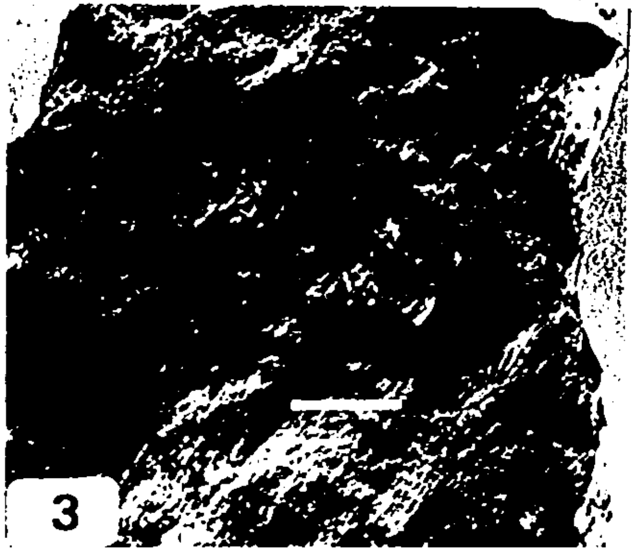
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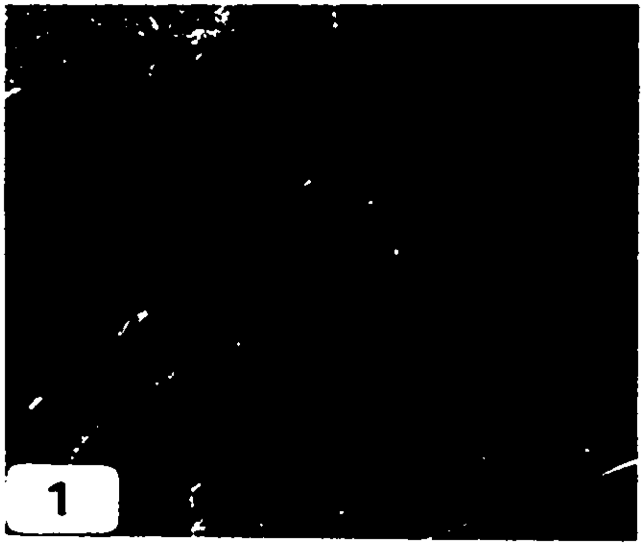
Explanation of Plate 3-8

Figs. 1-2. Planolites sp. (1) specimen from the 403 section showing frequent cross-overs, cm scale; (2) straight to slightly sinuous sample from the Sydenham Road section, cm scale.

Figs. 3-4. Rusophycus sp. (3) small specimen from Clappison Corner section, cm scale; (4) well-developed specimen from Sydenham Road section, x 1.

Fig. 5. Rhabdoglyphus sp. from the Jolley Cut Road section, note distinct invaginated calyces, cm scale (specimen courtesy of D. Kobluk).



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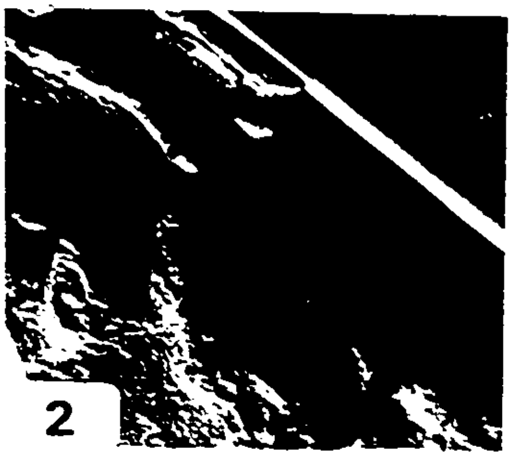

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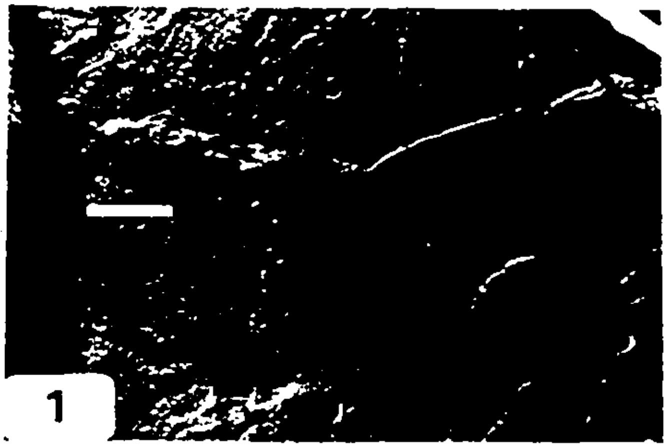
Explanation of Plate 3-9

Figs. 1-3. Palaeophycus sp. (1) well developed specimen from Sydenham Road section displaying frequent branchings, transverse view, scale bar equals 1 cm; (2) straight specimen from 403 section displaying collapsed structure, transverse view, scale bar equals 3 cm; (3) numerous straight to arcuate specimens displaying branching, from the Jolley Cut section, scale bar equals 1 cm.

Fig. 4. Planolites sp. strongly curved specimen from Clappison Corner section, scale bar equals 1 cm.

Figs. 5-6. Skolithos sp. from the Jolley Cut section; (5) longitudinal view showing open burrow, scale bar equals ½ cm; (6) infilled specimen, x 2.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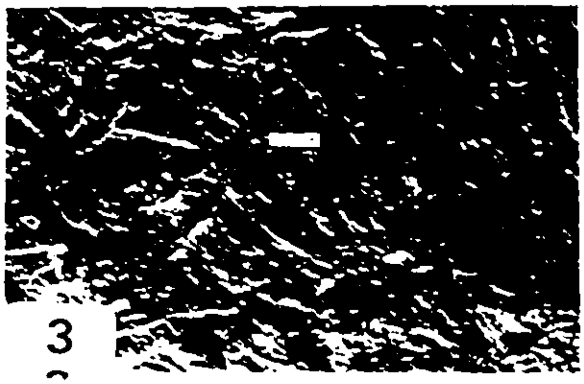
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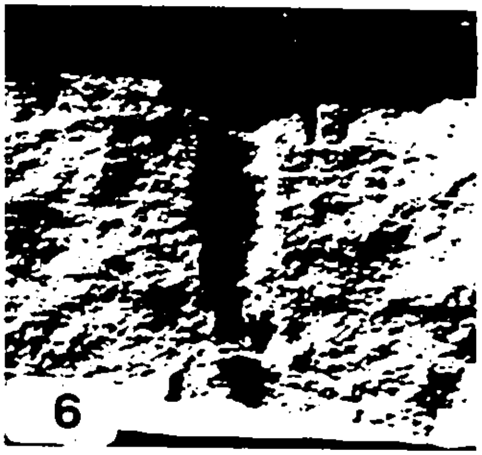
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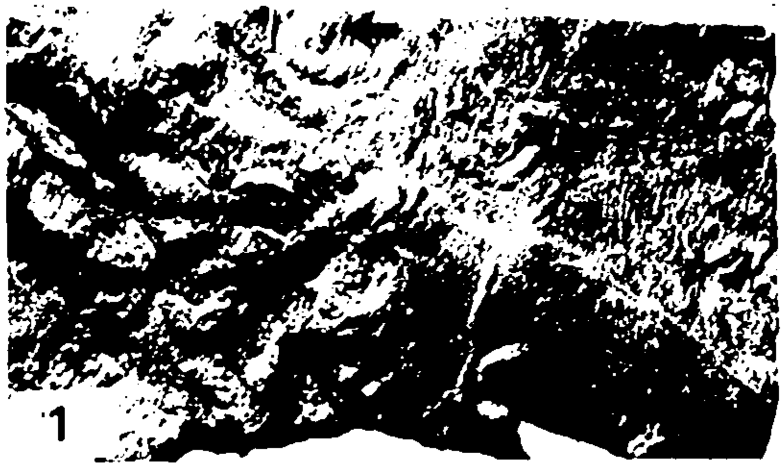
Explanation of Plate 3-10

Figs. 1-3. _Polycylindrichnus_ sp. (1) transverse view showing burrow aperture, arrow points to concentric nature of the infill, x 2 ; (2) longitudinal view showing the nature of the branching, x 2; (3) longitudinal view of one branch, note the similarity to _Cylindrichnus_, x 2. All specimens from the Jolley Cut section.

Figs. 4-5. _Skolithos_ sp. (4) S.E.M. micrograph of preserved lining x 200; (5) inclined specimen from the Sydenham Road cut, scale bar equals ½ cm.



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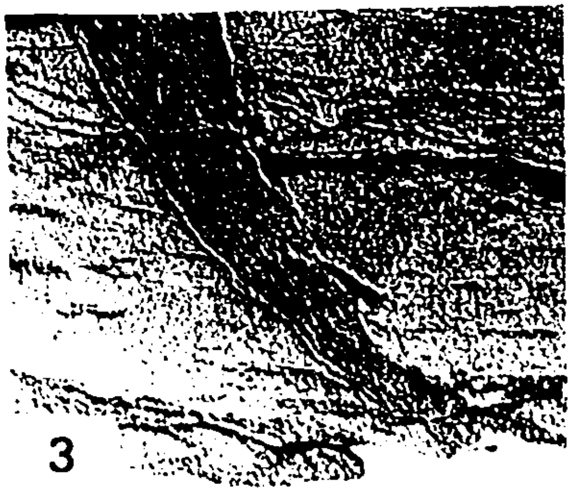

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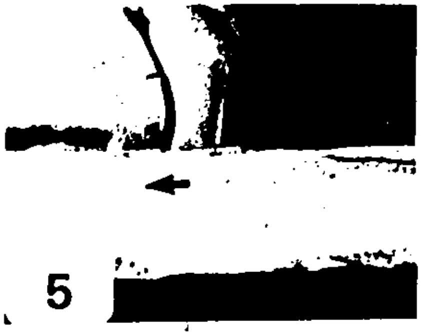

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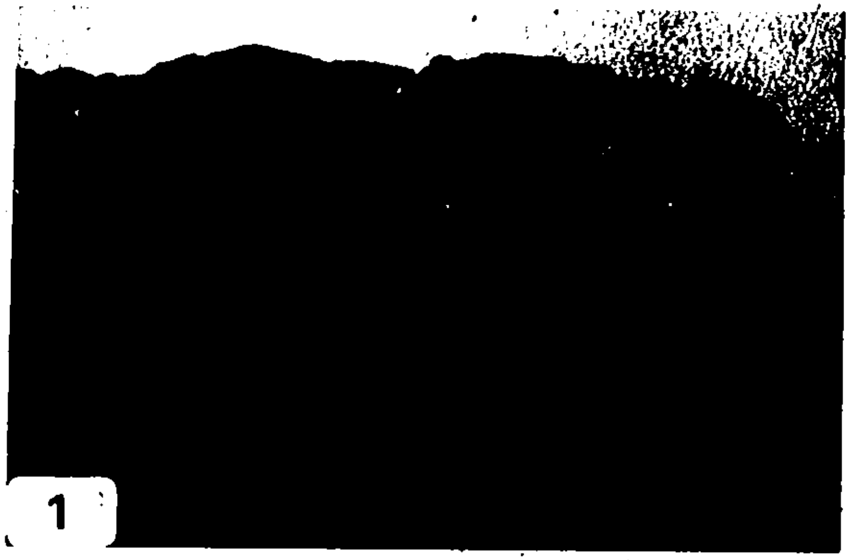
Explanation of Plate 3-11

Figs. 1-3. Teichichnus sp. (1) cut section of specimen showing the alignment of grains, x 2, (photo courtesy of D. Craig); (2) full relief specimen from the Jolley Cut section, x .75, (photo courtesy of D. Craig); (3) plan view of bedding plane specimen, note the well-developed spreiten structure, from the Sydenham Road section, scale bar equals 1 cm.

Fig. 4. Scalarituba sp. from the Sydenham Road section, scale bar equals 1 cm.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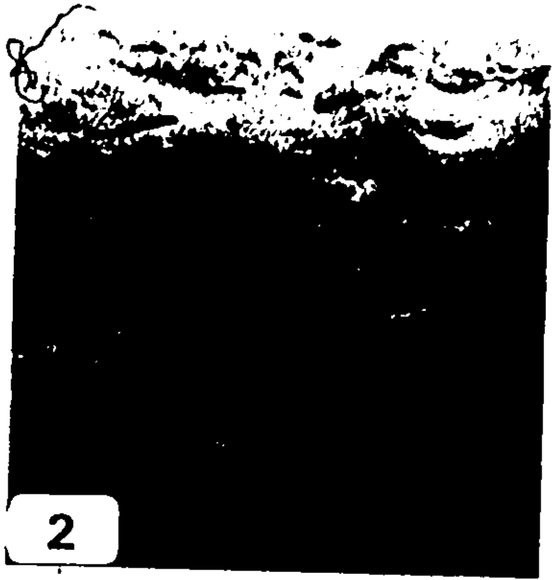
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Explanation of Plate 3-12

Fig. 1. Echiuroid feeding trace, from Sydenham Road section, probable burrows are located at apex of fan-shaped trace (courtesy of Dr. M. Risk). Scale bar equals 1 cm.

Fig. 2. Feeding trace of *Listriolobus pelodes* (courtesy of Dr. M. Risk). Scale bar equals 1 cm.

Fig. 3. ? *Caprionichnus* sp. from the Sydenham Road section, dime for scale.

Fig. 4. ? *Trichophycus* sp. from the Sydenham Road section, note the distinct horizontal striations, x 2.

Fig. 5. ? *Gordia* sp. from the Sydenham Road section, note cross-overs, scale bar equals 1 cm.


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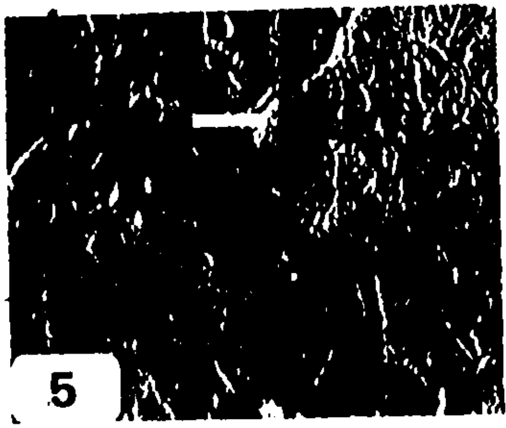
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CHAPTER 4

Thorold Ichnofossil Distributions

4-1. The Thorold Ichnofossil Suite

The Thorold Sandstone exhibits a varied and dense ichnofossil assemblage which is indicative of both soft-bodied and shelled organisms that are not represented (in most cases) by actual body remains. Although highly problematical each ichnogenus can be attributed to a particular animal group and ethological category (Table 4-1). Analysis of these data indicates that far from being the unfossiliferous unit as previously thought, the Thorold Sandstone contains structures resulting from the activities of tribolites, ?coelenterates, ?gastropods, ?arthropods, inarticulate brachiopods, and annelids (or other similar worm-like groups).

These ichnofossils represent a number of different ethological groups and can be classified according to Seilacher's (1953a) behavioural scheme as dwelling burrows (domichnia), feeding burrows (fodinichnia), grazing traces (passichnia), crawling traces (repichnia), and resting traces (cubichnia). Furthermore, different feeding strategies can also be differentiated. The Thorold ichnocoenoses contains structures representing filter-feeders, deposit feeders, and carnivores (see Table 4-1).

Table 4-1. Classification of Thorold ichnofossils according to probable originator, ethological group and trophic level.

Animal	Interpretation	Trophic Group*	Ichnogenus
Trilobites	Furrow		Cruziana
	Walking track		Diplichnites
	Swimming trace		Monomorphichnus
	Resting excavation		Rusophycus
Coelenterates	Dwelling/Feeding excavation	Carnivore?	Dolopichnus
Molluscs	Grazing burrow	Carnivore? Deposit-feeder?	?Scolicia
Annelids or similar "worm-like" organisms	Dwelling burrow	Filter-feeder	Arenicolites
	Dwelling burrow	Filter-feeder?	Bifungites
	Dwelling burrow	Filter-feeder	Diplocraterion
	Dwelling burrow	Filter-feeder	Skolithos
	Dwelling burrow	Filter-feeder/Carnivore	Polycylindrichnus
	Feeding burrow	Deposit-feeder	Arthrophycus
	Feeding burrow	Deposit-feeder	Chondrites
	Feeding burrow	Deposit-feeder	Fucusopsis

Table 4-1 continued.

	Grazing burrow	Deposit-feeder	*Lobichnus*
	?Feeding burrow	Deposit-feeder	*Planolites*
	Feeding burrow	Deposit-feeder	*Rhabdoglyphus*
	Grazing burrow	Deposit-feeder	*Scalarituba*
	Feeding burrow	Deposit-feeder	*?Trichophycus*
	Feeding burrow	Deposit-feeder	*Teichichnus*
	Feeding burrow	Deposit-feeder	*?Gordia*
	Feeding burrow	Deposit-feeder	*?Caprionichnus*
	Grazing burrow	Deposit-feeder	Echiuroid trace
	?Feeding burrow	Deposit-feeder	*Daedalus*
	?Feeding burrow	Carnivore?	*Palaeophycus*
Brachiopod	Dwelling burrow	Filter-feeder	*Lingulichnus*
Arthropod	Walking track	?	*Incisifex*

---

* Trophic group designation very tenuous, see Chapter 3 and contained references for individual ichnogenus interpretations and trophic level determinations.

Such information is extremely valuable in the interpretation of the variations in the distribution of specific ichnogenera and ichnofossil assemblages. Since ichnofossils are inherently linked to the physical properties of the sediment any distributional change in them will ultimately correspond to fluctuations in the physical characteristics of the depositional regime.

4-2. Distribution of Thorold Ichnofossils

A). Regional distribution

Ichnofossils were encountered in virtually every Thorold outcrop studied, with the exception of the Niagara Glenn section (N.G.). Table 4-2 summarizes the occurrence of specific ichnogenera in each outcrop investigated and indicates their relative abundances. Only specimens which could be reliably identified were recorded and their abundance was estimated in respect to the entire ichnocoenoses encountered at any one outcrop. For example, at the Vinemount section (Vn), the most abundant ichnogenus was Skolithos; Arthrophycus and Planolites were commonly encountered, and Palaeophycus was rarely recorded. Analysis of Table 4-2 indicates that of the ichnogenera identified, the majority of them were found in the Hamilton, Ontario area (sections Fr, Mb, J.C. and 403). Reasons for this apparent bias will be more closely examined in a subsequent section of this chapter.

Table 4-2. Ichnofossil occurrence in the Thorold Sandstone; A = abundant, C = common, R = rare.

	X	G	U	K	O	R	NG	A	RC	BF	GB	WR	Vn	Fc	Sc	20	AF	FR	MB	JC	403	WF	SR	RF	CC
<u>Arenicolites</u>										?						?			C	C					
<u>Arthrophycus</u>	A	A	A	A	A	C		C	C	C		C	C					?		?					
<u>Bifungites</u>																				R					
<u>Chondrites</u>												R		R		C	C	C	C	C	C	C	C	C	C
<u>Cruziana</u>																		C		C	C	C	C	C	C
<u>Daedalus</u>	A	A	A	A		A		C	C	C								?	?	?					
<u>Diplichnites</u>																				R	R		R		R
<u>Diplocraterion</u>								C				C						A	A	A					R
<u>Dolopichnus</u> Sp. A																				C					
<u>Dolopichnus</u> Sp. B								C																	
<u>Fucusopsis</u>																				R					
<u>Incisifex</u>																				R	R				
<u>Lingulichnus</u>																				C					
<u>Lobichnus</u>										C		C								R					

Table 4-2 continued.

	X	G	U	K	O	R	NG	A	RC	BF	GB	WR	Vn	Fc	Sc	20	AF	FR	MB	JC	403	WF	SR	RF	CC
Monomorphichnus																				R	R		R		R
Palaeophycus	R		R						R	R	R	R	R	R	C			C	C	C	C	C	C	C	C
Planolites	R	R	R	R	R	R		R	R	R	R	R	C	C	C	C	C	C	C	A	C	C	C	C	C
Polycylindrichnus																				R					
Rhabdoglyphus																				R					
Rusophycus																		C		C	C	C	C	C	C
Scalarituba																					R		C		C
Skolithos								C	C	C	C	A	A	A	A	A	A	A	A	A	C	C	C	C	C
Teichichnus																				R	R		C		C
Echiuroid trace																					R		R		R
?Gordia																					R		R	R	
?Caprionichnus																							R		
?Scolicia																							R		
?Trichophycus																				R	R		C		

B). Local distribution

Examination of Table 4-2, on the distribution of ichnogenera in the Thorold Sandstone, reveals that four distinct trace fossil suites can be distinguished. These assemblages are differentiated not only on the ichnogenera contained but also on their relative abundances (see Table 4-3).

Assemblage one was encountered in all of the New York State sections examined and consists of abundant specimens of Arthrophycus and Daedalus. In addition, a few rare samples of rather non-descript Palaeophycus and Planolites were also observed.

Assemblage two was recorded in outcrops extending westwards from DeCew Falls to Albion Falls. It consists of: abundant to common Skolithos; common Arthrophycus, Arenicolites, Daedalus, Diplocraterion, Dolopichnus sp. B, and Lobichnus; and common to rare Chondrites, Palaeophycus, and Planolites.

Assemblage three was encountered in the outcrops of the Hamilton, Ontario from the Flock Road section westwards to the Jolley Cut section. An extremely diverse ichnofossil suite was recorded from this area and consists of: abundant Skolithos and Diplocraterion; abundant to common Planolites; common Arenicolites, Chondrites, Cruziana, Dolopichnus sp. A. Lingulichnus, Palaeophycus and Rusophycus; and rare

Table 4-3. Synopsis of the four general ichnofossil assemblages recognized in the Thorold Sandstone.

Relative Abundance	Ichnofossil	
Assemblage I:	New York sections	
Abundant	*Arthrophycus*	
	Daedalus	
Rare	*Palaeophycus*	
	Planolites	
Assemblage 2:	DeCew Falls to Albion Falls	
Common to Abundant	*Skolithos*	
Common	*Arthrophycus*	*Lobichnus*
	Daedalus	*Diplocraterion*
	Arenicolites	*Dolopichnus* Sp. B
Common to Rare	*Chondrites*	*Planolites*
	Palaeophycus	
Assemblage 3:	Flock Road to Jolley Cut	
Abundant	*Diplocraterion*	
	Skolithos	
Abundant to Common	*Planolites*	
Common	*Arenicolites*	*Dolopichnus* Sp. A
	Chondrites	*Lingulichnus*
	Cruziana	*Palaeophycus*
	Rusophycus	
Rare	*Bifungites*	*Polycylindrichnus*
	Diplichnites	*Rhabdoglyphus*
	Fucusopsis	*Scalarituba*
	Incisifex	*Teichichnus*
	Lobichnus	? *Gordia*
	Monomorphichnus	

Table 4-3 -- Continued

Assemblage 4:	403 to Clappisons Corners Cut	
Common	*Chondrites*	*Rusophycus*
	Cruziana	*Scalarituba*
	Palaeophycus	*Skolithos*
Common to Rare	? *Trichophycus*	
Rare	*Diplichnites*	Echiuroid trace
	Diplocraterion	? *Caprionichnus*
	Monomorphichnus	? *Scolicia*
	? *Gordia*	

Bifungites, Diplichnites, Fucusopsis, Incisifex, Lobichnus, Monomorphichnus, Polycylindrichnus, Rhabdoglyphus, Scalarituba, Teichichnus, and ? Gordia.

The final suite, assemblage four, was encountered in outcrops west of Hamilton, Ontario from the 403 section westwards to the Clappison Corners section. It consists of: common Chondrites, Cruziana, Palaeophycus, Planolites, Rusophycus, Scalarituba, and Teichichnus; common to rare ? Trichophycus; and rare Diplichnites, Diplocraterion, Monomorphichnus, echiuroid traces, ? Caprionichnus, ? Gordia, and ? Scolicia.

C). Problems associated with ichnofossil distributions

As previously noted, there exists a noticeable discrepancy in the distribution of ichnofossils in the Thorold, in that the majority of the identified ichnogenera are from outcrops of the Hamilton, Ontario area. Although such a pattern is probably a true reflection of the distribution of trace-making organisms, a number of inherent difficulties are associated with ichnofossil collecting which may introduce a bias in their observed distributions. These problems are prevalent in the Thorold and warrant some mention.

1). Trace fossils are essentially interfacial structures and as such their recognition depends greatly on outcrop extent and physiography. Large outcrops with extensive, exposed bedding planes are much more likely to yield observable traces than are small, vertical exposures. In the Thorold, the Hamilton area outcrops are better exposed and much more extensive than in any other area. In fact, a number of the Thorold outcrops are very small, overgrown with vegetation, and lack horizontal exposures. As a result, trace fossil collecting in these areas is somewhat hampered.

2). In Ontario, outcrops of the Thorold are generally associated with the Niagara Escarpement and in some cases (the Balls Falls, Websters Falls, and Rock Chapel Falls sections) are quite inaccessible. Therefore, ichnofossil collecting is limited to dislodged float blocks which although may contain some specimens may not truly represent the entire assemblage. In addition, such outcrops do not allow, in some cases, for any stratigraphic placement of the samples.

3). A problem repeatedly encountered in the Thorold Sandstone involved the number of laterally-discontinuous beds. As a result, little stratigraphic control could be maintained both in a vertical and horizontal sense.

These problems, although present, did not seem to greatly affect the recognition of ichnofossils in this study. As with any branch of geology, one can not be entirely certain that every identifiable structure was encountered.

4-3. The Concept of Ichnofacies and Bathymetry

One of the major themes in paleontology is that organisms display a complex community structure (Walker, 1972). These body fossil communities are delineated by specific environmental constraints (Ziegler, et al., 1968), and tend to recur through time (Bretsky, 1969). Similarly, ichnofossils have also been observed to form characteristic associations which also repeat through much of geologic time. However, ichnofossil associations are unique in that trace fossils are insensitive indicators of animal speciation and thus recur through much longer periods of time than do body fossils (Seilacher, 1964a; Frey, 1975; Frey and Seilacher, in press).

Frey and Seilacher (in press) have stated that the strength of recurrence in ichnology is the fact that ichnofossils represent animal behaviour. Elders (1975) indicated that this behaviour, like the morphology of body parts, is subject to convergent evolution as dictated by particular modes of life and environmental requirements. In this way, identical structures, for example funnel-feeding burrows, have been utilized by a variety of morphologically different organisms (the lugworm Arenicola, the holothurian Leptosynapta, and the enteropneust Balanoglossus). Therefore, specific ichnofossils, although created by a variety of organisms, have extremely long-time ranges (Seilacher, 1977a).

This concept of recurring ichnofossil associations was first introduced by Seilacher (1964a). Originally, six different associations were established: the _Scoyenia_ ichnofacies; the _Glossifungites_ ichnofacies; the _Skolithos_ ichnofacies; the _Cruziana_ ichnofacies; the _Zoophycos_ ichnofacies; and the _Nereites_ ichnofacies. As with any new classificational scheme, a number of additional associations have been subsequently proposed. Chamberlain (1971a) proposed the erection of a _Chondrites_ ichnofacies which would occupy a position between _Zoophycos_ and _Cruziana_ associations and would be indicative of bathyal, upper slope environments. Although such a division may be warranted in the Carboniferous Ouachita succession of Oklahoma described by Chamberlain (1971a), _Chondrites_ is not so restricted in other deposits. It has been found to be indicative of a wide variety of environments ranging from tidal flats to deep-sea basins (Frey and Chowns, 1972; Chamberlain, 1978). Similarly, Ekdale (1977, 1978) and Ekdale and Berger (1978), studying the traces in deep-sea cores, have proposed a _Chondrites_-_Planolites_-_Zoophycos_ ichnofacies which would characterize such bathyal environments. Again all three of these ichnogenera are known from a wide variety of shallow and deep water deposits (Chamberlain, 1978) and any depth determinations based on them would be highly tenuous. The only subsequently proposed ichnofacies which warrants definition is the Trypanites ichnofacies recently erected by Frey and Seilacher (in press). It characterizes consolidated marine littoral and sublittoral omission surfaces which are widespread in the rock record. The ichnogenus Trypanites was chosen as the name-bearer because it is easily identified and widespread in hard substrates from the Cambrian to the Holocene (Warme, 1975; Kobluk, et al., 1978). Table 4-4 summarizes the characteristics and environmental implications of these seven ichnofacies.

In perhaps the most cited paper in ichnological literature Seilacher (1967a) stated that in marine environments the parameters which govern the abundance and distribution of tracemakers (i.e., temperature, food supply, agitation) tend to change progressively with water depth. As a result, a relative scale of bathymetry was established (fig. 4-1). It was in this context that ichnofossil research progressed. They were often viewed as an absolute indicator of water depth and a search for unique indicators was mounted. This more or less simplistic concept, although a valuable tool, was used to excess and gross generalizations began to appear in the literature. Ichnologists, as well as investigators in other branches of geology, perhaps looking for exact indicators, often mis-interpreted Seilacher's original concept and a definite bias was

Table 4-4. Recurring aquatic trace fossil assemblages and their environmental implications.

(The Scoyenia ichnofacies is distinguished on the basis of salinity; the Trypanites, Glossifungites, and Skolithos ichnofacies are differentiated from one another by substrate consistency, and from the Cruziana, Zoophycos, and Nereites ichnofacies by bathymetry -- or at least by variables which typically are depth-related). (Adapted from Seilacher, 1967a; Frey, 1975.) (After Frey and Seilacher, in press.)

Characteristic Trace Fossils	Typical benthic environment*
	Scoyenia ichnofacies
Vertebrate tracks, trails, and burrows, mainly of aquatic or semi-aquatic species but also of terrestrial species coming to water; insect and other arthropod traces; certain forms of Isopodichnus and Planolites; scattered snail and clam crawling traces and shallow burrows. Local diversity, abundance and complexity	Nonmarine clastics, especially continental "red beds," floodplain deposits, and similar lotic and lentic environments (Trewin, 1976). Lebensspuren of deep lakes may exhibit bathymetric zonations comparable to those of marine environments (Chamberlain, 1975b, Fig. 19.9); perhaps these traces should be grouped

Table 4-4 -- Continued

generally less than in marine or nearshore environments.	as a separate ichnofacies as yet unnamed.
Trypanites ichnofacies** (hard substrates)	
Cylindrical to vase-, tear- or U-shaped to irregular domiciles of endolithos, oriented normal to substrate surfaces, or shallow anastomosing systems of borings (sponges, bryozoans); excavated mainly by suspension feeders or "passive" carnivores. Raspings and gnawings of algal grazers, etc. (chitons, limpets, echinoids). Diversity generally low, although borings or scrapings of given kinds may be abundant.	Consolidated marine littoral and sublittoral omission surfaces (rocky coasts, beachrock, hardgrounds) or organic substrates (wood, shell, bone). Bioerosion is as important as, and indeed accelerates, physical erosion of the substrate (Warme, 1975; Bromley, 1978). Intergradational with the *Glossifungites* ichnofacies.
Glossifungites ichnofacies (firm substrates)	
Vertical cylindrical, U-shaped, or sparsely	Firm but unlithified marine littoral and

Table 4-4 -- Continued

ramified dwelling burrows; protrusive spreiten in some, developed mostly through growth of animals. Fan-shaped *Rhizocorallium*. Many intertidal species (e.g., crabs) leave the burrows to feed; others are mainly suspension feeders. Diversity typically low, but given kinds of burrows, may be abundant.	sublittoral omission surfaces, or stable, coherent substrates either in protected, low-energy settings (salt marshes) or in areas of somewhat higher energy, where semiconsolidated substrates offer resistance to erosion (Frey and Howard, 1969, Pl. 4, fig. 3).
Skolithos ichnofacies (shifting substrates)	
Vertical cylindrical or U-shaped dwelling burrows; protrusive and retrusive spreiten in some, developed mainly in response to substrate aggradation or degradation (escape structures); forms of *Ophiomorpha* consisting predominantly of vertical or steeply inclined	Littoral to infralittoral, relatively high-energy conditions; clean, well-sorted, shifting sediments, subject to abrupt erosion or deposition. (Higher energy increases physical reworking and obliterates biogenic sedimentary structures, leaving a preserved

Table 4-4 -- Continued

shafts. Animals chiefly suspension feeders. Diversity is low, yet given burrows may be abundant.	record of physical stratification; (Rhoads, 1975, Fig. 9.8; Howard, 1975).
Cruziana ichnofacies	
Abundant crawling traces, both epi- and intrastratal; inclined U-shaped burrows having mostly protrusive spreiten (feeding swaths; soft-sediment *Rhizocorallium*); forms of *Ophiomorpha* and *Thalassinoides* consisting of irregularly inclined to horizontal components; scattered vertical cylindrical burrows. Animals include mobile carnivores and both suspension and deposit feeders. Diversity and abundance generally high.	Infralittoral to shallow circalittoral substrates, below daily wave base but not storm wave base, to somewhat quieter offshore-type conditions; moderate to relatively low energy; well-sorted silts and sands, to interbedded muddy and clean sands; appreciable but not necessarily rapid sedimentation. A very common type of depositional environment, including estuaries, bays, and lagoons as well as continental shelves or epeiric slopes.

Table 4-4 -- Continued

Zoophycos ichnofacies

Relatively simple to moderately complex, efficiently executed grazing traces and shallow feeding structures; spreiten typically planar to gently inclined, distributed in delicate sheets, ribbons, or spirals ("flattened" forms of *Zoophycos* or, in pelitic sediments, *Phycosiphon*). Animals virtually all deposit feeders. Low diversity; given structures may be abundant.	Circalittoral to bathyal, quiet-water conditions; nearly thixotropic muds or muddy sands rich in organic matter but somewhat deficient in oxygen, below storm wave base to fairly deep water, in areas free of turbidity flows or significant bottom current. Watery surficial sediments are difficult to exploit by epibenthos, resulting in both low diversity and abundance and poor preservation of epistratal traces (*cf*. Frey, 1970). Where relict or palimpest substrates are present, especially if swept by shelf-edge or deeper water contour currents, this ichnofacies may be omitted

Table 4-4 -- Continued

	in the transition from infralittoral to abyssal environments.
Nereites ichnofacies	
Complex grazing traces and patterned feeding-dwelling structures, reflecting highly organized, efficient behavior; spreiten structures typically nearly planar, although *Zoophycos* forms are spiraled, multilobed, or otherwise very complex. Numerous crawling-grazing traces and sinuous fecal castings (*Neonereites*, *Helminthoida*, *Cosmorhaphe*), mostly intrastratal. Animals chiefly deposit feeders or "scavengers," although many may have "farmed" microbe cultures within their more or less permanent, open domiciles (*Paleodictyon*;	Bathyal to abyssal, mostly quiet but oxygenated waters, in places interrupted by intermittent turbidity flows (flysch deposits); or highly stable, very slowly accreting substrates (Hollister, *et al.*, 1978). In flysch or flysch-like deposits, pelagic muds typically are bounded above and below by turbidites. In more distal regions, the record is mainly one of continuous deposition and bioturbation. (The stable deep-sea floor is not universally bioturbated, however, at least not

Table 4-4 -- Continued

Seilacher, 1977b). Diversity and abundance significant in flysch deposits, less so in more distal regions.	equally intensively at every site).

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[*] Marine bathymetric zones indicated here are those reiterated by Ager (1963, fig. 2.3).

[**] The genus *Trypanites* is chosen as name-bearer for this ichnofacies because it is easily identified and is widespread in hard substrates from Cambrian to Holocene (Warme, 1975; Kobluk *et al*., 1978).

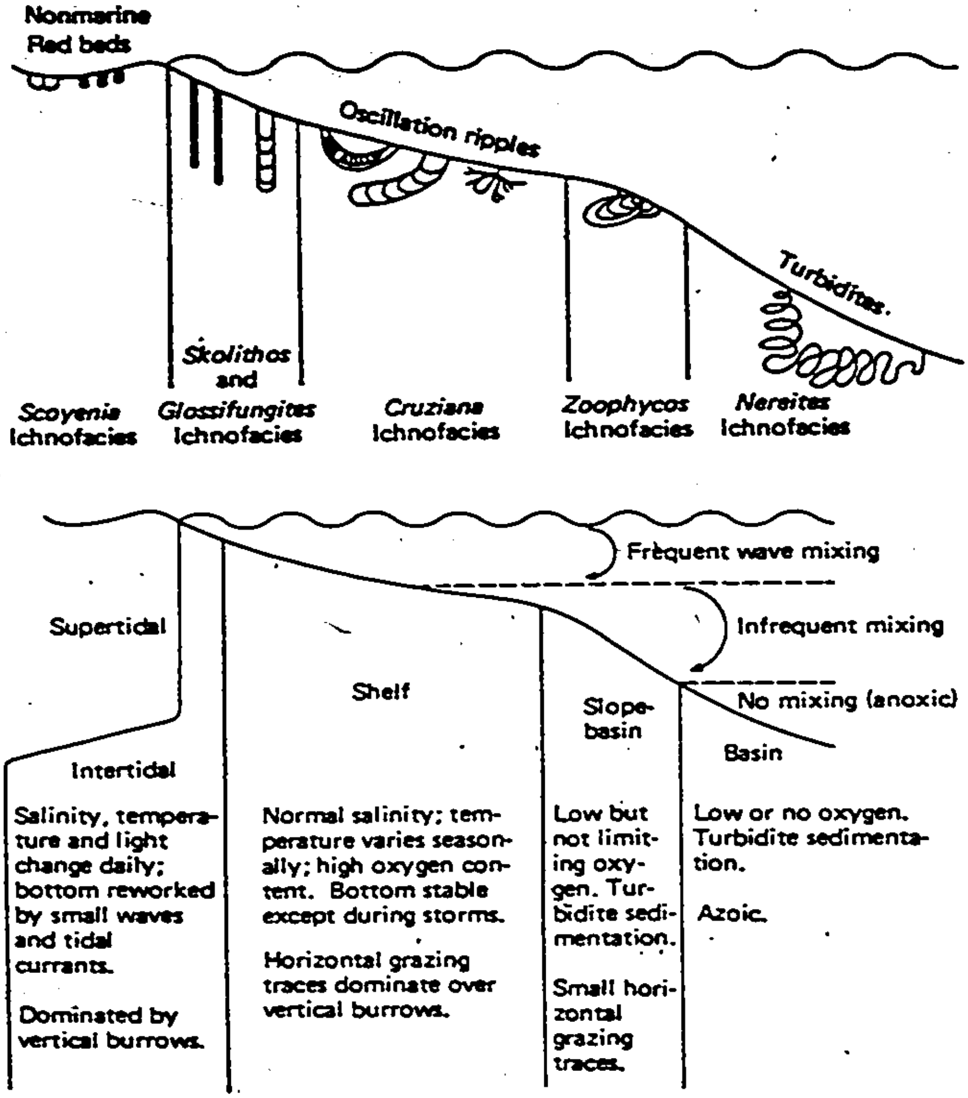


Fig. 4-1. Cross section of geosynclinal shelf and basin, showing: (Top) trace fossil assemblages (after Seilacher, 1967a); and (Bottom) gradients in important ecological parameters (after Rhoads, 1975).

introduced into the interpretation of ichnofossil distributions. This bias infers that when a specific ichnogenera was encountered in the rock record, an exact depth determination could be made.

One of the first ichnofossils used as a unique depth indicator was Ophiomorpha. Weimer and Hoyt (1964) concluded that the decapod crustacean Callianassa major was the probable originator of the Ophiomorpha burrow, and since Callianassa major was restricted to the shallow water shoreface facies, it could be used as a shoreline indicator. Subsequent studies reinforced this notion, and Ophiomorpha, as well as the closely related ichnogenus Thalassinoides, were viewed as strictly shallow water forms (Farrow, 1966; Kennedy, et al., 1969; Sellwood, 1971; Pickett, et al., 1971; among others). Kern and Warme (1974), however, discovered numerous specimens of both Ophiomorpha and Thalassinoides in the Upper Cretaceous Point Loma Formation of California, which was deposited in the bathyal environment. Additionally, they pointed out that modern callianassids have been recovered from water depths in excess of 600 m (Schmitt, 1921; Biffer, 1971). Frey, et al. (1978) also indicated that other analogs of the Ophiomorpha and Thalassinoides structures exist and include several additional species of Callianassa and Upogebia (Bromley and Frey, 1974; Frey, et al., 1978) and Axius (Pemberton *et al*, 1976). These organisms are not restricted to the shoreline facies but are found at nearly all depths (see discussion in Frey, *et al*., 1978). More recently, Stewart (1978) has discovered *Ophiomorpha* in the marsh facies of the Lower Cretaceous Wealdon Marls of the Isle of Wright, which indicates that it may not even be restricted to marine deposits. Bromley and Frey (1974) and Chamberlain (1975b) illustrate that similar pellet-lined burrows are created by fresh-water crayfish. It seems evident therefore that the ichnogenus *Ophiomorpha* was produced by a variety of different organisms in response to specific environmental energy levels and sedimentary properties which may or may not be depth-related (Stewart, 1978).

There exists in the trace fossil literature many more examples of ichnogenera which were once thought to be depth-restricted. The common ichnogenus *Zoophycus* was considered to be restricted to intermediate off-shore depths until Osgood and Szmuc (1972) discovered numerous specimens in the shallow-water facies of the Lower Mississippian Cuyahoga Formation of Ohio. Spiral burrows, once thought to be found exclusively in the abyssal *Nereites* ichnofacies, are known from recent intertidal fine sands (Roder, 1971; Risk and Tunnicliffe, 1978). *Skolithos*, a vertical dwelling burrow, was often used as a shallow-water indicator, but it has recently been described from deep-water canyon (Hayward, 1976), submarine fan (Crimes, 1977), and even abyssal environments (Ekdale, 1977, 1978; Ekdale and Berger, 1978).

This problem of depth indication also manifests itself when dealing with assemblages of ichnofossils. Hayward (1976), studying the Lower Miocene Waitakere Group of Northland, New Zealand, discovered a predominantly shallow-water ichnofossil suite consisting of *Skolithos*, *Planolites*, *Scalarituba*, and *Thalassinoides* in rocks deposited in a mid-bathyal (3000 m) canyon floor environment. Crimes (1977) described a mixed ichnofossil assemblage consisting of deep-water forms and shallow-water forms (*Arenicolites*, *Diplocraterion*, *Ophiomorpha*, *Pelecypodichnus*, *Skolithos*, and *Thalassinoides*) in Eocene deep-sea fan deposits from Northern Spain. Such wholesale displacements of entire ichnofossil assemblages, although presently rare, illustrates an important underlying theme in ichnology, in that ichnofossils reflect an animal's behavioural response to specific environmental conditions. In this way, it would not be unusual to find predominantly shallow-water ichnofossils in deep-water habitats if deposition occurred under conditions otherwise similar to those preferred by the trace-making organisms (Frey, 1971). For example, Crimes (1977) indicated that the middle fan environment consisted of fast-flowing sand-laden currents, sandy substrates, high oxygen levels, and a slow build-up of organic detritus; conditions very similar to an intertidal-shoreface environment. As such, a normally shallow-water ichnofossil assemblage developed in response to these conditions. Similarly, Frey and Seilacher (in press) indicated that grazing and feeding burrows of the Zoophycos ichnofacies may occur in shallower water than usual if waves and currents are minimal, deposited food is abundant, and oxygen levels are low.

This discussion is not meant to diminish the value of the concept of ichnofacies and depth relationships which, although valid when properly applied, must be viewed in terms of the entire spectrum of physical, chemical, and biological interactions (Frey and Seilacher, in press).

4-4. Significance of Ichnofossil Distributions

The ichnofossils found in the Thorold Sandstone are indicative of shallow-water, marine environments. Such near-shore habitats are subject to a complex array of both physical and biological interactions which result in a diverse spectrum of sedimentary regimes. Dörges and Hertweck (1975) have recently subdivided the littoral zone into three major environments based primarily on the position of mean-high water, mean low-water, and wave base (see fig. 4-2). In addition, faunistic investigations indicate that in the sublittoral mean wave base, and the border between recent and relict sediments (storm wave base) are distinct boundaries separating animal communities (Dorjes and Hertweck, 1975). Therefore, the sublittoral can be further sub-divided into three subenvironmental zones: (1) the upper sublittoral, located between mean low-water and mean wave base, is mainly influenced by surf, breakers, and strong wave oscillations; (2) the middle sublittoral, located between mean wave base and the boundary between recent and relict sediments, is mainly influenced by currents; and (3) the lower sublittoral, located between the recent-relict sediments border and the continental shelf-edge, where high-energy physical processes are less important (after Dörjes and Hertweck, 1975). Table 4-5 summarizes the zonation, terminology, and environmental characteristics of a generalized beach to off-shore profile.

The Thorold ichnocoenoses is characteristic of the nearshore Skolithos and Cruziana ichnofacies, as defined by Seilacher (1967a). These ichnofacies are ideally considered to be differentiated from one another by variables which typically are depth-related. They are composed of characteristic ichnogenera which display specific morphological traits which enable them

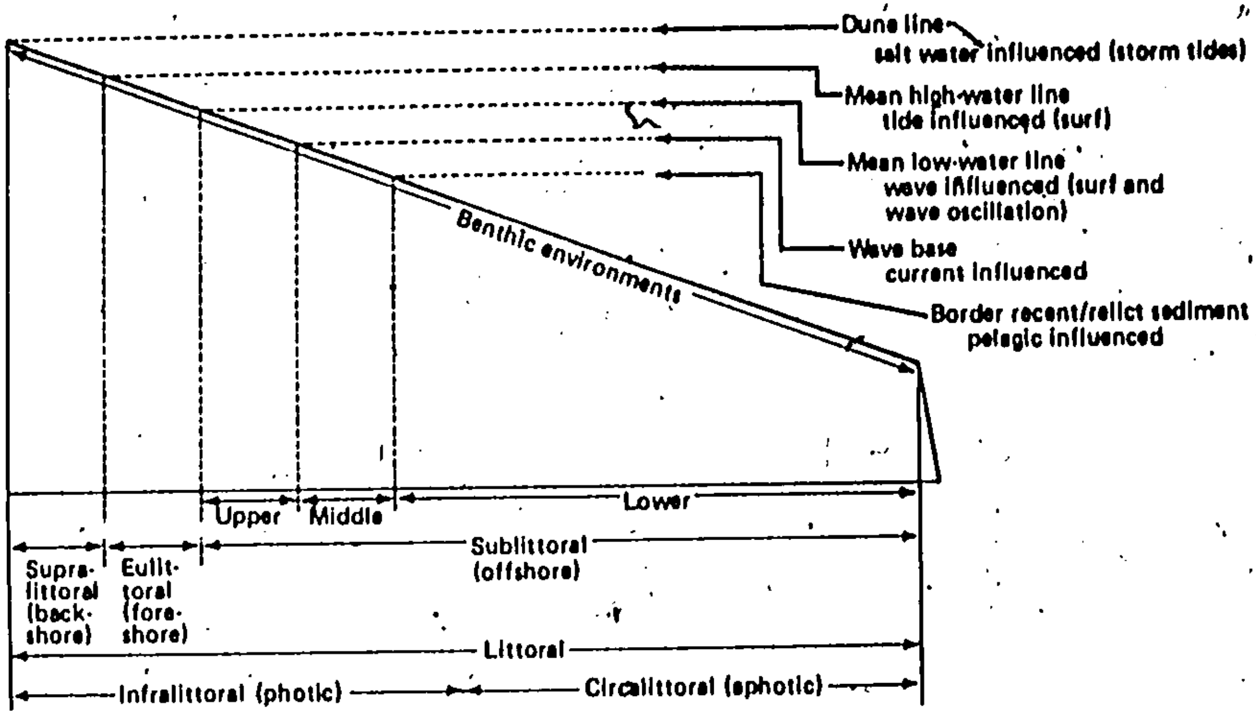


Fig. 4-2. Classification of marine environments. Compare with Table 4-5 (after Dörjes and Hertweck, 1975).

Table 4-5. Zonation, terminology, and environmental characteristics in a generalized beach-offshore profile (after Dorges and Hertweck, 1975).

Boundaries between environmental zones			Mean high-water line	Mean low-water line	Wave base
General (littoral) classification	Supralittoral	Eulittoral	Upper sublittoral	Middle sublittoral	Lower sublittoral
Beach-offshore classification	Dunes and backshore	Foreshore	Shoreface	Upper offshore	Lower offshore
Energy, sources and sedimentary processes	Eolian reworking; currents and wave action during spring tides and storms	Bidiurnal submersion; mainly wave action; periodically high reworking rate; low rate of bioturbation	Strong wave action; breakers, surf; high reworking rate; low rate of bioturbation	Low wave influence to sea bottom; sedimentation prevails over reworking; high rate of bioturbation	Exceptional storm wave influence to sea bottom; currents are main energy source; scarce or no sedimentation or reworking; considerable bioturbation
Sediments	Fine sand	Fine sand with medium sand	Fine sand with medium sand	Silty fine sand	Silt to clay, or coarse relict sediments

to exploit these diverse near-shore habitats. Table 4-6 summarizes the general characteristics and trends displayed by the trace fossils which compose these two closely related ichnofacies. The Skolithos ichnofacies is characterized by: predominantly full-relief structures consisting of vertical, cylindrical, and U-shaped burrows; few horizontal structures; high individual densities; low diversity, few mobile forms; and mostly filter-feeding organisms occupying dwelling burrows. The Cruziana ichnofacies, on the other hand, is characterized by: a mixed assemblage of vertical, inclined, and horizontal biogenic structures, low to medium individual densities, high diversity, some mobile forms, and predominantly deposit-feeding organisms selectively mining the substrate (see Table 4-4 and contained references).

Taken individually, the ichnogenera found in the Thorold are not restricted to any one particular ichnofacies (see Table 4-7). However, many of these forms do display a definite environmental preference. For example, Crimes (1977) illustrated that a typically shallow-water trace fossil assemblage was found in a deep-sea, submarine fan environment, in a bathymetric zone usually occupied by the Nereites ichnofacies. This suggests that these encountered ichnogenera were then part of the Nereites ichnofacies, which may not be

Table 4-6. General characteristics of the shallow-water *Skolithos* and *Cruziana* ichnofacies (see Table 4-4).

Ichnofacies	General Characteristics	Dominant Ichnogenera
Skolithos	Mostly fullrelief structures consisting of vertical cylindrical and U-shaped burrows. Few horizontal structures. High densities. Low diversity. Organisms mostly filter-feeders. Few mobile forms. Dwelling burrows dominant.	*Skolithos* *Arenicolites* *Diplocraterion*
Cruziana	Mixed assemblage of vertical, inclined and horizontal biogenic structures. Feeding burrows dominant. Low to medium density. High diversity. Organisms mostly deposit-feeders. Carnivorous mobile forms present.	*Cruziana* *Rusophycus* *Teichichnus* *Trichophycus*

entirely true. Crimes (1977) went on to stress that although found in deeper-water, these forms were found associated with a sedimentological regime which displayed physical and chemical characteristics typically encountered in much shallower water. Therefore, the organisms were responding to a specific environmental preference. In other words, they still represent the shallow-water Skolithos ichnofacies which has merely been displaced bathymetrically. When viewed in this light, many of the ichnogenera recorded from the Thorold can thus be assigned to a particular ichnofacies based on environmental preferences (Table 4-7).

B). Local ichnofacies determinations and interpretations

i). Assemblage One

The ichnocoenoses of Assemblage One consists of basically a bi-specific association of Arthrophycus and Daedalus. The individual burrow systems are well preserved and occur in relatively high densities. Martini (1966) characterized this assemblage as a mottled burrow zone, and inferred that it developed in response to the low energy conditions prevalent during Thorold time in New York State.

It is difficult to assign a specific ichnofacies to such a sparse association. Both ichnogenera are known from both the Skolithos and Cruziana ichnofacies

Table 4-7. Known ichnofacies associations of ichnogenera encountered in the Thorold.

Ichnogenus	Ichnofacies Range[1].	Environmental Preferences[1].
Arenicolites	*Skolithos* to *Nereites*	*Skolithos*
Arthrophycus	*Skolithos* to *Cruziana*	No preference
Bifungites	*Skolithos* to *Cruziana*	*Skolithos*
Chondrites	*Skolithos* to *Nereites*	no preference
Cruziana	*Skolithos* to *Zoophycos*	*Cruziana*
Daedalus	*Skolithos* to *Cruziana*	no preference
Diplichnites	*Skolithos* to *Zoophycos*	*Cruziana*
Diplocraterion	*Skolithos* to *Nereites*	*Skolithos*
Dolopichnus	*	*
Fucusopsis	*Cruziana* to *Nereites*	no preference
Incisifex	*	*
Lingulichnus[2].	*Skolithos* to *Nereites*	*Skolithos*, *Cruziana*
Lobichnus	*	*
Monomorphichnus	*Skolithos* to *Zoophycos*	*Cruziana*

Table 4-7 continued.

Palaeophycus	*Skolithos* to *Zoophycos*	*Cruziana*
Planolites	*Skolithos* to *Nereites*	no preference
Polycylindrichnus	*	*
Rhabdoglyphus	*Cruziana* to *Nereites*	*Nereites*
Rusophycus	*Skolithos* to *Zoophycos*	*Cruziana*
Scalarituba	*Skolithos* to *Nereites*	*Nereites*
Skolithos	*Skolithos* to *Nereites*	*Skolithos*
Teichichnus	*Cruziana* to *Nereites*	*Cruziana*
Echiuroid trace	*Skolithos* to *Nereites*	*
?*Gordia*	*	*
?*Caprionichnus*	*	*
?*Scolicia*	*Skolithos* to *Nereites*	*Cruziana*, *Nereites*
?*Trichophycus*	*Cruziana* to *Zoophycos*	*Cruziana*

* Insufficient data for accurate determination.

1. See Chapter 3 and contained references for ichnofacies ranges and environmental preference.

2. Also based on occurrence of *in situ* lingulid shells (See Chapter 7).

(see Table 4-7), and display little preference to either one. This implies that they probably form as a response to specific environmental conditions which may be locally prevalent in either zone. These conditions seem to be related to low energy levels, continuous deposition rates (as indicated by the steady vertical migration of both types), and relatively high levels of contained detritus. Martini (1966) suggested that such conditions may have been prevalent in this area during the deposition of the Thorold and indicated that they may reflect a lagoonal or tidal flat environment. The recognition and distribution of the ichnofossils in Assemblage One does not significantly alter this interpretation.

ii). Assemblage Two

The ichnocoenoses of Assemblage Two is typical of the very near-shore Skolithos ichnofacies of Seilacher (1967a), which is characterized by abundant to common vertical and U-shaped dwelling burrows (Arenicolites, Diplocraterion, Dolopichnus sp. B, and Skolithos). Such burrow systems are usually interpreted as the domiciles of filter-feeding organisms (see Chapter 3, and contained references), and often attain very high densities. Associated ichnogenera include: Arthrophycus, Chondrites, Daedalus, Lobichnus, Palaeophycus, and Planolites, all of which (except Daedalus) represent feeding burrows of infaunal organisms which are found in rather low densities.

Such an association develops in response to a variety of environmental conditions which include: high energy levels, high oxygen levels, and sandy substrates with low detritus levels (Seilacher, 1967a; Frey, 1971; Howard, 1972). As a result, filter-feeders dominate the biota and deposit-feeding and mobile carnivorous forms are selectively excluded (Howard, 1972). Similar trace fossil associations are well known from shallow-water foreshore to shoreface environments (Campbell, 1971; Howard, 1972; Spencer, 1976; among others). Such environments are subject to high water energies which tend to favour filter-feeding populations, here represented by the ichnogenera *Skolithos*, *Arenicolites*, and *Diplocraterion*.

iii). *Assemblage Three*

Of the four ichnofossil associations observed in the Thorold Sandstone, Assemblage Three is by far the most complex. Examination of Table 4-2 indicates that virtually every ichnogenera recognized in the study is found in the Hamilton, Ontario area. In addition, analysis of Table 4-7 suggests that a mixing of ichnofacies may be present, in that elements typically associated with the *Skolithos* ichnofacies occur in the same outcrop as elements which characterize the *Cruziana* ichnofacies.

[For the purpose of this discussion I will confine my remarks to the ichnocoenoses recorded from the

Jolley Cut section, since it is the most extensive and well-developed in the Hamilton area.]

Upon further examination, it was noted that the ichnofossils were found in discrete, recognizable zones which appeared to be more or less repetitive. The main body of the exposure consists of fine-grained sandstones, siltstones, and shales and is characterized by the following ichnogenera: Chondrites, Cruziana, Diplichnites, Fucusopsis, Incisifex, Lingulichnus, Lobichnus, Monomorphichnus, Palaeophycus, Planolites, Polycylindrichnus, Rhabdoglyphus, Rusophycus, Scalarituba, vertical to inclined Skolithos, Teichichnus, ? Gordia, and ? Trichophycus. Such an assemblage is reminiscent of the Cruziana ichnofacies of Seilacher (1967a) in which the diversity of forms is high, and individual densities are low. In general, the assemblage is indicative of a predominantly deposit-feeding population with many mobile forms also being present. Given normal circumstances, it is exactly the type of assemblage one would expect going off-shore from the Skolithos ichnofacies of Assemblage Two. It reflects decreasing water energy, decreasing grain size, and correspondingly increases in detritus and shale content (Howard, 1972), precisely the conditions described for this series of outcrops by Martini (1966).

Interspersed within this assemblage, however, are relatively thick sandstone layers which contain the following ichnogenera: Arenicolites, Bifungites, Diplocraterion, Dolopichnus sp. A, and Skolithos. This association is reminiscent of the one reported in Assemblage Two and referred to the Skolithos ichnofacies. It consists of predominantly filter-feeding organisms inhabiting dwelling burrows that attain very high densities and correspondingly low diversity.

Assemblage Three, therefore, is composed of a mixed ichnocoenoses which includes elements of both the Skolithos and Cruziana ichnofacies. Such a lack of facies specificity and the breakdown of the community concept should not come as a surprise. Crimes (1970b) has indicated that shallow water environments are extremely complex and often contain locally developed substrate types which are more commonly associated with other depth zones. This alternation of depth-related ichnofacies is often interpreted as resulting from a rise and fall of sea level. Although plausible, a more likely interpretation involves an alternation of sand and silt sedimentation at a constant water-depth (Crimes, 1970b), in which the different trace fossil assemblages reflect varying behavioural responses of the animals colonizing the two distinct habitats (Crimes, 1970b).

The distribution of the trace fossils in Assemblage Three is consistent with such an interpretation. The relatively thick fine-grained sandstone units which contain elements of the Skolithos ichnofacies can be viewed as the result of periodic sedimentological events which were not necessarily the result of a simple rise and fall of sea level. Vos (1977) recently described similar sequences from Upper Paleozoic strata in Morocco, and interpreted them as the result of storm deposits. Storms are known to be powerful geologic agents in the near-shore shelf whose frequency may be much more extensive than previously thought (Goldring and Bridges, 1973; Kelling and Mullin, 1975; Harms, et al., 1975; Kumar and Sanders, 1976). Hayes (1967) has demonstrated that such storms have the ability to move sand-size sediments on marine shelves; and Hjulstrom (1939) has indicated that high velocity currents more easily resuspend the sand fraction than they do the cohesive mud fraction.

Storm deposits have frequently been described from the lower shoreface and off-shore facies (Howard, 1972; Harms, et al., 1975; Vos, 1977; among others), and as storm washovers in a mixed tidal flat facies (see Vos, 1977; and contained references). The recognition of this seems to be based on specific lithologies, bedding, sedimentary structures and ichnofossils (Table 4-8).

Table 4-8

Selected Criteria for the Identification of Ancient Storm Deposits (see text for specific references)

A). <u>Lower Shoreface and Off-Shore Zone</u>

1). <u>Lithologies</u>: predominantly fine sandstones and coarse siltstones interlayed with shales and fine siltstones; individual units fining upwards.

2). <u>Bedding and sedimentary structures</u>: hummocky cross-stratification; ripple and ripple-drift cross-laminations; groove casts; linear, undulatory, and interference ripple marks; ball and pillow deformed bedding, armored mud balls.

3). <u>Ichnofossils</u>: Sandstones contain predominantly filter-feeding organisms as indicated by a burrowed upper surface consisting of vertical, cylindrical and U-shaped domiciles. Interlayed siltstones and shales characterized by numerous horizontal feeding burrows of predominantly deposit-feeding organisms.

B). <u>Storm Washovers in Tidal Flats</u>

1). <u>Lithologies</u>: massive sandstone unit recording a single event; unit tends to coarsen upwards and often terminates in a conglomeratic veneer cover.

2). <u>Bedding and sedimentary structures</u>: horizontal laminations and low angle cross-bedding; groove and flute casts; wrinkle marks, swash marks, rill marks and desiccation cracks, ripple-marks.

3). <u>Ichnofossils:</u> None observed, with the exception of root penetrations.

In the lower shoreface and off-shore facies, storm derived sediments consist of fine-grained sandstones and coarse-grained siltstones interlayered with shales and siltstones (Harms, et al., 1975). The sand deposition probably records a single storm event followed by the more typical deposition of silts and muds on the near-shore shelf. Vos (1977) indicated that such units may display: groove casts on the underside of beds; an abrupt flat to undulose base, ripple cross-lamination and ripple-drift cross-lamination (showing a sequence from type A of Jopling and Walker, 1968, into type B into in-phase lamination); and on upper surfaces showing a great variety of linear, undulatory, and interference ripples. In addition, Harms, et al. (1975) suggests that storm lain sandstone bodies may also display hummocky cross-stratification.

A number of additional sedimentary structures are also known to be associated with storm deposition. Deformed bedding with ball and pillow structures have been attributed to load casting, slumping and the eventual floundering of a sand body, which was deposited suddenly over a soft clay bottom (Kuenen, 1958; Potter and Pettijohn, 1963). The impetus of the floundering is thought to be related to a sudden energetic shock, such as storm waves (Kuenen, 1958). Bell (1940) has interpreted armored mud balls to be the result of rolling mud chips, obtained by rapid bank undercutting or by storm wave-erosion. Therefore, such features may also be associated with storm derived sediments.

Ichnofossils, being sensitive indicators of energy levels (Frey, 1971), may also be valuable in identifying such events. Howard (1972), investigating trace fossil distributions in the Upper Cretaceous Blackhawk Formation of Utah, found that off-shore sediments typically are composed of siltstones and shales with abundant horizontal feeding structures (horizontal _Asterosoma_, _Arthrophycus_, _Scolicia_, and _Teichichnus_). Such an ichnofossil assemblage, Howard (1972) felt indicated low energy conditions, slow continuous sedimentation rates, sediment rich in organics with a predominantly deposit-feeding biota, and an overlying water column either too turbid or too slow moving to support filter-feeding organisms. Interspersed periodically throughout this succession, Howard (1972) found relatively thick, fine-grained sandstone beds with rippled surfaces and predominantly vertical ichnofossils (_Ophiomorpha_, vertical _Asterosoma_, and "vertical curving tubes). He related this abrupt change in ichnofossils to higher energy conditions, rapid deposition, and a lack of organic detritus in the sediment which corresponded to a change in feeding behaviour from deposit-feeding to filter-feeding. Such an abrupt transition was related to the deposition of the sand units by sudden storms (Howard, 1972).

Storm derived sediments have also been recognized to extend landward from the backshore onto a mixed tidal flat as "storm washovers" (Andrews, 1970; McGowan and Scott, 1975; Vos, 1977; among others). The deposits consist of a single sandstone unit which displays horizontal laminations (Andrews and van der Lingen, 1969), low angle cross-beds (Vos, 1977), and a coarsening upward sequence of grains, often culminating in a post-storm conglomeratic veneer (Hayes, 1967; Vos, 1977). The underside of the unit is often marked by numerous flute and groove casts and the upper surface is usually a broad, flat, ripple-marked plane (Vos, 1977). Associated sedimentary structures may include wrinkle marks, which result from a strong wind blowing over a sediment surface which has a thin water cover (Reineck, 1969); and rill marks, which are erosional sculptures produced when a thin layer of water drains over a sedimentary surface (Cepek and Reineck, 1970). Such structures generally are associated with the change from subaqueous to subaerial conditions in tidal flat environments (Reineck, 1969). Ichnofossils, aside from root penetrations, have not been described from these storm washover deposits.

Table 4-8 summarizes the main features associated with storm derived sediments in both the off-shore and tidal flat environments.

The problem now arises, to which environmental zone does Assemblage Three of the Thorold Sandstone belong - the nearshore shelf or a tidal flat? Martini (1966, 1971b, 1972) indicated that exposures (containing this assemblage) in the Hamilton area, were representative of a beach (?) to tidal flat environment and cited the presence of lingulid brachiopods as indicative of such a designation.

The inarticulate lingulid brachiopod is commonly cited as an example of a very successful, evolutionary stable, and long-ranging organism (e.g., MacGinitie and MacGinitie, 1968; Rudwick, 1970) that very early ~~in~~ the Phanerozoic exploited a stable marine environment. Until very recently, lingulids were thought to have first adapted to the shallow, marine habitat in the Cambrian and to have lived successfully in this habitat to the present (Craig, 1952, 1954; Ferguson, 1962, 1963). Recent discoveries of lingulids in open shelf, deep shelf and basinal sediments of Paleozoic age (Pickerill, 1973; Watkins and Berry, 1977; Percival, 1978; Cherns, 1979), however, challenge this model and indicate that the history of habitat exploitation by lingulid brachiopods is more complex than previously thought (Pemberton and Kobluk, 1978b).

Most modern lingulids commonly occur in water depths ranging from the intertidal to 45 m (Craig, 1952); only rare specimens are found deeper, and only one specimen is known from as deep as 100 m (Hatai, 1939). Although fossil lingulids (when found without other brachiopods) are used to indicate shallow water environments in ancient sequences (Rudwick, 1965), clearly they were not restricted to the intertidal or immediate subtidal. By comparison with modern lingulid brachiopods, fossil lingulids may actually indicate water depths as great as 100 m.

There is fossil evidence that lingulids, in the lower Paleozoic, inhabited not only shallow water environments but also deeper marine environments even down to basinal depths. Following are examples of occurrences of deep and shallow marine brachiopods from the Lower Paleozoic (also see figs. 4-3 and 4-4).

One of the earliest occurrences of lingulids is in the shallow marine Lower Cambrian Poleta Formation (*Nevadella* tribolite zone) of the southwestern Great Basin of California and Nevada (Rowell, 1977). Pemberton and Kobluk (1978a) describe a slightly younger, *in situ* lingulid burrow (*Lingulichnus verticulis*) from the Lower Cambrian Bradore Formation of Labrador (*Bonnia-Olenellus* tribolite zone). The Bradore Formation represents a series of tidal-dominated silicilastic sand

Fig. 4-3. Selected occurrences of deep and shallow water lingulids in the Lower Paleozoics. [1 and 17 (Thayer, 1974); 2 (Watkins and Berry, 1977); 3 (Cherns, 1979); 4 (Ziegler, et al., 1968); 5 (Delong, personal communication, 1978; Titus and Cameron, 1976); 6 (Pickerill, 1973); 7 and 11 (Rowell and Brady, 1967); 8 (Pickerill, in press); 9 (Rowell, 1977); 10 (Pemberton and Kobluk, 1978a); 12 (Titus and Cameron, 1970); 13 (Bretsky, 1970); 14 (Johnson, 1975; Ziegler, et al., 1968); 15 (Martini, 1971b); 16 (Lawson, 1975)].

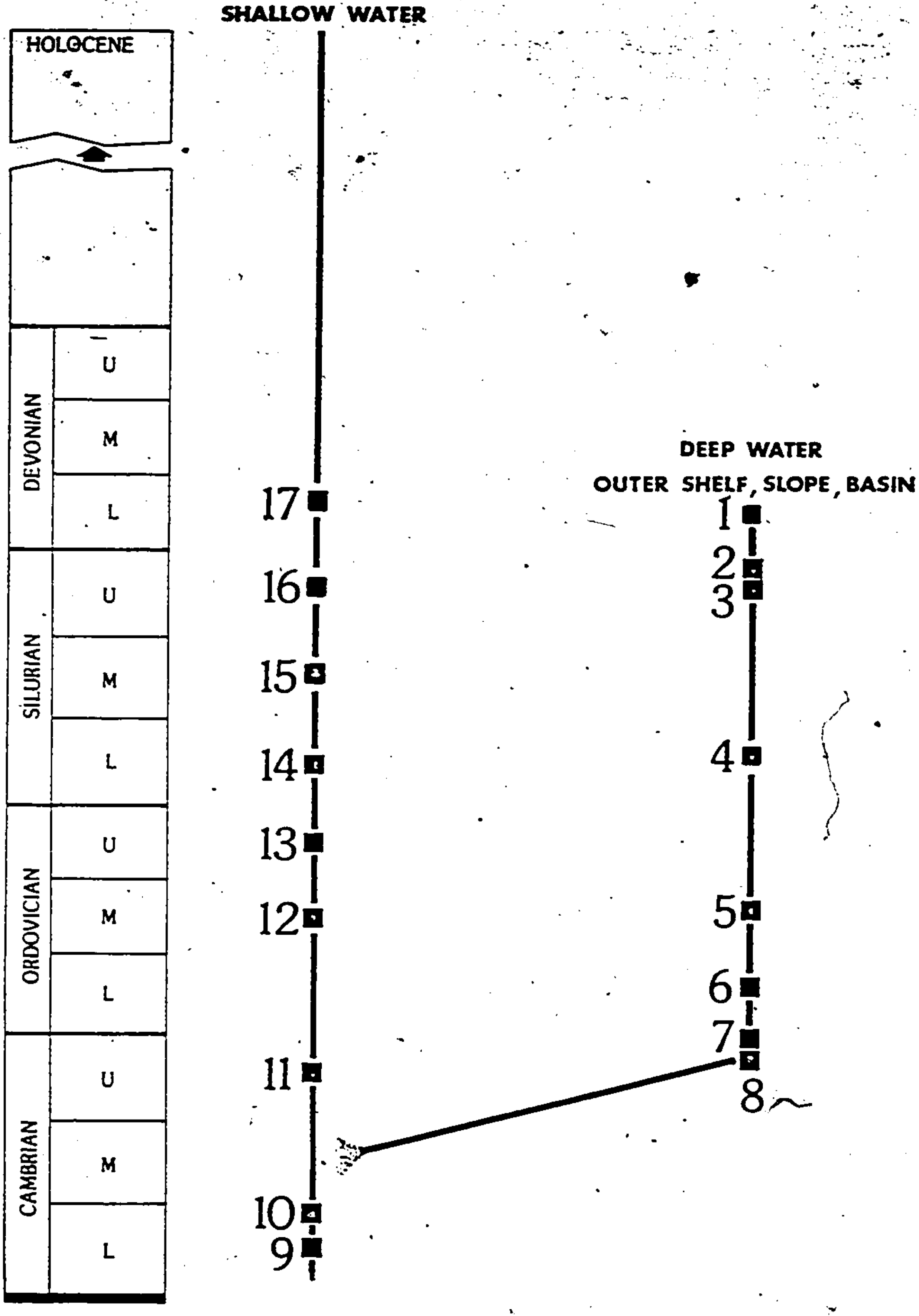
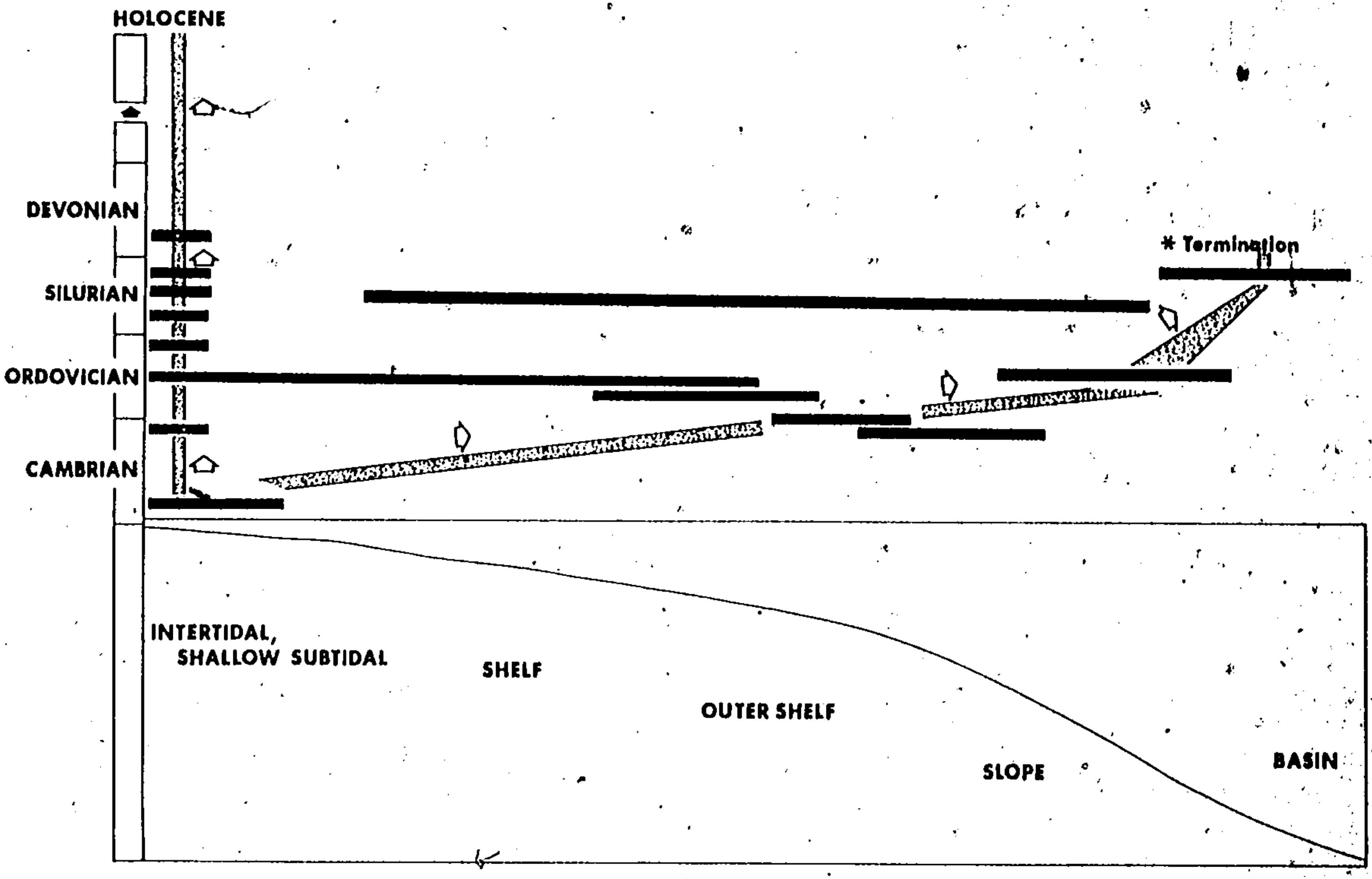

SHALLOW WATER
HOLOCENE
DEVONIAN
U
M
L
SILURIAN
U
M
L
ORDOVICIAN
U
M
L
CAMBRIAN
U
M
L
17
16
15
14
13
12
11
10
9
DEEP WATER
OUTER SHELF, SLOPE, BASIN
1
2
3
4
5
6
7
8

Fig. 4-4. Environmental range of Lower Paleozoic lingulid brachiopods (see fig. 4-3 for references).


HOLOCENE
DEVONIAN
SILURIAN
ORDOVICIAN
CAMBRIAN
* Termination
INTERTIDAL, SHALLOW SUBTIDAL
SHELF
OUTER SHELF
SLOPE
BASIN

shoals (Swett and Smit, 1971) deposited in very shallow water. Other examples of similar environments of Cambrian age, such as the Eriboll Sandstone of Scotland (Swett, et al., 1971) and the Chickies Quartzite of southeast Pennsylvania (Goodwin and Anderson, 1974) have neither lingulid burrows nor shells. This may be a function of preservation, but the Labrador occurrence (Pemberton and Kobluk, 1978a) certainly indicates that burrowing lingulids were present in shallow water environments as early as the Lower Cambrian.

Inarticulate brachiopods (including lingulids) are present in the three agnostid tribolite communities established by Jago (1973) for the Middle Cambrian of Tasmania. These three communities characterize facies from the inshore region through the inner-middle-outer shelf to basinal environments (Jago, 1973). These benthic communities described by Jago (1973) are simple and are composed primarily of agnostid tribolites, polymerid trilobites, inarticulate brachiopods, dendroids, hydroids, and sponges. Recent work on the Upper Cambrian of the Great Basin of Utah and Nevada (Pterocephaliid Biomere) by Rowell and Brady (1976) indicates that lingulid brachiopods are distributed throughout the available range of environments. They occur in deposits that characterize shallow water shoal, innershelf, outershelf, and upper slope environments.

The broad habitat tolerance exhibited by the Upper Cambrian lingulids continued through the Lower and Middle Ordovician. Pickerill (1973) described deepwater outershelf lingulids (Linguiasma tenuigranulata) from the Lower Ordovician of the Welsh Borderlands. They are part of a fauna equivalent to the strophomenid-trilobite community of Bretsky (1970). In addition to numerous horizontally-oriented shells on bedding planes, Pickerill described some in vertical life position. Recently, Titus and Cameron (1976) described the fossil communities of the Middle Ordovician Lower Trenton Group of New York. They found that the lingulid Lingula reciniformis was a common element of four of the six communities: the Triplesia community which characterized lagoonal deposits; the Trematis community, indicative of a deep shelf environment; the Geisonoceras community, associated with the shelf-basin transition; and the Triarthrus community, representing the shelf margin to basin environment (see Titus and Cameron, Fig. 7, p. 1221). Another important Middle Ordovician occurrence is from western Newfoundland, where lingulids are found in deposits associated with graptolites and turbidites in what is interpreted as a slope environment (DeLong, personal communication, 1978). None of these shells are found in life position; however, the shells are articulated and undamaged, and do not appear to have undergone any transport.

The classic shallow water lingulid community established by Ziegler, _et al_. (1968) from the Lower Silurian has also been recognized in the Upper Ordovician Oswego Formation of New York by Bretsky (1970). Bretsky (1969) has stated that this shallow-water-molluscan association originated in the Upper Ordovician and persisted until the Lower Permian.

Ziegler, _et al_. (1968) defined the shallow water lingulid community from the Lower Silurian (Cowleigh Park Beds) of Wales. This is one of several examples of Silurian shallow water lingulid communities containing _in situ_ lingulid shells (see also Johnson, 1975).

Investigations of the Upper Silurian Ludlovian deposits of the Welsh Borderlands indicate that two lingulids _Lingula lata_ and _Lingula lewisii_ are distributed over a wide range of environments from the shallow nearshore zone to the basin facies (Calef and Hancock, 1974; Lawson, 1975; Watkins and Berry, 1977). Shells of _Lingula lata_ are found in life position and are associated with graptolites in sediments interpreted as representing deep basinal environments (Cherns, 1979).

In a detailed analysis of the Lower Devonian Genesee Group of New York, Thayer (1974) found the lingulid brachiopod genus _Barroisella_ to be abundant in all environments from the near-shore facies to the basin facies. Although specimens from the graptolitic basin facies were found horizontal to the bedding, other specimens from different facies were found in the vertical in situ position (Thayer, 1974).

No examples of deep water lingulids are known from rocks younger than Lower Devonian, whereas many examples exist of shallow water lingulids (many in life position) from the Upper Devonian (Szmuc, et al., 1976) the Mississippian (Craig, 1952, 1954; Ferguson, 1962, 1963; and Osgood and Szmuc, 1972), the Pennsylvanian (West, 1972; and Hakes, 1976), and the Permian (Elias, 1937; and Yarrow, 1974).

Therefore, based on the available fossil evidence, the presence of lingulid brachiopods in the Lower Paleozoics cannot be used as the sole criteria in delineating paleoenvironments (Pemberton and Kobluk, 1978b).

In addition to the presence of lingulids, Martini (1966) also pointed out that the presence of rare mudcracks in the Thorold strata of this area was indicative of a tidal flat origin. Although well-developed mudcracks were not observed in this present study, their suspected occurrence warrants discussion.

Mudcracks are usually interpreted as being formed on the sediment surface during periods of subaerial exposure. There are, however, numerous examples of morphologically similar structures termed shrinkage cracks which form subaqueously (see White, 1961; Burst, 1965; and Donovan and Foster, 1972; among others). Such structures usually develop due to the mechanism of syneresis, which involves the expulsion of the liquid phase from the solid phase in a liquid-solid suspension (Jungst, 1934; Rich, 1951; White, 1961; Burst, 1965; Donovan and Foster, 1972). The impetus for their formation seems to be linked to changes in the salinity of the depositing medium (Van Straatan, 1954; Weiss, 1954; Donovan and Foster, 1972). Experimental studies conducted by Donovan and Foster (1972) resulted in the development of subaqueous shrinkage cracks in a clay-chalk mixture which was deposited by density flow in a sedimentation tank. Three months after the initial deposition of the sediment a weak Parazone (bleaching) solution was added to the overlying water, and two weeks later shrinkage cracks developed. They interpreted the crack formation as resulting from the interaction of the Cl^- ions (in the Parazone) with the sediment-water interface.

An alternate hypothesis, involving biogenic intervention, has also been postulated. In areas which have high numbers of deposit-feeding organisms, it has been shown that their burrowing activities greatly increases the water content of sediments (Chapman, 1949; Harrison and Wass, 1965; Rhoads, 1970; Pemberton and Risk, 1976). In addition, Ginsberg (1957) indicated that factors such as the mixing of muds and silts by organisms, the gel-like character of biogenically mixed sediments, and the escape of gasses produced by the bacterial decay of such things as fecal pellets, contribute to a rapid change in sediment packing. Later, true compaction during burial decreases porosity, develops new fabrics, and in silt and clay-sized sediments, produces some sort of physical cohesion between the particles. This later effect is similar to the change caused by desiccation (Ginsberg, 1957). Furthermore, Baldwin (1974) recently illustrated that preconditioning of patterns of stress relief in submarine sediments by sediment-water interface biogenic traces could effect subsequent crack development due to the mechanism of syneresis.

Either one of these proposed interpretations for the development of subaqueous shrinkage cracks, seem to be a viable alternative for the features described by Martini (1966) as mudcracks. Although the presence of well-developed, horizontal burrows strongly suggests a biogenic influence, the interpretation of storm deposits is consistent with abrupt salinity changes. During storm periods, extensive runoff seaward from land sources might decrease salinities locally and with the resumption of fair-weather conditions, salinities would return to normal. This abrupt increase in Cl^- ions might result in the similar reaction previously described by Donovan and Foster (1972).

Assemblage Three, therefore, can be interpreted as being characteristic of a lower foreshore to offshore environment, the resident ichnocoenoses being the elements of the Cruziana ichnofacies which makes up the majority of the section. Interspersed periodically within this ichnocoenoses are relatively thick, fine-grained sandstone units containing elements of the Skolithos ichnofacies, which are here interpreted as resulting from storm deposition.

The criteria for the recognition of such storm derived sediments in the lower shoreface to offshore zones have been summarized in Table 4-8. Thorold strata, in this area, contain a number of these diagnostic sedimentary features including: fining upward sequences of sandstone-siltstone-shale, basal groove casts, linear, undulatory, and interference ripples, ball and pillow structures, armored mud balls (Martini, 1966); ripple drift cross-laminations (Martini, 1974); and perhaps the most diagnostic feature of all, hummocky cross-stratification (R. G. Walker, personal communication, 1979). In addition, the resident ichnofauna is characteristic of the relatively quiet-water, and fine-grained sediments usually associated within this environment. In fact, a number of the recognized ichnogenera are known to be found almost exclusively in flysch sediments (Fucusopsis, Rhabdoglyphus, Scalaritubа, and ? Scolicia).

Another important ramification of the recognition of these storm-derived units concerns the ethological distribution of the trace-making organisms. The resident ichnocoenoses (the elements of the Cruziana ichnofacies) can be considered to represent a stable benthic community, whose populations are at or near the carrying capacity of the environment. Levinton (1970) has termed such assemblages as being resource-limited and noted that they usually occur in habitats with low physio-chemical stresses. The periodic influx of elements of the Skolithos ichnofacies represents one of the few examples of an opportunistic trace fossil assemblage. Examples of opportunistic species have long been known from body fossils (Waage, 1968; Levinton, 1970), and represent organisms which are not resource-limited, but instead are associated with unstable, physically-controlled environments (Levinton, 1970). Such species have been recognized based on the following criteria:

a). Distribution over a limited area (Waage, 1968);

b): Presence of species in thin but widespread isochronous horizons, indicating brief invasions (Waage, 1968).

c). Species found abundantly in several otherwise distinct faunal assemblages (Levinton, 1970);

d). Species appearing in great abundance in a facies with which it is not usually associated (Levinton, 1970); and

e). A species numerically dominates a fossil assemblage (Levinton, 1970).

In Assemblage Three of the Thorold Sandstone, the ichnocoenoses of the storm-derived sediments can be interpreted as being comprised of ichnogenera produced by opportunistic species. The resident ichnocoenoses was wiped out by the high physiological stress brought on by the influx of storm-derived sediments. These sediments were then in turn invaded by opportunistic species which attained very high densities in a short period of time. With the resumption of normal sedimentological conditions, the stress which limited the resident fauna was removed, which allowed for a recolonization. As the resident fauna re-established itself, conditions changed and the opportunistic species (here represented by _Arenicolites_, _Diplocraterion_, and _Skolithos_) were selectively excluded. These elements were later introduced with the next major storm event.

iv). _Assemblage Four_

The ichnocoenoses of Assemblage Four represents the westward continuation of the resident _Cruziana_ ichnofacies described from Assemblage Three. It consists of *Chondrites*, *Cruziana*, *Diplichnites*, *Diplocraterion*, *Monomorphichnus*, *Palaeophycus*, *Planolites*, *Rusophycus*, *Scalarituba*, inclined *Skolithos*, *Teichichnus*, echiuroid traces, ? *Gordia*, ? *Caprionichnus*, ? *Scolicia*, and ? *Trichophycus*. The assemblage is characterized by increases in feeding burrows and the traces of mobile organisms, and a corresponding decrease in dwelling burrows. Such domiciles when found are oriented obliquely to bedding planes.

The zones of dense vertical burrows observed in Assemblage Three and interpreted as resulting from storm deposition were not observed. The trace fossil assemblage is dominated by structures created by deposit-feeding and carnivorous mobile organisms, which are resource-limited. Such assemblages are characteristic of shallow water offshore environments which seem to be biologically controlled (Howard, 1972).

4-5. Summary

The trace fossils of the Thorold Sandstone are indicative of the shallow-water, nearshore *Skolithos* and *Cruziana* ichnofacies, and can be divided into four distinctive assemblages.

Assemblage One is restricted to the New York area and seems to be indicative of a tidal flat to low energy lagoonal environment (Martini, 1966).

Assemblage Two, from DeCew Falls westward to Albion Falls, is characteristic of the *Skolithos* ichnofacies, which seems to be indicative of tidal flat to shoreface environments. Such environments are dominated by physical processes related to the proximity of the shoreline. Assemblage Three consists of a mixed ichnocoenoses which contains elements of both the *Skolithos* and *Cruziana* ichnofacies. The resident ichnofossils are indicative of the *Cruziana* ichnofacies, which is characteristic of the lower shoreface to offshore environment. The elements which comprise the *Skolithos* ichnofacies are considered to result from storm deposits. Assemblage Four is a continuation of the resident *Cruziana* ichnofacies of Assemblage Three and indicates offshore deposition.

These four ichnofossil assemblages can be differentiated based on the lateral variations in ethological groups (Table 4-9). These variations correspond very closely to the observed lateral changes in sedimentary properties (Table 4-10) observed by Martini (1966).

Table 4-9

Lateral Variations Between Thorold Trace Fossil Assemblages

A). From Assemblage 1 to Assemblage 2.

1. Decrease in abundance of Arthrophycus and Daedalus
2. Introduction of abundant vertical dwelling burrows: Arenicolites, Diplocraterion, Dolopichnus sp. B, and Skolithos.
3. Density high, diversity low.
4. Few horizontal burrows.
5. Few mobile forms.

B). From Assemblage 2 to Assemblage 3.

1. Great increase in feeding burrows: Chondrites, Fucusopsis, Polycylindrichnus, Rhabdoglyphus, Scalarituba, Teichichnus, and Trichophycus.
2. Increase in density of horizontal burrows.
3. Increase in abundance of mobile forms: Cruziana, Diplichnites, Incisifex, Monomorphichnus, and ? Gordia.
4. Aside from discrete zones of dense dwelling burrows, there is a decrease in vertical forms.
5. Density low, diversity high.

C). From Assemblage 3 to Assemblage 4

1. Increase in abundance of feeding structures.
2. Decrease in abundance of dwelling burrows.
3. Increase in mobile forms.
4. Vertical burrows where present tend to be inclined.
5. Densities low, diversity high.

Table 4-10

Generalized Lateral Variations in Trace Fossil and Sedimentary Characteristics in the Thorold Sandstone, from Niagara Glenn Westwards to Clappison Corners

Trace Fossil Variations	Sedimentary Variations*
1. general increase in horizontal burrows	1. increase in shale content
2. general increase in feeding structures, corresponding to a general decrease in dwelling structures	2. general decrease in water energy levels
3. increase in diversity	3. increase in contained detritus
4. decrease in individual densities (aside from the opportunistic species found in the Jolley Cut section)	4. general decrease in overall grain size
5. general decrease in vertical forms; corresponding to an increase in oblique forms	

* After Martini, 1966.

CHAPTER 5

Proposed Re-classification of Some Selected Vertical Ichnofossils

5-1. Introduction

At present the field of ichnology is going through a rapid expansion and increased importance is being placed on the study of trace fossils in the paleoecological interpretation of rock units. Many difficulties have frequently arisen when it comes to the point of assigning ichnogeneric and ichnospecific names. This problem is due largely to the vast number of ill-defined ichnogenera and ichnospecies that have accumulated in the literature (Fursich, 1974a). Recently, there have been numerous proposals brought forth in hopes of clarifying this situation. Frey (1973) has suggested that the use of the ichnogenus as the basic nomenclature unit in trace fossil taxonomy might be a valid compromise to help solve the present difficulties. Since trace fossil systematics is not recognized by either the "International Code of Zoological Nomenclature" or the "Internal Code of Botanical Nomenclature," Sarjeant and Kennedy (1973) have proposed a separate code for the nomenclature of ichnofossils. This code is similar to the Botanical code and calls for the retention of binomial ichnofossil names and makes provisions for the special problems confronted by ichnologists.

In the study of ichnofossils, several classifications have been used. These range from stratinomic (Seilacher, 1953a) to phylogenetic (Seilacher, 1953a) to ethologic (Seilacher, 1964). Chamberlain (1971b) pointed out that difficulties arise in any system of classification of ichnofossils, partly because extensive comparison of morphology and ethology with modern organisms has not been made. Ichnofossils, for the most part, reflect behaviour of organisms and only to a small extent reflect the morphology. In this context, it can be shown that an organism may display more than one behavioural pattern and thus may produce more than one type of structure. Similarly, an organism may display a single behavioural pattern in varying sediments but produce two, different traces, this being based on grain size, sediment chemistry and degree of erosion or sedimentation. To confuse the issue further, different taxa behaving similarly may produce similar structures. Thus, very few ichnogenera can confidently be assigned to existing taxa, and many ichnofossils cannot confidently be assigned to ethological types (Chamberlain, 1971b). These inconsistencies illustrate the value of the Sarjeant and

Kennedy (1973) code in which they state that "... a nomenclature for trace fossils must be recognized for what it is, an essentially morphological classification for naming organically-induced structures in sediment, in rocks, and in the walls of body fossils. It should presuppose neither a knowledge of the nature of the organism whose activity produced the structure, nor the absence of such knowledge."

As stated earlier the morphology of trace fossils reflects the behaviour and, to a lesser extent, the morphology and size of the organisms responsible for creating them. Fursich (1973) correctly pointed out that the behavioural patterns responsible for the morphological features can bear quite different degrees of significance. Based on these consideration, Fursich (1973, 1974a, 1974b) has developed the concept of significant and accessory features for use in trace fossil systematics, in which morphological features resulting from behaviour at a high level of significance are called significant features and are used for classification at the ichnogeneric level. Morphological features resulting from behaviour at a low degree of significance are called accessory features and are used for classification at the ichnospecific level.

Considering the state of the classification of ichnofossils as previously outlined, only a few studies have attempted to revise groups of ichnofossils and possibly decrease the number of ichnogenera and ichnospecies, many of which are synonymous or poorly differentiated. Recent studies have attempted to revise the systematics of Diplocraterion (Fursich, 1974a), Rhizocorallium (Fursich, 1974b) and crustacean trace fossils (Fursich, 1973; Bromley and Frey, 1974; Frey and Howard and Pryor, 1978).

One of the most poorly understood groups of ichnofossils consists of vertical, single-entrance burrows. By far the most prolific ichnogenus in this group is Skolithos, and as Osgood (1970) stated, "It remains in a state of confusion and is badly in need of monographic study." Alpert (1974b) presented a systematic review of the ichnogenus Skolithos, conducted solely from the literature, actual type specimens were not examined, 35 species of Skolithos were placed into five distinctive ichnospecies. It must be stressed, however, that there exists in the literature a multitude of ill-defined ichnogenera that may or may not be referrable to two or three separate taxa.

5-2. Historical Perspective

In any classificational revision it is imperative that one have a clear understanding of the history of the forms being studied. The nomenclature of ichnofossils is a subjective process and is dependent on the views being expressed. In the early nineteenth century most biogenic structures were considered to be the remains of marine plants and were described as fucoids (see MacCulloch, 1814). It was not until the middle of the century that an animal origin was proposed for some of these structures.

Haldemann (1840) applied the name Skolithos to vertical, cylindrical structures in the Lower Cambrian Chickies Formation of southeastern Pennsylvania and described them as follows:

> "Fucoides ? linearis: Stem simple (never branched), rectilinear, surface nearly even. Diam. 1/8 to 1/4 in.; length several feet. Cylindrical or compressed. Locality, south of Reading and north of Columbia, Penn., being the oldest fossil in the state, occurring in the first stratified rocks above the gneiss. Obs. I discovered this fossil in 1835, and described it about three years ago as Skolithos linearis, proposing a subgenus for it, because its real nature could not be determined, and because the genus Fucoides is composed of heterogeneous materials. The characters of the subgenus Skolithos are: stem free, cylindric or subcylindric veriform or linear, never branched" (Haldemann, 1940, p. 5).

Haldemann's paper, however, was not widely distributed and was unillustrated and the ichnogenus Skolithos received little attention, until the work of Hall (1847). Hall, describing forms similar to Haldemann's, from the Potsdam Formation of eastern New York and western Massachusetts elevated Skolithos from the sub-generic to the generic rank and re-named the form "Scolithus". This was done because Haldemann (1840) had used the Greek form (Skolithos) and not the Latin form (Skolithus). However, as Howell (1943) points out, the original spelling should be retained (Article 19, International Code of Zoological Nomenclature). Hall (1847) still considered the form to represent a fossil plant and characterized it as such: "Stem free, simple, cylindric or subcylindric, veriform or linear, never branched" (Hall, 1847, p. 2).

Meanwhile in Europe similar forms were being examined from the Lower Ordovician of France by Rouault (1850), who proposed the names Foralites and Tigillites. Foralites characterized simple structures which penetrated the substrate at various angles; although some specimens were straight, most were gently curved (Rouault, 1850). Tigillites, on the other hand, characterized vertical structures that were never crowded and did or did not exhibit a funnel-shaped aperture (Rouault, 1850). Salter (1857) considered Foralites to be a synonym of Skolithos and also suggested that the ichnogenus Scolites should include not only vertical and diagonal structures but also horizontal burrows attributed to annelids. This proposal was not well received, and finally Nicholson

(1873) proposed the ichnogenus Planolites for horizontal burrows of annelid origin.

In the years 1860 to 1900 numerous examples of Skolithos burrows were being described from Eastern North America. These include studies of forms from the Lower Cambrian of Labrador (Billings, 1861); the Georgia Group of Vermont (Hitchcock, 1861); the Potsdam Sandstone of the Montreal area (Dawson, 1863); the Potsdam Santstone of Wisconsin (Whitfield, 1880); the Cincinnati Group of Ohio (James, 1881); the St. Peter's Sandstone of Minnesota (Winchell, 1884); the Chickies Sandstone of Pennsylvania (Wanner, 1890); and from numerous Cambrian deposits (Walcott, 1890b). These newly described forms (along with others not mentioned) were all concerned with Skolithos forms but in most cases new species were named. In addition, Chamberlain (1883) suggested that the burrow described by Whitfield (1880) from Wisconsin and named "Skolithus woodi", be renamed Arenicolites. He preferred this name because the annelidan character of the fossil had been determined. However, this suggestion did not meet with success and the ichnogenus Arenicolites was reserved for U-shaped forms (Whitfield, 1877).

James (1892) conducted the first analysis of the ichnogenus Skolithos in which all forms previously discussed, along with other reports not mentioned, were interpreted. These forms ranged in age from Lower Cambrian (*Skolithos linearis*; Haldemann, 1840) to Triassic ("*Scolithus* (*Fucoides*) *shepardi*"; Hitchcock, 1833) and based on morphological characteristics were inseparable (James, 1892). In spite of this fact, James (1892) proposed that these species names be retained for structures in rocks of different ages or geographical regions. The reasons for this are outlined below:

> "It cannot be considered as at all probable that the annelid living in the Lower Cambrian and making the perforations we know as S. *linearis* persisted in the same form through all later geological periods into Triassic time. Mr. Walcott does not think it probable that the same species ranged even through Cambrian time, to say nothing of a much greater time-range. Yet he places forms from the lower and upper Cambrian under the same specific name. On the same principle we should unite all the species, in whatever geological horizon they may occur, under one name, for there are no characters to distinguish one form from another. But this does not seem advisable, and under the circumstances I would propose that the geological position shall decide the name to be used. Thus, *S. linearis* might be applied to the forms from the Lower Cambrian rocks of the eastern United States; *S. canadensis* to those occurring in Upper Cambrian strata of the eastern United Stated, and S. *woodi* to those from strata of similar age in the Upper Mississippi Valley; *S. minutus* might be the name for the form in Calciferous strata; *S. minnesotensis* might be applied to the forms from the St. Peter, and *S. delicatulus* to those in Cincinnati rocks; *S. clintonensis* might be applied to those from Clinton and Medina strata, *S. verticalis* to those from the Portage, and *S. shepardi* to those from the Triassic. It is probable, also, that a name should be given to forms collected from other horizons, say *S. arisonicus*, to the form from the Grand Canyon in Arizona" (James, 1892, p. 43).

These comments reflect the ideas expressed by most paleontologists of the era, in which forms, however similar, are treated as different species if found in strata of different ages. They also reflect the views held by ichnologists at this time, in that the trace fossil was regarded as a biological entity.

In addition to simple vertical burrows, Torell (1870) described vertical burrows with trumpet-shaped apertures from the Lower Cambrian of Sweden. These burrows were characterized as follows:

> "Erect, linear, superiorly somewhat widened, breadth 3-6 mm. length of the fragment 60 mm; situated in funnels (breadth 30-40 mm, height 22-30 mm). Tentacles c. 20 (in one specimen 21, in two specimens traces are found), long, extending above the margin of the funnel. Maximum length of tentacles 34 mm.
>
> Locality: In a sandstone boulder of the Cambrian formation at Lungas, Västergötland.
>
> When the worm reaches the upper part of the funnel, it seems to thrive in a sheltering tube, as is the case of recent worms of the division Tubicola." (Torrell, 1870, p. 13)

The specimens described by Torell (1870) were not illustrated and were poorly described and thus received little attention. Further descriptions of Monocraterion burrows were restricted to early Paleozoic strata in North America (Lime, 1878; Miller, 1889; Matthews, 1891, 1901).

After the major work of James (1892), there followed a period of relatively limited interest in ichnofossils of this type until the work of Richter (1920, 1921). Richter (1920) proposed a revision and clarification of the ichnogenus "Scolithus". He restricted "Scolithus" to straight, closely packed, vertical forms, which were best typified by the specimens of the Cambrian of Sweden. Richter (1920) then proposed the ichnogenus Sabellarites (for forms from the Lower Devonian Koblenz Quartzite of Germany) for irregularly loosely packed specimens, which included most of the forms previously described under the ichnogenus "Scolithus". Richter (1921) later changed this to Sabellarifex, since the earlier name was preoccupied by Sabellarites, Dawson (1890), an annelid. Richter's views, however, were not popular and Westergard (1931) undertook a re-examination of the Lower Cambrian specimens from Sweden. He observed that some scattered tubes were straight and some closely packed tubes were wavy and concluded: ". . . as these different Scolithus forms [Scolithus and Sabellarifex of Richter] are connected by intermediate forms and occur associated they can hardly be distinguished" (Westergard, 1931, p. 14-15).

In the same paper Westergard (1931) also reexamined specimens of Monocraterion originally described by Torell (1870). Since Torell's report was not illustrated and no type specimens could be located, Westergard (1931) re-described forms from the Lower Cambrian Lingulid sandstone at Lugnas, Sweden as follows:

> "A sub-cylindrical tube, perpendicular to the bedding plane, usually straight, sometimes slightly curved, ends superiorly in a funnel. Tube generally 3-4 mm in diam., often slightly increasing in width upwards; fragments 6-8 cm in length frequent; longest specimen found 16 cm. Funnel in transverse section circular or fairly irregular, in vertical section wide or narrow, straight-sided, cup- or trumpet-shaped; varying in width and depth, often 10-15 mm, rarely 20 mm in diameter; greatest depth observed 22 mm (in one specimen 20 mm in diam.). The tube continues often through the funnel, and occasionally it is seen to end in a second funnel at a higher level" (Westergard, 1931, p. 11).

Westergard (1931) also suggests that the "tentacles" described by Torell (1870) were not observed and that it cannot be ascertained that there exists any actual connection between the "tentacles" and the funnel.

Fenton and Fenton (1934) in a now classic paper, regarded "Scolithus" as being constructed by phoronids; and offered the following re-definition of the ichnogenus:

> "Tubes or tube-fillings, in pure to moderately impure sand; linear to flexuous, never branched; commonly closely crowded,

> though in many cases widely spaced. Traces of finely annulate tubes preserved in fine sands, but lacking from coarse ones" (Fenton and Fenton, 1934, p. 344).

The next major work conducted on vertical ichnofossil forms was conducted, for over a decade, by Howell. In examining _Skolithos_ forms from the Hardyston Sandstone of Pennsylvania, Howell (1943) was the first to point out the change in spelling of _Skolithos_ to "_Scolithus_" by Hall (1847). He recommended that the original spelling be used and that "_Scolithus_" be abandoned. In addition, Howell established two new ichnospecies of _Skolithos_: _S. magnus_, from the Lower Cambrian Hardyston Formation of Pennsylvania (Howell, 1944); and _S. ingens_, from the Lower Cambrian Antietam Sandstone of Maryland (Howell, 1945). Howell (1946) also described a new ichnospecies of _Monocraterion_ (_M. clintonense_); and re-defined the ichnogenus _Foralites_ to include those _Skolithos_-like burrows that were inclined and gently curved (Howell, 1954). Describing _Skolithos_-like burrows from the Cambrian Tapeats Sandstone of Arizona, Howell (1957) proposed a new ichnogenus _Stipsellus_ for those forms that exhibit ring-like expansions at regular intervals along their length. In an analysis of two ichnospecies of _Skolithos_, Howell (1955, 1958) followed the procedure of James (1892) for the designation of _Skolithos_ ichnospecies. Howell (1955) suggested that Skolithos minnesotensis, although indistinguishable from S. linearis, should be retained for Skolithos specimens of Lower Ordovician age. Similarly, Skolithos woodi would be reserved for specimens from the Upper Cambrian (Howell, 1958).

With the initiation of the "Treatise on Invertebrate Paleontology," the volume including ichnofossils was the first attempt to clarify the many ichnogenera that had been proposed. In the treatise, Häntzschel (1962) differentiated the following single-entrance, vertical ichnogenera: Asabellarifex, Cylindricum, Histioderma, Sabellarifex, Skolithos, Stipsellus, and Tigillites. Häntzschel (1962) placed Monocraterion, Foralites, and Leptocraterion in synonomy with Tigillites and suggested that Asabellarifex and Sabellarifex might be included with Skolithos.

Perhaps the most studied and spectacular example of Skolithos is in the Lower Cambrian Eriboll Sandstone of northwest Scotland. These burrows are so prolific that the strata is referred to as "pipe-rock" and have been studied since the early work of MacCulloch (1814). The investigations of Peach and Horne (1907) and McNair and Reid (1929) distinguished five separate burrow zones, composed of three different sizes of "ordinary" pipes and one zone of "trumpet" pipe. These forms were all lumped under the ichnogenus "Scolithus." Hallam and Swett (1966) re-studied these forms and placed the "ordinary" pipes in the ichnogenus Skolithos and the "trumpet" pipes in the ichnogenus Monocraterion. They did, however, propose that the same organism responsible for creating the Skolithos burrow also constructed Monocraterion, the morphological differences being related to varying sedimentation rates. A similar explanation was also proposed by Goodwin and Anderson (1974).

The first systematic review of the ichnogenus Skolithos since James (1892) was conducted by Alpert (1974b). Of the more than 35 ichnospecies examined (solely from the literature), Alpert (1974b) recognized only five distinct ichnospecies. This distinction seems to be based mainly on burrow diameter. In addition, Alpert (1974b) suggested that the following ichnogenera be placed in synonomy with Skolithos: most specimens of Tigillites, Sabellarifex, and Stipsellus and also that the ichnogenera Foralites, Haughtonia, and Cylindricum most probably are referrable to Skolithos.

Finally, in the revised edition of the "Treatise on Invertebrate Paleontology," Häntzschel (1975) distinguished the following vertical, single-entrance ichnogenera: Cylindrichnus, Cylindricum, Histioderma, Monocraterion, Neoskolithos, Pilichnia, Sabellarifex, *Skolithos*, *Stipsellus*, and *Tigillites*. The only changes from Häntzschel (1962) involved *Monocraterion*, which was earlier placed in *Tigillites*.

The preceding outline, although not by any means complete, is a synopsis of the major studies conducted on vertical, single-entrance ichnofossils.

5-3. Present Classification

A). *Cylindrichnus* Toots, 1962, p. 64 [*C. concentricus*, M.]

Cylindrichnus is a subconical form, straight to weakly curved with a circular to oval cross-section. Diameters range from 10 to 20 mm, but most commonly fall in the range from 12 to 15 mm. The burrow is penetrated by a central core that ranges from 2 to 4 mm in diameter. The exterior wall is composed of concentric layers and is preserved in full relief. The burrow is orientated from inclined to vertical.

B). *Cylindricum* Linck, 1949, p. 19

Plugs (fillings of tubes) shaped much like a test tube; rounded at the lower end, not pointed. The walls are smooth, and diameters range up to 5 cm; lengths, although variable, have been recorded up to several centimeters. Usually preserved in groups in convex hyporelief and are orientated perpendicular to the bedding plane.

C). *Foralites* Rouault, 1850, p. 742

Simple burrows, which penetrate the rock in all directions from perpendicular to inclined, but always have an aperture at the upper surface of the bed in which they lie. The burrows range from 1 to 5 mm in diameter and from 12 to 76 mm. The aperture is never funnel-shaped. The burrows are sometimes nearly straight, but are usually curved.

D). *Histioderma* Kinahan, 1858, p. 70 [*H. hibernicum*]

Vertical burrow with the upper extremeties trumpet-shaped and the lower turned up at a right angle to the bedding plane. The upper portion of the burrow is marked by several ridges crossing each other at irregular intervals. Diameters usually 12 mm and length varies from 2 to 8 cm.

E). *Monocraterion* Torell, 1870, p. 13 [*T. tentaculatum*]

Trumpet-pipes; upper funnel structure penetrated by a central straight or slightly curved tube. The funnel may be simple or multiple (seen in transverse-section as a series of concentric rings); with diameters of from 1 to 4 cm and depths of up to 2 cm. The central tube exhibits diameters of up to 5 mm and lengths up to 16 cm. The wall may or may not possess a visible lining. The entire burrow is usually oriented perpendicular to the bedding but may also be slightly inclined and it never branches.

F). Pilichnia Chamberlain, 1971a, p. 223 [P. elliptica]

Large subcylindrical gallery 60 mm wide with an oval or elliptical cross-section. Irregularly sinuous, mainly vertical but also horizontally through the sediment.

G). Sabellarifex Richter, 1921, p. 50 [S. eifliensis]

Simple vertical burrows, cylindrical to subcylindrical and never branched. Walls are smooth and never annulated. Burrows are similar to Skolithos but are less straight and not as crowded. Oriented vertically to the bedding plane.

H). Skolithos Haldemann, 1840, p. 3 [Fucoides linearis]

Simple vertical burrows, cylindrical to subcylindrical in form, usually parallel to each other. Diameters range from 1 to 15 mm and are usually constant throughout the entire length of the burrow. Lengths are highly variable; commonly up to 30 cm. The inner walls are smooth but may be finely annulated. The burrows are commonly closely packed but have also been found in isolated occurrences. Oriented vertically to inclined.

I). Stipsellus Howell, 1957, p. 18 [S. annulatus]

Vertical, cylindrical burrows that never branch. Diameters range up to 12 mm and lengths have been recorded up to 15 cm. The diameter is usually constant throughout the specimen. The walls are smooth except that the burrow was expanded at regular intervals (approximately 12 mm apart) so that narrow (1 to 2 mm in length) ring-like expansions form. The burrows are oriented perpendicular to the bedding plane.

J). Tigillites Rouault, 1850, p. 740 [T. dufrenoyi]

Simple vertical burrows, without a special lining. The walls are generally smooth but may be annulated. Burrow diameters range from 2 to 15 mm and are usually constant throughout the entire length of the burrow. Burrow lengths range up to several cm. Openings may be parallel-sided or flare to form a funnel. The burrows are usually not crowded, and are found vertically or inclined.

In addition to these forms, a number of additional ichnogenera have been proposed to describe burrows of a similar nature. These ichnogenera have not received much attention: Haughtonia Kinahan, 1850, p. 118-120; Asabellarifex Klähn, 1932, p. 14; Neoskolithos Kegal, 1966, p. 17-25; Leptocraterion Stehmann, 1934, p. 17; and Trachyderma Salter, 1864, p. 290.

5-4. Analysis of the Morphological Features of Single-Entrance Vertical Ichnofossils

Vertical, single-entrance ichnofossils exhibit a great range in morphological variation. These variations may be biologically or ethologically controlled or may merely reflect local differences in substrate characteristics. Ichnogenera must be regarded as "form genera" since a host of very different organisms may be responsible for their creation. Analysis of the morphological features of these single-entrance forms will center around those criteria that have been used to differentiate them in the past. These features include:

A). Burrow sinuosity;
B). Burrow diameter;
C). Orientation;
D). Ornamentation and lining;
E). Degree of crowding;
F). Presence of funnel-shaped aperture.

A). Burrow sinuosity

Deviation from straightness has been used to differentiate certain single-entrance, vertical ichnofossils. Richter (1920, 1921), in a re-evaluation of the ichnogenus Skolithos, suggested that Skolithos be restricted to straight, closely packed, vertical forms;

and that sinuous, loosely packed forms be placed in the new ichnogenus *Sabellarifex*. Richter (1921) did state, however, that if transitional forms could be found the ichnogenus *Sabellarifex* would prove unnecessary. This criterion was met by Westergard (1931), who found some isolated burrows that were straight and some closely packed burrows that were sinuous. Based on the recognition of these transitional forms, Westergard (1931) placed *Sabellarifex* as a synonym of *Skolithos*. Subsequently, a number of studies have illustrated that sinuous *Skolithos* burrows are quite common (Howell, 1943, 1955; Frey and Chowns, 1972). In spite of this fact, the ichnogenus *Sabellarifex* has persisted in the literature (see Selly, 1970, for example). Howell (1955), studying the ichnospecies *Skolithos minnesotensis*, found forms ranging from straight to sinuous; although he recognized the similarity between the sinuous *Skolithos* and *Sabellarifex*, he chose to retain the name *Sabellarifex* for Devonian forms. Frey and Chowns (1972) placed sinuous forms in the ichnogenus *Skolithos*, but suggested that these sinuous forms might be referrable to *Sabellarifex*. More recently, Häntzschel (1975) recognizes *Sabellarifex* as a distinct ichnogenus, although he does point out its similarity to *Skolithos*.

Fenton and Fenton (1934) stated that departure from straightness does not seem to be a character on which new ichnogenera may be based. Studies of arenicolids, capitellids, sabellarids, and phoronids indicate that in each group there exists a wide range of burrows (or tubes) which are straight to sinuous (Fenton and Fenton, 1934). Howell (1943) observed that straight Skolithos burrows were found in fine-grained sandstone and as the grain size increased so did the sinuosity of the burrow. Howard and Frey (1975) observed that burrows of the polychaete Diopatra cuprea were straight in the intertidal environment and were more sinuous in subtidal sediments. Sinuosity in the burrow of Spiochaetopterus oculatus was determined to be the result of the organism bending around rocks, shells, and other obstacles in the sediment (Howard and Frey, 1975). Chisholm (1969) suggested that sinuosity in Monocraterion burrows was due in part to the exaggerating effects of the compaction of the sediment.

It seems evident that the deviation from straightness is a function of substrate characteristics. Thus, the sinuosity of burrows cannot be used as a distinguishing characteristic.

B). Burrow diameter

Similar ichnofossils of different sizes commonly occur in the same bed or formation and are sometimes interpreted as different ichnogenera. Farrisch (1973) has pointed out that although this may be of some limited value regionally, it often breaks down when these forms are compared with ones from other areas. Frey and Chowns (1972), in studying specimens from the Silurian of Georgia, suggested that forms over 1 cm in diameter are referrable to the ichnogenus Tigillites, while forms up to 1 cm are referrable to the ichnogenus Skolithos. This seems to be very arbitrary, and examination of burrow diameter data from a number of independent studies indicate that there exists considerable overlap in the diameter of these two ichnogenera. In addition, specimens attributed to the ichnogenera Cylindricum, Foralites, and Sabellarifex also fall into the range diameters exhibited by Skolithos and Tigillites (Table 5-1).

Numerous studies on the distribution and morphology of modern polychaete burrows (see Frey and Howard, 1972; and Howard and Frey, 1975; for examples) show that a wide variety of diameters exist in these single-entrance, vertical forms which may be referrable to Skolithos. Since the diameter of these forms is related to the size of the individual and does not reflect any deviation in morphology, the burrow diameter is not a significant feature. Since ichnogenera represent, more or less, "form genera,"

Table 5-1. Selected list of reported diameter ranges for various single-entrance, vertical ichnogenera.

Ichnogenus	Diameter Range (mm)	Reference
Skolithos	2-14	Langille, 1974
	4-15	Alpert, 1974
	10-20	Howell, 1944
	2-6	Curren and Frey, 1977
	3-15	Hallam and Swett, 1966
	2-10	Webby, 1968
	4-5	Goodwin and Anderson, 1974
	2-8	Frey and Chowns, 1972
Tigillites	2-15	Rouault, 1850
	10-25	Frey and Chowns, 1972
	1-5	Volk, 1966
	1-7	Boucek, 1966?
	2-20	Gregory, 1969
	3-10	Hayward, 1976
Sabellarifex	1-7	Richter, 1921
	1-5	Selley, 1970
Foralites	1-5	Rouault, 1850
	1-5	Howell, 1954
Cylindricum	5-15	Webby, 1968

relative size is not a distinguishing characteristic. It should be noted, however, that Alpert (1874b) used burrow diameter as one of the characteristics to delineate the ichnospecies of Skolithos. This character may thus prove valuable as an accessory feature for the establishment of ichnospecies.

C). Orientation

The ichnogenus Foralites was established by Rouault (1850) for single-entrance ichnofossils that were not oriented perpendicular to the bedding plane (Pl. 5-1, fig. 1). This distinction was not deemed significant by Salter (1857), who called for the suppression of the ichnogenus Foralites and included these inclined forms in the ichnogenus "Scolithus." Subsequently, numerous other workers have also placed inclined forms in the ichnogenus Skolithos (Whitfield, 1880; Picard, 1942; Howell, 1958; Curran and Frey, 1977; and Pickerill, 1977; among others) and Foralites was somewhat ignored. Howell (1954) re-introduced Foralites and suggested that this ichnogenus be restricted not only to single-entrance, inclined forms, but also to arcuate forms (Pl. 5-1, fig. 2).

Studies on modern burrows indicates that the penetration angle may merely be an environmental response (Frey, 1971). The burrow of the polychaete Diopatra cuprea is vertical in intertidal environments but is orientated at various angles in subtidal sediments (Howard and Frey, 1975). These deviations from the vertical were attributed to inhomogeneities within the sediment. Frey (1971) has pointed out that environmental stress plays an important role in burrow orientation; intertidal burrows are usually vertical in response to increased physical stress. Even within an homogenous substrate certain polychaete burrows exhibit a wide variety of orientations: Notomastus burrows are straight to arcuate and penetrate the substrate at any angle (Howard and Frey, 1975); Glycera americana also constructs vertical to gently curved burrows (Hertweek, 1972); and burrows of the polychaete Onuphus microcephala are vertical to inclined (Frey and Howard, 1969).

As was the case with burrow sinuosity, the orientation of these single-entrance forms depends on sediment consistency and environmental stress and is not a significant morphological feature on which to differentiate ichnogenera.

D). Ornamentation and lining

Vertical, single-entrance, ichnofossils display a variety of variations in ornamentation and lining, which may reflect local differences in sediment coherence (Frey, 1971). A number of ichnogenera, now under discussion, exhibit fine annulations along their length (Pl. 5-1, fig. 3). The annulations are present in some of the specimens attributed to Skolithos (Whitfield, 1880; Picard, 1942; Howell, 1958; Langille, 1974; and Pickerill, 1977; among others); Tigillites (Hantzschel, 1964, 1965, 1975; and Hayward, 1976; among others); and Monocraterion (Goldring, 1962; and Chisholm, 1968; among others). Chisholm (1968) and Cowie and Spencer (1970) observed that annulations on the burrow wall are only present where distinct laminations are present in the host rock; where these laminations are absent in the host rock, there are no annulations on the burrow wall. Langille (1974) and Hayward (1976) made similar observations and attributed them to varying resistence of the surrounding sediment.

In modern sediments an annulated burrow wall may be developed in a number of ways. Reineck (1958) illustrates that an annulated burrow wall may form as a result of an organism repeatedly re-opening its burrow and pushing aside loose sediment. Schäfer (1972) points out that annulations may form on a burrow wall constructed in a laminated sediment. In addition, a number of modern polychaetes construct annulated tubes as a result of morphological characteristics; those include some maldanid species and Sabellaria tubes (Schäfer, 1972) and tubes constructed by the chaetopterid polychaete Spiochaetopterus oculatus (Barnes, 1964; Howard and Frey, 1975). Goldring (1962) suggested that the faint annulations of the burrow wall in Monocraterion specimens from the Devonian of Devon might be used as a criteria for distinguishing between Monocraterion and Skolithos. As many Skolithos burrows are annulated, this would not be a significant morphological feature. The actual process of burrow annulation, although biologically controlled in some instances, seems to be merely a reflection of the physical aspects of the host rock. This distinction between physical and biological control of annulation would seem too difficult to distinguish and thus wall annulation does not appear to be a significant morphological feature.

A different type of wall sculpturing is expressed by ring-like expansions found at intervals along the burrow length. Howell (1957) ascribed these particular vertical forms to the ichnogenus Stipsellus (Pl. 5-2, fig. 1). These ring-like expansions are a prominent feature of the ichnofossil and do not appear to be the result of any differences in the consistency of the host sediment. Modern organisms create ring-like expansions in a number of ways. Some species of polychaetes such as Clymenella (and other maldanids, commonly called bamboo worms) have swellings at intervals along their length (Howell, 1945; Schäfer, 1972). Similarly, ring-like expansions are also known to occur in some species of phoronids (Benham, 1890) and pogonophorans (Ivanov, 1963). Schäfer (1972) also pointed out that many polychaetes use peristaltic motions which enable them to move rapidly back and forth in their dwelling burrow. Contraction of strong, circular musculature which runs along the body causes the burrow wall to be reworked, and this results in a regular transverse segmentation, which in no way represents a mold of the body segments of the polychaeta (Schäfer, 1972). Although the mode of formation of this sculpturing varies, both methods suggest strong biological control. This factor, easily recognizable in fossil form, is therefore deemed to be representative of behaviour at a significant level. The resultant morphological difference is interpreted to be of value in differentiating vertical ichnogenera.

In addition to wall ornamentation, vertical ichnogenera often display distinct linings. Examples of forms designated as Monocraterion, Sabellarifex, Skolithos and Tigillites are often described with either distinct or indistinct walls. Distinctiveness of the burrow wall may merely reflect substrate consistency (Rhoads, 1970). Vertical burrows created in high water-content sediments usually display indistinct walls, while burrows in low water-content sediments usually display distinct walls. Stehnmen (1934) established the ichnogenus Leptocraterion for a form, although identical to Monocraterion, which displayed a distinct lining. Häntzschel (1975) indicated that this was not sufficient grounds for the erection of a new ichnogenus and placed it in synonomy with Monocraterion. Since the presence or absence of a lining (usually expressed as a distinct burrow wall) seems to be a function of the substrate; it cannot be recognized as a significant morphological feature.

A distinctive type of lining has been described by Reineck (1958), which he termed "Räumauskleidung" or reaming and lining. This occurs as a response to slow continuous sedimentation; as sediment enters the dwelling burrow it is pressed against the wall by peristaltic and undulating movements, where it is mixed with mucus. The result of a number of such episodes is a burrow having a multi-layered lining (Pl. 5-1, fig. 4). Such linings have been observed in the burrows of the polychaete Nereis (Reineck, 1958; Schäfer, 1972; Howard and Frey, 1975) and the siphonal shafts of certain bivalves (Schäfer, 1972). The recognition of such multi-layered linings in fossil form has resulted in the erection of the ichnogenus Cylindrichnus by Toots, in Howard (1966). Although this multi-layered lining results as a response to sedimentation (by some organisms) it does reflect a distinctive ethological trait. The resultant morphological difference is considered to be of a significant level.

E). Degree of crowding

A number of morphologically similar ichnofossils have been separated into distinct ichnogenera based solely on their degree of crowding. Many of the early descriptions of Skolithos made mention that they were often found crowded together (Pl. 5-2, fig. 2). This crowding was so persistent in some areas that many of these beds became known as "pipe-rock" (see Hallam and Swett, 1966). Rouault (1850) defined the ichnogenus Tigillites to encompass single-entrance, vertical ichnofossils, with or without a funnel-shaped aperture, which do not show any significant degree of crowding. Forms of Tigillites that do not have a funnel-shaped aperture are indistinguishable from Skolithos (Hallam and Swett, 1966), and are presently distinguished from Skolithos in being less crowded (Häntzschel, 1962, 1976; Gregory, 1969; Hayward, 1976). Richter (1920, 1921) used burrow crowding as one of the criteria to distinguish between Skolithos and Sabellarifex (Skolithos was closely packed and Sabellarifex was loosely packed).

It has been correctly pointed out by Hallam and Swett (1966) and Frey and Chowns (1972) that the degree of crowding is clearly not a taxonomic characteristic. The original description of Skolithos by Haldemann (1840) was based on specimens that did not show any significant degree of crowding. Moreover, Westergard (1931) illustrated that Skolithos burrows in Sweden exhibit every gradation between closely crowded and widely spaced burrows. Based on these observations Westergard (1931) suggested that the ichnogenus Sabellarifex was indistinguishable from Skolithos. Similar observations were made by Hallam and Swett (1966), who suggested that Tigillites specimens (without a funnel-shaped opening) be placed in Skolithos.

The density of organisms occupying single-entrance, vertical burrows is controlled by a multitude of factors and cannot be used as a criterion for the differentiation of ichnofossils.

F). Presence of absence of funnel-shaped aperture

The significance of the presence or absence of a funnel-shaped aperture has long been debated by ichnologists. This dilemma is especially acute in the analysis of the ichnogenera Monocraterion, Skolithos, and Tigillites. Haldemann (1840) erected Skolithos for single-entrance, vertical ichnofossils; later Rouault (1850) established Tigillites to encompass forms that did or did not display a funnel-shaped aperture. Monocraterion was erected by Torell (1870) to encompass forms which possessed a funnel-shaped aperture exclusively. Since all three of these original descriptions were quite vague and unillustrated, much confusion on the assignment of these names has resulted. In the original version of the "Treatise on Invertebrate Paleontology," Häntzschel (1962) recognized only Skolithos and Tigillites; he placed Monocraterion in synonym with Tigillites. In the revised edition, however, Häntzschel (1975) recognized all three as distinct ichnogenera.

A number of explanations have been offered to account for the formation of a funnel-shaped aperture. Deecke (1906), in an attempt to interprete funnel-shaped forms from the Lower Cambrian Balka Sandstone of Denmark, suggested an inorganic origin. Observations on modern supratidal flats led Deecke (1906) to postulate that these structures were the result of rainwater collecting in depressions and later sinking due to capillary forces through an organic layer. Composite cones also developed if more organic-rich layers were encountered deeper in the sediment. Deecke (1906) states that the resultant cones have a concentric structure visible at the upper end. Andrée (1912) postulated a similar origin for funnel-shaped tubes in the Lower Devonian Ober-Koblenzschichten in the Marburg area of western Germany. The specimens from the Balka Sandstone were subsequently re-studied by

Bruun-Peterson (1973), who assigned them to the ichnogenus Monocraterion. Since the laminae pointed in the wrong direction, the hydraulic interpretation of Deecke (1906) was disregarded.

Boyd (1966) conducted experiments to ascertain if the deflection of the laminae observed in specimens of Monocraterion, from the Middle Cambrian Flathead Sandstone of Wyoming, was the result of drag caused by the downward penetration of the burrower. The results of these experiments, however, differed in both magnitude and character from the observed laminae disruption of the Monocraterion burrows. Boyd (1966) then postulated that the downbent laminae of the Monocraterion burrows was the result of wall erosion above the stabilized part of the burrow with the stabilized tube then extending upwards in response to continued sedimentation. Boyd (1966) observed that the burrows of Callianassa are alternately covered by water and exposed to the air; after exposure the upper rim of the burrow collapsed as runoff drained into the hole; later, sand and water was extruded from the bottom of the funnel-shaped depression and a central tube re-appeared. This process would thus give downbent laminae, with a funnel-shape, penetrated by a central tube (Boyd, 1966). A similar process was observed by Crimes, et al. (1977) for U-shaped burrows from beaches in Spain and by

Goodwin and Anderson (1974) for Monocraterion burrows from the Lower Cambrian of Pennsylvania.

In an analysis of the morphological features of the ichnogenus Diplocraterion, Fursich (1974a) stated that the presence or absence of funnel-shaped apertures is governed by the following:

a). Erosion - slight erosion is sufficient to remove a funnel-shaped aperture.

b). Sediment cohesion - except when heavily lined or excavated in very firm sediment, vertical tubes will always display some sort of funnel at the depositional interface.

c). Weathering - weathering usually accentuates the size of the funnels.

Fursich (1974a) concluded that because of these processes funnel-shaped apertures were controlled by environmental factors and not behaviour; thus the resulting morphology was not a diagnostic feature. However, he failed to mention the biological interactions that aid in the development of such structures.

Hallam and Swett (1966), investigating both Skolithos and Monocraterion burrows from the Lower Cambrian Eriboll Sandstone of Scotland, concluded that the funnel-shaped aperture exhibited by Monocraterion (Pl. 5-3, fig. 1) was indeed diagnostic. They also postulated that the same organism was responsible for the creation of both burrow types; Skolithos was formed during periods of negligible sedimentation, while Monocraterion represented a response to sediment influx. Goodwin and Anderson (1974) later interpreted Monocraterion as the funnel top of a Skolithos burrow. Their arguments mainly center around the fact that Skolithos burrows are found alone in beds associated with high energy sediments which terminate in a planar erosion surface (thus the Monocraterion top was eroded). Crimes, et al. (1977) correctly pointed out, however, that cross-stratified sets containing Skolithos burrows which terminate at an upper erosion surface do not prove that the burrows were eroded, but merely show that they were a later episode. Crimes, et al. (1977) also pointed out that in the Lower Ordovician of Spain, sandy beds with gradational upper contacts with overlying muds, contain only Skolithos burrows, despite the apparent absence of erosion. These observations led them to reject both the one-organism hypothesis and the erosion hypothesis.

Frey and Chowns (1972) differentiate Monocraterion on the presence of the funnel-shaped aperture. They concluded that this represents a feeding-structure, similar to that exhibited by Arenicola, and thus does have taxonomic value. Similar feeding structures are known to be produced by the enteropneust Balanoglossus

(Howard and Dorjes, 1972). It is of interest to note that these feeding funnels are easily preserved in recent sediments (Pl. 5-3, fig. 2), and thus their preservational potential is quite high. Frey and Howard (1972) stated that the dwelling structure of the polychaete Diopatra cuprea consists of a chitinous, vertical tube ~~that is~~ commonly surrounded at its upper end by funnel-like laminae (Pl. 5-3, fig. 3). This disruption of laminae is caused by the worm building up the upper portion of the tube for reinforcement (Myers, 1970). Increased sedimentation would result in a multi-funnel cone, which is similar to the multi-funnel cones exhibited by some samples of Monocraterion (Pl. 5-3, fig. 4).

It seems evident that regardless of which explanation is employed, the presence of a funnel-shaped aperture is representative of an ethological response which is highly significant. The fact that the structure may be related to increased sedimentation or reduced grain sizes is immaterial; the morphological difference is significant and should be used as a distinguishing characteristic.

5-5. Proposed Classification

The following criteria are considered of sufficient taxonomic significance to allow differentiation of ichnogenera:

a). the presence of distinct ring-like expansions along the burrow length;

b). the presence of a multi-layered lining; and

c). the presence of a funnel-shaped aperture.

The following criteria are deemed taxonomically unimportant:

a). burrow sinuosity;

b). burrow diameter;

c). burrow orientation; ?

d). presence of faint annulations on the burrow wall;

e). the presence of a single burrow lining; and

f). the degree of crowding.

Based on these criteria, the ichnogenera previously discussed can be grouped into one of four distinctive "form ichnogenera": Cylindrichnus, Monocraterion, Skolithos, and Stipsellus.

A). The Ichnogenus Cylindrichnus, Toots, 1962
(Pl. 5-1, fig. 4)

Cylindrichnus Toots, 1962, p. 64; Howard, 1966, p. 45; Kasiazkiewicz, 1970, p. 314.

non Cylindrichnus Bandel, 1967, p. 6 [= Margaritichnus, Bandel, 1973]

Asterosoma form Cylindrichnus, Frey and Howard, 1970, p. 160, 162; Frey, 1970, p. 12; Frey, 1972, p. 22.

Anemonichnus Chamberlain and Clark, 1973, p. 677.

i). Description

Subconical to cylindrical burrow, straight to weakly curved with a circular to oval cross-section. The burrow is penetrated by a central core. Width and length may be highly variable. Orientation may be from vertical to inclined (but never horizontal) and the burrow never branches. The exterior wall is composed of concentric layers.

ii). Geological range

Forms assigned to the ichnogenus Cylindrichnus are restricted in their distribution. Numerous specimens have been found in Upper Cretaceous deposits from the Mesaverde Formation of Wyoming (Toots, 1962); the Panther Sandstone of Utah (Howard, 1966; Frey and Howard, 1970); and the Fort Hays Limestone of Kansas (Frey, 1970, 1972; Frey and Howard, 1970). Additional specimens are known from the Lower Pennsylvanian Manning Canyon Shale of Utah (Chamberlain and Clark, 1973) and the Upper Eocene of the Polish Carpathians (Kasiazkiewicz, 1970). Numerous samples have also been recently discovered by the writer from the Lower Cambrian Forteau Formation of southern Labrador (Pl. 5-1, fig.4).

iii). Interpretation

In the original description of Cylindrichnus Toots (1962) mentioned the similarity of the multi-lining to the structures in modern nereid burrows described by Reineck (1958) and termed "Raumauskleidung" (or reaming and lining). Reineck (1958) attributed this multi-lining to the activity of the organism in its burrow responding to a slow continuous sedimentation rate; as sediment entered the burrow it was pressed against the burrow wall. Multi-lined burrow walls such as these have been recognized in the burrows of the polychaete Nereis (Reineck, 1958; Schäfer, 1962; Howard and Frey, 1975), the siphonal shafts of certain bivalves (Schäfer, 1972), and burrows of the thalassinid crustacean Callianassa (Schäfer, 1972). Howard (1966) referred to Cylindrichnus as merely the dwelling burrow of a filter-feeding organism. Frey (1970) suggested that it may be the vertical shaft of a crustacean formed ichnogenus Thalassinoides. Finally, Chamberlain and Clark (1973) proposed that sea anemones were the originators of these structures, the multi-layered infil being a response to vertical movements.

B). The Ichnogenus Monocraterion Torell, 1870

(Pl. 5-3, figs. 1, 4; Pl. 5-4, figs. 1, 2)

? Histioderma Kinahan, 1858, p. 70; Crimes and Crossley, 1968, p. 200; Crimes, 1970b, p. 109.

Monocraterion Torrell, 1870, p. 12; Prime, 1878, p. 12; Prime, 1878, p. 79; Miller, 1889, p. 519; Lesley, 1889, p. 417; Matthew, 1891, p. 160; Matthew, 1901, p. 135-136; Cole, 1901, p. 82; Bassler, 1915, p. 822; Westergard, 1931, p. 11-14; Howell, 1946, p. 33-35; Goldring, 1962, p. 233-234; Häntzschel, 1964, p. 92-93; Häntzschel, 1965, p. 57; Hallam and Swett, 1966, p. 103; Chisholm, 1968, p. 111-114; Swett, 1969, p. 635; Crimes, 1970a, p. 60; Swett, *et al.*, 1971, p. 408; Frey and Chowns, 1972, p. 28; Brun-Peterson, 1973, p. 513-524; Alpert, 1974a, p. 37-38; Goodwin and Anderson, 1974, p. 781-784; Langille, 1974, p. 66-70; Häntzschel, 1975, p. W182-W184; Crimes, *et al.*, 1977, p. 118-120; Pickerill, *et al.*, 1977, p. 242-245.

Monocraterion Volk, 1967, p. 98 (misspelling).

Tigillites Rouault, Cole, 1901, p. 82 (*partim*); Haug, 1922, p. 179; Boucek, 1938, p. 249; Häntzschel, 1962 (*partim*), p. W218; Webby, 1969, p. 1003; Häntzschel, 1975 (*partim*), p. W117.

Tigellites Barthel and Barth, 1972, p. 578 (misspelling).

Scolithus Hall, Peach and Horne, 1907 (*partim*), p. 372; Hogbom, 1924, p. 78; Macnair and Reid, 1929 (*partim*), p. 55.

Leptocraterion Stehmann, 1934, p. 17; Häntzschel, 1965, p. 52.

Sabellarifex Richter, Selly, 1970 (partim), p. 484.

i). Description

Vertical pipes which display a funnel-shaped aperture and never branch. The upper funnel structure is penetrated by a central straight or slightly curved tube (Pl. 5-4, fig. 1). This funnel may be simple or multiple (seen in cross-section as a series of concentric rings). Burrow dimensions are highly variable. The burrow wall may or may not exhibit a visible lining and is usually smooth but may display faint annulations. The entire burrow is usually oriented perpendicular to the bedding, may also be slightly inclined, but is never horizontal. Specimens in which the infilling has weathered out may not show a central tube, but will still display the distinctive expanded aperture (Pl. 5-4, fig. 2).

ii). Geologic range

The ichnogenus Monocraterion has been described from a number of Lower Cambrian deposits from around the world (Torell, 1870; MacNair and Reid, 1929; Westergard, 1931; Hallam and Swett, 1966; Swett, 1969; Swett and Smitt, 1972; Alpert, 1974a; Goodwin and Anderson, 1974; Langille, 1974; Crimes, et al., 1977; and Pemberton, et al., 1977). In addition, specimens have also been reported from the Middle Cambrian (Boyd, 1966); the Upper Cambrian (Crimes, 1970a); the Ordovician (Rouault, 1850); the Silurian (Howell, 1946; Frey and Chowns, 1972; Pickerill, et al., 1977); the Devonian (Goldring, 1962; Brun-Peterson, 1973); the Carboniferous (Chisholm, 1968), as well as the Lower Jurassic (Häntzschel, 1975).

iii). Interpretation

Peach and Horne (1907), investigating vertical burrows, both Skolithos and Monocraterion, from the Eribol Sandstone of Scotland, proposed that they represented the burrows of deposit-feeding annelids. Hallam and Swett (1966), studying these same forms, suggested that they represented the dwelling burrows of suspension-feeding annelids. The funnel-shaped aperture of Monocraterion was interpreted to be an escape feature which resulted from an influx of sediment. Langille (1974) noted that the funnels may represent a zone of sediment disturbance resulting from the alternating extension and retraction of a feeding apparatus; multi-funnels resulted from an influx of sediment in which the animal would adjust to its position. As previously outlined, Frey and Howard (1972) indicated that the dwelling tube of the polychaete Diopatra cuprea resembles Monocraterion.

C). The Ichnogenus Skolithos Haldemann, 1840
(Pl. 5-1, figs. 1-3; Pl. 5-2, figs. 2-4).

Skolithos Haldemann, 1840, p. 3; Howell, 1943, p. 6-16; Howell, 1957b, p. 17-18; Häntzschel, 1962, p. W214; Gekker and Ushakov, 1962, p. 857; Dalgarno, 1962, p. 7-8; Häntzschel, 1964, p. 88-91; Häntzschel, 1965, p. 85; Borrello, 1966, p. 25; Webby, 1968, p. 1002; Conybeare and Crock, 1968, Pl. 42, Pl. 43, fig. A; Swett, 1969, p. 635; Seilacher, 1969b, Pl. 1, fig. 2; Osgood, 1970, p. 325-327; Cowie and Spencer, 1970, p. 94-96; Banks, 1970, p. 30; Crimes, 1970a, p. 61; Crimes, 1970b, p. 101-103; Frey and Chowns, 1972, p. 26, 28; Greggs and Bond, 1972, p. 939; Germs, 1972, p. 865-866; Young, 1972, p. 5; Chamberlain and Clark, 1973, p. 680; Alpert, 1974a, p. 35-36; Alpert, 1974b, p. 661-663; Langille, 1974, p. 55; Peterson and Clark, 1974, p. 766-767; Copper, 1974, p. 375; Alpert, 1975, p. 510; Häntzschel, 1975, p. W106-W108; Pickerill, et al., 1977, p. 246; Crimes, et al., 1977, p. 126; Curran and Frey, 1977, p. 148-150; Baldwin, 1977, p. 27; Pickerill, 1977, p. 6; Miller, 1977, p. 1334; Ekdale and Berger, 1978, p. 273.

Fucoides verticalis Hall, 1843, p. 242.

Scolithus Hall, 1847, p. 2 (non Pascoe, 1873, p. 171 = insect); Hitchcock, et al., 1861, p. 356; Hunt, 1878, p. 135-139; Nathorst, 1881, p. 49; Barrois, 1882, p. 177; Whiteaves, 1883, p. 109; Ami, 1886; p. 304; Lebesconte, 1886, p. 793; Miller, 1889, p. 520-521; Dawson, 1890, p. 602; Wanner, 1890, p. 35-38; James, 1891, p. 32-44; Grabau and Shimer, 1910, p. 246; Högbom, 1915, p. 45-59; Bassler, 1915, p. 1153; Westergard, 1931, p. 14-16; Shimer, 1933, p. 192; Fenton and Fenton, p. 341-348; Twenhofel and Shrock, 1935, p. 137, Text - gis. 42E; Shimer and Shrock, 1944, p. 234; Moore, Lalicker and Fisher, 1952, p. 456; Shrock and Twenhofel, 1953, p. 258, 512-513, Text - figs. 8-5A, B, 11.12E; Andrews, 1955, p. 235; Seilacher, 1956; p. 164; Opik, 1959, p. 11-12; Häntzschel, 1965, p. 83; Lowry, 1966, p. 254-255; Andrews, 1970, p. 184; Swett, et al., 1971, p. 408; Swett and Smitt, 1972, p. 3230-3231; Goodwin and Anderson, 1974, p. 781-784.

Skolithus Hall, 1847, p. 2 (misspelling)

Scolithas Billings, 1862, p. 96 (misspelling)

Scolitus Fritsch, 1908, p. 18 (misspelling)

Scolithuus Sampelayo, 1915, p. 279 (misspelling)

Scollithus Sampelayo, 1915, p. 283 (misspelling)

Scolithos Seilacher, 1967a, p. 72 (misspelling)

Tubulites Rogers in Hall, 1847, p. 2 (nomen nudium; non Gesiver, 1758 = annelid; non Bein, 1932 = microproblematica); Häntzschel, 1965, p. 96.

Scolecolithus Roemer, 1848, p. 171; Goeppert, 1851, p. 189; Andrews, 1955, p. 235; Häntzschel, 1965, p. 83; Andrews, 1970, p. 194.

Tigillites Rouault, 1850, p. 740; Tromelin and Lebesconte, 1876, p. 624; Tromelin, 1877, p. 26; Crié, 1878, p. 687; Lebesconte, 1883, fig. 20, 21; non Lisson, 1904, p. 37-41 (U-shaped); Haug, 1922, Pl. 79, left; Boucek, 1938, p. 244-252; Peneau, 1946, p. 78; Melendez, 1950, p. 67; Lessertisseur, 1955, p. 60; Andrews, 1955, p. 251; Häntzschel, 1962 (partim), p. W218; Häntzschel, 1965 (partim), p. 92-93; Gubler, 1966, p. 181-182; Borrello, 1966, p. 25-26; Volk, 1967, p. 97-99; non Webby, 1968, p. 1003, Text - figs. 3, 4 (= Monocraterion); ? Gregory, 1969, p. 12-13; Heinberg, 1970, p. 232; Andrews, 1970, p. 215; Frey and Chowns, 1972, p. 28, 28; Häntzschel, 1975 (partim), p. W117; Hayward, 1976,

non Tigillites danieloi Rouault, 1850, p. 741 (? = Laevicyclus).

non Tigillites habichi Lisson, 1904, p. 41, Text - fig. 21; Douvillé, 1908, p. 362, figs. 2-4;

non Tigillites vertebralis Fritsch, 1908, p. 28, Pl. 5, figs. 7, 8 (branches downward); Boucek, 1938, p. 245-250, Pl. 17-19, Text - fig. 1.

Tigilites Prestwich, 1888, p. 39 (misspelling)

Foralites Rouault, 1850, p. 742 (*partim*); Tromelin and Lebesconte, 1876, p. 624; Delgado, 1885, p. 87-89; Peneau, 1946, p. 77; Melendez, 1950, p. 67, Pl. 2, fig. 3; Howell, 1954, p. 1-2; Andrews, 1955, p. 159; Häntzschel, 1965, p. 36; Andrews, 1970, p. 90.

non Foralites pomeli Rouault, 1850, p. 745 (horizontal; Melendez, 1950, Pl. 2, fig. 3.

non Foralites hoeninghausi Rouault, 1850, p. 743-744 (double tubes).

Forallites Bigsby, 1868, p. 30, 213 (misspelling).

Floralites Gubler, 1966, p. 182, 279 (misspelling).

Scolites Salter, 1857 (*partim*), p. 204; Häntzschel, 1965, p. 83.

non Scolites Salter, 1873, p. 2, 10 (= *Planolites*); Salter, 1881, p. 483; Prestwich, 18888, Text - figs. 10C.

non Scolecites Salter, 1873, p. 2, 10 (= *Planolites*); Häntzschel, 1965, p. 83.

? *Haughtonia kinahan*, 1859, p. 118-120; Häntzschel, non Scotolithus Linnarsson, 1871, p. 18 (star-shaped); Häntzschel, 1962, p. W242; Häntzschel, 1965, p. 83; Häntzschel, 1970, p. 210.

Arenicolites Whitfield, 1882 (partim), p. 177; Chamberlain, 1883 (partim), p. 127-128; Etheridge, 1888 (partim), p. 34.

Sabellarites Richter, 1920, p. 226 (non Dawson, 1890, p. 605 = tubes); Häntzschel, 1965, p. 81.

Sabellarifex Richter, 1921, p. 49 (pro Sabellarites); Häntzschel, 1962, p. W214-W215; Häntzschel, 1965, p. 81; Selly, 1970 (partim), p. 484; Häntzschel, 1975, p. W102.

Asabellarifex Klähn, 1932, p. 14; Häntzschel, 1962, p. W184; Häntzschel, 1965, p. 11.

? Cylindricum Linck, 1949 (not seen); Häntzschel, 1962, p. W189-W190; Häntzschel, 1965, p. 28-29; Webby, 1968, p. 1003; Häntzschel, 1975, p. W57-W58.

non Neoskolithos Kegel, 1966, p. 17-25 (inorganic)

? Pilichnia Chamberlain, 1971a, p. 223; Chamberlain, 1971b, fig. 6-9; Chamberlain and Clark, 1973, p. 679; Häntzschel, 1975, p. W95; Gutschick and Rodriguez, 1977, p. 202-203.

? Pilichna Chamberlain and Clark, 1973, p. 679, Pl. 3, figs. 1, 7, Text - figs. 3 (misspelled)

i). Description

Vertical, single-entrance, unbranched burrows, cylindrical to subcylindrical, lined or unlined. The burrows are straight to sinuous to arcuate and are often inclined (but never horizontal). Diameters and lengths are highly variable. The inner walls are smooth but may be finely annulated; sediment infill is usually structureless but may display a meniscus-fill.

ii). Geological range

The ichnogenus Skolithos ranges throughout the Phanerozoic, from the Late Precambrian to the Quaternary (Häntzschel, 1975).

iii). Interpretation

Like many ichnogenera, Skolithos has been interpreted in a multitude of different ways (Table 5-2). Most early workers interpreted Skolithos to be the remains of marine plants preserved in situ (Haldemann, 1840; Hall, 1847, 1852). Logan (1852) seems to be the first to have postulated an annelid origin for such structures. A rather unusual explanation was given by Billings (1865) who claimed to have discovered sponge spicules in the sediment of infill of Skolithos burrows from the Potsdam Sandstone of Eastern Canada, and concluded that they were the result of some type of sponge activity. An inorganic origin was postulated by Hogbom

(1915), who believed that Skolithos represented the passage of air through the sediment which was forced to the surface when the incoming tide covered a dry sand flat. This theory, however, did not gain much acceptance since Skolithos burrows never branch or intersect and are in some cases too straight and dense to represent anything else but an organic entity. Richter (1920, 1921), in his review of the ichnogenus, suggested that they were the fossilized tubes of the filter-feeding annelid Sabellaria. This view is still maintained by some later workers (Kirtley and Tanner, 1968; Copper, 1974).

Macnair and Reid (1929), in a most convincing argument, postulated that the Skolithos burrow was similar to the intertidal burrow of the lugworm Arenicola. This interpretation was dismissed by Wells (1945) who showed that Areieda constructs a J or L shaped burrow and not the simple vertical burrow that was assumed earlier. In a now-classic paper, Fenton and Fenton (1934) concluded that many dense associations of Skolithos may be the tubes of lophophorate-feeding phoronids. This was based on observations of the burrows of the phoronid Phoronopsis viridis in the tidal flat at Elkhorn Slough, California.

Seilacher (1964) introduced the ethological classification of ichnofossils in which it was recognized that there exists more than one originator for a

Table 5-2. List of tentative interpretations given to explain the origin of *Skolithos*.

Interpretation	Reference
Stems of marine plants preserved *in situ*	Haldeman, 1840 Hall, 1847, 1852
annelid burrow	Logan, 1852
sponge affinity	Billings, 1865
brachiopod pedicle perforations	Perry, 1872
inorganic-pathways of rising air bubbles	Hogbom, 1915 Geinitz, 1915
tubes of the filter-feeding annelid *Sabellaria*	Richter, 1920, 1921
burrow similar to the lug worm *Arenicola*	McNair and Reid, 1929
tubes of the phoronid *Phoronopsis viridis*	Fenton and Fenton, 1934
tubes of the filter-feeding annelid *Sabellaria*	Kirtley and Tanner, 1968 Copper, 1974
burrows of the polychaete *Onuphis microcephala*	Curran and Frey, 1977

particular ichnogenus. As a result of this, it is imperative to note that since there exists a multitude of possible originators, each separate example must be studied on its own and interpretations should be based on the particular characteristics displayed by it. For example, Curran and Frey (1977) present excellent data that indicate that Skolithos burrows in the Pleistocene of North Carolina were probably created by the burrowing polychaete Onuphis microcephala. Kirtley and Tanner (1968) and Copper (1974) suggest that some Skolithos burrows were probably created by sabellid polychaetes. With the advent of studies on modern burrows, it was shown that a multitude of polychaetes could be responsible for the creation of a Skolithos-like ichnofossil. These include, for example: Laeonereis culveri, Mesochaetopterus taylori, Onuphis eremita, Onuphis nebulosa (Hertweck, 1972; Curran and Frey, 1977); Clymenella torquata, Spiochaetopterus oculatus, Owenia fusiformis, Pista sp. (Howard and Frey, 1975).

D). The Ichnogenus Stipsellus Howell, 1957 (Pl. 5-2, fig. 1)

? Trachyderma serrata Salter, 1864, p. 290, Pl. 15, figs. 9a, b.

Stipsellus Howell, 1957, p. 18-19; Häntzschel, 1962, p. W218; Häntzschel, 1965, p. 80; Häntzschel, 1975, p. W112.

Stripsellus Howell, 1957, p. 18-19 (misspelling);
Häntzschel, 1965, p. 89.

Scolithus Hall, Picard, 1962 (partim), p. 11-14;
McKee, 1945, p. 46.

Skolithos annulatus Alpert, 1974b, p. 664.

Skolithos sp. Pickerill, et al., 1977 (partim),
p. 246.

non Stipsellus Dawson, et al., 1977, p. 179 (horizontal, branching).

i). Description

Vertical, cylindrical, single-entrance burrows that never branch. Diameters and lengths highly variable. The burrow walls are smooth except were expanded at regular intervals, so that narrow ring-like expansions form. The burrows are found perpendicular to the bedding plane but may be inclined (never horizontal).

ii). Geological range

The ichnogenus Stipsellus has received very little mention in the literature; the original description was based on specimens from the Lower to Middle Cambrian Tapeats Sandstone of Arizona (McKee, 1945; Howell, 1957). Certain forms from a Lower Cambrian formation in western Arabia described by Picard (1942) and placed in the ichnogenus Skolithos may be referrable to Stipsellus. Additional Lower Cambrian specimens have been seen by the writer in the Bradore Formation of southern Labrador. Pickerill, et al. (1977) stated that some vertical forms from the Silurian Chaleurs Group of Quebec resemble Stipsellus.

iii). Interpretation

Since very few samples of Stipsellus have been described not much is known about its probable originators. As previously discussed, the ring-like expansions are known from a number of modern organisms, most notably maldanid polychaetes (Howell, 1945; Schäfer, 1972).

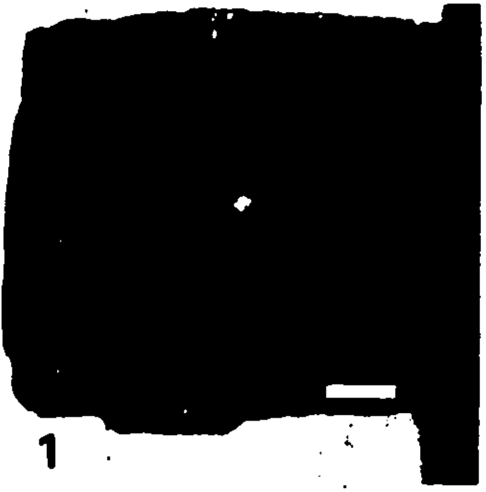
Explanation of Plate 5-1

Fig. 1. Inclined specimen of <u>Skolithos</u> sp., note that orientations vary from vertical to oblique, scale bar equals 1 cm (specimen courtesy of Princeton University).

Fig. 2. Arcuate specimen of <u>Skolithos</u> sp. (= <u>Foralites americanus</u> of Howell, 1954). From upper Cambrian Theresa Fm. of New York, X1. (Specimen No. 56432, Princeton University).

Fig. 3. Specimen of <u>Skolithos</u> sp. displaying distinct annulations, X2. (Specimen courtesy of the National Museum of Belgium).

Fig. 4. <u>Cylindrichnus</u> sp. from the Lower Cambrian Bradore Fm. of southern Labrador. Note the distinct nature of the multilayered lining. Scale bar equals 1 cm.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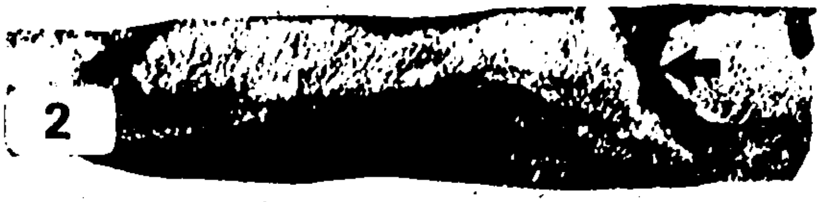
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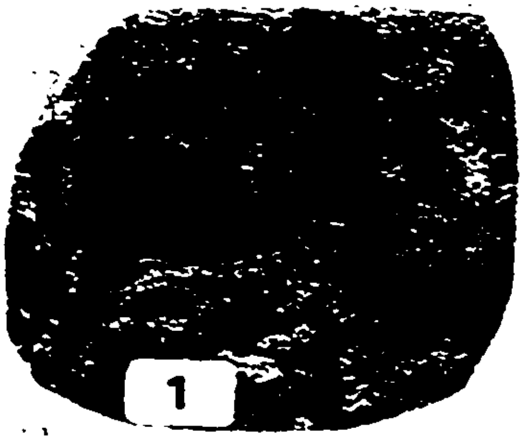
Explanation of Plate 5-2

Fig. 1. Stipsellus annulatus from the Cambrian Tapeats Fm. of Arizona, X1 (Specimen courtesy of the Grand Canyon National Park Museum, No. 8535).

Fig. 2. Dense assemblage of Skolithos linearis burrows from the Lower Cambrian Bradore Fm., southern Labrador, scale bar equals 1.5 cm.

Fig. 3. Variations in sinuosity displayed by Skolithos sp. burrows (specimens courtesy of Princeton University). Scale bar equals ½ cm.

Fig. 4. Skolithos linearis from the Lower Cambrian Bradore Fm., southern Labrador. Scale bar equals 1 cm.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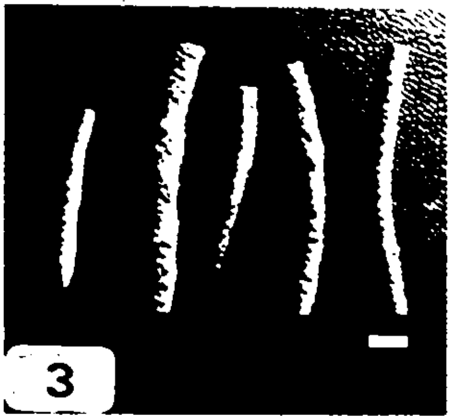
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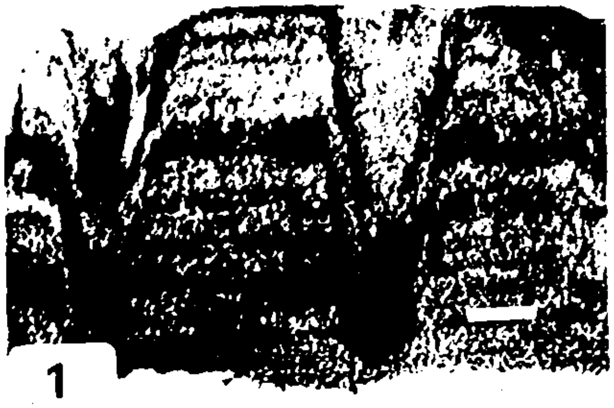
Explanation of Plate 5-3

Fig. 1. *Monocraterion* sp. from the Lower Cambrian Eriboll Sandstone, northwestern Scotland, in vertical section. Note downward deflection of sedimentary laminae. (Specimen courtesy of the Grant Institute of Geology, University ~~of~~ Glasgow, No. 22063). Scale bar equals 1 cm.

Fig. 2. X-ray radiograph of upper portion of *Balonoglossus* feeding burrow. Scale bar equals 3 cm. (after Howard and Dörges, 1972).

Fig. 3. X-ray radiograph of the dwelling tube of the polychaete *Diopatra cuprea*, from the Georgia coast. Note that the funnel-shaped depressions in the sediment laminae surrounding the upper portion of the tube (after Frey and Howard, 1972). Scale bar equals 1 cm.

Fig. 4. *Monocraterion* sp. from the Lower Cambrian Bradore Fm., southern Labrador. Bedding plane view showing central cylinder, X.75.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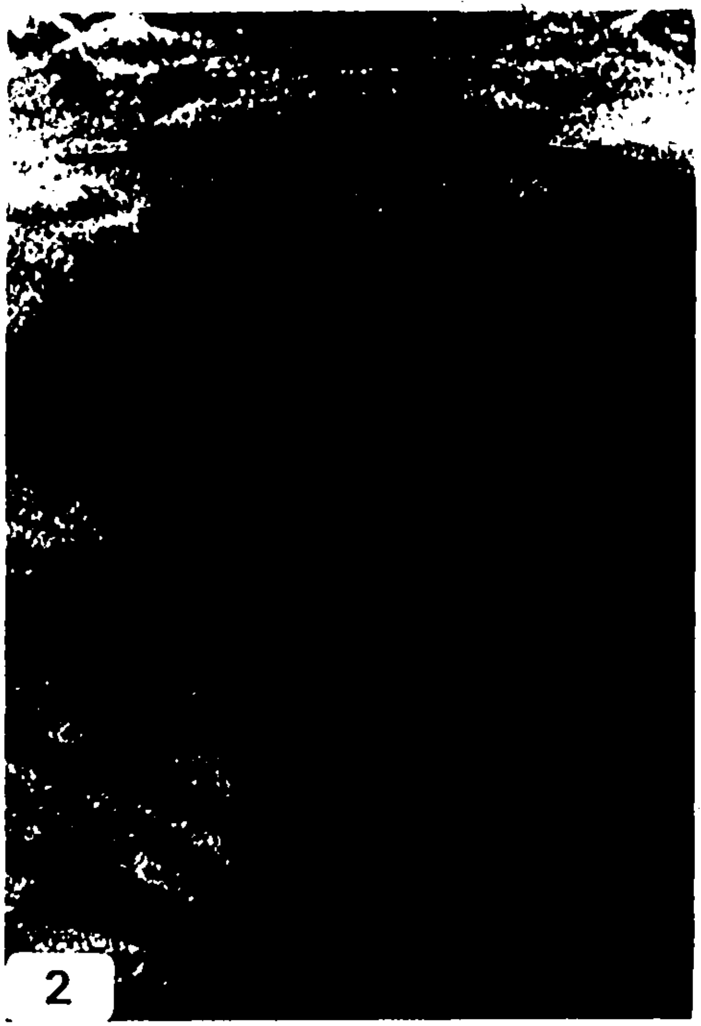
Explanation of Plate 5-4

Fig. 1. Monocraterion sp. from the Lower Cambrian Bradore Fm., southern Labrador, showing central shaft which ends abruptly. Scale bar equals 1 cm.

Fig. 2. Monocraterion sp. from the Lower Cambrian Bradore Fm., southern Labrador. Burrow resulting when the infill weathers out, note expanded aperture and sudden decrease in diameter. Hammer for scale.

1



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CHAPTER 6

Trypanites from Southern Ontario: Origin, Form and Zoological Affinities

6-1. Introduction

Many groups of metazoa are known to bore into hardgrounds and skeletons, among which are the cirripeds, sponges, polychaetes, sipunculids, phoronids, and pelecypods (Warme, 1975). Although the history of macroborings is long and includes borings in rocks as old as Lower Cambrian (James, _et al._, 1977), almost nothing is known with any degree of reliability, of the organisms responsible. A notable exception is the recent study by Pojeta and Palmer (1976) on the borings of mytilacean pelecypods from the Ordovician. There are many reasons for this lack of understanding, among the most prominent being the inherent difficulties in studying often poorly preserved and infilled fossil borings. An exceptionally well-preserved subaerial karst erosion surface on the Silurian of southern Ontario that underwent boring during the Devonian marine transgression (Kobluk, _et al._, 1977) provides the evidence for detailed analysis and interpretation.

The sub-Devonian (Gedinnian) disconformity is developed on the Upper Silurian Bertie Formation (formerly Bertie-Akron Formation: Caley, 1940, 1941; Telford and Tarrant, 1975). In the study area in southern Ontario, from Hagersville in the west to Port Colborne in the east (fig. 6-1), the lowest Devonian beds, the Oriskany Sandstone and the Springvale Sandstone Member of the Bois Blanc Formation (Emsian), directly overlie the Silurian Bertie Formation (fig. 6-2).

The disconformity at the top of the Bertie Formation represents extreme shallowing and subaerial exposure. The transgression, which covered the area with Oriskany orthoquartzitic sand, was followed by a second regression and period of subaerial exposure prior to the influx of Springvale glauconitic and quartzitic sands (Kobluk, et al., 1977). Both disconformity surfaces developed small scale Karst features, including an irregular to undulatory solution topography, ridges, solution holes and protuberances as well as ledges, solution-widened joints and surface pits. In addition, macroborings are commonly developed on the lips of joints, along ridges and ledges, and along the surfaces of both pre- and post-Oriskany disconformities; the borings were produced during intertidal and subtidal nearshore and shoreline phases of the Devonian marine transgression. The borings in the Bertie dolomite contain detrital quartz, clay, and

Fig. 6-1. Map of Niagara Peninsula, southern Ontario, indicating localities where Silurian-Devonian contact has been identified and field studies were undertaken (after Kobluk, et al., 1977).

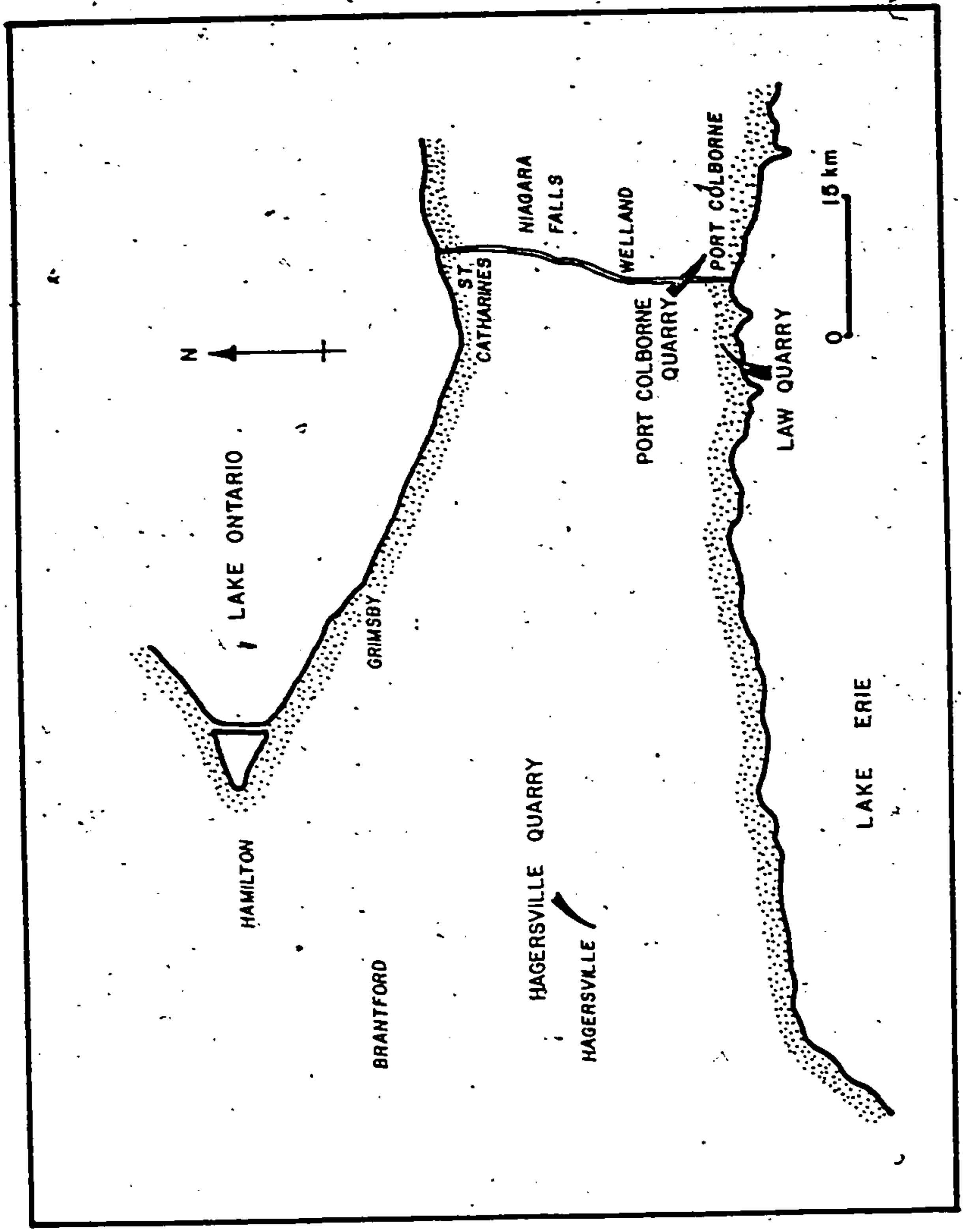
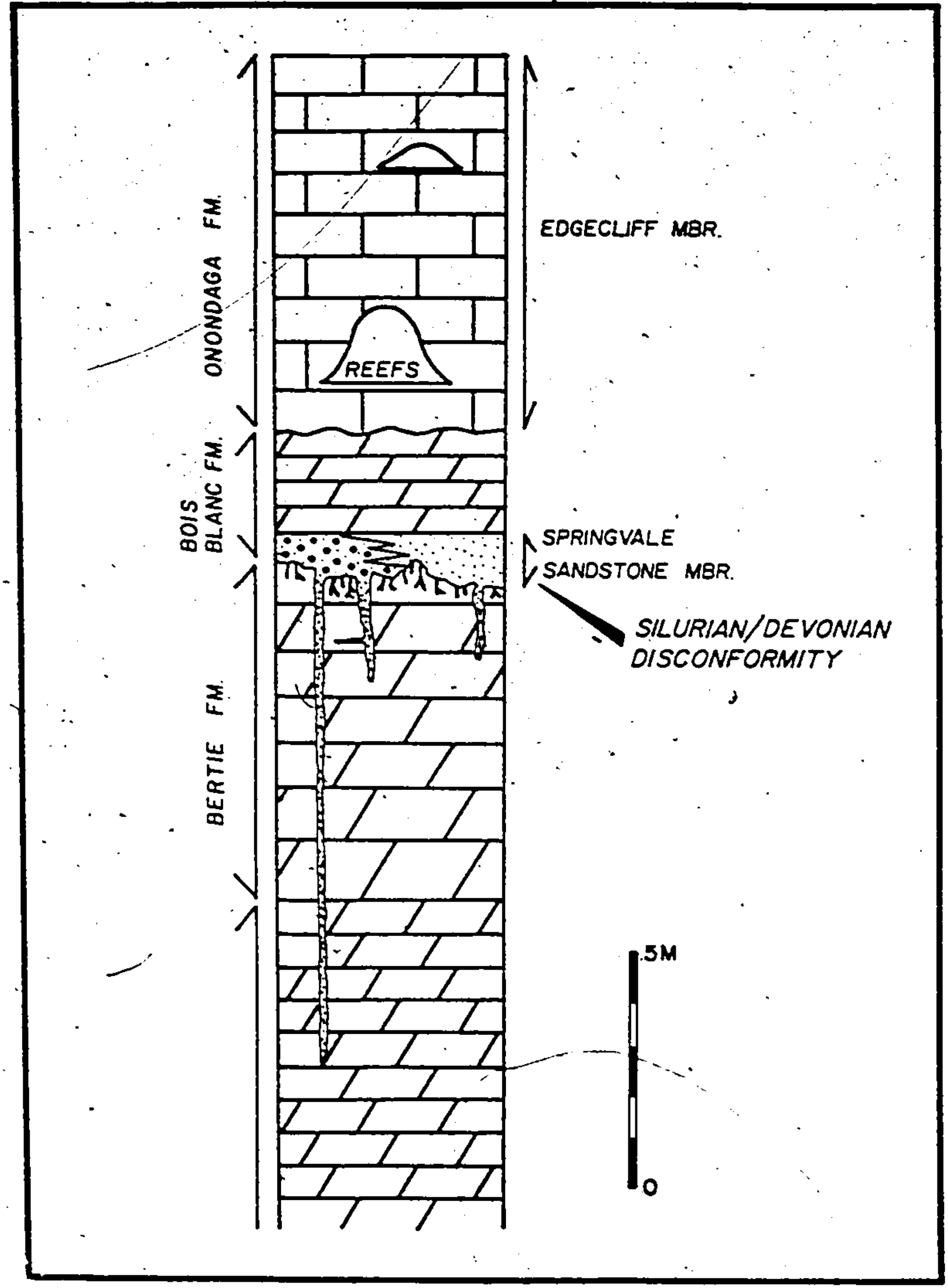

LAKE ONTARIO
N
HAMILTON
GRIMSBY
ST. CATHARINES
NIAGARA FALLS
WELLAND
PORT COLBORNE QUARRY
PORT COLBORNE
LAW QUARRY
0
15 km
LAKE ERIE
HAGERSVILLE QUARRY
HAGERSVILLE
BRANTFORD

Fig. 6-2. Composite stratigraphic section of the study area, showing relative position of the Silurian-Devonian disconformity (after Kobluk, _et_ _al_., 1977).


ONONDAGA FM.
EDGECLIFF MBR.
REEFS
BOIS BLANC FM.
SPRINGVALE SANDSTONE MBR.
SILURIAN/DEVONIAN DISCONFORMITY
BERTIE FM.
.5M
0

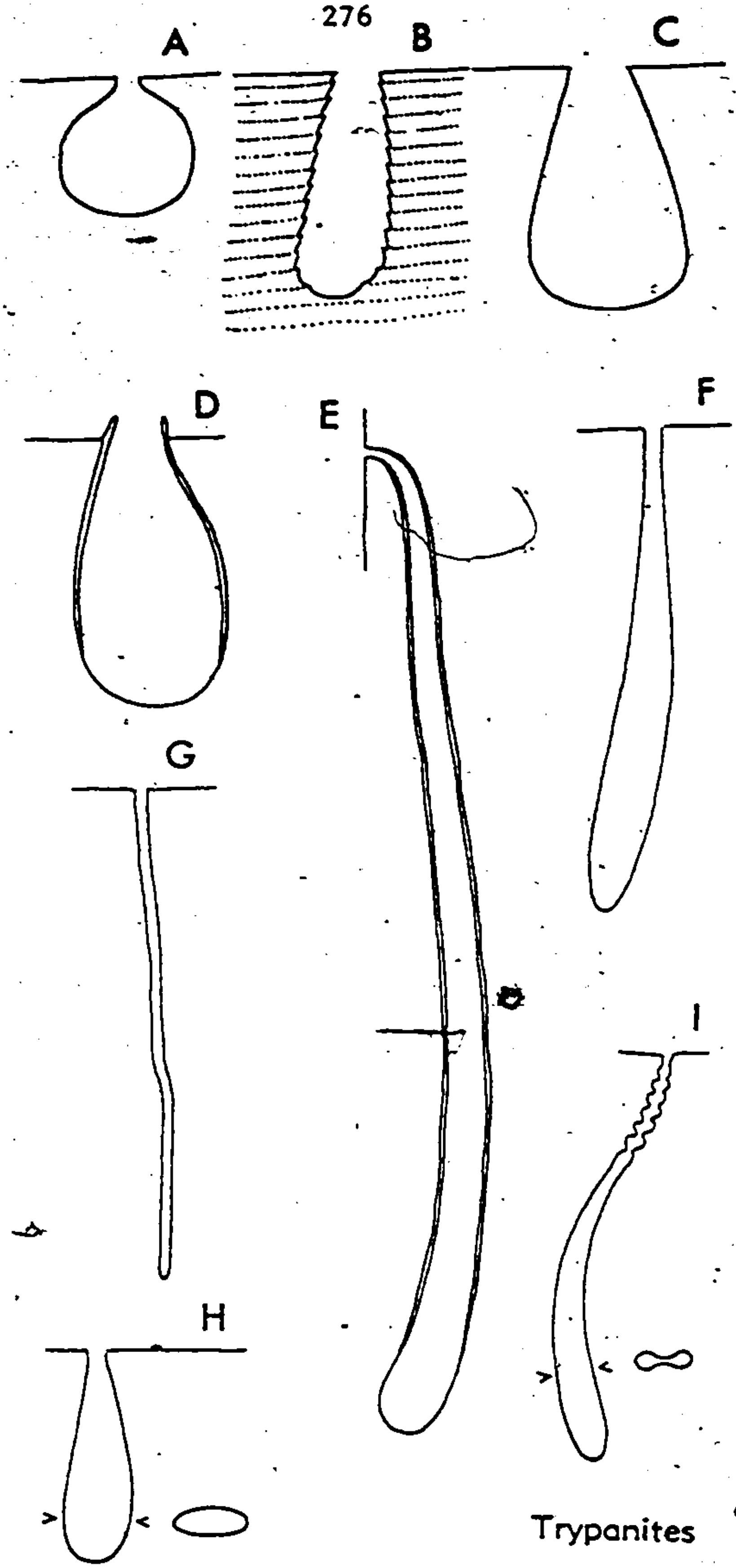
dolomite grains and rock fragments, and clearly indicate that the dolomitization of the Bertie sediments was pre-Devonian, possibly primary dolomitization.

These borings have been identified as belonging to the form ichnogenus Trypanites Magdefrau, 1932 (fig. 6-3), which includes any single-entrance, pouch-shaped boring (Bromley, 1972). Although well known from Paleozoic deposits as old as upper Lower Cambrian (James, et al., 1977), little work has been done on the zoological affinities of Trypanites. Bromley (1972) suggested that probable originators of these and similar borings include bivalves, polychaetes, sipunculids, and phoronids. Glazek, et al. (1971) concluded that borings attributed to the sabellid polychaete Potamilla could also be classified under the genus Trypanites.

6-2. The Ichnogenus Trypanites

Recently Bromley (1970, 1972) and Hantzschel (1975) pointed out the confusion which arises when fossil cavities are given the names of modern boring organisms. They suggested general ichnological names for groups of borings, such as Entobia Bonn for all borings possibly produced by sponges (Bromley, 1970), and Trypanites Magdefrau for all single-entrance, pouch-shaped borings (Bromley, 1972), as described above. Redescription of Trypanites involved grouping seven different ichnogenera into a synonymy. In addition,

Fig. 6-3. Schematic longitudinal sections of a range of forms of *Trypanites*. A: Subspherical boring of bivalve. B: *T. vadaszi* (Vitális). Boring of bivalve in wood. C and D: *T. clavatus* (Leymerie). Flask-shaped borings of bivalves with or without calcareous lining. E: Boring of teredinid bivalve (in wood with calcareous lining. F: Common form, generally with the work of sipunculids or annelids. G: *T. weisei* Magdefrau. Borings of sipunculids, phoronids or annelids. H: *T. cretacea*. and I: *T. biforans*. Borings of polychaetes (after Bromley, 1972).



Trypanites

Bromley (1972) suggested that 2 ichnospecies which were named after extant organisms, namely Polydora biforans Gripp, 1967, and Dodecaceria cretacea Voigt, 1971, should also be included in synonymy with Trypanites. Borings described from several deposits have been attributed to the recent sabellid polychaete Potamilla (Ellenberger, 1947; Radwanski, 1959, 1970; Holder and Hollman, 1969; and Glazek, et al., 1971). These are very similar in morphology to Trypanites and should be incorporated into this ichnogenus (Holder and Hollman, 1969; Voigt, 1970b; Glazek, et al., 1971). Recently, Hillmer and Schulz (1973) redefined borings attributed to Polydora biforans and established the new ichnogenus Ramosulcichnus for borings of this type. It is suggested that Ramosulcichnus be placed in synonymy with Trypanites.

A). Systematic paleontology

Ichnogenus Trypanites Magdefrau, 1932

Teredolites Leymerie, 1842, p. 2., Pl. 2, figs. 4-5

Gastrochaenolites Leymerie, 1842, p. 3, Pl. 3, fig. 1

Trypanites Magdefrau, 1932, p. 151

Nygmites Magdefrau, 1937, p. 56

Specus Stephenson, 1952, p. 51, Pl. 8, figs. 4-6

Martesites Vitalis, 1961, p. 124, Pls. 1-2
Vermiforichnus Cameron, 1967, p. 190,
figs. 1-2
Conchifora Muller, 1968, p. 68, figs. 3-7
Ramosulcichnus Hillmer and Schulz, 1973,
p. 9-10, Pl. 1, figs. 1-4

Diagnosis: Simple borings with a single opening to the surface.

Discussion: Pouch-shaped borings excluding those of acrothoracican cirripeds. From the single entrance the boring may extend as a subspherical crypt, a flask-shaped or conical cavity, as a long cylindrical tube or a flattened U-shaped chamber with figure-eight entrance. Borings in all hard substrates are included, with no age or size restriction.

6-3. Description of Modelling of Boring Morphology

The borings in the hard ground disconfirmity in Ontario have been preserved in two ways. Springvale Member sands have infilled most of the borings, forming well-preserved casts (Pl. 6-1). Locally, however, post-disconformity sedimentation by Oriskany orthoquartzites has plugged the entrances of many borings so that they have remained open and pristine (Pl. 6-2, fig. 1). Plate 6-2, figure 2, is a radiograph of a typical cut section illustrating this feature.

A model was developed in order to provide some basis, other than simple description, for comparing the fossil structures to modern borings. Direct measurements of the size and geometry of the borings were made in order to describe the morphology. Ratios of the dimensions of the borings were found to be independent of size, which permitted mathematical modelling of the borings.

Two slabs from the Silurian hardground were embedded (surface downward) in plastic casting resin, then immersed in hydrochloric acid. After acid digestion, the remains consisted of some undissolved carbonate, silica, and the quartz, clay, and glauconite infillings of the borings, as casts. Thirty-seven complete casts, as well as a large number of broken casts, were obtained in this fashion.

Typical borings are narrow, elongate structures that expand downwards gradually and end in hemispherical to hemielliptical terminations (Pl. 6-3, figs. 1-5). Plate 6-4 illustrates the high densities and spatial relationships of the borings within the hardground surface. The length of individual borings ranges from a few millimeters to over 6 cm. The average length is 1.4 cm (37 samples); the average width is 0.18 cm (37 samples). A few of the borings show branching as well as cross-cutting by adjacent borings

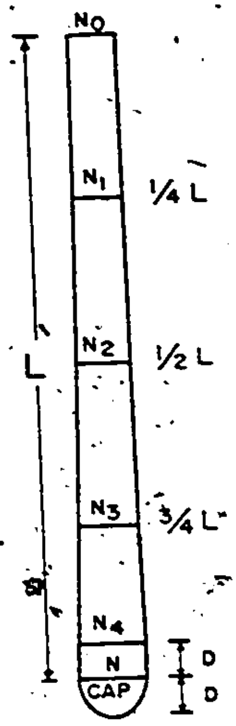
(Pl. 6-3, figs. 2, 3, 6), representing a later episode of boring. Most of the branchings appear to be invasions of the initial boring, probably by larval or juvenile forms, as suggested by the large contrast in branch lengths and diameters (Pl. 6-3, fig. 6). Branchings caused by one individual should tend to be more uniform in size.

To model the borings, 37 complete casts obtained by acid dissolution were used. The procedure is similar to that applied by Evans (1968a) in his study of the boring morphology of <u>Penitella penita</u>. Casts were measured using either a micrometer, a ruled grid under a binocular microscope, or from photographs; figure 6-4 summarizes the results.

Individual borings were found to increase in diameter distally from the aperture, becoming largest near the termination. The bottom of the boring, from the maximum diameter to the end, is here termed the cap (see fig. 6-4). All further measurements of the boring are taken relative to the maximum diameter N, which defines the top of the cap. D is the length of the cap measured from N to the end of the boring; L is the length from the top of the boring to N, and N_0, N_1, N_2, N_3, are the diameters of the boring measured at quarter of L intervals. N_4 is the diameter measured 1 cap length (D) from N (numerical analysis conducted by R. K. Yeo).

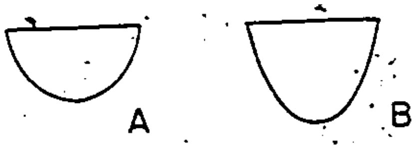
Fig. 6-4. Empirical models describing the morphology of the hardground borings. The bottom of the boring, from the maximum diameter to the end, is here termed the cap. All further measurements of the boring are taken relative to the maximum diameter N, which defines the top of the cap. D is the length of the cap measured from N to the end of the boring; L is the length from the top of the boring to N, and N_0, N_1, N_2, N_3 are the diameters of the borings measured at quarter of L intervals. N_4 is the diameter measured 1 cap length (D) from N. Diagrams indicate parameters measured and shapes of Type A and Type B caps. Morphotypes A and B represent the mean of their respective populations, and type A-B, the overall mean for the 37 specimens.

BURROW MORPHOLOGY



PARAMETER	MORPHOTYPE		
	TYPE A	TYPE B	TYPE A-B
D	0.558 (N) ± .024	0.800 (N) ± .086	0.632 (N) ± .103
L	18.6 (D) ± 2.4	15.4 (D) ± 2.6	17.0 (D) ± 3.2
N_0	0.675 (N) ± .038	0.747 (N) ± .043	0.719 (N) ± .035
N_1	0.731 (N) ± .085	0.805 (N) ± .038	0.774 (N) ± .072
N_2	0.830 (N) ± .062	0.873 (N) ± .036	0.855 (N) ± .053
N_3	0.900 (N) ± .056	0.940 (N) ± .024	0.924 (N) ± .045
N_4	0.981 (N) ± .008	0.970 (N) ± .018	0.974 (N) ± .016

CAP SHAPE



Two different populations are differentiated using the data gathered from measuring these parameters, which are here referred to as morphotypes A and B, based upon the proportions of the cap (see fig. 6-4). Cap type A defines a nearly perfect half-circle ($D = 0.50\ N$), whereas type B is elongated in the D direction ($D = 0.80\ N$). The separation of the two morphotypes was made at $D = 0.65\ N$, approximately the mean for the 37 specimens. This resulted in two almost equal populations ($n = 16$ for type A; $n = 21$ for type B). Morphotypes A and B represent the mean of their respective populations, and type A-B, the overall mean for the 37 specimens. The table in figure 6-4 presents the empirical data relating dimensions of a boring to a percentage of the parameters N or D. For example, given a type A boring with a maximum diameter (N) of 2.0 cm, the diameter of entrance to the boring (N_0) should be 0.5586 x (2.0 cm ± 2.4%).

In general, type A borings show greater variation in diameter, with a rapid increase in diameter to the cap. Type B borings tend to be slightly longer with more constant diameters. One feature not immediately apparent from the model is that in some cases, the N_0 diameter is greater than the N_1, indicating an enlargement just at the opening of the bore hole. Many of the borings are also gently curved or bent at angles of 120° to 160°, commonly near the top or base of the structure.

Another feature of the borings includes later penetration of the boring walls by endolithic algae (Kobluk, et al., 1977).

6-4. Survey of Modern Macroboring Organisms

A). Polychaetes

Many different species of polychaetes are known to be active borers, including representatives of the eunicids, sabellids, spionids, flabelligerids and cirratulids.

i). Eunicids

The morphology of the borings of eunicids follows two basic strategies. The most prolific consists of a branching network with many separate openings (Pl. 6-6, fig. 1), and is characterized by the species Eunice mutilata, Eunice schemacephala, Eunice kinbergi, Morphysa stylobranchiata and Palola paloloides (MacGeachy and Stern, 1976; McHuron, 1976; Bromley, 1978). These systems attain diameters of from .5 to 4 mm and lengths of up to 10 cm (MacGeachy and Stern, 1976). A different morphology, one of a long horizontal, meandering, U-shape, with two entrances, is displayed by the species Marphysa sanguinea (Warme, 1975), and Lysidice ninetta (Bromley, 1978). Systems of this type attain widths of up to 5 mm or more and are commonly many decimeters in length (Warme, 1975).

Boring is accomplished mainly by mechanical means; eunicids possess strong jaws, setae and acicula which are employed to physically excavate the boring system (Hartman, 1954). Dales (1963), however, points out that eunicids secrete mucus and suggested that this may aid in softening the rock matrix, thus facilitating the mechanical excavating process. This mechanical rasping of the substrate results in characteristic gouges on the burrow walls along the entire length of the boring (McHuron, 1976). This sculpturing, however, is less evident in the older (proximal) sections of the boring, where the walls have been smoothed by the constant passage of the worm (Bromley, 1978). Eunicid borings have been found in a wide variety of lithologies, from corals (Ebbs, 1966; James, 1969; MacGeachy and Stern, 1976; Bromley, 1978) and carbonate lithologies (McHuron, 1976) to purely terrigenous mudstones, siltstones and sandstones (Warme, 1975; McHuron, 1976).

ii). Sabellids

Initial investigation by Treadwell (1917) indicated that sabellids were not active borers but rather embedders, whose growth kept pace with that of the coral. Later studies by MacGeachy and Stern (1976) and Bromley (1978), however, have demonstrated that the sabellid Hypsicomus elegans is an active borer (based mainly on cross-cutting relationships of the boring and the corallites). The boring of Hypsicomus elegans is a vertical unbranched structure which exhibits a circular cross-section (fig. 6-5A) and attains diameters of from 1 to 4 mm and lengths of up to 20 cm (Bromley, 1978). Although the boring displays a uniform diameter throughout its length, MacGeachy and Stern (1976) noted that the distal end tapers rapidly to a blunt point. Bromley (1978) observed that the borings were lined with a chitinous sheath and as a result the walls display no sculpturing or ornamentation.

Another well-known sabellid borer is Potamilla, which excavates a straight boring with a circular cross-section (fig. 6-6 A). Diameters have been reported up to 6 mm and lengths up to 5 cm (Glazek, et al., 1971). Borings are isodiametric throughout their length and display no thickenings or constrictions (Radwanski, 1959). Glazek, et al. (1971) observed that Potamilla borings were rarely vertical, but instead were oriented obliquely. The borings are never found to bifurcate or to intersect one another (Radwanski, 1959) and commonly display a funnel-shaped aperture (Holder and Hollmann, 1969).

Fig. 6-5. Macroboring morphologies. A. Boring of sabellid polychaete Hypiscomus elegans, longitudinal section, X1 (after Bromley, 1978). B. Boring of flabelligerid polychaete Pherusa inflata, longitudinal section, X2 (after McHuron, 1976). C. Boring of gastrochaenid bivalve Gastrochaena hians, longitudinal section, X1 (after Bromley, 1978). D. Boring of pholadid bivalve Penitella penita, longitudinal section, X1 (after McHuron, 1976).

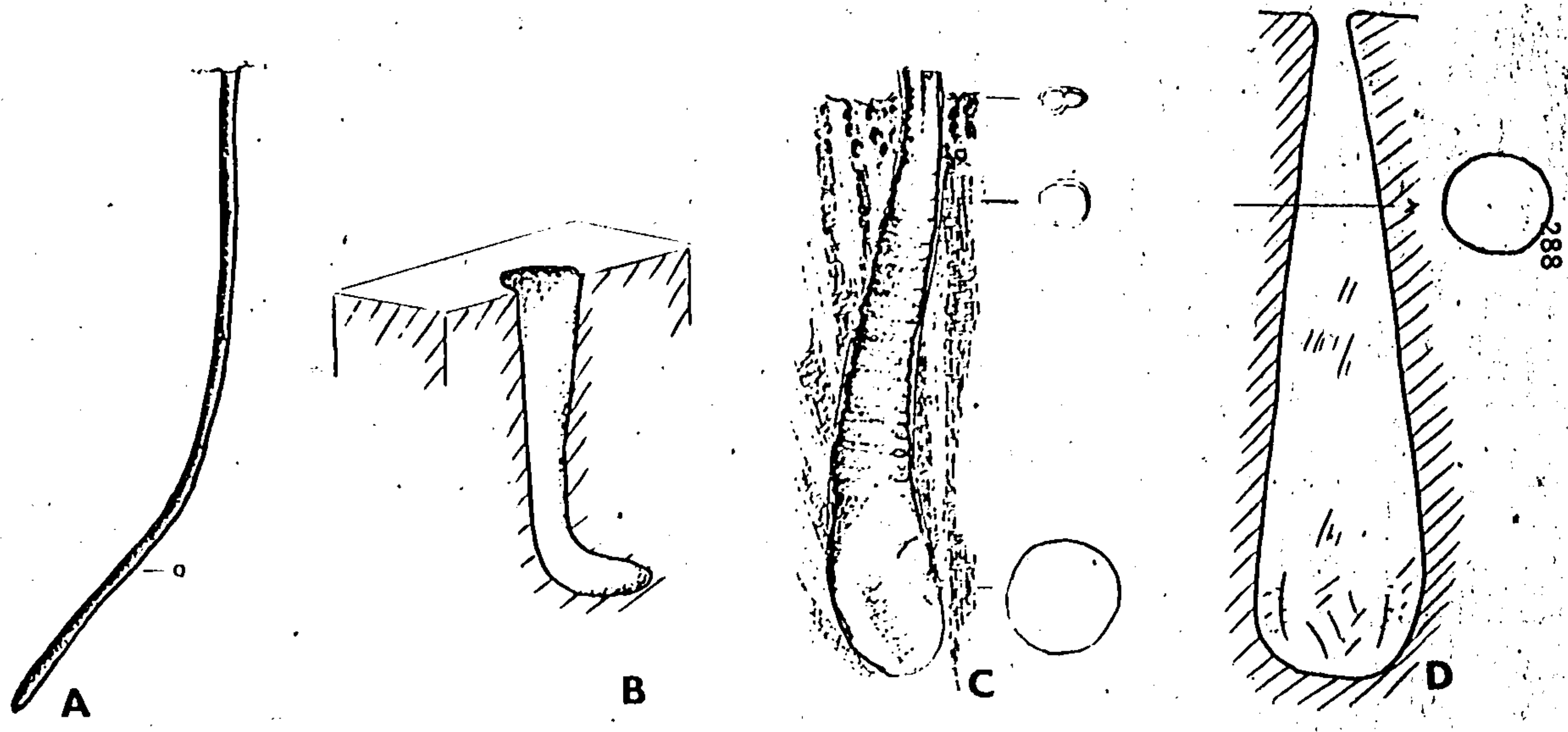
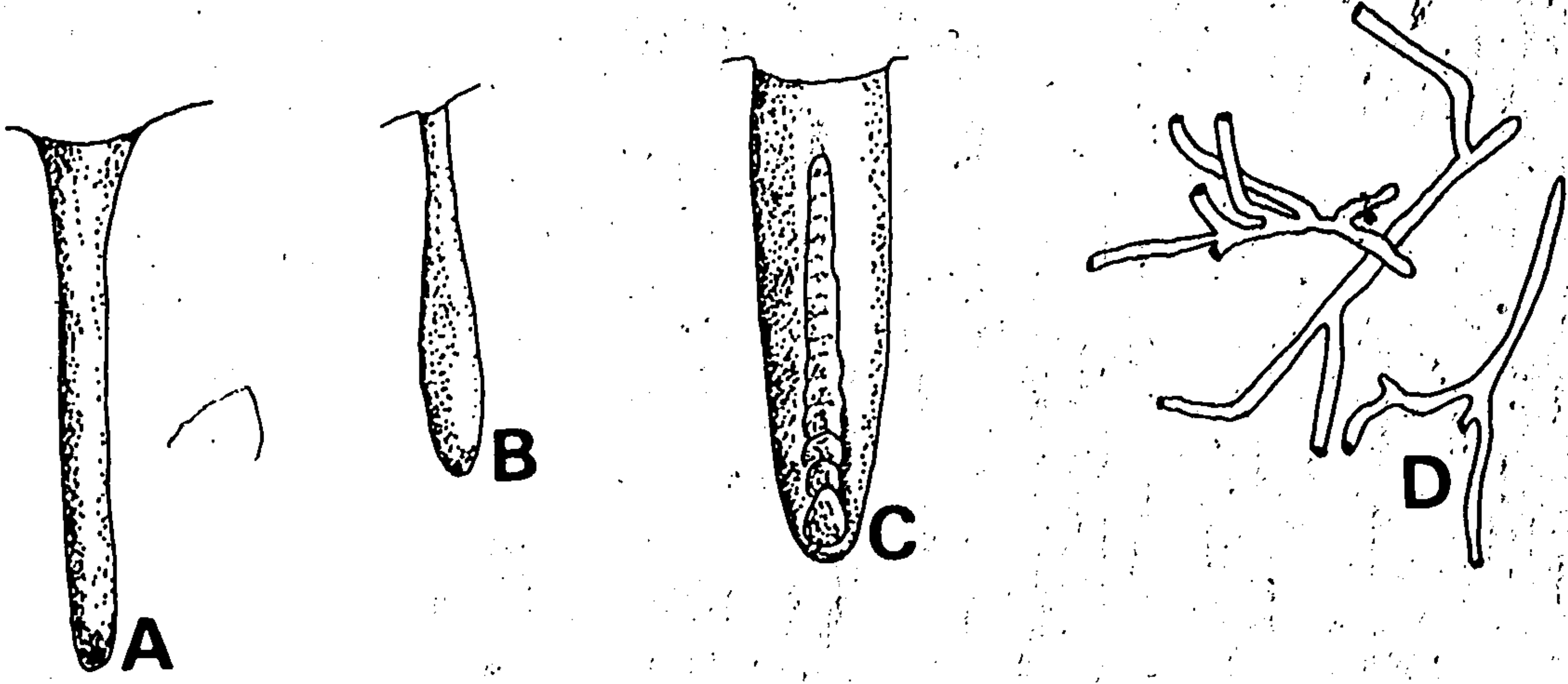

a
A
B
a
C
288
D

Fig. 6-6. Schematic longitudinal sections of the borings of organisms that create Trypanites-like traces. A: The sabellid polychaete Potamilla sp. (after Holder and Hollmann, 1969). B: The sipunculid Dendrostomum (after Bromley, 1970). C: The thoracican cirriped Lithotrya. The series of calcareous discs represent successive attachment positions of the animal (after Bromley, 1970). D: The phoronid Phoronis ovalis (after Bromley, 1970).


A
B
C
D

Bromley (1978) stated that it was unlikely that sabellids could bore with their head end due to its specialized prostomium. Likewise, sabellids are not able to double back within their narrow boring, which suggests that boring is accomplished by the posterior end. Lack of any obvious tools led Bromley (1978) to postulate that boring is done by chemical means. Similar observations were made by Knox (1951) for Potamilla borings. Sabellid borings have been found in shells and coral (MacGeachy and Stern, 1976; Bromley, 1978) and calcareous rocks (Holder and Hollman, 1969; Glazek, et al., 1971).

iii). Spionids

Blake and Evans (1972) state that only the members of the polydorid complex (Polydora, Pseudopolydora, and Boccardia) are capable of active boring. The polydorids are perhaps the most studied group of polychaete borers (Korringa, 1951, 1952; Hempel, 1957; Dorsett, 1961; Dean and Blake, 1966; Haigler, 1969; Cameron, 1969; Bromley, 1970; Blake and Evans, 1972). Although a large variety of morphologies and sizes exists in the borings of this group, the basic plan is quite similar. The boring is a straight, blind-end structure with a figure-eight or oval cross-section (Blake and Evans, 1972). McHuron (1976) states that polydorid borings often exhibit complex branching patterns while Hein and Risk (1975) observed that they are commonly U-shaped.

The mechanism of boring is a much debated issue, and has been summarized by Blake and Evans (1972). Two different theories have been postulated, mechanical boring utilizing the setae and chemical boring utilizing acid secretion. The principal proponent of the mechanical theory is Hempel (1957) who found scratch marks on the boring wall and worm setae in some specimens of Polydora ciliata. On the other hand, Haigler (1969) observed that species of Polydora etch carbonate and no inorganic material was discharged from an active boring, which both indicate that boring was chemical. Evans (1969) also observed that Polydora cancharum enlarged the branches of the boring simultaneously which also indicates chemical excavation. Hannerz (1956) and McHuron (1976) observed features of both mechanical (scratch marks) and chemical (etch marks) and suggested that both means were being utilized.

Polydorid borings are found in a wide range of sediment types both calcareous and noncalcareous (Blake and Evans, 1972; McHuron, 1976) as well as organic substrates (Blake, 1969; Haigler, 1969; Bromley, 1970).

iv). Flabelligerids

MacGeachy and Stern (1976) and McHuron (1976) were the first to suggest that the flabelligerid *Pherusa* was an active borer. Although no direct observations were made on the organism actively boring, the snug fit of the organism in the boring suggests that it was not occupying a pre-existing hole (MacGeachy and Stern, 1976). The borings of *Pherusa* are club-shaped, with a circular cross-section (fig. 6-5 B) and are generally quite small with diameters of from 1 to 2 mm and lengths of up to 25 mm (MacGeachy and Stern, 1976). The aperture shows a slight funnel shape (McHuron, 1976) and the boring tapers from the anterior and terminates in a point (MacGeachy and Stern, 1976). McHuron (1976) postulated that boring was accomplished by a combination of mechanical and chemical means. The only sculpturing found was faint annulations on the wall in the central portion of the boring (McHuron, 1976). Flabelligerid borings have been observed in coral, shells, and terriginous rocks (MacGeachy and Stern, 1976; McHuron, 1976).

v). Cirratulids

The cirratulid *Dodecaceria* is known to be an active borer in shells (Blake, 1969) and pebbles (Voigt, 1970b). The boring is similar to that of *Polydora* in that it is a sub-horizontal, flattened

U-shape (Evans, 1969). It differs in that the boring of Polydora has a figure-eight cross-section while Dodecaceria has an oval cross-section (Bromley, 1970).

vi). Fossil polychaete borings

Fossil borings attributed to polychaetes have recently been reviewed by Cameron (1969), Bromley (1970) and Warme (1975). As is the case with modern polychaete borings, forms similar to the polydorids have received the most attention. A number of ichnogenera have been established to encompass forms attributed to polydorids, including Polydora biforans (Gripp, 1967), Polydorites (Holder and Hollmann, 1969), Meandropolydora (Voigt, 1965), Caulostrepsis (Clarke, 1908), Ostreoblabe (Voigt, 1965), Ramosulcichnus (Hillmer and Schulz, 1973), and Vermiforichnus (Cameron, 1969a, 1969b).

Borings attributed to the sabellid Potamilla have been described from the Middle Jurassic of Western Europe (Holder and Hollmann, 1969), the Lower Jurassic of the Tatra Mountains (Radwanski, 1959), the Cretaceous of the Cracow Upland (Glazek, et al., 1971), the Paleocene of the Paris Basin (Ellenberger, 1947), the Eocene of the Tatra Mountains (Roniewicz, 1970), and the Miocene of the Holy Cross Mountains (Radwanski, 1970). In addition, Teichert (1945) established the ichnogenus Conchotrema for fossil forms in Permian brachiopods, that displayed polychaete affinities.

Bromley (1972) also suggested that certain forms of the ichnogenus Trypanites may have been created by polychaetes.

B). Phoronids

Phoronid borings (fig. 6-6 D) are irregularly winding tubes from .2 to .3 mm in diameter, and are of variable length (Bromley, 1970). The individual tubes are isodiametric throughout their length and, due to secondary boring by new individuals, a complex branching pattern results (see Bromley, 1970). Densities of up to 150 borings per square centimeter of Phoronis ovalis, in various shells, were recorded by Marcus (1949). Fossil borings attributed to phoronids have been restricted to Mesozoic deposits (Joysey, 1959; Voigt, 1970a, 1972; Perkins, 1971). Voigt (1972) has ascribed the ichnospecies Talpina ramosa to fossil phoronid borings.

C). Thoracican cirripeds

The literature dealing with borings of the thoracican cirriped Lithotrya has recently been reviewed by Bromley (1970), Ahr and Stanton (1973) and Warme (1975). These cylindrical bore holes with an oval cross-section (fig. 6-6 C) range in diameter from 5 to 8 mm and attain lengths of up to 10 cm (Bromley, 1970). The boring is commonly gently curved and tapers to a rounded end (Ahr and Stanton, 1973). Within the boring, a trail of abandoned basal plates are often well preserved (Pl. 6-6, fig. 2) along one side near the base (Bromley, 1970, 1978; Ahr and Stanton, 1973; McHuron, 1976). The genus Lithotrya bores by mechanical abrasion with the aid of calcified plates which occur on the surface of the peduncle and cover the capitulum (Ahr and Stanton, 1973). The borings are usually oriented perpendicular to the surface and are often found to penetrate upwards from overhanging surfaces (Ahr and Stanton, 1973; Bromley, 1978).

Although thoracican cirripeds date from the Triassic (Newman, et al., 1969), no fossil borings have been attributed to this group (Ahr and Stanton, 1973).

D). Sipunculids

Sipunculid borings (Pl. 6-6, fig. 3) are normally straight to gently curved with a circular cross-section, and terminate in a rounded, cupulate chamber (Rice, 1969). Because many species of sipunculids bore, the dimensions of the bore holes are highly variable (Rice, 1970). Bromley (1978) noted that the walls were unlined and did not display any sculpturing, but Seilacher (1969b) stated that sipunculid borings often show slight radial scratch marks. Rice (1969) and MacGeachy and Stern (1976) state that differences in diameter, length, and degree of twisting were sufficient to enable the borings of different species to be differentiated. Bromley (1978), however, does not feel that these differences were great enough to allow for such a differentiation and thus grouped the different species borings together.

Sipunculids bore with the aid of both mechanical and chemical means (Rice, 1969; Rice and Macintyre, 1972; Williams and Margolis, 1974). Chemical secretions from the epidermal glands weaken the intercrystalline bonds permitting detachment of the crystals by mechanical abrasion (Rice, 1969; Williams and Margolis, 1974). Rice (1969) noted that sipunculids are well suited for mechanical abrasion since many hooks, spines, and papillae are located on the introvert and along the body wall. This dual boring mechanism enables sipunculids to bore into a variety of substrates ranging from coral (MacGeachy and Stern, 1976; Bromley, 1978) to calcareous rocks (Rice, 1969; Williams and Margolis, 1974; Warme, 1975) to non-calcareous rocks (Warme, 1970, 1975).

Sipunculid borings (fig. 6-6 B) have been observed oriented at many different angles to the surface (Rice, 1969; Warme, 1970) and observations of modern sipunculids indicate that in high densities the closely packed borings commonly interconnect (Warme, 1970).

Although rare body fossils of sipunculids are known from as far back as the Middle Cambrian (Walcott, 1911) and Silurian (Weller, 1925); few reports of fossil sipunculid borings are known. Perkins (1971) has suggested that sipunculids may have been responsible for some of the borings in Cretaceous limestones and corals from Texas.

E). Bivalves

Boring is widespread in the class Bivalvia, and has arisen independently in seven super-families: Gastrochaenacea (Otter, 1937; Purchon, 1954); Hiatellacea (Hunter, 1949); Myacea (Yonge, 1951a); Mytilacea (Otter, 1937; Yonge, 1955; Hodgkin, 1962; Turner and Boss, 1962; Goreau, et al., 1969, 1970; 1972); Pholadacea (Turner, 1954, 1955; Evans, 1969a, 1969b); Tridacnacea (Yonge, 1936); and Veneracea (Otter, 1937; Yonge, 1958; Narchi, 1975). Of these, only three contain widespread boring genera: Gastrochaenacea, Mytilacea, and the Pholadacea (Warme, 1975). Turner (1954) noted that in bivalve borings the widespread range of form is useful since the type of boring is frequently diagnostic for a given group.

Bromley (1970) indicated that bivalve borings are of considerable importance to paleoecologists because:

a). they are abundant in Mesozoic and Tertiary rocks (hardgrounds and boulders) and shells;

b). they commonly contain the body fossil of the borer; and

c). owing to detailed knowledge of modern forms, identification and paleoecological interpretation of the ichnofossil is feasible.

i). Gastrochaenids

The borings of most gastrochaenids (fig. 6-5 C) are typified by the species *Gastrochaena bians* (Warme, 1975) which construct a long (up to 10 cm) club-shaped borehole (Bromley, 1978). The boring exhibits a circular cross-section and invariably posseses a calcareous lining composed of aragonite (Warme, 1975; MacGeachy and Stern, 1976; Bromley, 1978). Bromley (1978) pointed out that the aperture consists of two separate siphonal tubes which may be jointed (as in *Gastrochaena hians*) or widely separated (as in *Sponglerìa rostrata*). These siphonal tubes may be extended for some length beyond the substrate surface and encased in calcareous chimneys (Warme, 1975). Since the boring is lined, the external wall does not display any ornamentation, although the inner wall may show a coarse ribbing which is usually confined to the central portion of the boring (Bromley, 1978).

It is believed that gastrochaenids employ chemical dissolution as a boring means (Kühnett, 1933; Warme, 1975; Bromley, 1978). As a result, gastrochaenids have been noted to be restricted to calcareous substrates, mainly coral heads and large shells (Warme, 1975).

ii). *Mytilids*

Lithophaga, a common and well-studied boring, belongs to the family Mytilidae. Kühnett (1930) recognized 46 distinct species of *Lithophaga*, most of which bore. The borings of these different species, however, are somewhat similar and display a number of shared characteristics: spindle-shaped, lined, smooth walls, circular cross-section (Bromley, 1970, 1978; MacGeachy and Stern, 1976; Warme, 1975). The spindle-shaped outline (Pl. 6-6, fig. 4) results from the animal rotating in the boring. Since so many different species of *Lithophaga* exist, the dimensions of the borehole are highly variable (Warme, 1975).

The method of boring in *Lithophaga* is related to the rotation of the shell and has been attributed to a combination of chemical and physical means (Yonge, 1955; Turner and Boss, 1962; Soliman, 1969). An acidic solution is released by gland cells positioned on the margin of the mantle, which softens the substrate and facilitates the mechanical abrasion of the rotary movements of the valves (Yonge, 1955). Ciliary currents then in turn remove the loosened fragments from the boring (Hodgkin, 1962). Recent data, however, indicate that the chemical reagent used in boring by Lithophaga is not an acid but a calcium-complexing mucroprotein which would restrict the borings to calcareous substrates (Jaccarini, et al., 1968).

Although mytilid borings are well known in calcareous substrates (Yonge, 1955; Ansell and Nair, 1969; Bromley, 1970, 1978; MacGeachy and Stern, 1976; Warme, 1977), they have also been described from calcareous (35% calcium carbonate cement) quartz sandstones (Warme and Marshall, 1970), and non-calcareous, semi-consolidated mudstones (Haas, 1942).

Other well-known mytilid boring genera differ from Lithophaga in that they do not rotate in their boreholes (Yonge, 1955). As a result, they take on the outline of the borer and the borings of the genera Adula (Warme, 1975) and Botula (Yonge, 1955; Bromley, 1978), which are basically heart-shaped.

iii). Pholads

Pholads are another well-known group of bivalve borers; over 42 species have been identified along the North American coast (Turner, 1954, 1955). In a series of excellent papers, Evans (1967a, 1967b, 1968a, 1968b, 1968c, 1968d, 1970) outlined the life history, ecology and boring characteristics of the well-known pholad borer Penitella penita. The borings of most pholads (fig. 6-5 D) are straight, conical in shape and possess a narrow entrance and a large rounded terminus (Evans, 1970). The borings are usually oriented vertically and are circular in cross-section (Evans, 1968a).

Pholads bore mainly through mechanical means by a series of periodic rotating motions (Yonge, 1964). As a result they are not restricted to calcareous substrates and are known to bore into almost any kind of rock (see Warme, 1975, for details). Turner (1954) pointed out that pholads are able to bore into rocks that are much harder than their shell because they accumulate rock grains in the mucous coat covering the foot and shell and uses them to excavate the borehole (e.g., Pholas dactyles). Rock hardness does, however, affect the shape and ornamentation of the boring (Evans, 1970). In soft substrates (e.g., mudstones) spines on the shell produce deep parallel grooves on the wall, while in harder substrates the wall is smooth and the boring is shallow (Evans, 1970).

Although many pholads occur in high densities, the borings never interconnect or branch and in unusually high densities boring may even cease entirely if entrance to another borehole cannot be avoided

(Evans, 1970). Since many different species bore, the dimensions of the borings are highly variable; diameters of up to 8 cm have been attained (Zirfaea pilsbryi; Warme, 1975).

iv). Other bivalve borers

In addition to the three groups already examined, four other bivalve groups contain genera capable of boring. These, however, are of little consequence to the discussion at hand since the majority of them do not rotate, and thus the boring reflects the morphology of the shell, e.g., Petricola (Vereracea; Warme, 1975; Bromley, 1978); Platydon (Myacea; Warme, 1975); Hiatella (Hiatellacea; Warme, 1975); and Tridacna (Tridacnacea; Warme, 1975). The majority of these borings are heart-shaped in cross-section and irregular in outline.

v). Fossil bivalve borings

A multitude of fossil bivalve borings have been described from a wide range of deposits (see Radwanski, 1964, 1965, 1959; Keen, 1969a, 1969b; Turner, 1969; and Bromley, 1970, for complete details). These examples, however, are mainly restricted to Mesozoic and Tertiary rocks, since most boring genera evolved before then (Table 6-1). Recently, however, Pojeta and Palmer (1976) described the oldest boring bivalves,

Table 6-1. Geologic range chart of bivalve borers (ages taken from Treatise on Invertebrate Paleontology, Pt. N).

Superfamily	Family	Boring Genus[1]	Range
Gastrochaenacea	Gastrochaenidae		Jurassic-Recent
Hiatellacea	Hiatellidae	*Hiatella*	Permian-Recent
Myacea	Myidae	*Platydon*	Paleocene-Recent
Mytilacea	Mytilidae		Ordovician-Recent[2]
Pholadacea	Pholadidae		Jurassic-Recent
Tridacnacea	Tridacnidae	*Tridaena*	Tertiary-Recent
Verneracea	Petricolidae	*Petricola*	Eocene-Recent

[1] Genus mentioned only in those families that have only one or two boring genera.

[2] After Pojeta and Palmer, 1976.

mytilids from the Lower Ordovician, and pointed out that they represent the only Paleozoic bivalve borings.

6-5. Comparison With Recent Forms

Examination of the macroborings produced by recent endolithic organisms indicates that four different groups produce traces similar to the hardground Trypanites borings: phoronids, polychaetes, sipunculids and thoracican cirripeds. Table 6-2 summarizes the major attributes of each group.

Bivalve borings have been omitted, as probable producers, for a variety of reasons. In most cases, boring bivalve genera belong to superfamilies and families that did not evolve until the Mesozoic (see Table 6-1; and Turner, 1969). The mytilids, which are known to be active borers from at least the Lower Ordovician (Pojeta and Palmer, 1976) can be eliminated because: the borings of mytilids are usually lined, do not increase in diameter gradually but rather exhibit a rapid expansion due to the shape of the shell, do not branch and do not interconnect (see previous discussion for references). Other mytilid borings do not fit the general shape of the fossil forms and can thus be easily dismissed.

Although each of these four major groups display similar features to the fossil borings, all but one may be eliminated as producers of the borings.

Table I: FEATURES OF MODERN *TRYPANITES*-LIKE BORINGS

ORGANISM	SIZE Diameter	SIZE Length	REPORTED DENSITIES	METHOD OF BORING	SUBSTRATES ATTACKED	CROSS-SECTION	MAJOR FEATURES OF BORING	MAJOR REFERENCES
Phoronids: e.g. *Phoronis ovalis*	.2-.3 mm.	variable	150/cm^2	chemical	shells calcareous rocks	circular	Irregular winding tubes, which may result in an interconnected pseudo-colony. Isodiametric throughout length.	Joysey, 1959 Bromley, 1970 Voigt, 1970 Warme, 1975
Polychaetes: e.g. *Potamilla* sp.	4-6 mm.	3-5 cm.	8/2.2 cm^2	chemical	calcareous rocks shells corals	circular	Funnell-shaped aperture, isodiametric throughout length. Do not bifurcate or intersect, usually orientated oblique to an abrasion surface.	Knox, 1951 Holder and Hollmann, 1969 Glazek et al. 1971
Thoracican cirripeds: e.g. *Lithotrya* sp.	5-8 mm.	variable up to 10 cm.	1/sq.cm.	mechanical	calcareous rocks coral	oval	Borings are usually curved and taper to a rounded end, intersections common. Trail of abandoned basal plates well preserved along sides.	Bromley, 1970 Ahr and Stanton, 1973 Warme, 1975
Sipunculids: e.g. *Phascolosoma antillarum*	variable	variable	up to 700/sq.m.	mechanical and chemical	calcareous rocks non-calcareous rocks coral	circular	Straight to gently curved, smooth walled, terminating in a rounded cupulate chamber, orientated at any angle to surface, slight radial scratch marks near base, closely packed borings often interconnect forming a branching network.	Rice, 1969; 1970 Rice and MacIntyre, 1972 Williams and Margolis, 1974 Warme, 1975

Phoronid borings are dismissed because of their small size and isodiametric dimensions. Sabellid polychaete borings, represented by Potamilla and Hypsicomus, can be eliminated due to their isodiametric dimensions, flared aperture, the lack of bifurcations and interconnections and the fact that distal end tapers to a blunt point. Flabelligerid polychaete borings, represented by Pherusa, can be eliminated because of their flared aperture, lack of wall sculpturing, and the fact that the boring tapers from the anterior and terminates in a point. Other polychaete borings belonging to the eunicids, the cirratulids, and the spionids do not resemble the fossil specimens in their morphology. Ahr and Stanton (1973) summarized the features diagnostic of thoracian cirriped borings, as represented by Lithotrya, to be: a). the trail of abandoned basal plates; b). frequent interconnections; c). oval cross-sections; and d). tapering to a rounded end. The fossil borings (Pl. 2, figs. 1-5) do not possess a trail of abandoned basal plates, do not taper, and display circular cross-sections.

Modern sipunculid borings, however, closely resemble the Silurian examples both in size and morphology. Plate 6-5 illustrates the similarity between modern sipunculid borings of Phascolosma sp. from Florida reef rubble and the hardground borings.

A number of modern sipunculid borings were examined and two complete borings were measured in the same manner as the parameters for the fossil model discussed above. Table 6-3 lists a comparison between observed measurements and those predicted using the "N" value (maximum diameter) of the recent borings applied to a Type B Silurian model. A Type B model was used since the cap morphology of the sipunculid borings fell within the ranges of the Type B cap discussed previously. Predicted measurements closely paralleled actual measurements within the range of error of the model, except for diameters at 1/4 L (fig. 6-4). Actual diameters were smaller than predicted values, but this may be a function of the particular sipunculid species involved.

Because many of the hardground borings have remained open and pristine, many surface features remain unaltered (Pl. 6-2, fig. 1). Slight radial scratch marks are present (Pl. 6-3, figs.1, 2) similar to the ones described by Seilacher (1969b) for modern sipunculid borings.

Boring sipunculids are known from a wide variety of different environments, ranging from intertidal to subtidal (Rice, 1969). They are known to infest calcareous beach rock and living coral (Rice, 1970), as well as terrigenous sandstones and mudstones

Table 6-3

Comparison of predicted and observed measurements of two modern sipunculid borings taken from Florida reef rubble, based on the fossil hardground model

	Observed	Predicted	Observed	Predicted
N	2.4 mm	2.4	2.01 mm	2.01
L	3.55 cm	3.88 ± .42	2.6 cm	2.48 ± .39
D	1.63 mm	1.51 ± .24	1.53 mm	1.61 ± .17
N_0	1.24 mm	1.73 ± .13*	1.06 mm	1.5 ± .1*
N_1	1.9 mm	1.86 ± .09	1.59 mm	1.62 ± .08
N_2	2.13 mm	2.1 ± .09	1.81 mm	1.76 ± .07
N_3	2.23 mm	2.22 ± .06	1.9 mm	1.89 ± .05
N_4	2.32 mm	2.32 ± .04	1.96 mm	1.95 ± .04

Predicted values were obtained by applying the actual measurement of the maximum diameter of the borings (N) to the empirically derived multiplication factors found in Fig. 6-4.

* Indicates significant deviation from the observed value.

(Warme, 1970). Rice (1970) described borings attributed to Phascolosoma antillarum in exposed bedrock (composed of calcite with some aragonite and quartz) in densities of 415 per square meter. This type of environment is consistent with the paleoecological interpretation of the hardground proposed by Kobluk, *et al*. (1977).

6-6. Summary

Well-preserved hardground borings of genus *Trypanites* provides the opportunity for detailed morphological study and the determination of zoological affinities. The description and modelling of the fossil forms in association with comparison to modern borings suggests that the *Trypanites* morpho-type present probably were created by sipunculids. This suggests that sipunculids may have been widespread in the lower Paleozoic and that the process of the coastal erosion of limestones by the macro-endoliths was active in the Devonian.

Explanation of Plate 6-1

Longitudinal section of Trypanites, showing subparallel sides, and the glauconitic Springvale sand infill. The disconformity is developed below the dark sediment above the boring, and filling the small fracture. Scale bar equals 2.6 mm.

Explanation of Plate 6-2

Fig. 1. Slabbed section illustrating the open Silurian hardground borings. Note that ornamentation on the inner surface of the boring is well preserved. Metric scale.

Fig 2. X-ray radiograph of slabbed section of hardground borings in Bertie dolomite. The borings branch, interconnect, are never U-shaped, X1.

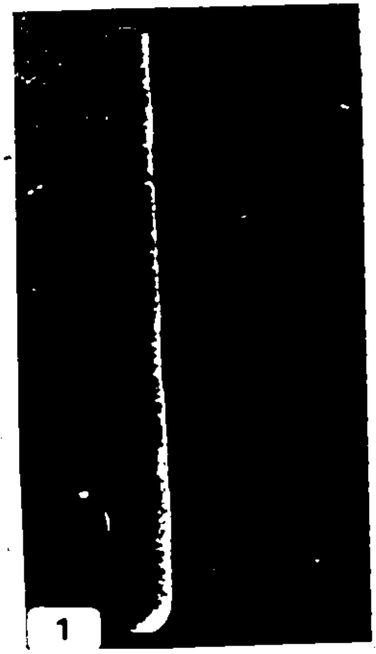
1

2

Explanation of Plate 6-3

Figs. 1-5. Glauconitic casts, the result of acid dissolution techniques, of Silurian hardground borings. Features include radial scratch marks (Fig. 1), interconnections (Fig. 2), and branches (Fig. 3). Scale in mm.

Fig. 6. Hardground boring casts showing multiple branchings and variability in branch sizes. Scale in mm.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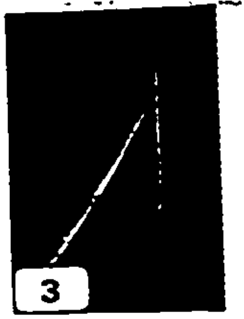
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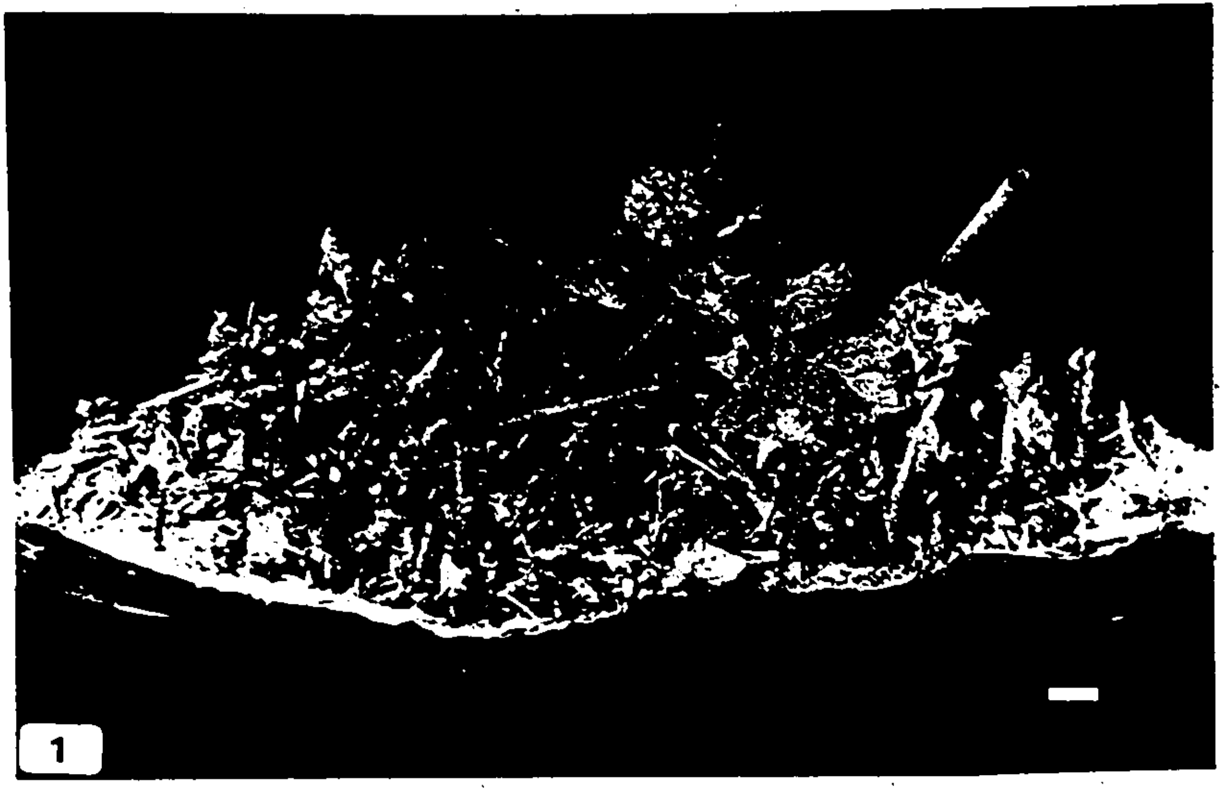
Explanation of Plate 6-4

Fig. 1. Dissolved remains of hardground material showing high densities and spatial arrangements of the glauconitic-filled boring casts. Side view. Scale bar equals 1.6 cm.

Fig. 2. Same specimens as in Fig. 1, in plan view. Scale bar equals 1 cm.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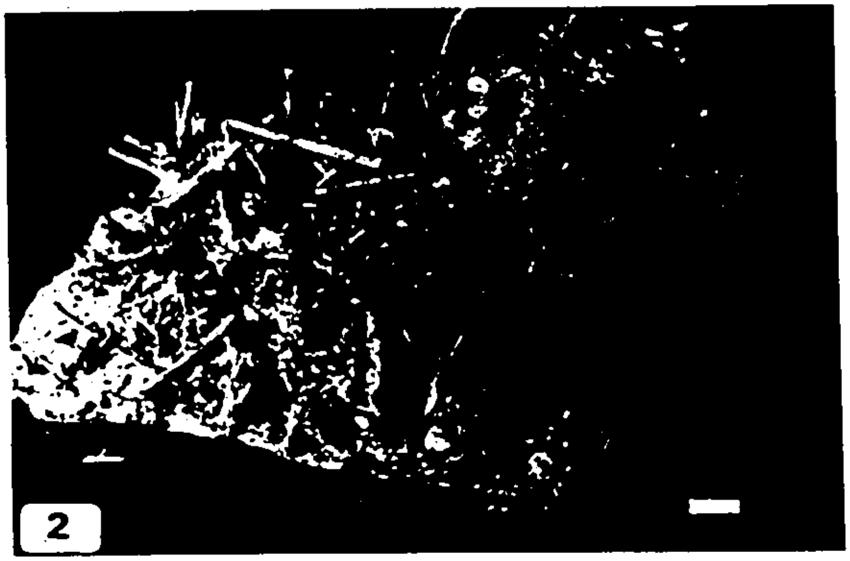
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Explanation of Plate 6-5

Fig. 1. Small coral head (<u>Montastrea annularis</u>) broken open to illustrate boring of modern sipunculid (<u>Phascolosoma</u> sp.), from Key Largo Florida. Metric scale.

Fig. 2. Silurian hardground boring. Note shape and similarity to recent sipunculid boring. Boring has remained open due to infilling by Oriskany sandstone seen in upper portion of boring. Metric scale.


1


2

Explanation of Plate 6-6

Fig. 1. Borings of eunicid polychaete *Eunice* sp. from reef rubble, Pirate Bay, Tobago. Millimeter scale.

Fig. 2. Boring of thoracican cirriped *Lithotrya* sp. from reef rubble, Pirate Bay, Tobago; note series of abandoned calcareous discs which represent successive attachment positions of the animal. Millimeter scale.

Fig. 3. Boring of sipunculid *Dendrostomum* sp. (courtesy of Dr. M. Rice). Millimeter scale.

Fig. 4. Boring of mytilid bivalve *Lithophaga nigra*, from reef rubble, Pirate Bay, Tobago. Millimeter scale.

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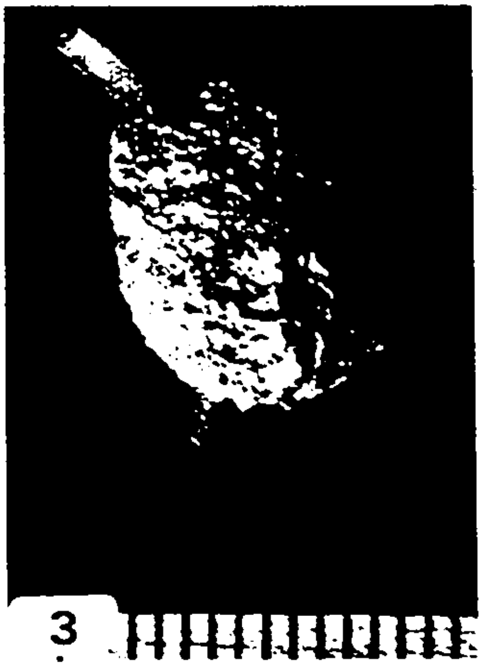
2



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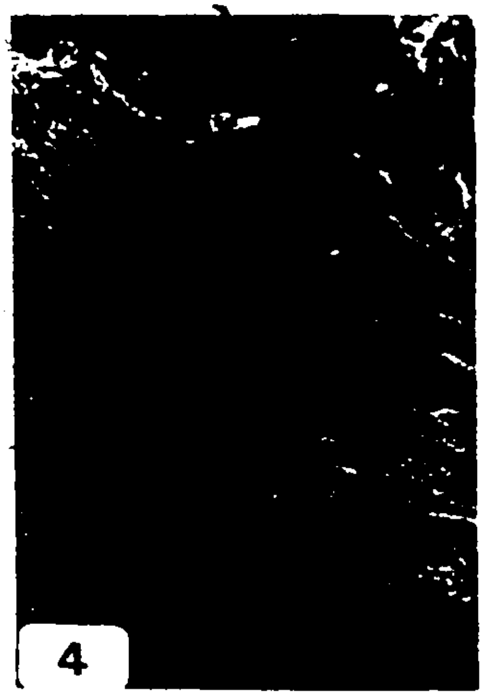

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CHAPTER 7

Oldest Known Brachiopod Burrow: The Lower Cambrian of Labrador

7-1. Introduction

Almost every significant aspect of the life history, physiology, and ethology of lingulid brachiopods has received attention (see Craig, 1952; Chuang, 1956, 1962, 1964; Ferguson, 1963; and Paine, 1963). Recently there has been an upsurge of interest in the burrowing methods of lingulids (Thayer and Steele-Petrovic, 1975) and in their relationship to the sediment substrate (Paine, 1970). There are numerous accounts of fossil lingulids found in the vertical position and considered to be preserved _in situ_. Table 7-1 documents the occurrences of _in situ_ or vertical lingulid fossils in Paleozoic rocks. Many more fossils _in situ_ examples probably await recognition, in light of the recent study by Thayer and Steele-Petrovic (1975) on the burrowing dynamics of the recent lingulid _Glottidia pyramidata_; they demonstrated the lingulid burrows are U-shaped and that shells may also assume oblique or nearly horizontal positions within the sediment, as illustrated by Yatsu (1902) for recent species, and Pickerill (1973) for fossil lingulids.

Table 7-1: Examples of *in situ* preservation of Paleozoic lingulids (expanded from Paine, 1970).

Lithology	Preservation	Age	Reference
Sandstone	burrow preserved	Cambrian	This study
Shale	pedicle preserved	Ordovician	Walcott, 1888
Sandstone	shells vertical	Ordovician	Davidson, 1874-1882
Slate	shells vertical	Ordovician	Opik, 1930
Siltstone	shells vertical	Ordovician	Bretsky, 1970
Siltstone	shells vertical	Ordovician	Pickerill, 1973
Sandstone	shells vertical	Silurian	Ziegler *et al.*, 1968
Sandstone	shells vertical	Silurian	Pemberton (unpub. thesis data)
Sandstone	shells vertical	Silurian	Martini, 1971
Coral: *Heliolites*	shells vertical	Silurian	Richards and Dyson-Cobb, 1976
Coral: *Heliolites*	shells vertical	Silurian	Newall, 1970
Chalk	shells vertical	Devonian	Hecker, 1960
Sandy shale	shells vertical	Devonian	Cooper, 1937
Siltstone	burrow preserved	Devonian	Szmuc *et al.*, 1976

Table 7-1 continued.

Siltstone	shells vertical	Devonian	Thayer, 1974
Sandstone	pedicle preserved	Mississippian	Hall and Clark, 1892
Shale	shells vertical	Mississippian	Craig, 1952, 1954
Shale	shells vertical	Mississippian	Ferguson, 1962, 1963
Siltstone	shells vertical	Mississippian	Osgood and Szmuc, 1972
Siltstone	burrow preserved	Pennsylvanian	Hakes, 1976
Shale	shells vertical	Pennsylvanian	Edwards and Stubblefield, 1947
Shale	shells vertical	Carboniferous	Young, 1866

Although fossil shells of lingulid brachiopods are not uncommon, preserved burrows of lingulids are very rare. Two new ichnogenera have been established for burrows attributed to lingulids: Lingulichnus (Hakes, 1976) ~~and~~ Lingulichnites (Szmuc, Osgood, and Meinke, 1976). Because Lingulichnus has taxonomic priority due to publication date and in order to avoid confusion, Szmuc et al. (1977) called for the supression of the ichnogenus Lingulichnites and placed it in synonymy with Lingulichnus.

This paper describes a well-preserved specimen of Lingulichnus verticalis Hakes from the Labrador Group (Bonnia-Olenellus zone) of southern Labrador. Rocks assigned to the Labrador Group record deposition during initial phases of the Lower Paleozoic transgression onto the eastern continental margin of North America during the late Lower Cambrian time. In Labrador the Lower Cambrian comprises two formations: the lower, the Bradore Formation, is a series of conglomerates, sandstones and minor siltstones; the upper, the Forteau Formation, is a series of siltstones, shales, and fossiliferous limestones containing archaeocyathid reefs (Schuchert and Dunbar, 1934; James and Kobluk, 1978). The Lingulichnus burrows were found in a red subarkosic sandstone unit near the top of the Bradore Formation. This unit also contains abundant Skolithos linearis burrows.

7-2. Systematic Ichnology

Lingulichnus verticalis Hakes (1976)

Lingulichnites amygdalinus Szmuc, Osgood and Meinke (1976).

A). Description

Tongue to spade-shaped vertical burrow with the widest dimension at the top. The aperture and upper tongue-like part are elliptical in transverse section, displaying two planes of symmetry; one would pass between the valves and the other bisect the valves and form a ninety degree angle with the first. The single most diagnostic feature is the basal projection down from the main chamber.

Age range of known forms

Lingulichnus is known from only two locations, the Upper Devonian Chagrin Formation of Ohio (Szmuc, et al, 1976) and the Upper Pennsylvania Rock Lake Shale Formation of Kansas (Hakes, 1976). In addition, specimens referrable to Lingulichnus are known from the Silurian Thorold Formation of Ontario (see Chapter 3). Examples of lingulid shells found in situ in Paleozoic rocks range in age from Ordovician to Pennsylvanian.

B). Interpretation

The Lower Cambrian form (Pl. 7-1, fig. 1) is almost identical to the specimen illustrated by Szmuc, *et al.* (1976, fig. 2B, p. 165); it differs only in its larger size. The upper spade-like chamber in the Labrador specimen is 4.1 cm. long and 3.5 cm. wide; the basal stem is 5.7 cm. long and 1 cm. wide, giving the entire burrow a length of 9.8 cm. This burrow is large; however, there are examples of both recent and fossil lingulids that attain these dimensions. In a study of the recent species *Lingula unguis*, Chuang (1962) describes specimens that are 5.2 cm. in length and 2.2 cm. in width. Pickerill (1973) described specimens of *Lingulasma tenuigranulata* (Pl. 7-1, fig. 2) that attain lengths of up to 4.5 cm. and widths of up to 3.2 cm.

7-3. Discussion

Examination of Table 7-1 shows that most of the examples of vertically oriented lingulids are from fine-grained siliclastic sediments. Until recently it was commonly accepted that lingulids lived in these fine grained sediments exclusively (Craig, 1952; Ferguson, 1963). Quantitative studies conducted on a wide range of recent species, however, have shown that extant lingulids prefer shallow sandy areas (Paine, 1970) and that the paleoenvironmental distribution of fossil lingulids is produced primarily by a preservational bias (Thayer and Steele-Petrovic, 1975). The reasons for this preference for sandy areas have been outlined by Thayer and Steele-Petrovic (1975) as follows:

1). Fine-grained material can pass between the setae and can thus foul the mantle cavity.

2). Fine-grained sediments usually exhibit high water contents and low shear strengths and thus are unable to support the pedicle.

3). Because of the low shear strength, fine-grained sediments are easily resuspended, causing clogging of suspension-feeding organisms (Rhoads and Young, 1970).

The Lower Cambrian Bradore Formation is interpreted, on the basis of physical sedimentary structures, to be a series of tidal-dominated, near-shore sand shoals (Swett and Smit, 1972). These sandstone units are devoid of body fossils so that ichnofossils present the only clue to the biologic component. The sample of Lingulichnus occurs in a medium-grained sandstone near the top of the Bradore Formation and is found in association with the ichnogenera Skolithos, Monocraterion, and Dolopichnus. Table 7-2 summarizes the known ichnogenera that are associated either with Lingulichnus or with vertical in situ lingulid shells.

Table 7-2. Ichnogenera associated with *in situ* lingulids.

Age	Formation	Location	Preservation	Associated Ichnogenera	Reference
Cambrian	Bradore	Southern Labrador	burrow	*Skolithos*, *Monocraterion*, *Dolopichnus*	Present study
Ordovician	Pen-y-Garnedd	North Wales	shells vertical, burrow	*Skolithos*, *Planolites*, *Teichichnus*	Pickerill, 1973
Silurian	Grimsby	N.E. New York S.W. Ontario	shells vertical	*Skolithos*, *Arthrophycus*, *Daedalus*, *Planolites*, *Chondrites*	Martini, 1971 Pemberton, unpub. data
Silurian	Thorold	N.E. New York S.W. Ontario	shells vertical	*Skolithos*, *Planolites*, *Rusophycus*, *Dolopichnus*, *Arenicolites*, *Chondrites*, *Teichichnus*, *Arthrophycus*, *Diplocraterion*	Pemberton, present study
Mississippian	Cuyahoga	Ohio	shells vertical	*Zoophycos*, *Palaeophycus*	Osgood and Szmuc, 1972
Pennsylvanian	Rock Lake Shale	Kansas	burrow	*Tigillites*, *Planolites*, *Asteriactes*, *Lockeia*, *Cochlichnus*, *Didymaulichnus*, *Chondrites*, *Isopodichnus*, *Rusophycus*, *Conostichus*, *Curvolithus*	Hakes, 1976

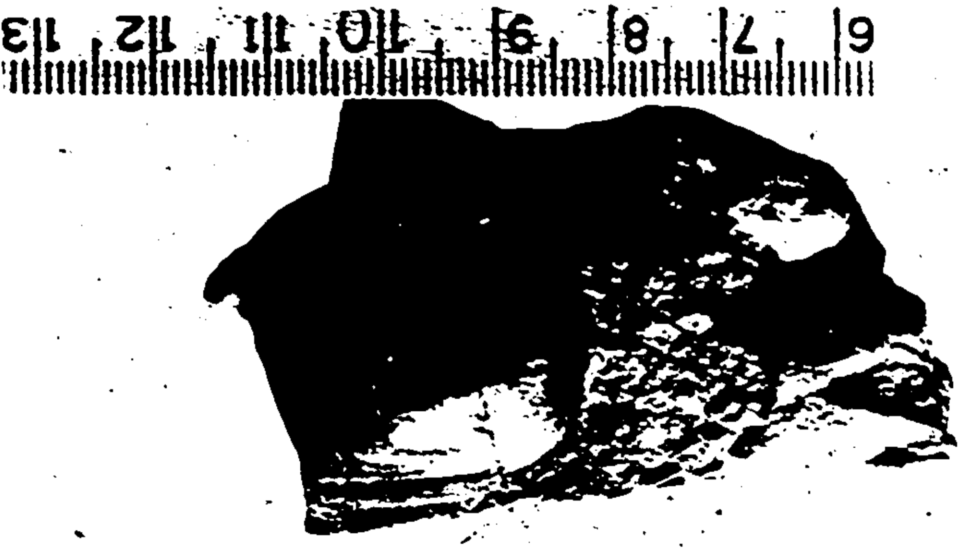
These data indicate that _in situ_ lingulids are generally found with ichnofossils that characterize relatively shallow, sandy areas (the _Skolithos_ zone of Seilacher, 1967). Therefore, the distribution of _Lingulichnus_ and its association with other ichnogenera conforms with the known paleoecology of lingulid body fossils. This points out the importance of establishing zoological affinities for ichnofossils since in high energy environments even organisms with hard parts may be represented only by their traces.

Another consequence of the occurrence of the Lower Cambrian _Lingulichnus_ burrow concerns the evolution of the ethology of lingulids. The burrowing mode of life of lingulids is known previously from as far back as the Ordovician (see Table 7-1). Rudwick (1970) indicated that Cambrian forms lack the parallel-sided shell form characteristic of those that are known to burrow and suggested that these forms normally led an epifaunal life. However, the discovery of _Lingulichnus_ in Lower Cambrian strata suggests that the infaunal habitat was exploited by at least some lingulids as early as the Lower Cambrian and probably has remained essentially unchanged since that time.

Explanation of Plate 7-I

Fig. 1. Lingulichnus verticalis from the Lower Cambrian Bradore Formation of Southern Labrador. Scale bar is 1 cm. The specimen is housed in the paleontological collection of the Royal Ontario Museum. Number R.O.M. 37226.

Fig. 2. Lingulasma tenuigranulata from the Lower Ordovician Pen-y-Garnedd Fm. of North Wales. Centimeter scale. (Specimen courtesy of Dr. R. K. Pickerill, University of New Brunswick.)



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CHAPTER 8

Spatial Distribution of Some Selected Vertical Ichnofossils

8-1. Introduction

Spatial pattern is one of the most important characteristics of any group of living organisms (Connell, 1963). Preliminary studies on the spatial distribution of organisms were first introduced by plant ecologists (see Greig-Smith, 1957; for review) and have since been applied to animal populations (Salt and Hollick, 1946; Holme, 1950). Three main types of distribution have been recognized in natural populations: uniform, aggregated, and random.

A non-random spatial distribution pattern implies some sort of constraint on the population. Aggregation is thought to be caused by gregarious behavior, reproductive habits or heterogeneity of the environment, such that individuals are clumped in the more favourable parts of the habitat (Connell, 1963). A uniform pattern results from negative interaction between the individuals (Holme, 1950), such as competition for food. A distribution pattern that is completely uniform is one where the individuals are situated in a hexagonal pattern.

Although the analysis of the spatial distribution of populations of extant organisms is widespread, few studies have been attempted on fossil populations. Miller (1956) has used nearest-neighbour relationships in an attempt to determine the current direction, in the Pennsylvanian Mecca Black Shale. This study, however, was not related to the dynamics of the fossil *in situ* population but instead was concerned with its relation to a physical property (the water current).

It has long been known that ichnofossils possess certain characteristics that set them apart from body fossils:

1). Since ichnofossil morphology reflects certain functions and behavioural patterns, rather than body shape, it has been shown that different organisms may create similar traces when their ethology is alike (Chamberlain, 1971b). Therefore, many types of ichnofossils may occur through many periods or even eras of geologic history, which facilitates long-range facies comparison (Seilacher, 1964).

2). Seilacher (1964) has also shown that significant types of traces are facies-specific, regardless of what organisms produced them.

3). Of particular significance to this study is that ichnofossils cannot be reworked. Thus, every ichnocoenosis represents part of an actual benthic community (Seilacher, 1964).

4). Although ichnofossils occur in most sedimentary sequences, they seem to be most abundant in clastic series. Often these clastic units are devoid of body fossils and thus, ichnofossils represent the only clue to their biotic component.

5). Selacher (1964) points out that while preservation affects body fossils in a negative sense (secondary solution, disintegration, or deformation) ichnofossils seem to improve rather than degrade, through diagenetic processes.

6). Field studies in the Bay of Fundy shows that living tubicolous polychaetes may be analagous to some vertical ichnogenera (Featherstone and Risk, 1977). Careful seiving of tubeworm populations indicates that the majority of the tubes on the Fundy flats are inhabited by living worms at any one time (M. J. Risk, personal communication).

These characteristics and observations indicate that ichnofossils may represent the only fossil element that may be conducive for such a spatial distribution analysis.

8-2. Techniques

In the analysis of the spatial distribution of selected vertical ichnofossils, two independent techniques have been employed: the distance to the nearest neighbour (Clark and Evans, 1954), and the coefficient of dispersion (Clapham, 1936).

A). The distance to nearest neighbour

The technique of using the distance to the nearest neighbour in analyzing the dispersion of an individual population was first introduced by Hertz (1909). Subsequent development of the technique was by Spooner, quoted in Holme (1950). Dice (1952) was the first to use distance to nearest neighbour in measuring a departure from randomness. The technique was further refined by Clark and Evans (1954, 1955) and Clark (1955). This has been used effectively in the analysis of populations of the bivalves Tellina (Holme, 1950); Mya and Petricola (Connell, 1956); and the amphipod Erichthonium braziliensis (Connell, 1963).

This measure of spacing is a measure of the degree with which the distribution of individuals in a population departs from that of a random distribution (Clark and Evans, 1954). The physiography of outcrop patterns necessitates two types of measuring procedures. In areas where large horizontal bedding planes are exposed (as in the Lower Cambrian Bradore Formation), quadrats of a standard size were constructed. Random areas were chosen on these exposed bedding planes by throwing a hammer, the point at which the hammer hit was used as the center of a quadrat. Roped quadrats were stretched over the resultant area and all burrows were charted and the distance to the nearest neighbour recorded. In areas where large bedding planes were not exposed (such as the Thorold Formation) an alternate procedure had to be used. Large blocks were extracted from the vertical outcrop face at the horizon to be analyzed. The area of the sample was determined by using a Keuffel and Esser Planimeter (accurate to within 1%), and all burrows were charted and the distance to the nearest neighbour recorded.

The equations used (Table 8-1) and the procedure outlined below is summarized from Clark and Evans (1954).

In a population with N individuals and a density (p), the distance (r) from each individual to its nearest neighbour is measured. The mean observed distribution is given by:

$$\bar{r}_A = \Sigma\, r/N$$

and the mean distribution expected if the population is a random one is given by:

$$\bar{r}_E = 1/2\sqrt{p}\ .$$

The ratio $\bar{r}_A/\bar{r}_E$ (R) is then used as a measure of the departure from the random expectation. In a

Table 8-1

A List of Symbols and Definitions of Concepts, Employed in a Measure of Spacing Based on the Mean Distance Between the Nearest Neighbour (after Clark and Evans,1954)

N:	number of measurements
r:	distance to nearest neighbour
p:	density per unit area
Σr:	summation of the measurements of distance to nearest neighbour
Σr^2:	summation of squares of the measurements of distance to nearest neighbour
$\bar{r}_A = \Sigma r/N$:	the means of the series of distance to the nearest neighbour
$\bar{r}_E = 1/2\sqrt{p}$:	mean distance to nearest neighbour expected in an infinitely large random distribution of density p
$R = \bar{r}_A/\bar{r}_E$:	the measure of the degree to which the observed distribution departs from random expectation with respect to the distance to nearest neighbour
$c = \dfrac{\bar{r}_A - \bar{r}_E}{\sigma_{\bar{r}_E}}$:	standard variate of the normal curve
$\sigma_{\bar{r}_E} = 0.26136/\sqrt{Np}$:	the standard error of the mean distance to nearest neighbour in a randomly distributed population of density p

random distribution R will equal unity; under conditions of aggregation, R will approach zero; and under conditions of maximum spacing R will be greater than unity. If the value of R indicates that a given population is not randomly distributed, the significance of the departure of $\bar{r}_A$ from $\bar{r}_E$ can be tested by the normal curve. The test of significance of the measure is given by:

$$c = \frac{\bar{r}_A - \bar{r}_E}{\sigma_{r_E}}$$

where c is the standard variate of the normal curve, and σ_{r_E} is the standard error of the mean distance to the nearest neighbour in a randomly distributed population of the same density as the observed population.

B). <u>The coefficient of dispersion</u>

In the analysis of the distribution of organisms over a specific area many investigators have used Fisher's "coefficient of dispersion." The method was introduced in studies of plant ecology by Clapman (1936) and Blackman (1942) and in terrestrial and marine ecology by Salt and Hollick (1946), Holme (1950), and Barnes and Marshall (1951).

The coefficient of dispersion is given by:

$$\frac{\Sigma\,(x - \bar{x})^2}{\bar{x}\,(n-1)}$$

where $\Sigma(\chi - \bar{\chi})^2$ is the sum of squares of the deviations of individual units (χ) from the mean ($\bar{\chi}$) of all the units (n) comprising the sample.

The coefficient is unity when the population is randomly distributed, less than one if the population is over-dispersed (evenly distributed), and greater than one if it is under-dispersed (aggregated). The significance of the departure from unity is tested by:

$$1 \pm 2\sqrt{2N/(n-1)^2}$$

where n is the number of units in the sample (Holme, 1950). Where n is less than 10, this latter expression is greater than unity, so that samples numbering less than 10 can not be tested for an even distribution.

In the present study, it was found that only populations from large horizontal bedding planes could be analyzed, due to the fact that a standard quadrant size must be employed. Where this method was used, a frame, of standard size, was constructed and thrown "randomly" over the exposed bedding plane. The resultant area was then sampled and the burrow density recorded.

8-3. Ichnogenera Analyzed

Three different ichnogenera have been selected for this analysis: Skolithos, Monocraterion and Diplocraterion (Table 8-2).

Skolithos and Monocraterion burrows were studied from the Lower Cambrian Bradore Formation of southern Labrador. The Bradore Formation consists of a series of conglomerates, sandstones and minor siltstones deposited in what has been interpreted to be a series of tidal-dominated, nearshore, sand shoals (Swett and Smit, 1972; James and Kobluk, 1978). Skolithos linearis burrows are usually confined to the quartzitic sandstone beds and are analogous to the classic "pipe-rock" facies of the Eriboll Sandstone of Scotland (Swett, et al., 1971). Monocraterion burrows are restricted to an arkosic sandstone layer which lies above the Skolithos horizon. Although present, Skolithos is not found in abundance in the Monocraterion horizon.

In response to the difference in lithologies coupled with extensive coastal outcrops, erosion has exposed large horizontal bedding surfaces. These surfaces allow for the implementation of both of the spacing techniques previously outlined.

An extensive "population" of Skolithos burrows were studied from the Middle Silurian Thorold

Table 8-2. Ichnogenera selected for spatial distribution analysis.

Form	Ichnogenus	Formation	Age	Location
Vertical Shafts	*Skolithos*	Bradore	L. Cambrian	Labrador
	Monocraterion	Bradore	L. Cambrian	Labrador
	Skolithos	Thorold	M. Silurian	Ontario
U-shaped	*Diplocraterion*	Thorold	M. Silurian	Ontario
Multi-entranced	Extant burrows of *Axius serratus*	————	Recent	Strait of Canso, Nova Scotia

Formation of the Niagara Peninsula. Due to outcrop limitations only the distance to the nearest neighbour technique could be employed.

In an attempt to gain information on the techniques application to multi-entranced forms, the ichnogenus Diplocraterion was sampled from the Thorold Formation. As with the Skolithos zone, only the distance to the nearest neighbour technique could be used.

8-4. Results of Spatial Distribution Analysis

A). Skolithos burrows

i). Skolithos linearis: Bradore Fm.
(Pl. 8-1, fig. 1)

In order to determine the coefficient of dispersion quadrats, 20 cm by 20 cm, were constructed and the bedding plane exposure was sampled. In all, 20 quadrats were counted (Table 8-3); densities per 400 sq. cm. ranged from 92 to 212 with a mean density of 142. This corresponds to a coefficient of dispersion of 9.85 (Table 8-4). The limits of the coefficient of dispersion for a random distribution at n = 20 are: 0.3342 to 1.6658. Analysis of these data therefore reveals that the Skolithos population is significantly aggregated.

In order to determine the interactions of the individuals within the population, a nearest

Table 8-3. Density counts of Skolithos burrows from the Bradore Formation

Quadrat Number	Number of burrows
1	99
2	106
3	201
4	212
5	114
6	92
7	110
8	196
9	198
10	142
11	111
12	132
13	127
14	125
15	150
16	136
17	156
18	180
19	105
20	147

Table 8-4. Coefficient of dispersion for Skolithos burrows from the Bradore Formation

Number of Quadrats	Total number of burrows	Average mean density (no./20 cm^2)
20	2839	142

Coefficient of dispersion = 9.85

Limits of the coefficient of dispersion for random distribution

at n = 20

0.3342 - 1.6658

Table 8-5. Distance to nearest neighbour analysis of Skolithos burrows from the Bradore Formation: Quadrat SB-1

Quadrat size: 400 sq. cm.

Number of burrows: 99

Distance to nearest neighbour (in cm)

0.6	0.6	1.5	1.2	1.4	1.5	0.8	1.2	2.0	1.5
0.6	0.6	1.5	1.0	1.3	1.4	0.8	1.2	1.6	1.4
0.5	0.7	1.0	1.0	1.3	1.0	1.3	1.4	1.6	1.4
0.5	0.7	1.0	1.5	1.0	1.0	1.3	0.6	1.2	0.8
0.8	1.0	1.8	1.5	1.0	1.0	1.6	0.6	1.2	0.8
0.8	1.0	1.8	0.9	0.9	1.0	0.8	0.5	1.0	1.2
1.0	0.8	0.4	0.8	0.9	0.7	0.8	0.5	1.0	1.0
1.0	0.8	0.4	0.8	0.5	0.7	1.0	1.5	0.8	1.4
0.5	0.5	0.5	1.0	0.5	1.4	1.0	1.0	0.8	1.0
0.5	0.5	0.5	1.0	0.7	1.0	1.2	1.0	1.4	

Sum of distances to nearest neighbour = 97.5 cm

Table 8-6. Distance to nearest neighbour analysis of <u>Skolithos</u> burrows from the Bradore Formation: Quadrat SB-2

Quadrat size	400 sq. cm.
Number of burrows:	106

Distance to nearest neighbour (in cm)

0.8	0.5	1.8	1.5	1.2	1.0	1.4	0.6	0.5	1.2	1.6
0.8	0.5	1.6	1.4	1.2	1.0	1.3	0.6	0.5	1.2	1.6
1.2	0.6	1.6	1.4	1.4	1.5	1.3	0.7	0.6	0.5	1.2
1.2	0.6	1.2	1.0	0.6	1.5	1.1	0.7	0.6	0.5	1.2
1.8	0.8	1.2	1.0	0.6	0.8	1.1	1.0	0.8	0.8	0.5
0.9	0.8	1.0	1.2	0.5	0.8	0.9	1.0	0.8	0.8	0.5
0.9	1.0	1.0	1.2	0.5	1.0	0.9	0.8	0.7	0.5	
1.1	1.0	0.8	0.7	1.5	1.0	0.4	0.8	0.7	0.5	
1.1	0.5	0.8	0.7	1.0	1.6	0.4	0.5	0.5	0.4	
1.2	0.5	1.4	1.0	1.0	1.2	0.7	0.5	0.5	0.4	

Sum of distances to nearest neighbour = 96.9 cm

Table 8-7. Distance to nearest neighbour analysis of Skolithos burrows from the Bradore Formation: Quadrat SB-3

Quadrat size: 400 sq. cm.
Number of burrows: 162

Distance to nearest neighbour (in cm)

0.9	0.8	1.7	1.5	1.1	1.0	1.3	0.5	0.8	0.4
0.9	0.8	1.4	1.4	1.1	1.0	1.2	0.5	0.8	0.4
0.6	1.2	1.4	1.4	1.3	0.7	1.2	0.7	0.6	1.0
0.6	1.2	1.2	1.0	0.6	0.7	1.0	0.7	0.6	1.0
0.5	1.4	1.2	1.0	0.6	0.9	1.0	1.0	0.8	1.6
0.5	0.9	1.0	1.2	0.5	0.9	0.9	1.0	0.8	0.9
0.7	0.9	1.0	1.2	0.5	1.5	0.9	0.8	0.7	0.9
0.7	1.0	0.9	0.7	1.3	1.5	0.4	0.8	0.7	1.1
0.5	1.0	0.9	0.7	1.0	1.6	0.4	0.5	0.5	1.1
0.5	1.2	1.6	0.9	1.0	1.2	0.7	0.5	0.5	1.2

0.8	1.1	1.2	1.0	1.2	0.5	0.6
0.8	1.1	1.2	1.0	1.2	0.5	0.6
0.4	0.5	0.4	0.5	0.5	1.3	
0.4	0.5	0.4	0.5	0.5	0.8	
0.8	0.6	0.7	0.7	0.5	0.8	
0.8	0.6	0.7	0.7	1.5	0.5	
1.1	0.5	0.4	0.5	0.4	0.5	
1.1	0.5	0.4	0.5	0.4	0.5	
0.4	0.5	0.4	0.5	0.5	1.2	
0.4	0.5	0.4	0.5	0.5	1.2	

Sum of distances to nearest neighbour = 133.7 cm

Table 8-8. Distance to nearest neighbour analysis of *Skolithos* burrows from the Bradore Formation: Quadrat SB-4

Quadrat size: 400 sq. cm.

Number of burrows: 201

Distances to nearest neighbour (in cm)

0.7	0.8	1.8	1.6	1.4	1.2	1.4	0.6	1.2	1.8
0.7	0.8	1.6	1.4	1.4	1.2	1.3	0.6	1.2	1.8
0.6	1.3	1.6	1.4	1.5	1.6	1.3	1.2	0.5	1.4
0.6	1.3	1.5	1.0	0.7	1.6	1.1	1.2	0.5	1.4
0.8	1.8	1.5	1.0	0.7	1.0	1.1	1.1	0.8	0.6
0.8	1.0	1.0	1.2	0.6	1.0	0.9	1.1	0.8	0.6
1.0	1.0	1.0	1.2	0.6	1.1	0.9	0.8	0.7	1.0
1.0	1.1	0.8	0.7	1.6	1.1	1.4	0.8	0.7	1.0
0.5	1.1	0.8	0.7	1.1	1.7	1.4	1.5	0.5	1.5
0.5	1.2	1.5	1.2	1.1	1.3	1.7	1.5	0.5	1.5

0.8	1.5	1.8	0.9	0.6	1.2	0.6	1.3	1.2	1.3	1.1
0.8	1.3	1.5	0.9	0.6	1.2	0.6	1.2	1.2	1.3	
0.5	1.3	1.5	1.2	1.2	1.5	1.1	1.2	1.4	1.4	
0.5	0.9	1.4	1.2	1.2	1.5	1.1	1.0	1.4	0.6	
0.8	0.9	1.4	1.5	1.1	0.8	1.0	1.0	1.0	0.6	
0.8	1.1	1.1	1.0	1.1	0.8	1.0	0.8	1.0	0.5	
1.0	1.1	1.1	1.0	0.8	0.7	0.9	0.8	1.1	0.5	
1.0	0.6	0.8	0.8	0.8	0.7	0.9	1.3	1.1	1.5	
0.6	0.6	0.8	0.8	1.5	1.0	1.6	1.3	1.5	1.0	
0.6	1.1	1.4	1.1	1.5	1.0	1.6	1.6	1.3	1.0	

Sum of distances to nearest neighbours = 215.5 cm

Table 8-9. Distance to nearest neighbour analysis of *Skolithos* burrows from the Bradore Formation: Quadrat SB-5

Quadrat size: 400 sq. cm.
Number of burrows: 212

Distance to nearest neighbour (in cm)

1.8	1.2	0.8	0.7	1.2	1.3	1.6	2.0	0.8	1.7	1.0
1.8	1.2	0.8	0.7	1.2	1.3	1.4	1.8	0.8	1.7	1.0
1.2	0.6	1.0	0.6	1.6	1.7	1.4	1.8	1.5	0.6	1.2
1.2	0.6	1.0	0.6	1.6	0.7	1.2	1.7	1.5	0.6	1.2
0.6	0.7	1.1	0.8	1.2	0.7	1.2	1.7	1.8	0.7	0.5
0.6	0.7	1.1	0.8	1.2	0.8	1.4	1.2	1.2	0.7	0.5
1.0	0.8	0.9	1.0	1.2	0.8	1.4	1.2	1.2	1.2	
1.0	0.8	0.9	1.0	1.2	1.6	0.9	1.0	1.1	1.2	
1.3	0.6	1.4	0.5	1.8	1.2	0.9	1.0	1.1	1.5	
1.3	0.6	1.4	0.5	1.5	1.2	1.4	1.7	1.4	1.5	

0.8	0.8	1.5	1.7	1.3	1.1	0.8	0.9	1.7	0.7	1.2
0.8	0.8	1.4	1.4	1.3	1.1	0.8	0.9	1.7	0.7	1.2
0.5	1.3	1.4	1.4	1.5	1.5	0.5	1.1	1.3	1.1	1.0
0.5	1.3	1.3	1.1	0.8	1.5	0.5	1.1	1.3	1.1	1.0
1.8	1.5	1.3	1.1	0.8	1.1	0.8	1.0	0.6	1.1	0.5
1.8	1.1	1.0	1.2	0.5	1.1	0.8	1.0	0.6	1.1	0.5
1.0	1.1	1.0	1.2	0.5	1.1	1.1	0.9	1.1	0.9	
1.0	0.7	0.8	0.7	1.6	1.1	1.1	0.9	1.1	0.9	
0.6	0.7	0.8	0.7	1.2	1.7	0.4	1.3	1.2	1.4	
0.6	1.1	1.4	1.2	1.2	1.4	0.4	1.3	1.2	1.4	

Sum of distances to nearest neighbour = 240.4 cm

Table 8-10. Results of distance to nearest neighbour analysis of *Skolithos* burrows from the Bradore Formation

Quadrat	Area (sq.cm.)	N	P	Σr	$\bar{r}_A$	$\bar{r}_E$	R
SB-1	400	99	0.248	97.5	0.985	1.005	0.98
SB-2	400	106	0.265	96.9	0.914	0.972	0.94
SB-3	400	162	0.405	133.7	0.825	0.786	1.05
SB-4	400	201	0.503	215.5	1.072	0.705	1.52
SB-5	400	212	0.53	240.4	1.134	0.687	1.65

Table 8-11. Tests of significance of nearest neighbour analysis: Skolithos burrows from the Bradore Formation

Quadrat	R	σ_{r_E}	c
SB-1	0.98	0.053	0.377
SB-2	0.94	0.049	1.184
SB-3	1.05	0.032	1.218
SB-4	1.52	0.026	14.115**
SB-5	1.65	0.025	17.88**

+ c = 1.96, P = 0.05 : significant

** c - 2.56, P = 0.01 : highly significant neighbour analysis was conducted on five of the above quadrats. These were selected to be representative of the observed density range. Each burrow was located and the nearest neighbour was determined and measured (Tables 8-5 to 8-9). A summary of the results of this analysis is given in Table 8-10. The two quadrats reflecting lower densities (SB-1 and SB-2) did not display any significant departure from the random (R = .98, for SB-1; and R = .94 for SB-2). The quadrat representing the middle density (SB-3) similarly did not display any significant departure from the random (R = 1.05). In contrast, the two quadrats reflecting the higher densities (SB-4 and SB-5) did show a departure from the random in the direction of uniform spacing (R = 1.52 for SB-4; and R = 1.65, for SB-5). Tests of significance (Table 8-11) illustrate that while quadrats SB-1, SB-2, and SB-3 can be considered random, the higher density quadrats were significantly uniform (c = 14.115 for SB-4; and c = 17.88 for SB-5).

ii). Skolithos: Thorold Sandstone (Pl. 8-1, fig. 2).

The analysis of the spatial distribution of Skolithos burrows in the Thorold proved to be much more complicated than in the Bradore Formation. There exist no large exposed horizontal bedding surfaces in which to sample. As a result, large blocks were

Table 8-12. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation: Quadrat ST-1

Quadrat location: Ball's Falls

Area of Quadrat: 200.18 sq. cm.

Number of burrows: 23

Distances to nearest neighbour (in cm)

1.5	0.9	0.4	1.2	1.7
1.4	0.9	0.4	1.6	2.1
1.4	1.9	1.0	1.6	2.1
1.6	3.3	2.8	2.3	
0.9	1.2	1.2	1.7	

Sum of distances to nearest neighbour = 35.1 cm

Table 8-13. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation: Quadrat ST-2

Quadrat location:	Ball's Fall's
Area of quadrat:	154.9 sq. cm.
Number of burrows:	23

Distances to nearest neighbour (in cm)

2.6	0.6	1.5	2.3	0.7
0.5	2.2	0.6	2.2	0.5
0.5	0.4	0.6	0.9	0.5
1.5	0.4	1.6	0.8	
0.6	1.9	2.1	0.8	

Sum of distances to nearest neighbour = 26.3 cm

Table 8-14. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation: Quadrat: ST-3

Location of quadrat: Flock Road

Area of quadrat: 128.7 sq. cm.

Number of burrows: 36

Distances to nearest neighbour (in cm)

0.5	0.8	1.5	1.1	1.5	1.0	1.4	1.6
1.4	1.4	1.5	0.8	1.0	1.0	0.6	
1.0	0.8	1.1	1.5	0.8	1.0	0.9	
0.9	0.8	1.1	0.8	0.9	1.5	0.9	
0.9	0.8	1.1	0.5	0.3	1.4	1.2	

Sum of distances to nearest neighbour = 36.7 cm

Table 8-15. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation: Quadrat: ST-4

Location of quadrat: Flock Road

Area of quadrat: 70.5 sq. cm.

Number of burrows: 18

Distances to nearest neighbour (in cm)

0.9	1.2	1.1	1.0
0.9	1.5	1.1	1.5
1.5	1.5	1.4	1.0
0.6	1.3	1.4	
0.6	0.5	1.0	

Sum of distances to nearest neighbour = 20 cm

Table 8-16. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation: Quadrat: ST-5

Location of quadrat:	Highway 403
Area of quadrat:	96.4 sq. cm.
Number of burrows:	34

Distances to nearest neighbour (in cm)

0.6	0.5	0.8	0.8	0.7	0.4	0.6
0.6	0.7	0.9	0.8	0.7	0.4	0.9
0.9	0.7	0.8	0.9	1.0	0.5	0.7
0.9	0.7	0.8	0.6	1.0	0.7	0.7
0.8	0.8	1.3	0.6	0.5	0.6	

Sum of distances to nearest neighbour = 26 cm

Table 8-17. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation. Quadrat: ST-6

Location of quadrat: Highway 403

Area of quadrat: 100.6 sq. cm.

Number of burrows: 38

Distances to nearest neighbour (in cm)

0.6	0.4	1.1	0.3	0.6	0.3	0.5	0.7
0.6	0.6	1.1	0.3	0.6	1.2	0.5	1.2
0.7	0.5	2.1	0.3	1.7	0.7	0.5	0.7
0.7	0.5	1.9	0.4	0.6	1.0	0.5	
0.4	2.2	1.3	0.4	0.3	1.0	0.5	

Sum of distances to nearest neighbour = 29.8 cm

Table 8-18. Distance to nearest neighbour analysis of *Skolithos* burrows from the Thorold Formation. Quadrat: ST-7

Location of quadrat: Sydenham Road

Area of quadrat: 359.6 sq. cm.

Number of burrows: 64

Distances to nearest neighbour (in cm)

1.2	0.6	1.6	1.7	2.2	1.1	0.6
0.7	3.1	4.8	2.3	1.5	1.0	1.0
0.6	0.9	1.4	1.8	0.9	0.5	0.8
0.5	0.9	1.4	0.5	0.8	0.5	0.8
0.5	1.6	1.5	0.5	0.8	0.6	0.5
0.5	1.0	1.0	1.3	1.3	1.3	4.4
0.8	0.8	1.7	0.7	0.7	2.0	0.9
0.7	0.6	0.8	0.5	0.5	3.1	1.1
1.1	1.1	0.6	0.6	0.6	0.6	1.6
1.1						

Sum of distances to nearest neighbour = 75.2 cm

Table 8-19. Distance to nearest neighbour analysis of <u>Skolithos</u> burrows from the Thorold Formation. Quadrat: ST-8

Location of quadrat: Jolly Cut Section

Area of quadrat: 166.7 sq. cm.

Number of burrows: 69

Distances to nearest neighbour (in cm)

0.6	0.5	0.9	0.4	0.6	1.0	0.7
0.6	0.5	0.4	0.3	0.6	1.5	1.0
1.8	1.0	0.4	0.3	0.6	0.4	1.6
1.8	1.2	0.8	0.6	0.7	0.4	1.0
2.0	1.1	0.8	0.7	0.5	0.6	0.3
0.7	1.1	0.4	0.7	0.5	0.7	0.3
0.7	1.3	0.4	0.7	0.4	1.2	0.4
0.8	0.7	0.4	0.6	0.4	0.7	0.4
0.8	0.7	0.4	0.6	0.5	0.7	
0.4	0.9	0.7	0.7	0.6	0.7	

Sum of distances to nearest neighbour = 49.7 cm

Table 8-20. Results of distance to nearest neighbour analysis of Skolithos burrows from the Thorold Formation

Quadrat	Area (sq.cm.)	N	P	Σr	$\bar{r}_A$	$\bar{r}_E$	R
ST-1	200.1	23	0.115	35.1	1.53	1.474	1.04
ST-2	154.9	23	0.148	26.3	1.14	1.3	0.88
ST-3	128.7	36	0.279	36.7	1.019	0.947	1.08
ST-4	70.5	18	0.255	20	1.111	0.990	1.12
ST-5	96.4	34	0.352	26	0.765	0.843	0.907
ST-6	100.6	38	0.378	29.8	0.787	0.813	0.966
ST-7	359.6	64	0.178	75.2	1.175	1.185	0.991
ST-8	166.7	69	0.414	49.7	0.720	0.777	0.927

Table 8-21. Tests of significance of nearest neighbour analysis: Skolithos burrows from the Thorold Formation

Quadrat	R	σ_{r_E}	c
ST-1	1.04	0.161	0.3478
ST-2	0.88	0.142	1.106
ST-3	1.08	0.082	0.878
ST-4	1.12	0.122	0.992
ST-5	0.907	0.076	1.03
ST-6	0.966	0.069	0.39
ST-7	0.991	0.077	0.134
ST-8	0.927	0.049	1.157

+ c = 1.96, P = 0.05 : significant

** c = 2.58, P = 0.1 : highly significant

extracted from a specific horizon known to contain abundant burrows. The surface area was measured using a planimeter and all measurements were recorded for 8 quadrats, from five different localities (Tables 8-12 to 8-19). A summary of the results of this analysis is given in Table 8-20. In all eight quadrats R-values indicated no departure from the random. In addition, all of the tests of significance (Table 8-21) confirmed that there was no departure from the random. The Skolithos population therefore seems to be randomly dispersed.

B). Monocraterion: Bradore Formation (Pl. 8-1, Fig. 3)

The Monocraterion burrows were sampled in the same manner as were the Skolithos burrows from the Bradore Formation. In the determination of the coefficient of dispersion 20 quadrat (1 m by 1 m) counts were made along a single bedding surface (Table 8-22). Densities ranged from 7 to 26 per square meter with a mean density of 11.5. This corresponds to a coefficient of 2.568 (Table 8-23). The limits of the coefficient of dispersion for a random distribution at n = 20 are: 0.3345 to 1.6658. Analysis of these data therefore indicates that the Monocraterion population as a whole is slightly aggregated over the entire bedding plane.

A nearest neighbour analysis was then conducted on eight quadrats, representing the full range of observed densities (Tables 8-24 to 8-31). A summary of the results of this analysis is given in Table 8-32. Tests of significants (Table 8-33) illustrate that all quadrats were significantly uniform.

C). Interpretation of Skolithos-Monocraterion data

Spatial distribution analysis of the ichnogenera Skolithos and Monocraterion reveals the following:

1). The Skolithos population from the Bradore Formation as a whole seems to be aggregated.

2). Individuals within this population interact in two observed ways; at low densities they seem to be randomly dispersed, while at high densities they appear to be uniformly spaced.

3). The individual elements of the Skolithos population from the Thorold Sandstone are randomly dispersed.

4). The Monocraterion population from the Bradore Formation as a whole seems to be slightly aggregated.

5). Individuals within this population interact negatively and a uniform spacing pattern results.

Table 8-22. Density counts of *Monocraterion* burrows from the Bradore Formation

Quadrat Number	Number of burrows
1	7
2	7
3	9
4	10
5	12
6	16
7	26
8	26
9	10
10	10
11	9
12	8
13	12
14	7
15	14
16	9
17	10
18	11
19	9
20	9

Table 8-23. Coefficient of dispersion for Monocraterion burrows from the Bradore Formation

Number of Quadrats	Total number of burrows	Average mean density (no./sq. m.)
20	231	11.5

Coefficient of dispersion = 2.568

Limits of the coefficient of dispersion for random distribution

at n = 20

0.3342 - 1.6658

Table 8-24. Distance to nearest neighbour analysis of _Monocraterion_ burrows from the Bradore Formation. Quadrat: MB-1

Area of quadrat:	1 sq. m.
Number of burrows:	7

Distance to nearest neighbour (in cm)

22	23.4	30.4
22	26.6	
23.4	26.6	

Sum of distances to nearest neighbour = 174.4 cm

Table 8-25. Distance to nearest neighbour analysis of <u>Monocraterion</u> burrows from the Bradore Formation. Quadrat: MB-2

Area of quadrat: 1 sq. m.

Number of burrows: 7

Distances to nearest neighbour (in cm)

27.3	34.8	33.4
24.6	25.5	
34.8	25.5	

Sum of distances to nearest neighbour = 205.9 cm

Table 8-26. Distance to nearest neighbour analysis of <u>Monocraterion</u> burrows from the Bradore Formation. Quadrat: MB-3

Area of quadrat:	1 sq. m.
Number of burrows:	9

Distances to nearest neighbour (in cm)

21.7	27.8	28.3
21.7	27.8	[illegible]4.7
30.3	28.3	24.7

Sum of distances to nearest neighbour = 235.3 cm

Table 8-27. Distance to nearest neighbour analysis of *Monocraterion* burrows from the Bradore Formation. Quadrat: MB-4

Area of quadrat: 1 sq. m.

Number of burrows: 10

Distances to nearest neighbour (in cm)

22.1
38.4
40.9
11.8
11.8
17.8
17.8
24.3
35.2
33.4

Sum of distances to nearest neighbour = 253.5 cm

Table 8-28. Distance to nearest neighbour analysis of *Monocraterion* burrows from the Bradore Formation. Quadrat: MB-5

Area of quadrat: 1 sq. m.

Number of burrows: 12

Distances to nearest neighbour (in cm)

16.6	52.1	22.1
16.6	15.7	36.6
13.3	15.7	36.6
13.3	22.1	38.6

Sum of distances to nearest neighbour = 299.3 cm

Table 8-29. Distance to nearest neighbour analysis of *Monocraterion* burrows from the Bradore Formation. Quadrat: MB-6

Area of quadrat: 1 sq. m.

Number of burrows: 16

Distances to nearest neighbour (in cm)

19.6	9.2	8.2	20.6
19.6	9.2	28.8	21.5
15.8	13.5	18.7	29.8
15.8	13.5	18.7	52.5

Sum of distances to nearest neighbour = 314.2 cm

Table 8-30. Distance to nearest neighbour analysis of <u>Monocraterion</u> burrows from the Bradore Formation. Quadrat: MB-7

Area of quadrat: 1 sq. m.

Number of burrows: 26

Distances to nearest neighbour (in cm)

14.6	14.8	16.4	19.6	20.2
13.1	14.8	27.6	13.9	12.8
20.1	20.1	18.1	15.5	12.8
19.6	20.1	18.1	10.5	26.1
19.6	16.4	13.6	10.5	26.1
13.1				

Sum of distances to nearest neighbour = 448.1 cm

Table 8-31. Distance to nearest neighbour analysis of *Monocraterion* burrows from the Bradore Formation. Quadrat: MB-8

Area of quadrat: 1 sq. m.

Number of burrows: 26

Distances to nearest neighbour (in cm)

21.6	17	14.3	20.4	14.2
33.7	17	14.3	20.4	14.9
17.9	29.9	12.6	40.6	14.9
17.9	13	13.5	19.8	23.9
19.4	13	12.6	14.2	21.6
23.9				

Sum of distances to nearest neighbour = 496.5 cm

Table 8-32. Results of distance to nearest neighbour analysis of <u>Monocraterion</u> burrows from the Bradore Formation

Quadrat	Area (sq.cm.)	N	P	Σr	$\bar{r}_A$	$\bar{r}_E$	R
MB-1	10,000	7	0.0007	174.4	24.91	18.87	1.32
MB-2	10,000	7	0.0007	205.9	29.4	18.87	1.56
MB-3	10,000	9	0.0009	235.3	26.14	16.67	1.57
MB-4	10,000	10	0.001	253.5	25.35	15.82	1.6
MB-5	10,000	12	0.0012	299.3	24.84	14.49	1.72
MB-6	10,000	16	0.0016	314.2	19.64	12.5	1.57
MB-7	10,000	26	0.0026	448.1	17.24	9.8	1.75
MB-8	10,000	26	0.0026	496.5	19.09	9.8	1.94

Table 8-33. Tests of significance of nearest neighbour analysis: <u>Monocraterion</u> burrows from the Thorold Formation

Quadrat Number	R	σ_{r_E}	c
MB-1	1.32	3.734	1.618*
MB-2	1.56	3.734	2.82**
MB-3	1.57	2.904	3.261**
MB-4	1.6	2.614	3.646**
MB-5	1.72	2.178	4.798**
MB-6	1.57	1.634	4.370**
MB-7	1.75	1.005	7.403**
MB-8	1.94	1.005	9.244**

* c = 1.96, P = 0.05 : significant

** c = 2.56, P = 0.01 : highly significant

D). Multiple-entrance vertical burrows

A significant number of marine organisms dwell or feed in burrows with more than one opening at the sediment-water interface. These types of burrows are also prolific in ancient sedimentary deposits. In order to investigate the application of the spatial distribution techniques previously discussed two burrow systems were studied (Table 8-2): 1. The ichnogenus Diplocraterion, representing U-shaped fossil forms, from the Middle Silurian Thorold Sandstone; and 2. Vertical burrow systems attributed to the thalassinid crustacean Axius serratus from recent sediments of the Strait of Canso, Nova Scotia.

i). Diplocraterion: Thorold Sandstone (Pl. 8-1, fig. 4)

The ichnogenus Diplocraterion is locally abundant in selected horizons in the Thorold Sandstone, at the Jolly Cut section in Hamilton. During the course of sampling the Skolithos population from this section numerous large slabs containing abundant specimens of Diplocraterion were found. These specimens were treated in a similar manner as were the Skolithos specimens previously discussed. One important difference however, between two ichnogenera was noted. Skolithos is merely a single burrow of rather small dimensions and measurements could be taken from the center of one burrow to the center of another. Diplocraterion consists of two vertical tubes joined by spreiten, which results in the specimen occupying a greater area. Clark and Evans (1954) suggest that the measurement of distance to the nearest neighbour in individuals that occupy an area ~~is~~ applicable only to the centers of the individuals and distances should be taken accordingly. Consequently, the distance to the nearest neighbour in the Diplocraterion population was measured from the center point of each individual (i.e., midway between the two vertical elements).

Six quadrats were sampled, each burrow was located, and the nearest neighbour was determined and measured (Tables 8-34 to 8-39). A summary of the results of this analysis is given in Table 8-40. In all 6 quadrats there exists an R-value indicative of a departure from the random. Tests of significance (Table 8-41) illustrate that all quadrats were significantly uniform.

There exists, however, a question in the reliability of the measurement of the distance to the nearest neighbour analysis in U-shaped burrows of this type. The spatial distribution of a population is influenced by many of the important physical and biological parameters that control the abundance and behavior of the individuals of the population

Table 8-34. Distance to nearest neighbour analysis of <u>Diplocraterion</u> burrows from the Thorold Formation. Quadrat: DT-1

Area of quadrat: 294.8 sq. cm.

Number of burrows: 128

Distance to nearest neighbour (in cm)

1.1	1.1	0.8	0.8	0.7	0.7	0.8
1.2	1.2	0.2	0.2	0.9	1.0	1.4
1.4	0.9	0.9	1.4	1.1	0.9	0.2
0.2	0.9	1.1	1.1	1.2	1.3	1.3
1.1	0.3	0.3	0.7	0.5	0.5	1.3
1.3	1.1	1.1	1.5	0.7	0.7	0.3
0.3	0.8	0.3	0.3	0.7	0.7	0.1
0.1	1.9	1.0	1.0	1.3	0.8	1.0
0.1	0.1	0.8	1.5	1.7	1.0	1.0
0.8	0.9	0.9	0.2	0.2	1.5	1.5
0.5	0.5	1.0	0.7	0.7	1.1	1.1
1.1	1.1	1.3	1.0	1.0	0.6	0.5
1.1	1.1	1.4	1.3	1.3	0.6	0.6
0.9	1.2	1.0	1.0	1.3	1.3	1.1
1.4	1.0	1.0	1.2	1.1	1.2	1.4
1.2	1.2	1.2	1.1	1.1	1.6	2.0
1.2	1.6	1.3	0.1	1.1	1.5	1.7
1.5	1.6	1.2	1.4	1.2	1.3	0.9
1.3	1.2					

Sum of distances to nearest neighbour = 124.1 cm

Table 8-35. Distance to nearest neighbour analysis of *Diplocraterion* burrows from the Thorold Formation. Quadrat: DT-2

Area of quadrat: 172.1 sq. cm.

Number of burrows: 64

Distances to nearest neighbour (in cm)

1.2	1.4	1.2	1.1	1.6	1.0	1.0
1.0	1.0	1.5	0.9	0.9	0.9	0.8
1.4	2.0	1.3	1.0	1.0	1.3	1.2
1.2	1.3	0.9	0.9	1.4	1.0	1.0
0.6	0.6	1.0	1.0	1.1	1.1	1.3
1.3	1.3	0.5	0.5	0.3	0.5	1.0
0.7	0.3	0.7	1.7	2.0	0.9	0.8
0.5	0.8	1.4	1.4	0.2	1.1	1.1
1.2	1.1	1.2	1.6	1.0	1.0	1.1
1.0						

Sum of distances to nearest neighbour = 67.3 cm

Table 8-36. Distance to nearest neighbour analysis of _Diplocraterion_ burrows from the Thorold Formation. Quadrat: DT-3

Area of quadrat: 332.2 sq. cm.

Number of burrows: 114

Distances to nearest neighbour (in cm)

1.4	1.2	1.4	0.7	1.2	1.4	1.0
1.6	1.5	1.2	1.1	1.5	1.1	0.7
1.0	1.1	1.2	1.2	1.2	1.0	1.2
1.2	1.6	1.6	1.7	1.0	1.0	1.0
1.2	1.2	1.3	1.1	0.8	0.8	1.1
1.1	0.7	0.7	0.8	0.8	1.3	1.1
1.1	1.7	1.4	0.6	0.6	1.2	1.3
0.9	0.8	0.8	1.0	0.8	0.9	0.8
1.0	1.7	1.7	1.1	0.9	1.3	0.9
1.3	1.0	1.4	1.3	1.2	1.3	0.7
0.7	0.7	1.6	1.3	1.1	1.4	1.3
1.2	0.9	0.9	1.3	1.2	1.0	1.6
1.0	1.2	1.0	1.0	1.3	1.5	1.4
0.9	1.5	1.3	2.1	1.5	1.2	1.1
1.2	1.2	0.6	1.1	1.1	0.6	1.0
1.8	0.7	0.7	1.0	1.8	0.8	0.9
0.9	1.2					

Sum of distances to nearest neighbour = 127.3 cm

Table 8-37. Distance to nearest neighbour analysis of *Diplocraterion* burrows from the Thorold Formation. Quadrat: DT-4

Area of quadrat: 153 sq. cm.

Number of burrows: 48

Distances to nearest neighbour (in cm)

1.0	1.1	1.0	0.9	0.7
1.3	1.2	1.0	1.5	1.4
1.3	1.1	1.1	1.5	1.2
0.7	2.0	0.6	0.7	0.7
1.7	1.4	1.1	1.6	1.3
1.3	0.7	1.3	1.2	1.7
1.3	1.1	0.7	1.1	2.4
1.1	1.1	1.6	1.3	1.1
1.2	1.4	1.2	1.5	
0.6	1.1	1.4	1.3	

Sum of distances to nearest neighbour = 58.5 cm

Table 8-38. Distance to nearest neighbour analysis of <u>Diplocraterion</u> burrows from the Thorold Formation. Quadrat: DT-5

Area of quadrat: 197.4 sq. cm.

Number of burrows: 72

Distance to nearest neighbour (in cm)

1.1	1.1	1.0	0.5	1.6	1.3	0.9
1.0	1.0	1.0	0.9	1.1	0.7	0.3
0.7	0.6	0.1	0.1	0.9	0.6	0.4
0.7	1.2	0.8	0.8	1.4	0.9	0.9
0.5	0.5	0.9	1.1	1.4	1.4	1.5
0.1	0.1	0.7	0.6	0.6	1.5	1.5
0.4	0.8	1.5	0.8	0.8	0.7	0.7
0.8	0.7	1.2	0.3	1.3	1.3	1.4
0.5	1.6	0.8	0.8	0.7	0.1	0.1
0.8	0.8	1.5	1.5	0.7	1.7	1.2
0.9	1.2					

Sum of distances to nearest neighbour = 67.2 cm

Table 8-39. Distance to nearest neighbour analysis of <u>Diplocraterion</u> burrows from the Thorold Formation. Quadrat: DT-6

Area of quadrat: 236 sq. cm.

Number of burrows: 111

Distances to nearest neighbour (in cm)

0.5	0.5	0.8	0.1	1.7	1.9	0.8
0.8	1.3	1.2	0.7	1.2	0.7	0.1
0.1	1.3	1.0	1.0	1.1	1.3	0.1
0.3	0.3	0.9	0.9	1.4	0.8	0.8
0.8	1.7	1.1	1.1	1.3	1.1	1.4
0.8	0.8	0.8	0.6	0.1	0.1	1.3
0.9	0.9	0.9	0.9	0.5	0.5	1.2
1.0	0.2	0.2	0.2	0.1	1.4	0.2
0.2	0.1	1.6	0.9	0.9	1.3	1.3
1.9	1.9	1.1	1.1	1.2	1.6	1.0
1.0	0.1	0.1	0.1	0.1	0.2	0.2
1.3	1.0	1.8	1.5	1.5	1.3	2.0
1.2	1.0	1.0	1.4	1.0	1.0	1.0
0.1	0.1	1.0	1.2	1.3	1.2	1.4
1.2	1.2	1.2	1.4	1.3	1.3	1.2
1.0	1.0	1.3	1.3	1.1	1.0	

Sum of distances to nearest neighbour = 101.9 cm

Table 8-40. Results of distance to nearest neighbour analysis of *Diplocraterion* burrows from the Thorold Formation

Quadrat	Area (sq.cm.)	N	P	Σr	$\bar{r}_A$	$\bar{r}_E$	R
DT-1	294.8	128	0.434	124.1	0.97	0.759	1.278
DT-2	172.1	64	0.372	67.3	1.052	0.82	1.28
DT-3	332.2	114	0.343	127.3	1.117	0.854	1.31
DT-4	153	48	0.314	58.5	1.219	0.893	1.37
DT-5	197.4	72	0.365	47.2	0.933	0.79	1.18
DT-6	236	111	0.47	101.9	0.918	0.729	1.26

Table 8-41. Tests of significance of nearest neighbour analysis: *Diplocraterion* burrows from the Thorold Formation

Quadrat Number	R	σ_{r_E}	c
DT-1	1.278	0.035	6.03*
DT-2	1.28	0.054	4.296**
DT-3	1.31	0.0418	6.29**
DT-4	1.37	0.067	4.87**
DT-5	1.18	0.051	2.8 **
DT-6	1.26	0.036	5.25**

* c = 1.96, P = 0.05 : significant

** c = 2.58, P = 0.01 : highly significant

(Levinton, 1972b). It has been shown that strong negative or positive interactions between individuals is a direct cause of the spatial distribution patterns exhibited by many populations (Holmes, 1950; Teal, 1958; Johnson, 1959; and Connell, 1963; among others). In this regard, U-shaped burrows present a special problem of measurement that may not be rectified.

Organisms that utilize a U-shaped burrowing mode, do so for a variety of reasons; these may vary from feeding method, as in Balanoglossus and Arenicola (Schäfer, 1972) or for ventilation purposes (Vogel and Bretz, 1972). In most U-shaped burrows the two tubes take on different functions; one is a feeding tube while the other serves as a fecal tube. This differentiation of use is reflected to some degree in the morphology of each tube. In recent sediments, when the burrow is active these differences can be recognized.

It is common, however, to find U-shaped fossil burrows on bedding surfaces which have been truncated by erosion, which results in an inability to distinguish between the tubes. An organism feeding in a U-shaped burrow exerts its strongest influence in the feeding tube, the site of active nutrient uptake. The fecal tube, which is used primarily for the passive passage of wastes, would be relatively ignored.

Individuals of a population would thus be more concerned with any interference with its feeding sphere than with the burrow as a whole. As a result any negative interactions between individuals (competing for a food supply) would probably be translated at the feeding tube of the burrow. This is illustrated in the modern burrows of <u>Arenicola</u>, where the feeding tube may change position frequently while the fecal tube remains stationary (Schäfer, 1972).

Therefore in the determination of the spatial distribution of U-shaped burrows (such as <u>Diplocraterion</u>, <u>Corophioides</u>, <u>Arenicolites</u>, <u>Bifungites</u>, and inclined <u>Rhizocorallium</u>) it may well be more advisable to consider the distance between feeding tubes and not the entire burrow.

ii). <u>Axius serratus</u>: Strait of Canso

In addition to U-shaped ichnogenera there exists another group of burrow complexes that possesses more than one opening to the sediment-water interface. These may take the form of vertical feeding structures, such as <u>Phycodes</u>, <u>Teichichnus</u> or <u>Tricophycus</u> or dwelling burrows with multiple openings such as <u>Ophiomorpha</u>, <u>Thalassinoides</u> or <u>Polycylindrichnus</u>. Unfortunately, no fossil specimens were found in sufficient numbers to warrant investigation. However, the spatial distribution of burrow complexes attributed to the thalassinid crustacean Axius serratus is included to illustrate the difficulties that structures of this type may present.

A coefficient of dispersion analysis was conducted on the burrows attributed to Axius serratus in the Strait of Canso (for location details, see Pemberton, 1976). In the determination twenty quadrat counts were made in each sub-area (Ship Harbour and Pirate Harbour). Within each quadrat, counts were made to determine the total number of burrows, the number of main burrow openings, the number of auxillary burrow openings, and the total number of burrow complexes (Tables 8-42 and 8-43). In each area a coefficient of dispersion was obtained for the total number of burrows and the total number of burrow complexes (Table 8-44).

In Pirate Harbour the mean density (number per square meter) of the total number of burrow openings is 19.25, with a corresponding coefficient of dispersion of 0.7429; the number of burrow complexes shows a mean density of 12, with a corresponding coefficient of dispersion of 0.3246. Similarly, the mean density of burrow openings in Ship Harbour is 14.1, with a corresponding coefficient of dispersion of 0.4621; and a mean density of burrow complexes of 8.75, corresponding to a coefficient of dispersion of 0.1789. The

Table 8-42. Random burrow densities taken from Ship Harbour. Each quadrat is one square meter

Quadrat	Total No. of burrows	No. of main burrow openings	No. of auxiliary burrow openings	Total no. of burrow complexes
SH-200	16	10	6	10
SH-201	17	9	8	9
SH-202	17	9	8	9
SH-203	18	11	7	11
SH-204	12	7	5	7
SH-205	12	9	3	9
SH-206	18	10	8	10
SH-207	12	8	4	12
SH-208	10	7	3	7
SH-209	14	10	4	10
SH-210	18	11	7	11
SH-211	14	9	5	9
SH-212	15	9	6	9
SH-213	14	8	6	8
SH-214	12	7	5	7
SH-215	14	8	6	8
SH-216	10	7	3	7
SH-217	12	9	3	9
SH-218	13	9	4	9
SH-219	14	8	6	8

Table 8-43. Random burrow densities taken from Pirate Harbour. Each quadrat is one square meter

Quadrat	Total No. of burrows	No. of main burrow openings	No. of auxiliary burrow openings	Total no. of burrow complexes
PH-100	19	12	7	12
PH-101	27	15	12	15
PH-102	22	13	15	13
PH-103	18	10	8	10
PH-104	26	15	11	15
PH-105	20	12	8	12
PH-106	21	13	8	13
PH-107	21	14	7	14
PH-108	16	10	6	10
PH-109	15	11	4	11
PH-110	19	12	7	12
PH-111	14	9	5	9
PH-112	17	10	7	10
PH-113	18	12	6	12
PH-114	23	14	9	14
PH-115	19	13	6	13
PH-116	24	15	9	15
PH-117	14	10	4	10
PH-118	15	9	6	9
PH-119	17	11	6	11

Table 8-44. Coefficient of dispersion for Axius serratus, in Strait of Canso

	Number of quadrats	Total no. of burrows	Ave. mean density (no./sq m)	Coefficient of dispersion
I <u>Pirate Harbour</u>				
A. Total no. of burrows (main openings plus auxiliary openings)	20	385	19.25	.7429
B. Burrow complexes	20	240	12	.3246
II <u>Ship Harbour</u>				
A. Total no. of burrows (main openings plus auxiliary openings)	20	282	14.1	.4621
B. Burrow complexes	20	175	8.75	.1789

Limits of the coefficient of dispersion for random distribution

at n = 20

0.3342 - 1.6658

limits of the coefficient of dispersion for a random distribution at n = 20 are 0.3342 - 1.6658.

Analysis of these data reveals that in both Ship Harbour and Pirate Harbour extreme care must be taken in the discrimination of the number of burrows present. When all burrow openings (main openings plus auxillary openings) are counted, the coefficient of dispersion falls within the limits of a random distribution. When only the number of burrow complexes are used, the coefficient of dispersion indicates a uniform distribution. Thus the intermixing of auxillary openings connected to main burrow openings or burrows of other organisms may result in erroneous results (Pemberton, 1976). In the analysis of the spatial distribution of Nephrops norvegicus, Chapman and Rice (1971) may have used all burrow openings in the area sampled, which not only consisted of main openings, but also auxillary openings and burrows of the crab Goneplax rhomboides. This may have affected the results obtained as outlined in Atkinson (1974).

It is possible to differentiate between burrow openings in modern active burrow systems. Pemberton, et al. (1976) observed that one main Axius burrow may be associated with up to three auxillary holes. The relationship between main openings and auxillary openings was established by squirting a potassium permanganate solution down the main opening and observing from which holes the dye is expelled. This dye irritates the shrimp and is actively pumped out of the system (Pemberton, et al., 1976). It is extremely difficult, however, to discern burrow complexes in fossil form unless subtile relationships remain intact and are observable. This would suggest that techniques related to the determination of the spatial distribution of complex multi-entranced ichnofossils be approached with caution.

E). Interpretation of data on multi-entrance ichnofossils

Investigations of the spatial distribution of multi-entranced burrows suggest the following:

1). Nearest neighbour distances should be made from feeding tube to feeding tube. If the distinction cannot be made an analysis should not be attempted.

2). Care must be taken to discern between main openings and auxillary openings in multi-entranced forms. Only burrow complexes should be used in the coefficient of dispersion analysis.

8-5. Discussion

A). Deposit-feeders versus suspension-feeders

The spatial distribution of a population is influenced by many of the important physical and biological parameters that control the abundance and behavior of the individuals of the population (Levinton, 1972a). Environmental heterogeneity has been shown to be a principal cause in the aggregational distribution exhibited by many species, for example, the filter-feeding bivalves Mya and Petricola (Connell, 1956) and Modiolus demissus (Connell, 1963). Harriston (1959) has demonstrated that this is particularly true for species that exist only under a limited range of environmental conditions. Strong negative interactions between individuals, due to direct interference or territorial behavior, is a principal cause of uniform distributions (Holme, 1950; Johnson, 1959; Connell, 1963; among others). Random distributions have been ascribed to a variety of factors, which include: random larvae settlement (Connell, 1955); an abundance of resources (Harriston, 1959); random movements of individuals (Levinton, 1972a); random distribution of resources (Levinton, 1972a); or wrong sample area (Risk, personal communication).

There exists a differentiation between the spatial distributions exhibited by suspension-feeding organisms and deposit-feeding organisms. Levinton (1972b) has shown that this difference is related to the availability of food. Suspension-feeders feed on a variety of substances such as plankton, dissolved organic matter, organic aggregates and bacteria. These resources tend to fluctuate in quantity with time (Harvey, 1950; Levinton, 1972b), and thus there exists a changing qualitative food supply available for suspension-feeding populations. Levinton (1972b) suggests that suspension-feeders must therefore maintain an adaptive strategy which maximizes the general nature of the food source and results in inhibiting the development of narrow food preferences. Since the majority of suspension-feeders are immobile they must feed on a resource that passes by them. Analysis of the mode of feeding of suspension-feeders by Levinton (1972b) indicates that no two closely located individuals of the same suspension-feeding species or of a different species have access to the same food particle. Therefore, each individual's food is unique and competitive exclusion by exploitation does not take place and all individuals are independent (Levinton, 1972b).

Deposit-feeders also feed on a number of food items such as plankton, dissolved organic matter, plant debris (which has been mechanically broken down), diatoms, and bacteria. Newall (1965, 1970) and Hargrave (1970) have shown that bacteria is often the major food source of a deposit-feeder. Zobell (1938) has demonstrated that bacteria are very abundant in fine-grained marine sediments. The activities of deposit-feeding organisms such as corophagy, biogenic reworking and bacterial conversion of detritus results in a constant recycling of food throughout the system (Rhoads and Stanley, 1965; Rhoads and Young, 1970). This implies that a relatively stable food supply is exploited by deposit-feeding organisms (Levinton, 1972b). As opposed to suspension-feeders, deposit-feeders are usually mobile, either moving through the sediment or grazing directly on the food source. Analysis of the mode of feeding of deposit-feeders by Levinton (1972b) indicates that all individuals in an area have access to approximately the same food supplies. As a result, differences in feeding efficiency or digestion efficiency can be utilized to enable one species to exclude another by competition. This competitive interaction leads to trophic specialization (Turpaeva, 1959) and adaptations to different substrate types by different species (Levinton, 1972b).

This differentiation in food supply and mode of feeding has led Levinton (1972b) to conclude that deposit-feeders display uniform spatial distribution or random distribution (in the presence of an abundant food supply). Suspension-feeders, on the other hand, usually exhibit an aggregated spatial distribution over large areas and random distributions within the aggregates.

Analysis of previous studies on the spatial distributions exhibited by modern organisms confirms Levinton's hypothesis. Table 8-45 summarizes data that indicate that a differentiation indeed exists between certain trophic types and their spatial distributions.

Holme (1950) has shown that the deposit feeding bivalve *Tellina tenuis* displays a uniform distribution pattern which is correlated with the foraging activities of the inhalent siphon on the mud surface. Several species of the scavenging decapod crustacean *Uca* also exhibit uniform distributions; of the three species studied, *Uca pugilator* (Crame, 1941; Teal, 1958; Weis, 1976), *Uca pugnax* (Pearse, 1914; Weis, 1976), and *Uca minax* (Ono, 1965) all were found to be extremely territorial. Two species of tube-dwelling, deposit-feeders have also been shown to exhibit populations that are uniformly spaced, the sabellid *Spirorbis boreali* (Wisely, 1960), and the nephthydid *Nepthys incisa* (McCall, 1977). The deposit-feeding bivalve *Nucula proxima*, on the other hand, displays an aggregated spatial pattern for the entire population, with individuals randomly distributed within the aggregate (Levinton, 1972a). This has been attributed to the fact that *Nucula* is a non-siphonated, free-burrowing form which lacks the means for territorial

Table 8-45

A comparison of the population dispersion of selected marine organisms

Type of Feeding	Species	Dispersion Pattern	Reference
Suspension-feeder	Barnacles	uniform	Crisp, 1961
	Modiolus demissus	random	Connell, 1963
	Mulinia lateralis	random	Hughes, 1970; Jackson, 1968
	Mya arenaria	random	Connell, 1956
	Petricola pholadiformis	random	Connell, 1956
	Phoronopsis viridis	random-low densities uniform-high densities	Johnson, 1959
Deposit-feeder	*Nepthys incisa*	uniform	McCall, 1977
	Nucula proxima	random	Levinton, 1972
	Scobicularia plana	random	Hughes, 1970
	Spirorbis boreali	uniform	Wisely, 1970
	Tellina tenuis	uniform	Holme, 1950; Connell, 1955
	Uca pugilator	uniform	Teal, 1958
	Uca pugnax	uniform	Connell, 1963

defense. Since it does not have a permanent burrow it does not establish a territory (Levinton, 1972a). Recently, many studies have been conducted on the spatial pattern displayed by the deposit-feeding lobster *Nephrops norvegicus* (Dybern and Hoiseter, 1965; Chapman and Rice, 1971; Atkinson, 1974; Farmer, 1974). Considerable variation has been found to exist in the spatial pattern of the burrows, from aggregations (Dybern and Hoiseter, 1965; Chapman and Rice, 1971), to random (Atkinson, 1974), to uniform (Farmer, 1974). All studies agree, however, that in the presence of high densities, territorial behaviour is strong and a degree of spacing will result. From these selected examples, the spatial distributions exhibited by deposit-feeding organisms seem to be food-related.

Suspension-feeding organisms, on the other hand, exhibit spatial patterns that are usually random or aggregated. Variation in substrate conditions has been cited as the principal cause in the aggregated distributions displayed by the suspension-feeding bivalved *Mya arenaria* and *Petricola pholadiformis* (Connell, 1956); *Modiolus demissus* (Connell, 1963); and *Mulinia lateralis* and *Gemma gemma* (Jackson, 1968). However, individual relationships within the aggregates proved random for *M. arenaria* and *P. pholadiformis* (Connell, 1956) and *M. lateralis* (Jackson, 1968).

Similar results have been reported for the phoronid Phoronopsis viridis by Johnson (1959); the entire population was aggregated but individuals were randomly dispersed within the aggregate. Epifaunal suspension-feeding barnacles, on the other hand, display a uniform spatial distribution which is related to space requirements (Crisp, 1961). From these selected examples, the spatial distribution of suspension-feeding organisms seems to be substrate (or environmentally) controlled. Competition for food does not play a prominent role.

B). Nature of trace-maker

Perhaps one of the most important aspects of the study of the spatial distribution of ichnofossils is its role in aiding in the identification of the trace-making organism. At present it is extremely difficult to assign a specific organism to a specific trace. This can only be done on those rare occasions when the trace-maker is preserved within the trace, such as with the examples illustrated by Cameron (1967) and Pickerill and Forbes (1978). In a now classic study Seilacher (1964) has classified ichnofossils by ethological grouping; assignment to these groups is usually based on the morphology of the ichnofossil. The determination and recognition of the spatial distribution of selected ichnofossils may aid in further refining the ethological classification of a particular trace.

Analysis of the data previously presented on the spatial distribution of Skolithos burrows is significant in a number of ways. The nature of the Skolithos-making organism has long been debated and a number of tentative assignments have placed it in groups ranging from inorganic gas bubbles to fossilized algae (see Chapter 5 for a more detailed examination). It is generally conceded now that Skolithos represents the dwelling burrow of a suspension-feeding organism. This assignment is based primarily on morphological features. A spatial distribution analysis may provide additional quantitative data on this problem and may aid in the refinement of the present state of knowledge.

The entire Skolithos population found in the Bradore Formation was found to be distributed in aggregate, based on the coefficient of dispersion. Analysis of the spatial pattern of the individuals within the aggregate, by the distances to nearest neighbour method, shows that at high densities they are distributed uniformly. Since only a distance to nearest neighbour analysis was done on the Skolithos burrows from the Thorold Formation, nothing concrete can be said about the dispersion of the entire population, but individuals within the population were distributed randomly at all observed densities. The only other study conducted on the spatial distribution of Skolithos concerned a population from the Upper Ordovician Ely Springs Dolomite of Nevada (Miller, 1977). The population was found to not significantly depart from the random; sample size was 100 sq. cm and although no procedural data are given, this would represent the interactions of the individuals within the population.

A significant feature of the distance to nearest neighbour method is that it allows for a comparison of observed densities between different samples, even if the quadrat areas are not standard. The density (p) used in the method is defined as the number of individuals per unit area (Clark and Evans, 1954); in both areas analyzed, this would be the number of individuals per square centimeter. A comparison of the observed densities of Skolithos from both areas (Table 8-46) reveals the following:

1). Observed densities per square cm from 5 sampled quadrats in the Bradore Formation ranged from .248 to .53.

2). At densities recorded as .248, .265 and .405 per square cm, the individuals were randomly dispersed.

Table 8-46. Comparison of density data of *Skolithos* from the Bradore and Thorold Formations.

Formation	Quadrat No.	Density	Distribution
Bradore Fm.	S.B. - 1	.248	random
	S.B. - 2	.265	random
	S.B. - 3	.405	random
	S.B. - 4	.503	uniform
	S.B. - 5	.53	uniform
Thorold Fm.	ST - 1	.115	random
	ST - 2	.148	random
	ST - 3	.279	random
	ST - 4	.255	random
	ST - 5	.352	random
	ST - 6	.378	random
	ST - 7	.178	random
	ST - 8	.414	random

3). At densities recorded as .503 and .53 per square cm, the individuals were uniformly dispersed.

4). Observed densities per square cm from 8 sampled quadrats in the Thorold Sandstone ranged from .115 to .414.

5). At all recorded densities the individuals were randomly dispersed.

These data indicate that the recorded densities in the Thorold Skolithos population may not be high enough for the individuals to display an uniform dispersion pattern. The highest density in the Thorold (.41 per sq. cm) was observed at the Jolly Cut Section (ST-8). A comparable density (.405 per sq. cm) was observed in quadrat SB-3 from the Bradore. Both displayed random distributions. Uniform spacing in the Bradore Formation did not occur until densities exceeded .5 per sq. cm. There are no density data given for the Skolithos population from the Upper Ordovician Ely Springs Dolomite (Miller, 1977).

Therefore, the spatial pattern of Skolithos burrows from both areas suggests that the entire population is dispersed in aggregations. Within these aggregations, the individuals are distributed randomly except that at very high densities (possibly exceeding .5 per sq. cm) that individuals are uniformly dispersed. This is very characteristic of the pattern displayed by suspension-feeding organisms, as previously outlined. Of special interest is the study done by Johnson (1959) on the phoronid *Phoronopsis viridis* from the intertidal sands of Tomales Bay, California; the entire population was dispersed in aggregation throughout the area, which he attributed to a response to environmental features (although no discernible differences were found between colonized and non-colonized areas). Within the aggregate, the individuals were distributed randomly in areas of low density and uniformly in areas of high density (Johnson, 1959). This is not unlike the pattern displayed by *Skolithos*. Johnson (1959) attributed the uniform distribution at high densities to the expansion of the lophophore during feeding. The similarity between the spatial patterns exhibited by *Skolithos* and *Phoronopsis* is especially interesting since Fenton and Fenton (1974) attributed *Skolithos* burrows to suspension-feeding phoronids.

For the first time, therefore, spatial distribution analysis quantitatively shows that *Skolithos* probably was the dwelling burrow (or tube) of a suspension-feeding organism. In addition, it can be shown that the *Skolithos*-maker was probably a lophophorate or tentacular-crowned suspension-feeder.

C). Differentiation of ichnogenera

One of the many enigmas that plague ichnofossil workers is the well known Skolithos-Monocraterion problem (see Chapter 5 for a complete synopsis). Hallam and Swett (1966), while investigating the ichnofossils of the Lower Cambrian pipe-rock of Scotland, concluded that Skolithos and Monocraterion were produced by the same worm-like organism, responding to different sedimentation regimes. Skolithos was formed during periods of negligible sedimentation, while Monocraterion was formed in response to sediment influx. More recently, Goodwin and Anderson (1974), investigating the Lower Cambrian Chickies Formation of Pennsylvania made similar conclusions and interpreted Monocraterion as merely the funnel-shaped top of a Skolithos burrow. They reached this conclusion based on the following:

1). Monocraterion funnels are always attached to Skolithos tubes.

2). Where Skolithos occurs alone in the Chickies, it is associated with higher energy tangential cross-stratification in sets separated by planar erosion surfaces. Thus Monocraterion funnels were eroded.

3). The difference in spacing is attributed to difference in time of submergence and persistence of tidal currents.

It has been pointed out, however, by Crimes, et al. (1977) that:

1). Although the lower Monocraterion tubes are similar to Skolithos, it does not necessarily follow that the lower tube represents Skolithos.

2). The cross-cutting of the cross-laminae by Skolithos, which terminate at an upper erosion surface, does not prove that the burrows were eroded; it indicates only that they are a later feature.

3). Other deposits with sandy beds with gradational upper contacts with overlying muds have only Skolithos burrows, despite the apparent absence of erosion.

Crimes, et al. (1977) therefore reject the erosion hypothesis of Goodwin and Anderson (1974) and although they agree with the sedimentation hypothesis of Hallam and Swett (1966), they reject the same-organism theory.

The study of the population structure of Skolithos and Monocraterion from the Lower Cambrian Bradore Formation may shed additional light on this problem. The Bradore Formation of Southern Labrador is analogous to the Chickies and Eribol Formations (Swett and Smit, 1972), where both Hallam and Swett (1966) and Goodwin and Anderson (1974) did their investigations. Similar tidal-origins have been postulated for all three formations (Swett, et al., 1971; Swett and Smit, 1972; Goodwin and Anderson, 1974).

In contrast to the Skolithos findings, analysis of the Monocraterion burrows indicates that while the entire population is dispersed in aggregates, the individuals are uniformly dispersed at all densities. Analysis of these data in conjunction with studies on modern organisms (previously discussed) suggests that the spatial patterns of Monocraterion burrows resemble that of a deposit-feeding or carnivorous form, in which negative interactions are common.

Suspension-feeding and deposit-feeding populations are not only separated by their mode of feeding and spatial arrangement, but are also somewhat facies-controlled. Infaunal suspension-feeders reach their maximum abundance in well-sorted sandy sediments. Sanders (1958) has determined that a median grain size of 0.18 mm diameter should theoretically be most favorable. Deposit-feeders, on the other hand, reach maximum abundance in finer-grained silts and clays (Sanders, 1958). This is correlated with food abundance, since silts and clays offer larger surface areas for bacterial production (Newell, 1965). In the Bradore Formation, the Skolithos "pipe-rock" is associated with clean quartzitic sandstones and do not contain Monocraterion burrows. On the other hand, Monocraterion burrows are associated with arkosic sandstones which contain much more detrital material and do have some Skolithos burrows.

The difference in spacing of Skolithos and Monocraterion burrows observed by Goodwin and Anderson (1974) (and attributed to a difference in time of submergence and persistence of tidal currents) may in fact be related to a difference in feeding strategies, as shown by the Bradore examples. Since these feeding strategies are somewhat facies-controlled, the observations of Hallam and Swett (1966) and Goodwin and Anderson (1974) are valid to some degree. Monocraterion burrows were probably produced at times of negligible sedimentation or slow deposition by low velocity currents, which would be consistent with detrital input. Skolithos, on the other hand, would be produced in the main after deposition of beds from high velocity currents, including those producing tangential cross-bedding. The one-organism hypothesis of the formation of Skolithos and Monocraterion (Hallam and Swett, 1966; Goodwin and Anderson, 1974) is rejected. The spatial distributions of the two burrow types suggest that they were created by organisms employing different feeding modes. This, in association with morphological studies (see Chapter 5), indicates that Skolithos and Monocraterion were indeed created by distinct organisms.

D). Summary of the applications of the measure

The determination of the spatial distribution of selected ichnogenera could be potentially useful in a number of ways. The technique may aid in the determination of the mode of feeding of a portion of the soft-bodied biota. The trophic analysis of body fossils has long been known to be of significant value in paleoecological reconstructions (see Walker, 1976). However, the soft-bodied fauna (as represented by ichnofossils) has often been ignored in the reconstruction of fossil communities, which may be due to a lack of adequate methodology. Thus, the spatial distributional analysis of ichnofossils may serve as an additional tool for extracting information for use in such paleoecological studies.

The analysis may also aid in problems dealing with ichnofossil taxonomy and nomenclature, an example of which is the Skolithos-Monocraterion problem outlined earlier. Analysis of this type will provide quantitative data (for the first time) in which comparison with specimens of different ages can be made.

E) Summary of the limitations of the measure

Although useful, the measure does have a number of limitations. It is suggested that the measure does not lend itself (at this time) to U-shaped or multiple-entranced burrow systems, for reasons previously outlined. Care must be taken to be sure that all samples are from a single bedding plane or horizon. In areas where extensive horizontal exposures are found it is suggested that both techniques be employed. This will give information on both the spatial distribution of the population as a whole and also on the dispersion of the individuals within the population. The two-fold analysis system is widespread in studies dealing with the determination of the spatial distribution of extant organisms (Hughes, 1970). In areas where extensive horizontal exposures are missing, it is suggested that the distance to the nearest neighbour analysis will give data on the distribution of individuals within the population. These in turn can be used as a comparison with other areas.

Explanation of Plate 8-1

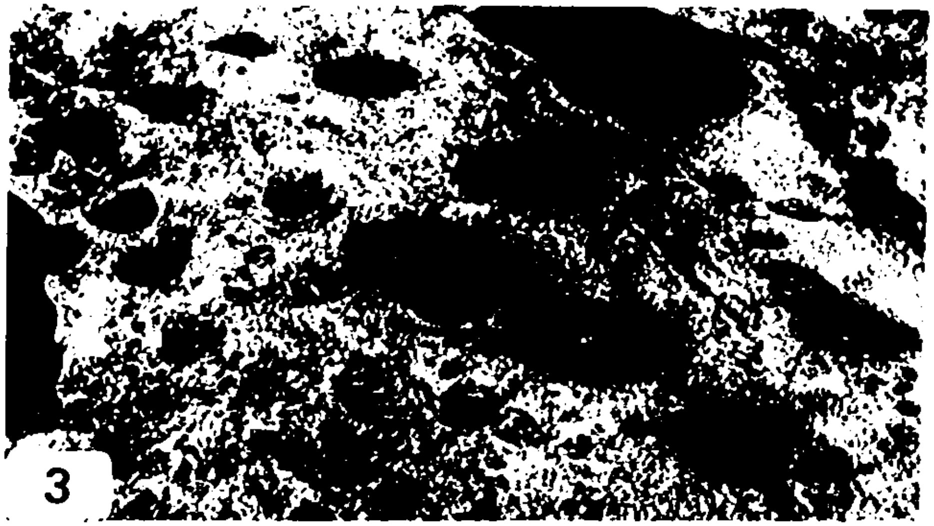
Fig. 1. Skolithos linearis from the Lower Cambrian Bradore Fm., southern Labrador. Scale bar equals 1 cm.

Fig. 2. Skolithos sp. from the Middle Silurian Thorold Sandstone, southeastern Ontario, X1.

Fig. 3. Monocraterion sp. from the Lower Cambrian Bradore Fm., southern Labrador. Bedding plane view, X.25.

Fig. 4. Diplocraterion sp. from the Middle Silurian Thorold Sandstone, southeastern Ontario. Bedding plane view. Scale bar equals 1 cm.


1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