

MACRO-BORINGS IN CRETACEOUS OYSTERS  
FROM DRUMHELLER, ALBERTA

MACRO-BORINGS IN CRETACEOUS OYSTERS FROM DRUMHELLER, ALBERTA:

TAPHONOMY AND PALEOECOLOGY

by

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A Thesis

Submitted to the Department of Geology  
in Partial Fulfillment of the Requirements  
for the Degree  
Bachelor of Science

McMaster University  
June 1983

BACHELOR OF SCIENCE (1983)  
(Geology)

McMASTER UNIVERSITY  
Hamilton, Ontario

TITLE: Macro-borings in Cretaceous Oysters from  
Drumheller, Alberta: Taphonomy and  
Paleoecology

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NUMBER OF PAGES: ix, 69

## ABSTRACT

Macro-borings and other biogenic structures found in Ostrea glabra valves were examined using a dissecting microscope, SEM and X-radiography. Shells were collected from in situ and transported oyster beds of the Bearpaw-Horseshoe Canyon Formation transition (Upper Cretaceous) at Drumheller, Alberta. Emended diagnoses for Entobia, Talpina and Zapfella were proposed and systematic descriptions of these ichnogenera along with Oichnus were done. Repair blisters and partitions apparently formed by the oyster in response to irritations were also described and interpreted. It was confirmed that statistical analysis could differentiate between round holes drilled by naticids and muricids. It was possible to define fossil micro-environments on the basis of an interpretation of taphonomy and paleoecology considered within the sedimentary context.

## ACKNOWLEDGEMENTS

I thank Dr. M.J. Risk for his willingness to supervise this thesis and provide financial assistance. I am grateful to Dr. S. George Pemberton for providing a stimulating introduction to ichnology and direction for this project. The Alberta Research Council generously financed field work and made their facilities available. McMaster University also provided research facilities. Anna Wong provided both technical assistance and encouragement.

I also wish to acknowledge the fine photographic work of Jack Whorwood and efficient typing done by Linda Hillier.

Heartfelt thanks to my family, friends and colleagues who provided assistance in a variety of ways.

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## CHAPTER 1

### INTRODUCTION

Trace fossils evidence the life activities of ancient organisms (Warme, 1975). Macro-borings are often sufficiently distinctive that they indicate the presence of a member of a particular group of borers (Bromley, 1970).

Few species are preserved as body fossils in the Drumheller oyster beds. Macro-borings make an important contribution to the reconstruction of the fossil community that existed. Drumheller macro-borings occur, almost exclusively, in Ostrea glabra valves. This affords a unique opportunity to study boring morphotypes in a single substrate. The distinct shapes of borings described thus are a result of different attack strategies rather than a reflection of substrate properties. Hardness, curvature and chemical composition are held constant. The purpose of this study is to compare the ichnofauna found in cemented and unconsolidated oyster beds and draw conclusions concerning taphonomy and paleoecology of these units.

### Study Area

The unit investigated in this study is located about 11 kilometers southeast of Drumheller (Fig. 1). Walls of the Willow Creek and Red Deer River valleys provide almost uninterrupted exposure of nearly flat lying Upper Cretaceous and Paleogene strata. Of specific interest for the present study is the unconsolidated glauconitic sand containing oyster fragments and the calcium carbonate-cemented oyster beds above this. Both are found in unit 4 of the Upper Cretaceous Horseshoe Canyon Formation (Rahmani, 1981) (Figs. 2 and 3). The sand typically is somewhat less than 3 m thick, while the cemented beds are generally approximately 1 m in thickness, occasionally up to 3 m.

### Depositional Setting

The Bearpaw and Horseshoe Canyon Formations crop out in an 850 kilometer arc through central and east Alberta. To the west, the Bearpaw thins and the Edmonton Group (containing the Horseshoe Canyon Formation) and Belly River thicken. These units were deposited during the Mesozoic to Cenozoic when widespread transgressions and regressions lead to the accumulation of alternating marine and terrestrial deposits. In the study area, the Horseshoe Canyon Formation consists of continental clastics while the Bearpaw is characterized by marine mudstones.

Figure 1. Location of field area (from Rahmani, 1981; used with permission).

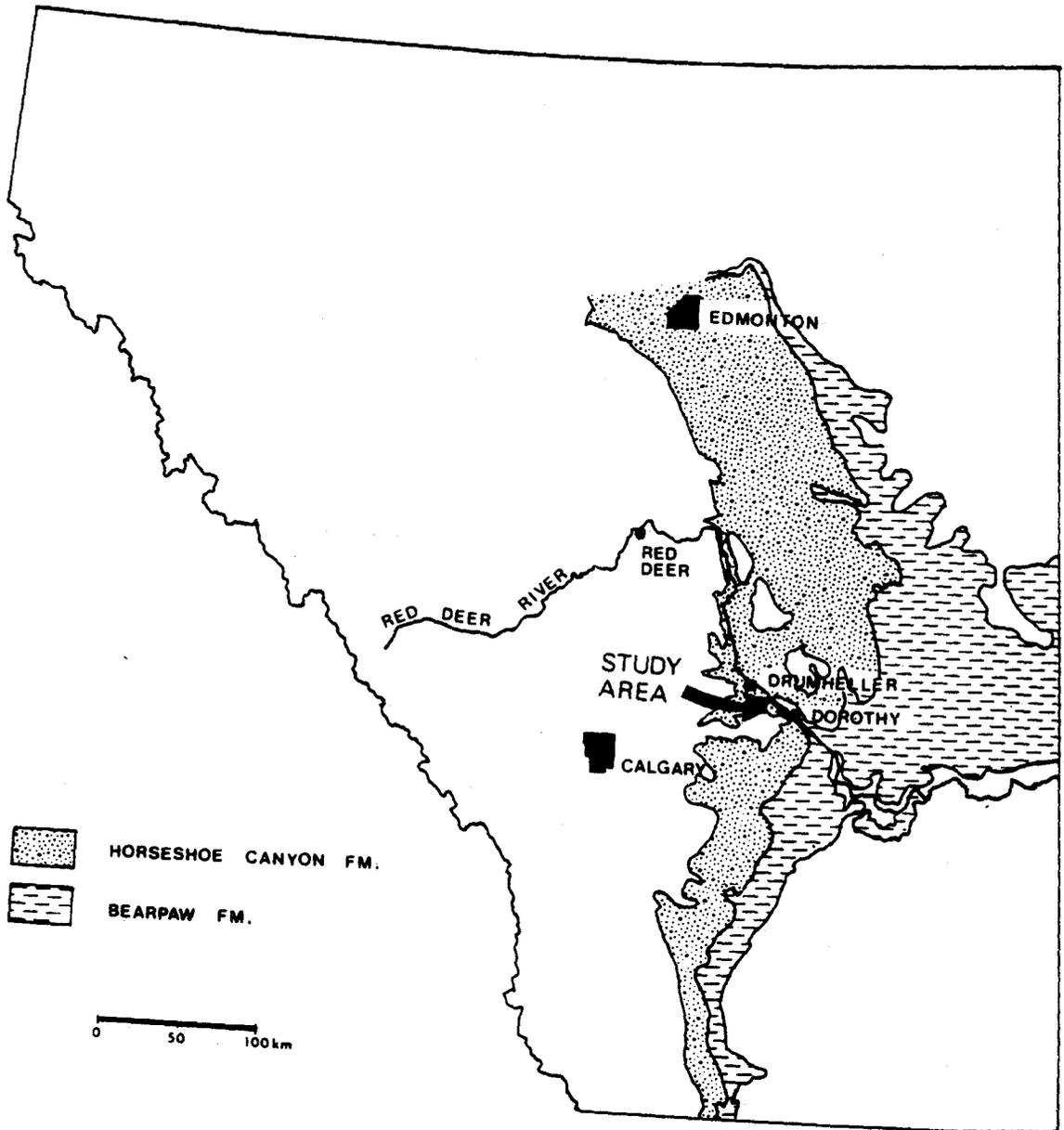
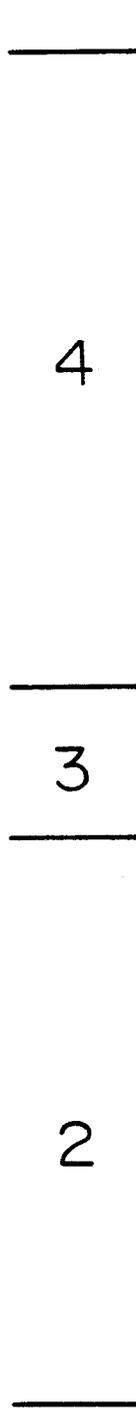
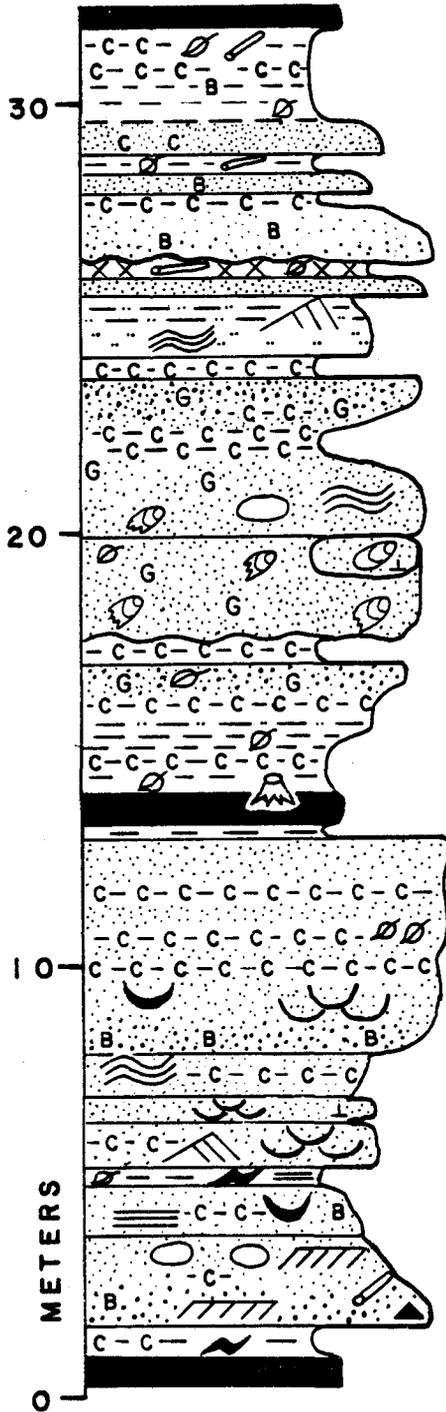


Figure 2. Schematic diagram of the Bearpaw-Horseshoe Canyon Formation transition (from Rahmani, 1981; used with permission).

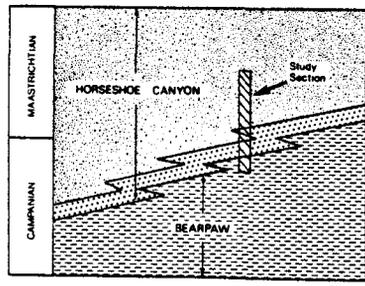
Figure 3. A portion of the stratigraphic column of WC 3, showing position of the oyster beds (after Rahmani, unpub. data).

# WC 3

# LEGEND



- BURROWS
- LEAF IMPRINTS
- COAL CHIPS
- SILICIFIED TREES
- OYSTERS-CLAMS (WHOLE)
- OYSTERS (FRAGMENTED)
- G GLAUCONITE
- B BENTONITE
- C CARBONACEOUS
- ⊥ CALCAREOUS
- CONCRETIONS
- TROUGH CROSS-STRATIFICATION
- TABULAR, PLANAR CROSS-STRATIFICATION
- CURRENT RIPPLES
- PARALLEL STRATIFICATION
- WAVY BEDDING
- FLASER BEDDING
- LOCALLY DERIVED CLASTS
- IRONSTONE BAND
- SANDSTONE
- SILT STONE
- SHALE
- COAL



Schematic diagram of the Bearpaw-Horseshoe Canyon Formations transition.

### Previous Work

Bearpaw-Horseshoe Canyon transition in the Drumheller area has been studied by Shephard and Hills (1970) and Rahmani (1981). These authors propose that the deposits represent an easterly prograding delta supplied by clastics derived from the tectonically uplifted Cordillera. The underlying Bearpaw represents a prodelta facies characterized by fine-grained sediment and much bioturbation. The presence of glauconite in the oyster bed indicates marine influence.

There is some difference of opinion concerning the relative importance of fluvial and tidal processes in delta development. This is reflected in contrasting interpretations of the significance of the oyster beds.

Shephard and Hills (1970) suggest that the delta is analogous to that formed by the Mississippi River, and thus river-dominated. They suggest that the oysters thrived in a partially restricted bay on the higher more stable portions where thick sands of a previous distributary channel underlay the bay. Currents traveled eastward from the open end of the bay. Tidal currents were allowed access following subsidence and lead to the erosion of the oyster beds. Partial restriction of the bay is also called upon to account for the discontinuous black shale.

Rahmani (1981), on the other hand, suggests that a tide-dominated environment typified by the Ord River Delta better

PLATE I OUTCROP

Fig. A: Sampling site WC3  
Cemented oyster beds form a resistant ledge.  
Beneath unconsolidated sand containing oyster fragments  
supports sparse vegetation.

Fig. B: WC3  
Unusually thick  $\text{CaCO}_3$ -cemented oyster bed.  
Unconsolidated sand with abundant oyster fragments can  
be seen in foreground (hammer is 35 cm in nature).

Fig. C: WC3  
Closer view of  $\text{CaCO}_3$ -cemented material.  
Large Ostrea glabra valves are the main constituent of  
this rock. Glauconite is also present.



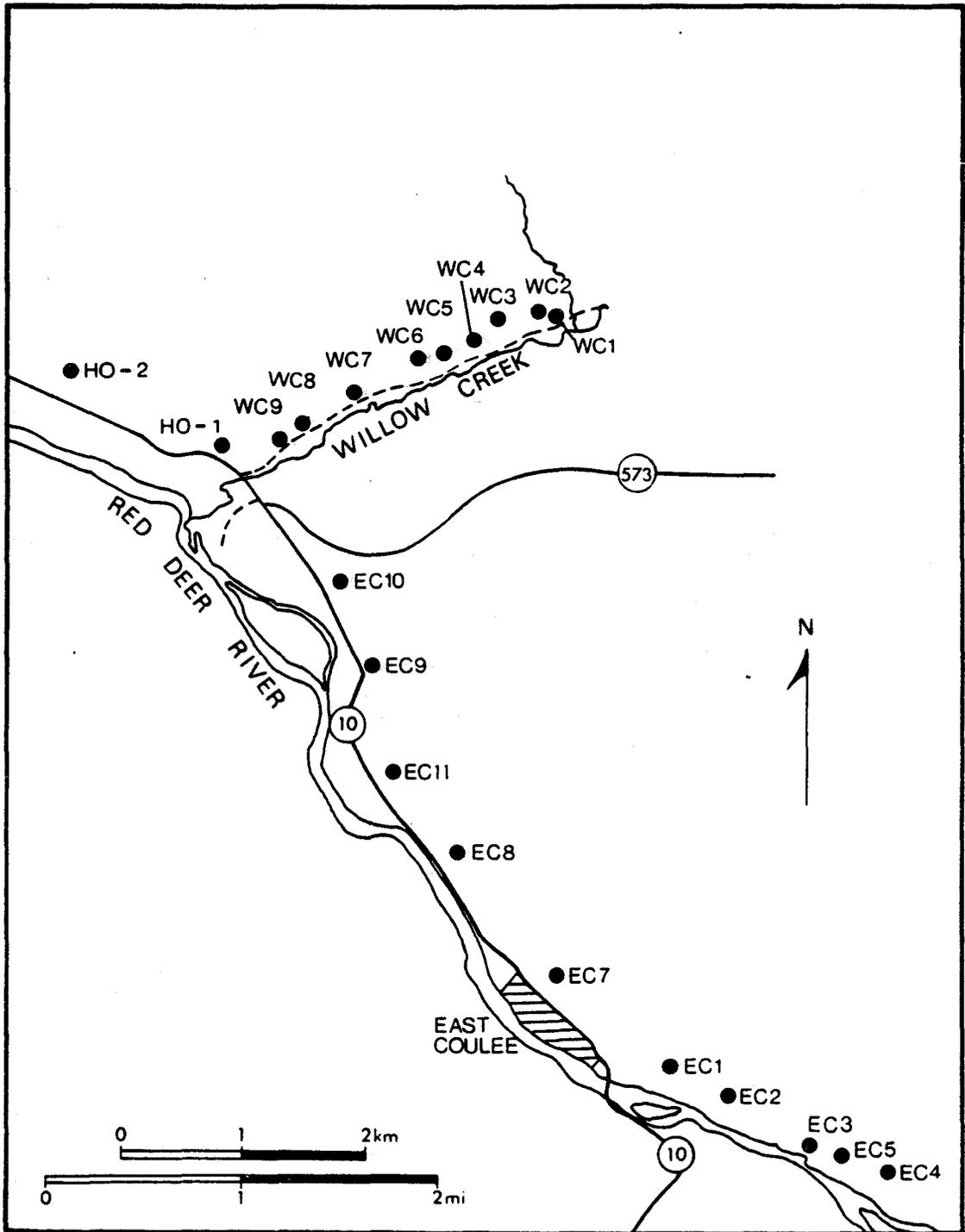
explains the features exhibited at Drumheller. The oyster beds are interpreted as marking a transition from barrier island to back-barrier tidal and open bay lagoonal environments. Oyster fragments at the base of unit 4 (Fig. 2) are interpreted as channel lag deposits. Rahmani (1981) conjectures that there was an initial northwest transgression of the sea. Following this, southeast progradation of tidal flats over barrier islands occurred due to seaward migration of back-barrier tidal channels. Peat swamps also prograded and were discontinuous behind the barrier bay complex.

#### Methodology

Oyster (Ostrea glabra) shells containing macro-borings were collected from unconsolidated sand at sites WC2-8 and EC10 (Fig. 4). Site WC1 and WC9 had only rare highly abraded shell fragments that lacked macro-borings. A visual examination of carbonate-cemented beds was made and several blocks dissected in a search for epibionts and bored shells. Measurements and descriptions of biogenic structures in 260 specimens were made using a binocular dissecting microscope equipped with an ocular micrometer. When necessary specimens were cleaned in an ultrasonic bath.

Round holes (Oichnus) were visually divided into 10 forms based on those suggested by Carriker and Yochelson (1968, Fig. 2, p.B4) with the addition of "J", an incomplete parabolic hole

Figure 4. Location of sampling sites (from Rahmani, 1981; used with permission).



with a concave to flat bottom generally lacking a countersunk edge. Group "k" consists of holes for which form could not be determined due to sediment infill. Following Reyment (1966) measurements were taken for the maximum and minimum diameter of borehole entrance and termination. In the case of borings that did not completely penetrate the substrate, diameters were measured at the base of the boring.

Galleried borings (Entobia) were divided into 3 forms based on the author's criteria. The terminology of Groot (1977) was adopted for descriptions. Parameters measured using x-radiography in addition to the binocular microscope include diameter of surface apertures, dimensions of chambers, the length and diameter of the canals connecting chambers (rootstocks). "Rootlets", the tiny extensions emanating from chamber walls, could not be identified and were not measured. A qualitative estimate of relative penetration depth and the relationship between chambers was also made.

Approximately another 100 shells with intertwined tunnel systems (Talpina) were arbitrarily divided into sub-samples with high, moderate and low boring densities.

In addition, scanning electron microscopy was employed on a sub-sample containing representatives of each ichnogenus. Statistical analysis was done on a Cyber 170 using a program modified by Ms. A. Wong.

## CHAPTER 2

### THE ORGANISMS THAT BORE INTO CALCIUM CARBONATE

#### Borings in CaCO<sub>3</sub>

Borings are trace fossils produced by an organism penetrating a hard substrate (Bromley, 1970). Specialized structures and/or secretions are often used to accomplish this task. The sculpture and form of a boring may closely reflect the morphology of the borer, in particular, the boring apparatus and the manner in which it was used (Seilacher, 1969; Bromley, 1970; McHuron, 1972). The substrate that is selected by an organism may indicate the mode of penetration. Borers depending on chemical dissolution will be restricted to materials responsive to the secretions they produce (Warne, 1975a). The boring will also reflect the purpose it was intended to serve. It may have provided a predator with access to a shell-bearing prey, in which case the boring will completely penetrate a shell from the exterior to the interior. Other organisms rasp to obtain nutrients from the shell. Borings may be domiciles affording protection to soft-bodied organisms (Carriker and Yochelson, 1968). Borings providing shelter tend to be deep and distinctive (Warne and McHuron, 1978). An organism may also penetrate a hard substrate in order to support body organs in a position enabling optimal functioning (Warne and McHuron, 1978). Thus, a knowledge of modern forms and their function

provides insights into the characteristics of organisms responsible for fossil borings. Borings are of great value in situations such as the study area, where body fossils of bioeroders are not preserved. Traces are the sole evidence of the presence of the instigator and its relationship with the shelled host (McHuron, 1972; Feldmann and Palubniak, 1973; Arua, 1982).

### Fossil Borings

Macro-borings in skeletal carbonate have been reported from deposits as old as Lower Cambrian (James *et al.*, 1977). Carriker and Yochelson (1968) describe borings in brachiopod shells from the Middle Ordovician. Shell borings are usually small, distinctive and not readily mistaken for soft-sediment structures (Warne, 1975a). Borings must have characteristic shapes to be distinguished from (inorganic) dissolution-caused features which more closely reflect the structure of the substrate (Boekschoten, 1966). Bromley (1970) has presented a strong case for naming traces on the basis of morphology. Formal names of borings should be separate from those of the organism responsible.

### Survey of The Organisms That Bore Into Calcium Carbonate

Members of almost every phylum of both plants and animals have been reported to bore into solid substrates (Warne, 1975a). Organisms that penetrate  $\text{CaCO}_3$  are active in a wide

variety of environments from intermediate depths of water to supratidal flats (Blatt et al., 1980, p.505).

Groups of organisms producing macro-borings include: gastropods, cephalopods, sponges, polychaetes, sipunculids, phoronids, tubellarians cirripedes, bryozoans, amphineurans, echinoids, and brachiopods. Modern examples of borers are easily studied and, in the case of species relevant to commercial oyster farming, a great deal of work has been done (see Pearse and Wharton, 1938; Guida, 1976).

The same organism may create a variety of morphotypes due to factors such as hardness, structure and restriction of substrate. Conversely, several groups may produce traces that would be placed in the same ichnogenus (Cameron, 1969; Bromley, 1970; Warme, 1975a; Warme and McHuron, 1978). In spite of these limitations, fossil borings are often characteristic of a group of boring organisms and therefore are often useful for environmental interpretations (Kobluk et al., 1978).

Borings have been arbitrarily divided into macro-borings and micro-borings, the former being those that can be recognized by the naked eye, generally greater than 0.5 mm (Kobluk et al., 1978). This paper is restricted to a consideration of macro-borings.

#### GASTROPODS

Organisms such as muricid and naticid gastropods along with sipunculids drill into hard substrates producing round

holes (Seilacher, 1969). Carriker and Yochelson (1968) suggested that predatory muricids and naticids use a combination of chemical and/or mechanical processes to penetrate shells of bivalves on which they prey. They found that gastropods from which the accessory boring organ had been excised could not bore. Secretions of this organ have the ability to etch carbonate. A specific enzyme, carbonic anhydrase, has been found to be responsible for this ability in the species Urosalpinx cinerea (Carriker and Smith, 1969). The degree of penetration appears to be governed by the depth to which secretions enter and soften the shell. The diameter of the borehole is equivalent to that of the accessory boring organ. Once the shell is softened, flakes are rasped off by radular action (Carriker and Yochelson, 1969). The mechanical aspect of boring is manifest in scratches often associated with borings.

The differences between the straight-walled borings of muricids and parabolic-walled naticid borings (Plate II, Fig. A,B) may be due to specializations in the structure and functioning of the boring apparatus, in particular the accessory boring organ (Carriker, 1969). Muricids have a mushroom-like papilla with a long stalk. Their radula is stenoglossate (radular formula 1-1-1, Carriker and Yochelson, 1968; Parker, 1982, p.104). Systematic radula rotation may contribute to cylindrical form (Zeigelmeier, 1954 in Reyment, 1966). Naticids possess a short-stalked padlike accessory boring organ. The

PLATE II OICHNUS

- Fig. A: Oichnus paraboloides. This specimen illustrates the parabolic walls characteristic of naticid borings. The borehole tapers significantly over its length and has an irregular termination. This, and most examples from Drumheller lack an obvious bevel.
- Fig. B: A pair of Oichnus paraboloides that do not completely penetrate the substrate. Entobia cretacea also occurs within the shell fragment. Note the dendritically branching arrangement of surface apertures of Entobia.
- Fig. C: Cylindrical Oichnus simplex has the straight walls found in muricid excavations. Borehole lacks significant tapering and has a near circular cross section; axis is somewhat oblique to shell surface.
- Fig. D: Multiple Oichnus simplex borings. This shell contains 13 borings initiated from both the interior and exterior surfaces. Most shells contained only a single boring. O. simplex falling in the smaller size range tended to incompletely penetrate Ostrea valves.



radula is taenioglossate, formula 2-1-1-7-2 (Carriker and Yochelson, 1968; Parker, 1982, p. 1010).

There are several other groups of gastropods that bore. These include: parasitic Capulidae that gain access to gills through an oval hole; Oleacinidae rasp irregular patches possibly to obtain  $\text{CaCO}_3$  or prey on shelled host; limpets graze and form resting hollows; the metabolic processes of periwinkles cause dissolution cavities; vermetids form a groove which is lined by the shell of the organism (Bromley, 1970). Okadaia elegans is an intertidal nudibranch Opisthobranch known to bore smooth round beveled holes with diameters 0.57-0.80 mm in calcareous tubes of annelids (Young, 1969).

#### CEPHOLOPODA

Some species of octopi drill holes of various shapes in mollusc shells using their salivary papillae. The minute (2x3 mm) borings allow venom to be injected, incapacitating the prey. Possibly, extinct species of cephalopods drilled holes in the past (Carriker and Yochelson, 1968; Bromley, 1981).

#### SPONGES

Several groups of boring sponge are known. As described by Groot (1977), clionids generally bore dwelling cavities consisting of somewhat globular chambers linked to one another by rootstocks. Chambers communicate to the surface through oscular

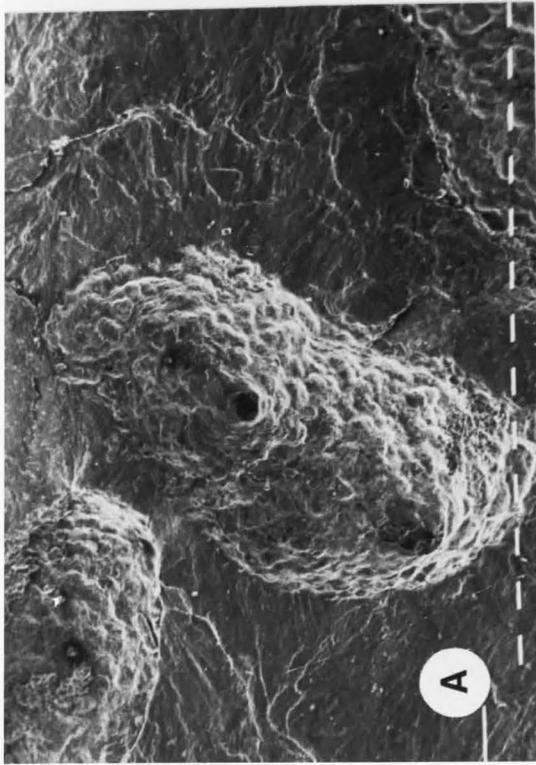
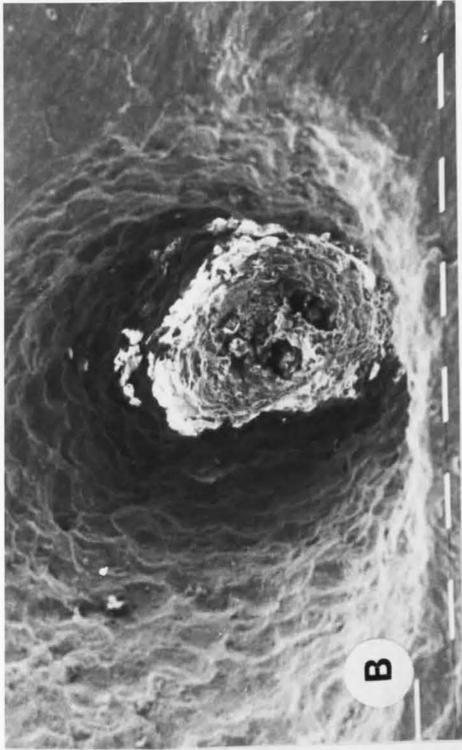
and ostial openings (Plate III).

The manner by which clionid sponges excavate has long been a matter of speculation. Hancock (1849) first argued that clionids were responsible for the cavities in which they dwell. He suggested that the substrate was removed by mechanical action of the spicules. Warburton (1958) suggested chemical means were employed, by demonstrating the initiation of boring prior to the development of spicules and also associated with regions of the sponge lacking spicules. However, Warburton detected acid neither in the tissue of boring sponges nor in the titrated solution in which they were living. Also, the amount of dissolved  $\text{CaCO}_3$  did not increase significantly. He concluded that boring was initiated by very localized use of secretions, followed by mechanical chip removal due to contractions of the sponges tissue. Rützler and Rieger (1973) have since documented the liberation of chips by cellular action. Filopodial extension and etching secretions are involved. They calculated that only 2-3% of eroded material is removed through dissolution. The combined chemical and mechanical actions of clionids result in the production of 40-60 $\mu$  chips and a peculiar scalloped pattern in the substrate (Rützler and Rieger, 1973).

Sponges of the genus Siphonodictyon also bore domiciles. They create a single spherical cavity with ostial and oscular apertures to the surface (Rützler, 1971). It is likely they

PLATE III SEM COMPARISON OF "A" AND "D" TYPE CHAMBERS

- Fig. A: A dumb-bell shaped excavation apparently formed through the merging of two shallow "A" chambers each possessing its own connection to the surface. (scale = 100 $\mu$ m).
- Fig. B: "D" chamber with scalloping preserved and connections to the surface visible at the base. Note size and gross morphology is comparable to Oichnus. (scale = 100 $\mu$ m).
- Fig. C: A pair of "A" chambers that have lost scalloped texture through abrasion. Chambers are shallow ellipsoidal and their long axes run parallel to shell surface. (scale = 100 $\mu$ m).
- Fig. D: "D" chamber lacking scalloping on walls. Chamber is roughly cylindrical with long axis perpendicular to shell surface. This type of chamber is typical of Entobia sp<sup>a</sup>. (scale = 100 $\mu$ m).



bore in a manner similar to clionids, because colony interiors show similar scalloping (Risk, pers. commun.).

#### POLYCHAETES

Many polychaete worms bore into coral, limestone, dead and living shells to seek shelter (Carriker and Yochelson, 1968). They make use of a combination of boring tools including: mandibles, setae, uncini, tentacles and/or mucus along with body-fluid pressure. Long single or branching unclustered "tubes" are produced with diameters ranging from .05 to 3 mm. The agglutinated tube is rarely reserved. Ornamentation reflects the manner in which appendages were used (Cameron, 1969; McHuron, 1972; Rodriguez and Gatschick, 1977). Polychaete worm damage in oyster shells is generally due to spionids (Bromley, 1970). Polydora websteri, which is active in temperate zones, makes isodiametric "U"-shaped boreholes open at both ends (Bergman et al., 1982). The limbs often converge at the surface creating a dumbbell-shaped cross-section (Cameron, 1969).

#### SIPUNCULIDS

Sipunculids exactly fit their domiciles; thus, they are believed to create them. Mode of boring is poorly understood. Mechanical methods may include the use of spine- and hook-bearing papillae powered by body fluid pressure. These may be combined with chemical dissolution to create straight

to sinuous narrow club-shaped borings. The single oval to circular entrance is narrower than the remainder of the boring (Rice, 1969; Bromley, 1970; McHuron, 1972).

#### PHORONIDS

Three species of phoronids bore beneath the periostracum of mollusc shells (Hyman, 1959). Complexly tangled psuedo-colonies emanate from a single individual (Bromley, 1970). Borings parallel shell surface and open to the exterior by a bend of 90° (Hyman, 1959). The winding tunnels and surface apertures have approximately the same diameter, ranging from 0.2 to 0.3 mm. Densities of up to 150 borings/cm<sup>2</sup> occur (Bromley, 1970). The borings are a dwelling place for the filter-feeding "worms" and penetration is probably achieved by chemical means. The borings are generally found on the exterior surface, although they do occur on the interior as well and may be accompanied by clionid borings. Phoronids are generally found in the upper littoral zone and may live in brackish water (Joysey, 1958; Hyman, 1959, p. 263-268).

#### TURBELLARIANS

Turbellarians bore through shells, particularly those of young oysters, in order to prey upon soft tissue. Their penetrations are minute (less than 0.2 mm) with an oval or keyhole-shaped cross-section (Carriker and Yochelson, 1968; Bromley, 1970).

## CIRRIPEDES

Acrothoracians are naked barnacles that embed in  $\text{CaCO}_3$  substrates including dead and living shells and coral (Seilacher, 1969; Rodriguez and Gutschick, 1977; Barnes, 1980). They are widespread in tropical coastal waters and are also found in temperate zones (Boekschoten, 1966). Mechanical abrasion by chitinous or carbonate peduncular studs produces small shoe-like traces and  $\text{CaCO}_3$  "dust" as a by-product (Joysey, 1959; Bromley, 1970). Arua (1982) reported lengths of 1.0-1.8, and widths of 0.15-.08 mm for elongate surface apertures. Smaller (0.08 to 0.03 mm long) comma-shaped apertures may also occur. Some apertures possess a slit-like extension and a ridge formed by the protrusion of the  $\text{CaCO}_3$  lining (Bromley, 1970).

## BRYOZOA

Members of two orders of bryozoa are known to bore. They produce superficial traces which may be only partially buried. Ctenostomatous bryozoa probably employ phosphoric acid to form slender (.04-.11 mm in diameter) frequently branching stolons which communicate repeatedly with the surface at enlarged zooid cavities (Bromley, 1970). Apertures may be circular, slit-like or reniform depending on species responsible. Colonies radiate from a centre of growth and change considerably with age. Colonization is generally initiated on the inner surface of the shell (Boekschoten, 1966; Brunton, 1966; Bromley,

1970). Boekschoten (1966) found ctenostomata borings restricted to depths of 50 to 112 meters. Electra monostachys is a member of the order Cheilostomata. This species etches CaCO<sub>3</sub> under reduced salinity conditions (Bromley, 1970). Traces produced consist of shallow oval depressions with dimensions 0.24x0.15 mm which are arranged in rows and occur at depths greater than 22 m (Boekschoten, 1966).

#### AMPHINEURA

Amphineura (chitons) are bioeroders that are abundant in the intertidal zone and also found in deeper water. They employ a radula (that may be mineralized) to rasp for algae. Traces formed range from shallow depressions to deep slot-like holes. Dimensions up to 5 cm in diameter and 7 cm in depth have been reported (Warme, 1975a).

#### ECHINOIDS

Echinoids leave distinctive grazing scratches on rock and shell. "Stars" composed of 5 sets of parallel scratch pairs at approximately 72° to one another are formed by the action of Aristotle's lantern. "Stars" are generally superimposed on one another (Bromley, 1975). Echinoids also excavate dwellings in rock using spines and dentition. Hemispherical cavities are found in harder substrates while deeper (up to 15 cm) slots which may branch are created in shale and lime-

stone (Warme, 1975a).

#### BRACHIOPODS

Three orders of brachiopods penetrate  $\text{CaCO}_3$  with divided pedicles in order to secure themselves (Bromley, 1970). The resulting grooves with diameters up to  $100\mu\text{m}$  are randomly arranged (Bromley, 1981).

Only a small number of the borings described above actually occur in the Drumheller specimens. Many different boring morphotypes may occur in carbonate substrates, and in some cases the densities and diversities of such borings may be very high. The absence of a particular boring type may have significant paleoenvironmental implications.

## CHAPTER 3

### INTEGRATED STUDIES ON BIOEROSION

#### Review Papers

There are several comprehensive papers surveying marine borers. Bromley (1970), Warne (1975a) and Warne and McHuron (1978) are useful guides to the identification of borings and the organisms possibly responsible for these traces. To date, no one has attempted to devise assemblages of borings that are more sensitive to paleoenvironmental conditions than Seilacher's (1967) all-inclusive Trypanites ichnofacies. Bromley (1970) tackles the difficult question of taxonomy of ichnofossils. He gives a model description of Entobia cretacea, discusses methods of studying Entobia and also ecological and sedimentological considerations. Warne (1975a) makes a useful distinction between borings in rock and shell produced by the same group. These borings may differ markedly due to the properties of the substrate.

#### Bioerosion in Modern Environments

Modern studies of bioerosion have generally been done on reefal environments (Bergman et al., 1981). Risk and MacGeachey (1978) survey taxa of reef eroders and propose a succession of bioeroders. Little quantitative work has been done (Bergman et al., 1981). Notable exceptions are: Rützler (1975) estimated that boring potential of sponges is about  $256 \text{ g CaCO}_3/\text{m}^2$

substrate.yr (with more than 75% of removal in the form of chips); Bromley (1978) reviews estimates of bioerosion for single species and estimates combined rate of bioerosion in one locale (predominantly due to clionids and parrot fish) as about 1.3mm/yr; and Bergman et al. (1981) demonstrated that the compressive strength of Pecten valves was inversely proportional to intensity of Polydora websteri bioerosion.

Comparison of bioerosion attributable to modern taxa with fossil traces has been done by many authors. Examples include: gastropods (Carriker and Yochelson, 1968); cirripeds (Seilacher, 1969); echinoids (Bromley, 1975); and, sipunculids (Pemberton et al., 1980).

### Bioerosion in Fossils

Borings may provide valuable information to the geologist in a number of ways. Table 3.1 gives a brief summary of the applications that have been made. Trace fossils are generally autochthonous; however, borings may be reworked with the substrate in which they occur (Bromley, 1970). Borer or host may be environmentally restricted, providing paleoecological and/or taphonomic information depending on whether the substrate is preserved in situ or has been transported (Boekschoten, 1966).

Table 3.1 Contributions of Macro-borings in CaCO<sub>3</sub> to Sedimentary Geology  
(modified from Frey and Seilacher, 1980)

Discipline and Components	References	
	Modern	Ancient
<u>1. Palaeontology</u>		
A. Fossil record of soft-bodied animals (often to genus or species level)	Lawrence, 1968 Pemberton <u>et al.</u> , 1980	
B. Patterns of activity by benthic organisms	Boekchoten, 1966	Stanton <u>et al.</u> , 1981
C. Infaunal or epifaunal shelled host		Arua, 1982
D. Orientation during life		Seilacher, 1969
E. Diversity of fossil assemblages	Lawrence, 1968	Arua, 1982
F. Evolution of metazoan and of behaviour		Seilacher, 1969 Stanton <u>et al.</u> , 1981
<u>2. Depositional environments &amp; paleoecology</u>		
A. Salinity	Hartman, 1958 Hopkins, 1962	Lawrence, 1969
B. Bathymetry	Hartman, 1958 Pang, 1973	
C. Hydraulic energy level	Bromley, 1978	Pickerill, 1976
D. Rates of deposition	Reyment, 1966	Carriker, 1969
E. Hardness of substrate at time of boring		Warme and McHuron, 1978
F. Trophic web in community structure		Stanton <u>et al.</u> , 1981
G. Sequence of colonization	Risk and McGeachy, 1978	Bottjer, 1982
<u>3. Sedimentology</u>		
A. Sediment produced by boring organisms	Rützler and Rieger, 1973 Kobluk, 1981	
B. Substrate destruction	Hein and Risk, 1975	Bromley, 1975
C. Carbonate cycling and diagenetic change	Summarized in Blatt <u>et al.</u> , 1980, p.505	

Table 3.1 (continued)

4. Taphonomy

A. Evidence of reworking	Wiedmann, 1972	Bromley, 1970
B. Exposure to contrasting environments	Wiedmann, 1972	
C. Indication of amount of substrate lost through dissolution		Seilacher, 1969

5. Stratigraphy

A. Marks marine disconformities		Bromley, 1975
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### Ecological Distribution of Boring Clionids

Several studies relating distribution of boring sponges to environmental conditions suggest that borings produced by sponges (Entobia) may be useful in paleoenvironmental reconstruction. (This will be discussed further in Chapter 5.) Hopkins (1956) used assemblages of clionids and their relative abundance to distinguish 6 zones diagnostic of estuarine waters of differing salinities. Hartman (1958) simply divided common species into two groups. Cliona vastifica-like species have small surface apertures and delicate "camerate" internal galleries. Vastifica-like species can tolerate a wide range of salinities; they dominate both very shallow and deep waters but are less important in the intervening littoral zone. Euryhaline species are typified by Cliona celata which has large apertures and more massive "palmate" internal galleries (Bromley, 1970). There are many other investigators who have contributed to our knowledge of the distribution of boring sponges. Their work is summarized in Table 5.2.

## CHAPTER 4

### DESCRIPTIONS OF MACRO-BORINGS AND OTHER BIOGENIC STRUCTURES

The aim of this study was to make paleoecological interpretations based on the evidence of trace fossils. Macro-borings described include the ichnogenera Oichnus, Entobia, Talpina and Zapfella. Ichnofossils are classified on the basis of conformity to a morphological diagnosis (Bromley, 1970). It was believed that the existing diagnoses for Entobia, Talpina and Zapfella were inadequate, and emended diagnoses were proposed. Examples of biogenic structures that appeared to be repair blisters and partitions within Ostrea glabra valves were informally described.

Ichnogenus Oichnus (Bromley, 1981, p.60)

Diagnosis: "Circular to subcircular holes of biogenic origin bored into hard substrates. The hole may pass right through the substrate as a penetration, where the substrate is a thin shell; or end within the substrate as a shallow to deep depression or short, cylindrical pit" (Bromley, 1981, p.60).

Remarks: Examples that do not completely penetrate the substrate can be distinguished from shallow round oyster attachment scars (Plate X, Fig. C) by their sharp walls and absence of a raised rim. Oichnus may have micro-borings visible on the boring wall and thus resemble Entobia chambers with rootstocks. However, Oichnus are isolated from one another even when multiple

borings occur within the same specimen (Plate II, Fig. B,D).

Description: The vast majority of borings are initiated from the exterior shell surface (Plate II). Most of those initiated from shell interior are incomplete (Forms H,G and I). Many Oichnus have a reddish ring about their entrance; this was also common around attachment scars. Furrows are often associated with Oichnus; they are not unequivocally of biogenic origin. Abrasion has been superimposed on circular holes in the form of worn and broken surfaces. The few macro-borings that were found in CaCO<sub>3</sub>-cemented material belong to the ichnogenus Oichnus. It was not possible to determine if one valve was preferred over the other or to describe the relative distribution of borings over the shell surface.

Shell layers are seen on the boring walls since conchiolin layers are more resistant to dissolution than is the carbonate. Diameter of the borehole entrance is equal to, or, more commonly, greater than the diameter of the distal end. Cross section at entrance is also significantly rounder than at the termination.

Oichnus paraboloides (Bromley, 1981, p.61)

Diagnosis: Oichnus having a spherical parabaloid form, truncated in those areas where the boring penetrates right through the substrate. Where it does not so penetrate, the paraboloid may be deformed by a slightly raised central boss.

Description: Refer to Table 4.1.

Remarks: A significant number (21%) of the borings that

Table 4.1 Summary of Statistical Analysis of Oichnus

Ichnogenus	<u>O. paraboloides</u>	<u>O. simplex</u>
Forms	C, F, I, J,	A, B, D, E, G, H
Probable Group Responsible	Naticids	Muncids
Sample Size	N = 59	N = 108
<u>Roundness</u>		
range in slope	0.51-0.88(1.06) <sup>J</sup>	0.94-1.02
range in correlation coefficients	0.79-0.99	0.99-1.000*
range in y-intercept	-0.19-0.70	-0.24-0.09(0.5) <sup>G</sup>
<u>Tapering</u>		
range in slope	0.80-1.47	(.97) <sup>G</sup> 1.01-1.05
range in correlation coefficients	0.66-0.99	0.88-1.000*
range in y-intercept	(-0.2)0.32-0.89	-0.01-0.69
<u>Size of entrance</u>		
maximum diameter	0.91 <sup>I</sup> - <u>2.4</u> -4.1	0.8- <u>2.1</u> -4.7
minimum diameter	0.96- <u>2.4</u> -3.6	0.80- <u>1.9</u> -4.6
<u>Description</u>		
cross section	deviates significantly from circular	nearly round
slopes	deviate from unity	close to unity
y-intercepts	rarely near zero	generally near zero
degree of taper	pronounced	slight
correlation	wide scatter in values	close to perfect correlation
size	narrow range, larger mean	wide range, smaller mean

<sup>I</sup>It was not possible to measure the minimum diameter corresponding to 0.91 mm.

<sup>J</sup>Form J has only 5 points.

\*Rounded off to 3 decimal places.

<sup>G</sup>Form G has only 2 points.

did not completely penetrate the shell lacked a raised central boss. When complete penetration does occur, the distal cross-section is often highly irregular in outline and uncentered.

Oichnus simplex (Bromley, 1981, p.60)

Diagnosis: "Oichnus having a simple cylindrical or subcylindrical form, axis more or less perpendicular to the substrate surface. Where the substrate is not penetrated right through, the distal end is flattened hemispherical."

Description: Refer to Table 4.1. A large number (44%) did not completely penetrate the substrate, these are members of forms G and H.

Remarks: The axes of most examples are oblique to the shell surface.

Discussion of Figs. 5 and 6: Borehole dimensions are generally highly correlated. The two supergroups corresponding to Oichnus paraboloides and O. simplex were found to contrast markedly with respect to roundness, tapering and size (Table 4.1). "Roundness" was determined by relating maximum and minimum diameters. A perfectly round cross section will have the same diameter measured in all directions. This state is illustrated by the closely dashed line on Fig. 5. "Tapering" was best illustrated by a comparison of minimum entry and termination diameters of boreholes. A cylindrical borehole that does not taper will be isodiametric throughout. This is shown graphically by the closely dashed line on Fig. 6. Regression lines for

Figure 5. Roundness of Borehole Entry. Maximum diameter vs. minimum diameter.

— — — O. simplex

————— O. paraboloides

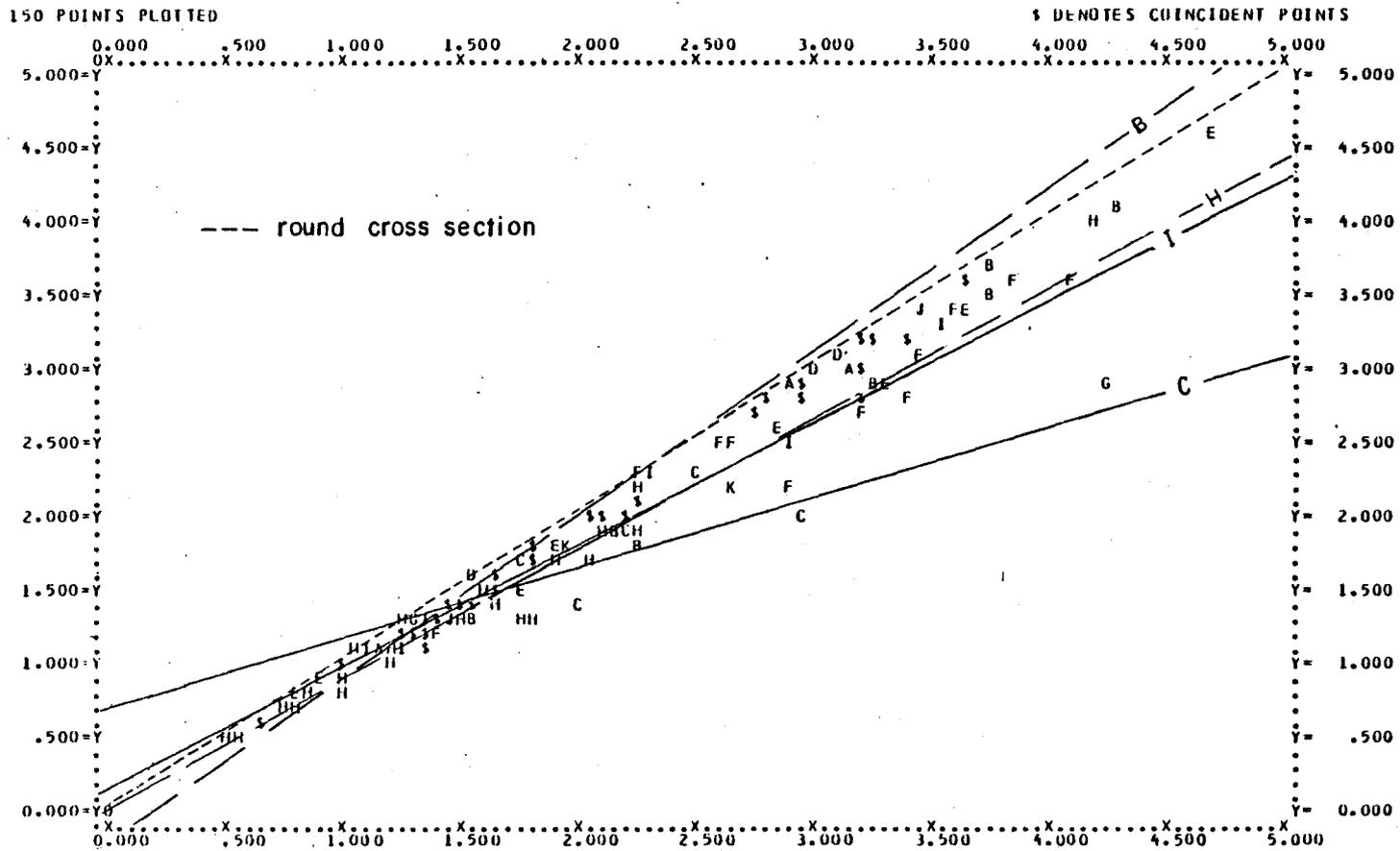


Figure 5

Figure 6. Tapering along Borehole Length.  
Minimum termination diameter vs.  
minimum entry diameter.

\_\_\_\_\_ O. simplex

\_\_\_\_\_ O. paraboloides



forms that were nearly circular or cylindrical and those with insufficient data were omitted for clarity. Those with insufficient data were G and J with 2 and 5 points respectively. Incomplete borings, particularly forms H and I, tended to be small in diameter (mean maximum 1.5 and 2.2) when compared to their respective ichnospecies as a whole (mean maximum 2.1 and 2.4). They dominated the smaller size range ( 2.5 mm). Forms F and D comprised most of the mid-range (2.25-3.5 mm) while B and E had a significant number of larger boring. Size distribution skewed toward smaller sizes. The results reported in Table 4.1 corroborate well those obtained by Reyment. He also found that O. paraboloides-like holes were larger and more strongly conical than O. simplex examples.

Ichnogenus Entobia (Bronn, 1837)

Emended Diagnosis: Shallow excavations in calcium carbonate consisting of closely-spaced, interconnected, spherical, ellipsoidal or cylindrical chambers. Diameters commonly 0.2 to 20 mm, sometimes fused into crypts up to 40 mm. Minute perforations connecting to subsurface chambers may be the sole surface manifestation, although chambers may be exposed.

Description: Chambers were divided into two types, A and D. Type A chambers are those typical of "camerate" clionid borings. They are generally somewhat ovoid in form with root-stocks and the long axes of chambers running parallel to the shell surface.

Type D chambers are Oichnus-like, approximating a cylinder in form. Their long axis extends a considerable depth into the shell. Small cylindrical channels frequently emanate from the hemispherical base. Walls are rougher and less clearly defined than Oichnus. Contact between wall and base is more gradational. In Oichnus there is a definite distinction between borehole wall and base. In Entobia, on the other hand, the chamber wall forms a fairly continuous surface. The characteristic scalloped nature of clionid excavations (Rützler and Rieger, 1973) visible under low magnification, may occasionally be seen in both forms (Plate III, Fig. A,B).

Remarks: No formal diagnosis appears to exist in the literature. The published statement that comes closest follows: "Borings attributable to sponges of the family Clionidae" (Bromley, 1970, p.78). This is not a diagnosis; it does not give any descriptive information concerning the morphology of the ichnogenus. Also, it is likely to promote a tendency, which is already far too prevalent, to first interpret and then describe trace fossils. This prevents objective descriptions from being made. It is unlikely that any descriptive diagnosis of practical value for identification could include all the wide range in forms produced by clionids (see Table 5.1). This may, in fact, be a major asset in refining the taxonomy of borings. For example, the emended diagnosis stated above would exclude the borings of

rare clionids that excavate single-chambered dwellings. Thus a new ichnogenus would be erected to define taxonomically such borings. This would make recognition of an ichnogenus more meaningful. It is desirable to put all similar borings produced in substrates with the same composition by the same species into a single ichnogenus. Thus, single chamber initiations of sponge colonies should be included in the emended diagnosis. Borings occur in shell, dead and living coral algae and carbonate rocks. They are dwelling cavities affording protection to soft-bodied clionids. The clionid may overgrow the substrate, and in the extreme some species become free-living (Groot, 1977). This along with the forces of mechanical abrasion and chemical dissolution that may act on the substrate, may expose clionid excavations and obliterate surface apertures.

Entobia cretacea (Portlock, 1842 in Bromley, 1970, p.78)

Diagnosis: "Clionid sponge borings showing extreme development of the camerate or 'string-of-beads' form. Young parts of the boring extend in an exploratory fashion as separate branches into the matrix (Plate V, Fig. C). These are swollen at somewhat regular intervals into more or less spherical chambers which in the mature parts have diameters of about 1.5-4 mm. Interconnecting canals are slender (0.1-0.7 mm). In the oldest most crowded parts of the boring, development of new and growth of old chambers restricted the substrate to thin partitions; and caused the shape of the chambers to become polygonal (Plate IV,

PLATE IV ENTOBIA CRETACEA

- Fig. A: SEM showing the forking of two branches. Globular type "A" chambers dominate this ichnospecies . A large chamber at the point of divergence is typical. It may be the result of the fusion of two or more chambers.
- Fig. B: SEM. Crowded chambers acquire a polygonal shape. Boring density of clionids may be very high. Note the occurrence of a "D" type chamber on the left-hand side. (scale = 100 $\mu$ m).
- Fig. C: X-radiograph showing the palmate form of immature portions of the colony. (size is 1.4 mm in nature).
- Fig. D: X-radiograph showing an overview of frequently branching "string-of-beads" form typical of mature portions of E. cretacea. Bright spots are surface apertures. (size is 1.6 mm in nature).

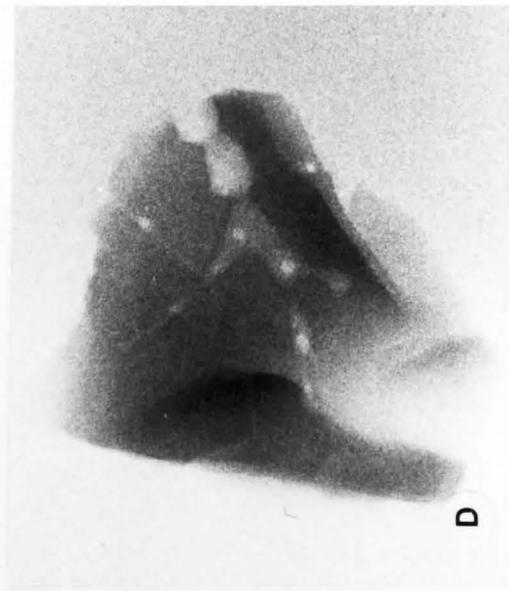
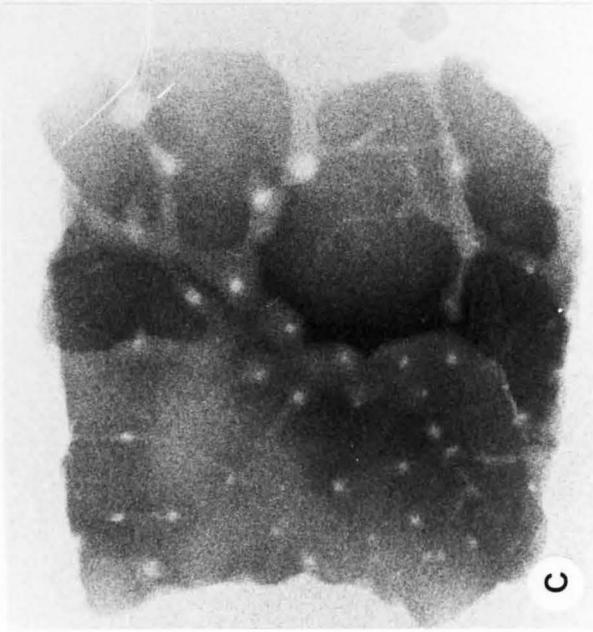
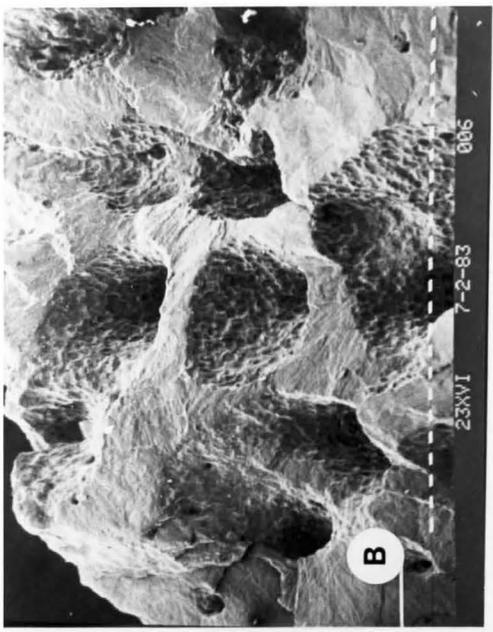
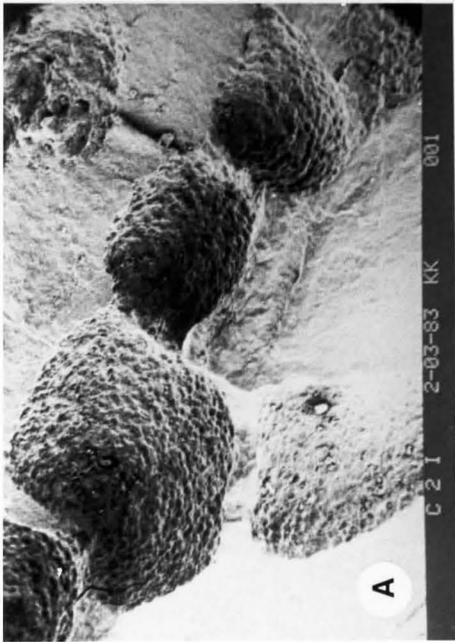


PLATE V SEM DETAILS OF ENTOBIA

- Fig. A: Scalloped ornamentation reflects the action of clionid sponges in removing  $\text{CaCO}_3$  "chips". Two distinct sizes of chips were removed. Those removed during rootstock excavation were significantly smaller than those etched from chamber wall. (scale =  $100\mu\text{m}$ ).
- Fig. B: "Chip" that has been etched from the substrate but not yet dislodged. Sponges produce distinctive multifaceted sediment grains. Shape of chips suggests that attack is not purely mechanical.
- Fig. C: Delicate excavations emanate in an exploratory fashion from chamber walls. With time the sponge expands chamber dimensions.

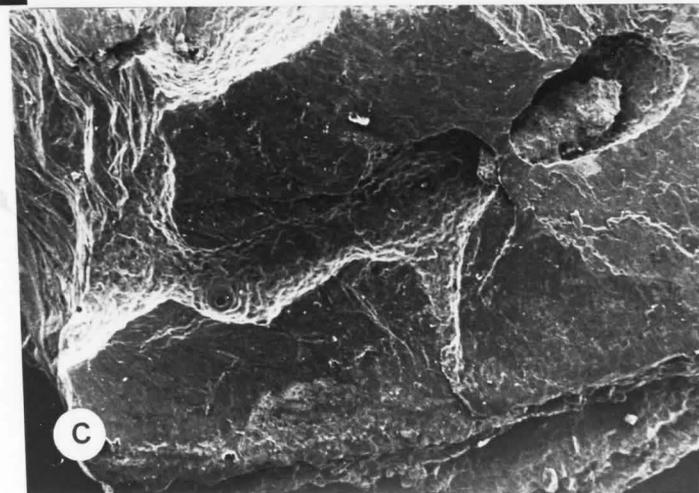
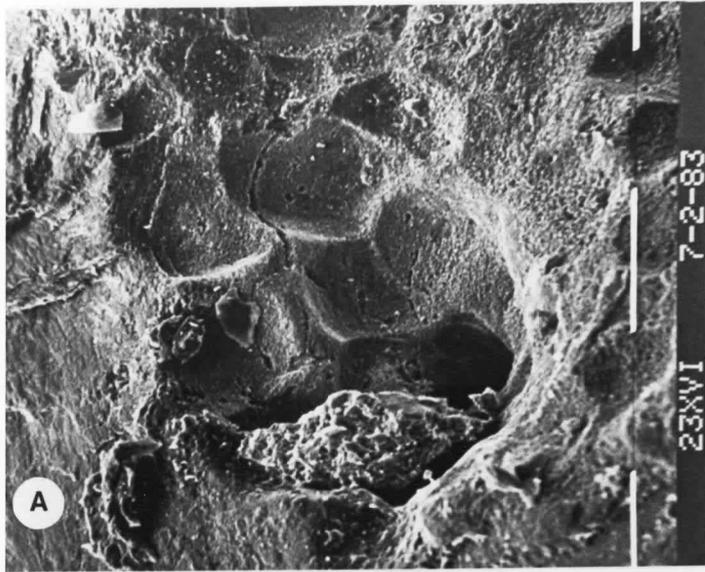


PLATE VI SEM OF SURFACE APERTURES OF ENTOBIA

- Fig. A: Surface aperture and the connection leading to it from chamber. Apertures are irregular in outline, approximately circular. Saw marks are visible on the edge of the specimen. (scale = 100 $\mu$ m).
- Fig. B: Another view of the surface connection illustrated in Fig. A. Note that the diameter does not vary significantly as it passes through the shell layers. Length is considerable. (scale = 100 $\mu$ m).
- Fig. C: Closely-packed apertures of Entobia cretacea. (scale = 100 $\mu$ m).

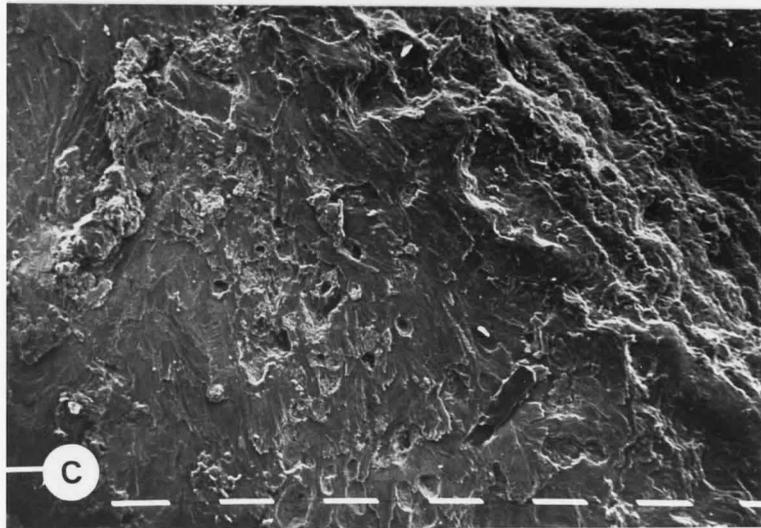
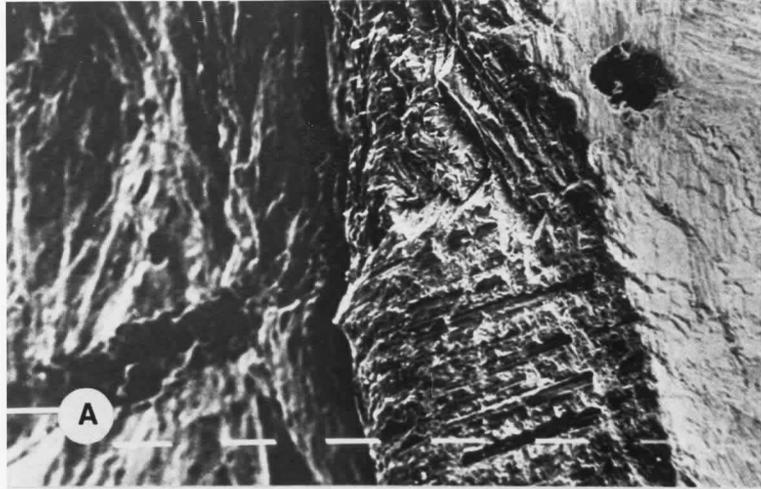


Fig. B). Except between a few pairs of chambers the thin partition walls remained intact and the chambers are not fused. The walls are penetrated not only by interconnecting canals but also by more slender, pinprick holes which in mould preservation appear as slender spines radiating from the chambers. Surface pores, one to four per chamber are fine (0.13-0.7 mm). Wall ornament pits range from 20 to 65 $\mu$  but are mostly about 50 $\mu$  across" (Bromley, 1970).

Description: Refer to Table 4.2. Type A chambers predominate, although D chambers also occur. E. cretacea was found in both "thick" and "thin" shell fragments. Chambers were more frequently exposed than found concealed within the substrate. This may be accounted for in two ways. First, the borings are very close to one shell surface (generally the exterior). Secondly, the shells have been subjected to abrasion and dissolution. Evidence for this will be discussed elsewhere. Size and depth of penetration is less than D chambers.

Remarks: Includes Cliona vastifica-like forms of Lawrence (1969). Chambers are clearly related to one another, although they may not form an obvious string in crowded situations (Plate IV, Fig. B). Up to 3 orders of branching may occur. Branching angles range from 10-90 (Pickerill and Harland, 1983). The size of chambers decreases along a branch. Fused chambers are common at the junction between branches

Table 4.2 Descriptions of *Entobia* from the Cretaceous at Drumheller

	Surface Apertures (range and average in mm)		Tendency to a) fuse b) encrust	Comments	"A" chambers	"D" chambers	Rootstock		Connections to surface	Comments
	a) small b) large						a) diameter b) length			
<i>E. cretacea</i> N = 17	.05-.12-.18 .14-.29-.58 .04-.21-.73†		a) no b) rare	Linear to dendritic pattern usually discernible	.27-4.09 <u>1.13x.90</u> Dominate	.64x2.50 <u>1.56x1.16</u>	a) .14-.29-.82 b) .18-.39-.82		.08-.28-.73	Chambers clearly related. Fused chambers noted.
<i>Entobia</i> sp. "a" N = 10	.16-.36-.58†		a) no b) not evidenced	Apertures rarely seen. When noted often elliptical. Dimensions <u>.34x.54</u>	.51x2.68 <u>1.50x.96</u> Dominate	.54-2.73 <u>1.70x1.61</u> Dominate	a) .18-.3-.68 b) .16-.29-.33		.09-.36 <u>.19-.16</u>	Branching pattern not seen. There may be only .54mm between closely spaced chambers. Fused chambers noted.
<i>Entobia</i> sp. cretacea, "a" N = 3	.18-.36-.27†		a) no b) not evidenced	Pattern not distinct	.91-1.82 <u>1.48x.97</u>	.36x1.64 <u>1.30x.67</u> Dominate	a) not seen b) .09-.2-.36*		not seen	Dendritic arrangement of chambers discernible but not striking. Fused chambers not seen.

<sup>c</sup> No distinction made between "mature" and "immature" portions of the boring.

See text for definitions of "A" and "D" chambers.

N Number of specimens measured.

† No distinction between large and small apertures possible.

\* Based on one specimen.

(Plate IV, Fig. A). They generally involve 2 or 3 chambers. The result is a large chamber rather than a massive crypt.

Entobia sp. "a"

Diagnosis: Numerous closely-spaced cylindrical and ellipsoidal holes that extend less than about 5.0 mm into the substrate. Diameters range from about 0.4 to 3.0 mm. Branching pattern not seen. "D" chambers predominate.

Description: Commonly found on the thick umbo region of abraded shells. Exposed on the exterior surface. Scalloped ornament and surface apertures rarely preserved. Apertures when present are often elliptical. The chambers occasionally show interconnections but these have usually been obscured by abrasion (Plate VII, Fig. A,B).

Remarks: May be similar in appearance to multiple cylindrical Oichnus; however, it should be possible to distinguish one from the other. Entobia sp. "a" chambers have rougher walls and the borehole has no distinct base.

Entobia sp. cretacea, "a"

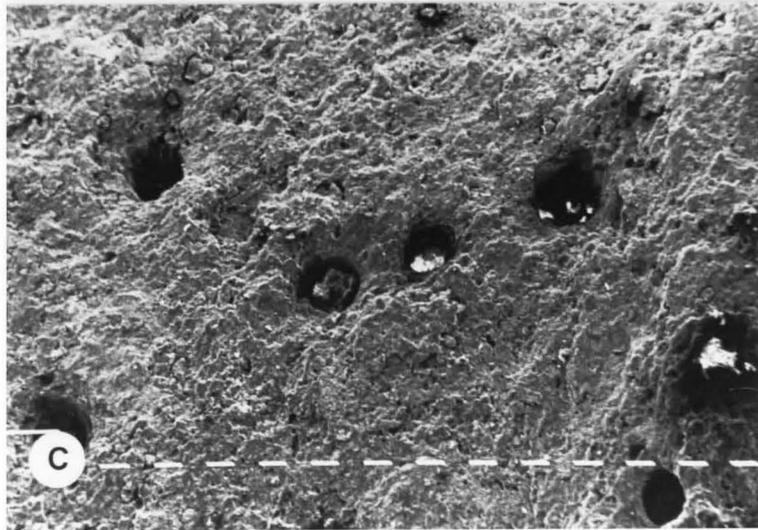
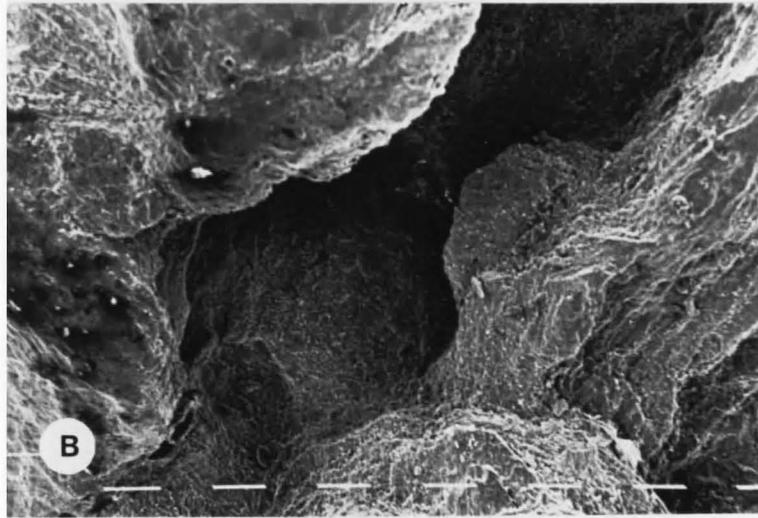
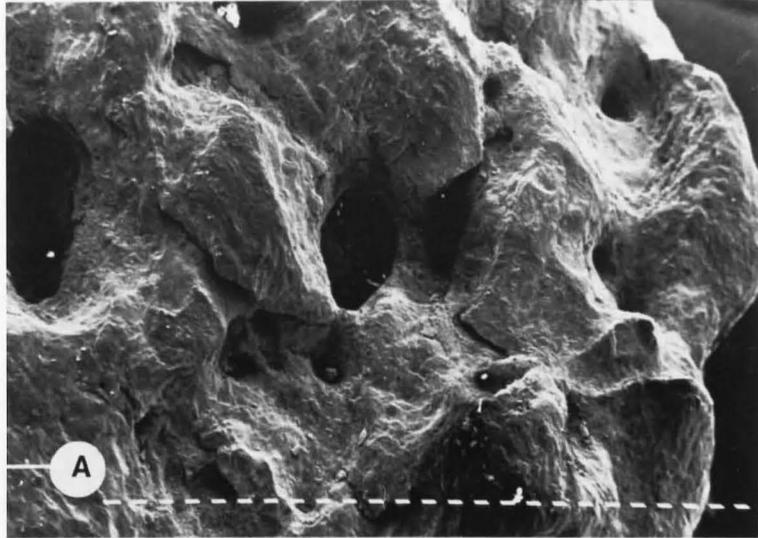
Diagnosis: An intermediate form with characteristics of both Entobia sp. a and E. cretacea. "D" chambers predominate. Branching pattern seen but less well developed than in E. cretacea.

Description: Location of borings same as Entobia sp. a.

Discussion: It is likely that Entobia sp. a and E. cretacea were produced by the same species of borer. In one

PLATE VII SEM OF ENTOBIA SP "A"

- Fig. A: Karst-like relief on shell surface is typical of Entobia sp. "a". Both mechanical abrasion and chemical dissolution appear to have played a role in exposing chambers and obliterating connections between them. Type "D" chambers abound. (scale = 100 $\mu$ m).
- Fig. B: Type "A" chambers occur occasionally. Rootstock between chambers has been enlarged. (scale = 100 $\mu$ m).
- Fig. C: Apertures on surface of abraded specimen appear to be more truly circular than those on well preserved specimens. Density of apertures is approximately 5/mm<sup>2</sup>. (scale = 100 $\mu$ m).



example, 2 distinct layers of chambers paralleled the shell surface. E. cretacea occurred in a layer proximal to the exterior. Chambers were sufficiently close to the surface that some were fully exposed. The layer near the interior consisted of Entobia sp.a. The chambers were not exposed and had longer connections (up to 0.5 mm) to the surface. Both intra- and inter-layer rootstocks were observed. Apertures to the exterior were significantly larger (0.38-0.48-0.54 mm) compared with those seen on shell interior. A common borer is also suggested by the existence of the intermediate form Entobia sp. cretacea, "a".

Ichnogenus Talpina (von Hagenow, 1840, p.671)

Emended Diagnosis: Shallow borings consisting of gently curving, isodiametric, smooth-walled, often branched, complexly intertwined tunnels; diameter ca. 2 mm. Tunnels enter substrate at about 90, then parallel substrate surface; numerous oval or circular cross sections generally seen (modified from Hantzschel, 1975, p.133).

Description: Qualitative estimates of low, moderate and high densities correspond to averages of 17.6, 56.2 and 121 borings/cm<sup>2</sup>, respectively (Plate IX). The highest density of borings observed was about 160 borings/cm<sup>2</sup>. The majority of effected shells (52%) had been bored to a "moderate" extent and only a small proportion (17%) had been highly bored. For low to moderate boring densities, shell exterior had been affected.

PLATE VIII SEM COMPARISON OF TALPINA AND ENTOBIA

- Fig. A: Talpina are smooth-walled isodiametric cylinders that curve gently and run parallel to shell surfaces. Branches are fairly common but not closely spaced. (scale = 100 $\mu$ m).
- Fig. B: Entobia may also have gently curving, approximately isodiametric connections. This portion is exposed at shell surface; however, long connections may run at any angle to the surface. (scale = 100 $\mu$ m).
- Fig. C: Close up of leftmost boring in Fig. A. Branches in Talpina may represent new borings initiated from the wall to the original borehole. Average branching angle is 34°. (scale = 100 $\mu$ m).
- Fig. D: Close up of cylindrical boring closest to chambers in Fig. B. Scalloped wall ornamentation distinguishes it from Talpina. (scale = 100 $\mu$ m).

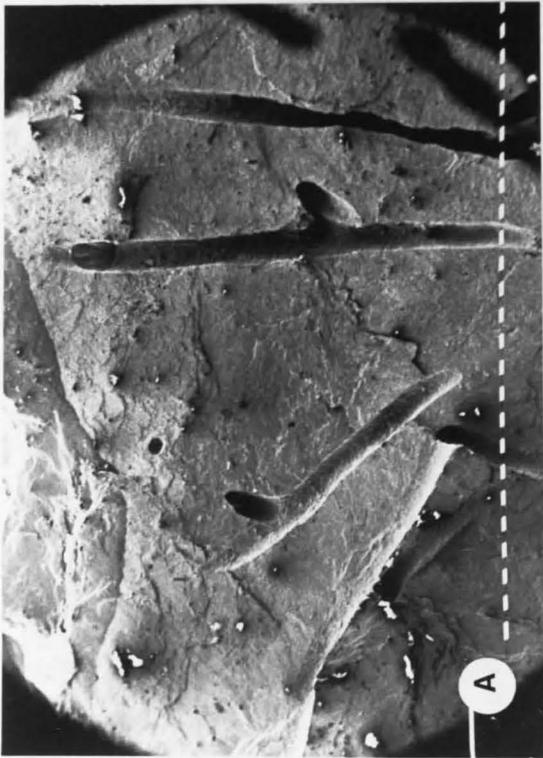
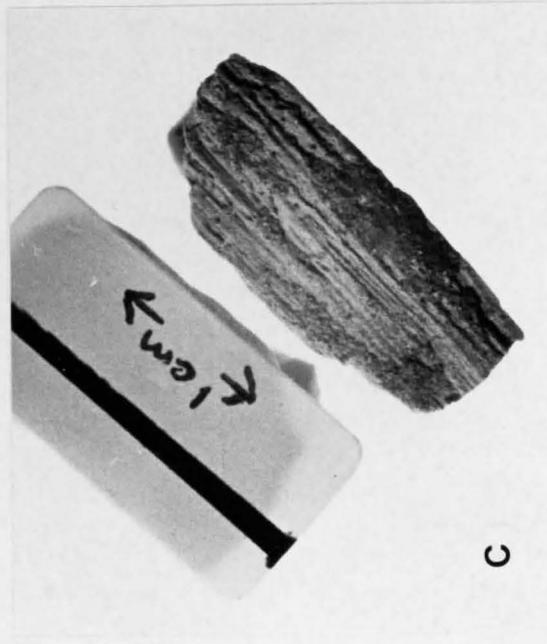
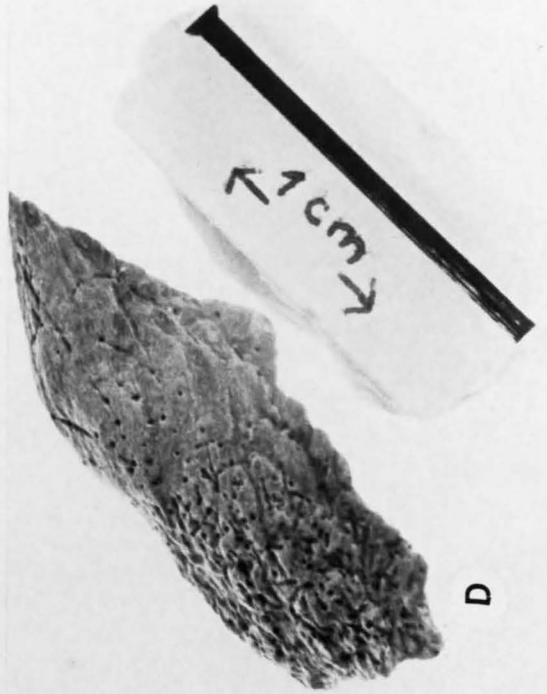
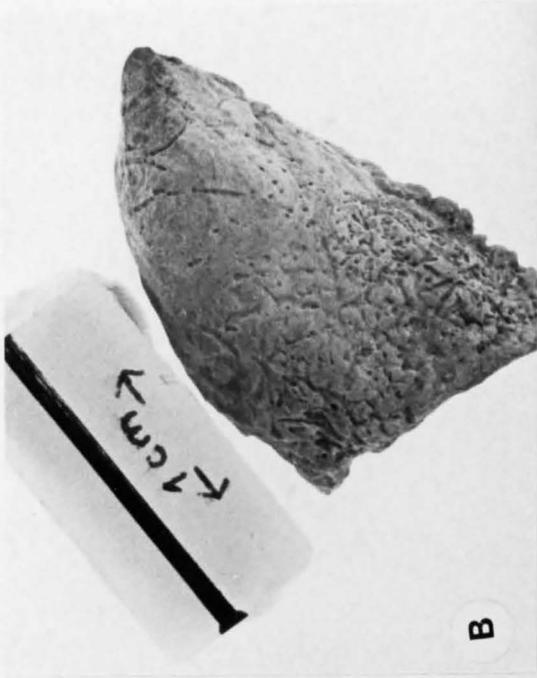


PLATE IX TALPINA

- Fig. A: Talpina revealed on interior shell of shell. Borings of this type are most commonly found on exterior surface of the shell.
- Fig. B: Density of Talpina borings shows a sharp contrast between portion near umbo and at a distance from it. The umbo area with low boring density has had less exposure to attack. It was buried while the area away from the umbo was exposed.
- Fig. C: Another view of the specimen shown in Fig. A. Minute circular cross sections are revealed. Talpina borings parallel laying; this suggests that boring is accomplished by chemical dissolution.
- Fig. D: Another view of the specimen shown in Fig. B. Talpina parallel the curved surface of the Ostrea shell. The void created by Talpina have accelerated shell destruction particularly in the area with high density of borings. Note the occurrence of Talpina on previously broken shell edges.



Specimens that had moderate to high boring density had been attacked on both surfaces, especially at shell margins. There was commonly a sharp distinction between bored and unbored areas on a given specimen (Plate IX, Fig. B,D). Borings were often concentrated on highly convex portions of shell exteriors or both surfaces of shell margins and notably absent from the remainder of the shell. These observations have significant implications concerning taphonomy (Chapter 5).

Talpina dominate the ichnofauna at the EC10 site. They are found on oyster valves that are almost complete. They obscure and thus post-date oyster attachment scars. A single example was retrieved from the cemented material at this location. Talpina represents a smaller proportion of borings at other sampling sites.

Remarks: Borings occurred most frequently on shell exteriors. Boring diameter did not vary substantially between specimens (N=22); measurements obtained were 0.13-0.21-0.45 mm. Lengths of 1.27-2.30-4.77 mm were measured, but represented only part of the total extent of the boring. Length was generally proportional to diameter. "Branches" often prove on closer inspection to be the intersection of two tunnels or the initiation of a new tunnel at the wall of a previously existing boring. Average branching angle is about 34 .

Discussion: The diagnosis provided by Häntzschel (1975) is overly restrictive and not entirely accurate. The treatise

illustration itself consisted of gently curving tunnels rather than "straight tunnel systems" (Häntzschel, 1975, p.133).

Restricting substrate of occurrence to "rostra of belmnoids" (Häntzschel, 1975, p.133) eliminates isomorphous borings occurring in other substrates including those discussed in this paper. Should it be demonstrated that this form is restricted to  $\text{CaCO}_3$ , then diagnosis given above should be emended.

Ichnogenus Zapfella (de Saint-Seine, 1956, p.449)

Emended Diagnosis: deep sac-like bore holes with an elliptical opening which is rounded at the posterior end and pointed at the anterior termination (modified from Bromley, 1970; Teichert, 1975).

Remarks: Similar to Rogerella but lacking slit at anterior end and ridge-forming  $\text{CaCO}$  lining.

Description: Three examples were found on the exterior surface of loose shell material (Plate X, Fig. A). Lengths had a range and mean of 1.91-2.22-2.73 mm. Width was measured at points  $\frac{1}{4}$  length ( $W_{\frac{1}{4}}$ ) and  $\frac{1}{2}$  length ( $W_{\frac{1}{2}}$ ) away from anterior end. Values of 1.14-1.27-1.57 mm and 0.54-0.85-1.09 mm, respectively, were obtained. Widths were normalized with respect to length and it was found that  $W_{\frac{1}{4}} = .38 \pm 0.10(L)$  and  $W_{\frac{1}{2}} = .57 \pm 0.03(L)$ .

#### REPAIR BLISTERS

One Ostrea glabra valve exhibited repair blisters (Risk, pers. commun.) on the shell interior, directly below Entobia cretacea chambers (Plate X, Fig. B). Blisters resemble mounds,

PLATE X BIOGENIC STRUCTURES FROM UNCONSOLIDATED SAND

- Fig. A: Zapfella has a distinctly elliptical cross section. The posterior end is round; the anterior pointed. Zapfella is the characteristic form resulting from the activity of boring barnacles.
- Fig. B: Repair blisters are seen in the uppermost portion of an Ostrea valve interior. The mound-like structures consist of conchiolin. They were formed by a living oyster in response to the threats of a clionid sponge which bore through the shell from the exterior.
- Fig. C: Oyster attachment scars can be distinguished from incomplete borings of predaceous gastropods. The scars are shallow and have poorly defined walls.
- Fig. D: Partitions resemble a flattened strip of putty. They are found on the interior of Ostrea valves and were probably created as a response to irritation caused by a parasitic worm.



B

← 10 μm



D

← 10 μm



C

← 10 μm



A

← 10 μm

often coalesce, and have considerable vertical relief (up to several mm). Dimensions of 1.0 x 1.0 mm to 1.5 x 3.0 mm (length and width) were noted. Occasionally the mounds are pierced by minute tunnels that appear to be associated with Entobia.

#### PARTITIONS

Two oysters exhibit partition on their valve interiors (Plate X, Fig. D). The structures vary in height, width and form over their length. Portions resemble a narrow (1.1-2 mm) strip of flattened putty. In other parts a sharp-edged distinct ridge with a width of 0.5-1.4 mm is formed. In the main, the partitions are gently curving occasional sharp twists. Lengths of 4.5 to 20 mm were noted. It is important to ascertain that partitions are indeed formed by the shell-bearing organism and not by another individual cementing itself to the valve. Another possibility that must be ruled out is that ridges result from growth restriction. The material forming the partitions appears to be of a similar composition as the shell interior and continuous with it. There is no indication of a break between the two in the form of hematite staining of entrapped sediment.

## CHAPTER 5

### PALEOECOLOGY OF THE OYSTER BEDS

Evidence concerning the paleo-communities that existed in the oyster beds at Drumheller comes from both body fossils and traces. Fossil content of the CaCO<sub>3</sub>-cemented beds differed from that of the unconsolidated sand. As will be discussed later it is likely that this difference reflects an actual difference in the paleo-communities and is not simply a taphonomic artifact.

#### Taphonomic Considerations

In studies concerned with the nature of ancient environments it is essential to "undo" the modifications made by processes acting on a fossil since deposition. Let us consider the evidence concerning post-depositional alteration.

In the cemented beds, predominance of Ostrea glabra that remain articulated, presence of thin-shelled Corbula sp. and lack of sorting indicate that significant transportation has not occurred (Feldmann and Palubniak, 1973). The cemented beds are essentially in situ. Thus, the species represented as fossils were a part of the living community. Borings attributable to muricid gastropods were found but their shells were not. The progressive dissolution of Littorina in marshes associated with oyster reefs has been documented by Wiedmann (1972).

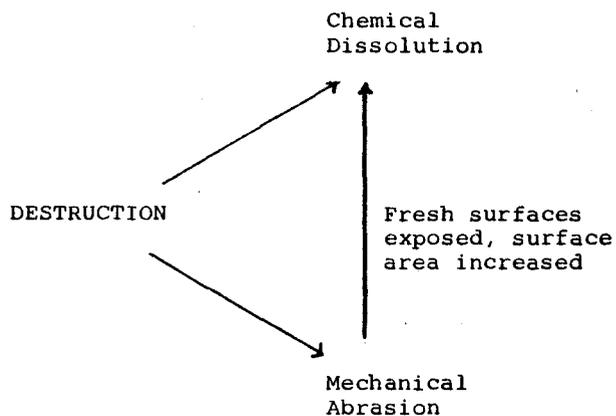
Possibly, the non-preservation of these hard parts can be attributed to dissolution of aragonite. Mechanical abrasion was not in evidence.

The situation appears to be strikingly different for the unconsolidated sand. Disarticulation and destruction of oyster valves indicates that the "shell concentrate" has been transported (Feldmann and Palubniak, 1973). Fairly restricted size ranges in shell fragments were noted. Sites WC2-8 had small thin shell fragments while at EC10 Ostrea glabra valves were almost complete. This suggests hydraulic sorting occurred (Stanton and Nelson, 1980). There is evidence of both mechanical and chemical destruction in the oyster shells found in this unit (Table 5.1). Mechanical destruction was evidenced first and foremost by the fragmentation of oyster valves. The fragments had irregular surfaces and edges.

Oysters are prone to abrasion during transportation due to their weight and sizeable surface area (Driscoll, 1970). The greatly reduced thickness of Willow Creek specimens is the result of considerable abrasion. It is likely that Willow Creek specimens were subjected to oscillatory wave action. Such movement results in much destruction but little travel (Feldmann and Palubniak, 1973). Possibly, the oysters at EC10 were subjected to unidirectional currents or were quickly isolated from hydraulic transport and thus remained intact (Feldmann and Palubniak, 1973). Mechanical destructions occurred both prior to the excavation of

Table 5.1 A Comparison of the Effects of Chemical Dissolution and Mechanical Abrasion

TYPE	EFFECTS	EXAMPLES
Chemical Dissolution	Details of ornamentation lost	<u>Entobia</u> scalloping lost <u>Q. paraboloides</u> bevelling, bossed base not seen
	Ultrastructure of substrate revealed	<u>Oichnus</u> shell layering seen on borehole wall
Mechanical Abrasion	Borings seen in relief	<u>Talpina</u>
	Substrate fragmented	<u>Oichnus</u> broken apart
DESTRUCTION	Destruction accelerated by void space	<u>Entobia</u> : only shells that are not intensively bored remain intact, fracture lines follow branches <u>Talpina</u> areas with high boring density pronounced shell reduction
	Structures with relief removed	<u>Zapfella</u> CaCO <sub>3</sub> ridge removed Repair Blisters seldom seen Partitions seldom seen
	Substrate thickness reduced	<u>Entobia</u> chambers exposed, still show scalloping



borings and following it. Shell destruction predated borings initiated on broken edges. Destructive effects were superimposed on other borings (Table 5.1). In these cases destruction must have post-dated boring. Specimens where borings were initiated on broken surfaces and then defaced themselves were taken to indicate that reworking of material occurred.

Findings of this study suggest it may be possible to relate the degree of detail preserved in trace fossils to the intensity and type of destruction to which they had been subjected.

At Drumheller there appears to be a hierarchy of preservation with Oichnus simplex being the most "resistant" boring. The least resistant fossils are those which are shallow and poorly defined. No grazing traces were positively identified at Drumheller. This suggests these traces are "unstable" with respect to the destructive forces in effect. Ornamentation appears also to be quickly obliterated. Very few examples of O. paraboloides had either the countersunk edge or raised base preserved (Carriker and Yochelson, 1968). Similarly, there were many examples of Entobia that lacked the scalloped ornamentation seen on well-preserved specimens.

Modifications to gross morphology require more extreme forms of destruction. Entobia sp.a appears to have been attacked both chemically and physically to the point where the surface has been destroyed and chamber walls modified (Plate VII, Fig. A). The most resistant trace appears to be Oichnus simplex. It has

a very simple form and is lacking in ornamentation. Dissolution may reveal layering of shell on boring wall, abrasion mar the exterior openings, but it takes considerable mechanical force for the boring to be broken apart. Oichnus simplex generally removes a small proportion of the substrate in a manner that does not greatly weaken the substrate. This promotes preservation of this ichnofossil in contrast to that of intensively bored Talpina and Entobia.

Overall, the type and degree of destruction found at Drumheller is heterogenous. In many specimens mechanical destruction is most pronounced, in others chemical dissolution predominates, in most both occur.

#### Cemented Beds

There are few traces in the cemented beds. The presence of oysters has long been used as an indication of brackish conditions (Berquist and Cobban in Feldmann and Palubniak, 1973). Members of the genus Ostrea, however, require more saline, less turbid water than estuarine Crassostrea (Hopkins, 1957). Corbula sp. also tends to inhabit brackish water (Pemberton, pers. commun.). There were also rare examples of a "Membranipora-like" cheilostomatous bryozoa (Bassler, 1953, p.157). The general lack of epizoans may indicate that water conditions were somewhat turbid. Ichnofossils that were present were Oichnus simplex and Talpina. These traces indicate organisms with a tolerance

PLATE XI MATERIAL FOUND IN CaCO<sub>3</sub> -CEMENTED BEDS

- Fig. A: Typical composition of cemented beds. Large complete and frequently articulated Ostrea glabra valves are numerous. The small thin-shelled bivalve in the lower part of the photograph is Corvula sp. Articulated bivalves were also found.
- Fig. B: Oichnus simplex in an Ostrea glabra valve. Borings are rare in cemented material. Oichnus and Talpina were only two forms represented.
- Fig. C: Body fossil of a Membranipora-like bryozoa. Epizoans were scarce at the Drumheller location. This may indicate that environmental conditions were inappropriate for them at the time these deposits were formed.



for low to normal marine salinities were present as will be discussed later.

### Unconsolidated Sand

In this unit, fragmented Ostrea glabra and associated encrusting bryozoa are the only body fossils preserved. The Ostrea glabra shells and the trace fossils left in them are the primary source of information regarding composition of the fossil community. Traces that were preserved in this unit include Oichnus, Entobia, Talpina, Zapfella, repair blisters and partitions. Their significance is discussed below.

### Oichnus

These small round holes are attributed to gastropods; O. paraboloides is the work of naticids, O. simplex due to muricids (Bromley, 1981). These are the only families known to attack molluscs to any extent (Stanton and Nelson, 1980).

Many environmental parameters effect snails, temperature being among them. Predaceous gastropods are more common in the tropics (Parker, 1982, p.1010). There were contrasts in attack strategies that were noted for the two gastropod groups. A large proportion of muricid borings were incomplete. The muricids were also more likely to initiate boring on the shell interior. Thus, they may be considered "less selective" (Reyment, 1967) with respect to the substrate they bore.

Statistical analysis reported earlier (Table 4.1) indicates that it is possible to differentiate between muricid and naticid borings on the basis of roundness, tapering and size. This distinction is useful in a number of ways. Some genera of muricids (for example, Murex) can tolerate lower salinity water than can naticids (Caspers, 1957). Thus, the occurrence of muricid borings in cemented beds along with the absence of naticid borings may indicate brackish water. Naticids only inhabit soft substrates, muricids generally dwell on hard ones (Taylor et al., 1980). The absence of O. paraboloides in the cemented beds suggests the substrate was hard, and that only transported shells were exposed to naticids. Naticids attack both infauna and epifauna, whereas muricids are restricted to epifauna (Reyment, 1967). Shells containing O. paraboloides may have been buried when bored; those exhibiting O. simplex were exposed. Naticids eat only living organisms; muricids eat carrion as well as live tissue (Reyment, 1967).

Finally, the ability to distinguish between muricid and naticid traces allows conclusions about the relative abundance or activity of these two groups in the past. This contributes to reconstruction of the fossil community structure. Gastropods are the dominant predator preserved from ancient communities (Taylor et al., 1980). This, along with the fact that bivalves are the most important prey of naticids and muricids, makes it essential to understand the role of predaceous gastropods in

ancient communities. Taylor et al. (1980) review the history of predaceous gastropods and conclude that muricids were more abundant than naticids in the Cretaceous, and that the reverse has been true from the Eocene to the present day. This explains the contrast between the findings of this study (more boreholes attributable to muricids) and those of Adegoke and Tevesz (1974) in the Eocene where the majority of gastropod borings were of naticid origin.

There is little conclusive evidence that Oichnus were excavated in living oysters. The number of borings initiated from the exterior far outweighs those begun from the interior, but this may simply indicate that the exterior was more likely to be exposed post mortem. An abundance of attachment scars of larval oysters occur on specimens containing Oichnus. This suggests that the shell was within a reproducing oyster bank. However, dead shells are not uncommon in oyster banks and are a popular substrate for larval attachment.

Size distributions were skewed toward smaller sizes. This is probably a reflection of gastropod reproductive habits. In modern environments juveniles make up the majority of the population. It may also indicate a greater number of incomplete borings by smaller individuals.

Small O. simplex tend to be incomplete. This suggests that juveniles or small muricid species: a) were not able to completely penetrate thick Ostrea valves; b) were more likely to

bore into dead shells and then abandon boring; c) were dislodged before boring was complete. The third possibility is supported by Adegoke and Tevesz (1974), who reported that muricids have a small foot and are thus less stable.

### Entobia

Borings consisting of multiple interconnected chambers are believed to be produced by clionids (Bromley, 1970). In addition many of the borings at Drumheller provide more "direct" evidence of sponge origin in the form of scalloped wall ornament (Kobluk, 1981).

There has been some debate concerning the possibility of using Entobia as an indicator of salinity, although assemblages of recent clionids can define salinity zones (Hopkins, 1956). Boekschoten (1966) emphasizes that a major stumbling block in determining assemblage is that it may be impossible to use fossil sponge borings (Entobia) to identify species. Even in rare cases of superb preservation ambiguity may exist due to substrate control of boring morphology. Old (1941) also suggests that substrate influences boring produced. He reported that Cliona vastifica galleries were arranged dendritically in thin scallop shells and lacked a discernible pattern in thick shells. In this study, however, it has been demonstrated that Entobia may have either a distinctly dendritic or unpatterned arrangement in thick shells. Groot (1977) found that size, not shape, was affected and that substrate chosen might be an indicator

of the species responsible. (Refer also to Table 5.2.) Variation in the morphology of borings produced by the same species may lead one to conclude that more species were active than was actually the case. For example, Hancock (1849) made the unlikely claim that he could distinguish 12 species of cliona in a single shell. The question to be answered is whether variation within a species is greater than variation between species. Bromley reported that in modern sponges: "in many cases the empty borings were sufficiently characteristic to allow identification to the species level" (Bromley, 1978, p.174). Finally, the same boring may be created by different species. This may not be an insurmountable problem with respect to the utility of Entobia as a paleoenvironmental indicator.

As has been mentioned Lawrence (1969) simply divided borings into two morphotypes: those resembling C. vastifica and those more akin to C. celata. The former group was found in shells he believed to be deposited under lowered salinities.

Entobia from Drumheller illustrate the complications that may arise from imperfect fossil preservation. A common problem is the enlargement of surface perforations and chambers (Boekschoten, 1966). This did not appear to be greatly significant at Drumheller. The loss of characteristic scalloped wall texture (Plate III) was in all likelihood due to dissolution. Abrasion has reduced the thickness of the shell making it impossible to determine the depth of penetration. Frequently, chambers

Table 5.2. Summary of surface aspect, excavation style and environmental observations of several species of modern boring sponges (after Hopkins, 1956, 1962; Hartman, 1957, 1958; Hechtel, 1965; Rützler, 1971; Pang, 1971, 1973; Rützler and Rieger, 1973; Groot, 1977; Bromley, 1978; Rützler and Bromley, 1981).

Species	Surface Apertures (in mm)			Excavations (in mm)				Environmental Observations		
	Ostial Oscular	Tendency to fuse to encrust	Pattern	Chambers Dimensions Description	Rootstock	Rootlet	Connection to Papillae	Salinity (‰) normal; still functions=f; critical=c;	Substrate	Distribution and Depth Hydraulic Energy Level
<i>Cliona celata</i>	.8-2.5 2.-4.5 .3-1.5-10	no no	--	2-6-8 LS *3 shell spherical, may fuse, linear or branched pattern in shells		2 LS diminutive in shells	limited depth of boring	1-22-30 ≤15 20 f 10 c	limestone shell algae	tide pools, subtidal 1-25m deep, lower estuary with > 1/4 marine salinity
<i>C. vastifica</i> <sup>v</sup>	.2-.4 .6-1.4 .1-1.0†	-- seldom	reticulate in thin shells, random in oysters, young colonies linear	1-3 LS 1-3 coral .2-.5 shell				10-21-30 11-13	limestone shell algae	intertidal < 1m, shallow subtidal, deep water. All but v. high energy
<i>C. viridis</i>	.2-1-2 <sup>+</sup> LS .1-.5-1.1 <sup>+</sup> shell, .1-1.5 <sup>+</sup> coral	yes --	--	2 LS 1-3 coral  smaller in shell		inter-connected			limestone shell algae	littoral terrace < 1m, deep water
<i>C. vermifera</i>	1.04 1.08 10x2 <sup>+</sup> LS .5-1.5 <sup>+</sup> coral	occasionally often	none	2x12 LS 1.64x3.48 coalesce at intersections open habit, no pattern		numerous cylindrical diameter .26-.32 1-3 coral	length 1-2		limestone coral coral rock not shell	littoral < 8m, 18-52m. All but v. high energy
<i>C. lobata</i>	.2-.5 .8-1.6	-- --	reticulate					14-17-22		upper estuary
<i>C. truitti</i> <sup>v</sup>	.1-.3* .4-.6*	no no	--					6-18 salinity far below marine		
<i>C. schmidtii</i>	1.02 1.83	no no	--	1.17x2.56 spherical to ellipsoidal irregular outline	narrow and elongate				coral coral rock	15-47m
<i>C. janitrix</i>	.58 .70	no no	--	5.11x1.58 spherical to cylindrical					coral dead coral	15-28m

Table 5.2b

<i>C. lampa</i> <sup>v</sup>	.72 1.20 .5-1.5 <sup>†</sup>	occasionally no	-- --	<u>1.08x1.58</u> spherical to ellipsoidal, honeycomb in x-sec, when closely spaced <u>.5x1.5</u>	slender	penetration .5-80mm from substrate surface	coral coral rock shell	.5-36m quiet shallow water
<i>C. carribaea</i> (v. similar to <i>C. viridis</i> )	large papillae with symbiotic algae	no no	--	3.7- <del>4.2</del> -5.8 cylindrical, ragged outline, bifurcate, fusion among closely spaced chambers		short, wide channel	coral	1-2m <20m. All but v. high energy
<i>C. delitrix</i>	3.05x4.05 7.85x9.65	yes yes	--	-- cylindrical, perpendicular to surface			coral dead coral	22-34m
<i>C. reponaca</i>	.69 1.11	yes yes	none	<u>1.21</u> cylindrical	short and wide		coral coral rock	--
<i>C. langae</i>	not visible	-- yes		<u>2.31</u> irregular, confluent, extend 2.4cm into corallum			coral dead coral	15-30m
<i>C. laticavicola</i>	2.55 )x 2.83 )x 2.18 )† 2.54 )†	yes --	none	<u>4.61</u> <sup>x</sup> <u>1.12</u> <sup>†</sup> substrate controlled	diameter 1-2 various lengths		coral coral rock	coral coral rock
<i>C. aprica</i>	1.05x1.67 <sup>x</sup> .98x1.52 <sup>†</sup>	yes yes	none	1.20 <sup>x</sup> 1.24 <sup>†</sup> spherical to ellipsoidal irregular outline confluent	1-2 long 2-3 wide		coral	coral
<i>C. rhodensis</i>	.5-2-3 2-3-4.8	uncommon no		unfused, sub-spherical 10x10 to 12x20 fused crypts up to 20x40	numerous and fine <.5		limestone Mg-calcite cement	abundant sealevel -3m common to 9m found to 90m
<i>C. rovigensis</i>	.4-.8 --						limestone between adjacent lithodomus burrows	littoral
<i>C. amplicarata</i>	few, large <sup>†</sup>			single, large, spherical	length up to 30			all but v. high energy

Table 5.2c

<u>C. flavifodina</u>	large <sup>†</sup>			large, noncamer- ate, smooth- walled				all but v. high energy
<u>C. pauciapins</u>						dead coral reef rock		only low hydraulic energy tolerated
<u>Spheciospongia Othella</u>				large, noncamer- ate network, ir- regular wall sur- faces reflect substrate			dead coral reef rock	
<u>Thosa mollis</u>						walls of abandoned lamellibranch burrows		littoral 2-8m
<u>Alectona jamaicensis</u>	.51 .54	no --	6.2 spher- ical to el- lipsoidal	3.2 long .42 wide				
<u>Siphonodictyon brevitulatum</u>	1.71 .11 confluent papillae 7.8x2	-- --	44.7 single, spherical	none			--	
<u>S. mucosum</u>	.023-.15 .3-5.5	no no		250cm <sup>3</sup>				coral
<u>S. cacharouense*</u>	.1-.14 4-8	no		500cm <sup>3</sup>	none	length varies with substrate 3.8-9.8		coral 5-32m
<u>S. coralliphagum</u>	.1-.25 2.0-10 or simply opening of channel to surface	yes yes	ostia distri- buted over surface, oscu- la elevated	spherical 5-10 ovoid 10-20 larger axis par- allel to sub- strate	none	endolith forms have 1 or 2 connections to surface at 20-40 to perpendicular to surface diameter .5-1.8		coral

## Symbols:

v -c vastifica-like species

\* based on a single specimen

† no distinction between ostial and oscular papillae made

x shallow water form

‡ deep water form

are exposed, so that information concerning the size distribution and density of surface apertures is lacking. Exposure also makes it difficult to determine whether the sponge overgrew the substrate. Fragmentation may result in the preservation of only a small portion of a boring system. This prevents the preservation of branching patterns. Guida (1977) suggests that in in situ oysters the mere presence or absence of clionid borings is significant. He found that approximately half the oysters of the lower third of the inter-tidal zone were infested with clionids. Above this zone few oysters were affected. This zone that is free of clionid borings corresponds to Hopkins' (1956) "zero zone". With respect to taxonomy, Old (1941) concluded that spiculation is the best criterion for species identification. Kobluk (1981) has documented the preservation of spicules from the Lower Cambrian. However, it is unlikely that spicules will routinely be found. The best strategy for ichnologists to follow is to establish context of depositional environment and make detailed descriptions of traces. Then comparison with data from Recent studies can be done and limited inferences drawn.

Table 5.2 has been constructed to gather data relevant to geologists wishing to make paleoenvironmental interpretations. Cliona is the predominate boring sponge in modern environments although other groups may have been important in the past. Possibly, with relevant data readily available, paleontologists will make more complete and comparable descriptions. This might

result in a) the erection of new ichnospecies, and b) substantiated association of particular forms with given paleoenvironments.

Examples of Entobia from Drumheller have very small surface apertures and chambers, especially when it is taken into account that dissolution is likely to have enlarged the excavations. The loss of scalloped texture is taken as evidence of dissolution. The only clionid species with papillar openings in the range found for Entobia is C. trutti. Data on chamber size are lacking; however, surface apertures are generally proportional in size to chamber dimensions. Therefore, C. trutti probably has minute chambers.

E. cretacea is characterized by a camerate form as is C. trutti and other vastifica-like species. Interpretations that can be made for Entobia borings are limited by the incomplete clionid data. E. cretacea appears to be related to C. trutti, and thus to C. vastifica, on the basis of form and dimensions. This implies that the instigator of E. cretacea was able to tolerate brackish water. Further evidence that C. trutti was responsible would indicate a restricted range of salinity from 6-18%, which is far below normal marine (36%). There is only one example of Entobia that was without doubt excavated in a living oyster, and it is discussed later in this report. Guida (1977) found that clionid damage was 10% greater in dead oysters than in living. No examples of Entobia were found in the cemented beds. It is likely that the majority of clionid

boring were excavated in dead shells.

The cemented oyster beds are completely barren of Entobia and thus were probably located in the mid to upper inter-tidal zone (Guida, 1977).

### Talpina

The closely-packed cylindrical borings described in this paper are most similar to phoronid dwellings. Other possible borers have been eliminated on the following grounds: polychaetes produce unclustered borings (Rodriguez and Gutschick, 1977) and bryozoan stolons branch frequently and at high angles (Bromley, 1970).

Borings tended to parallel shell surface (Plate IX, Fig. A,B). This may be an avoidance of conchiolin layers, supporting the hypothesis that chemical boring was employed. Phoronids generally dwell in the upper littoral zone and may live in brackish water (Hyman, 1959). As filter-feeding organisms, they cannot tolerate high rates of sedimentation. Talpina are ubiquitous, particularly in the EC10 section. The intensity of boring and surface coverage makes them useful taphonomic indicators.

As was described earlier borings are frequently concentrated on shell margins or convex exterior. In the first case the shell was probably lying with concave side up with sediment covering the exterior. Specimens corresponding to the

second description were positioned with convex exterior pointed upward and margins buried in sediment. In other cases one end appears to have been buried while the other was exposed (Plate IX, Fig. B,D).

It appears that for valves containing these borings essentially all exposed surfaces were bored. Thus, absence of boring indicates areas that were covered by sediment. This indicates portions of the shell were exposed for varying lengths of time and that reworking occurred. Borings frequently were noted on rough edges caused by shell abrasion during transport; thus they postdate transport.

### Zapfella

These borings are attributed to marine acrothoracians. The absence of a CaCO<sub>3</sub> ridge and the somewhat truncated form can be taken as evidence that the shell has been reduced; in modern examples, the aperture is smaller than the remainder of the boring (Bromley, 1975). Seilacher (1969) believed that barnacles bored only live shells; however, this has since been disproved (Rodrigues and Gutschick, 1977). Thus, the examples of Zapfella supply taphonomic information.

### REPAIR BLISTERS

Conchiolin repair marks are formed by living oysters in an attempt to seal off perforations made by borers. Boekschoten

(1966) found these structures in living oysters attacked by sponges. He concluded that shells lacking blisters were probably live when bored.

The association of blisters with Entobia cretacea indicates that live oysters coexisted with the clionid species responsible for E. cretacea (probably a vastifica-like sponge). The corollary would be that the remainder of shells were dead when attacked by Entobia, since evidence of repair is missing. However, considering the amount of substrate that has been lost (and repair marks with it in all likelihood) it would be unwise to draw such a conclusion in all cases. Another important point to note is that the boring did eventually penetrate the inner surface. Apertures may be seen on both surfaces, in spite of the fact that the organism was alive when first attacked.

#### PARTITIONS

The partitions described resemble those figured by Pearse and Wharton (1938). These were built by the oyster to protect itself from the parasitic flatworm Stylochus inimicus, the "oyster leech". This parasite cannot tolerate salinities below 6‰ for more than 2 weeks and 15‰ are required for egg development. Temperatures must be above 10 C.

The partitions cannot be unquestionably attributed to S. inimicus or any similar organism, until more is known about other irritants that might elicit such a response. Thus, con-

clusions concerning temperature and salinity can only be tentative at this time.

### Paleoecological Implications

At Drumheller, soft-bodied organisms and skeletal matter consisting of aragonite, silicae and chitin are not seen. However, there is evidence of the activity of organisms that possessed soft-bodies or unstable hard-parts. This evidence is predominately in the form of borings in the shells of Ostrea glabra. Lawrence (1968) estimates that under the conditions of preservation described (his third case) only 23% of the total living oyster community would be represented with a significant proportion of that evidence in the form of trace fossils. This suggests that species diversity in the in situ oyster was considerably higher than the fossil evidence substantiates. Despite this, the origin species diversity was probably low suggesting low salinity, agitated conditions (Feldmann and Palubniak, 1973; Warme, 1975a).

Three levels of organism interaction can be seen (Table 5.3). Direct interaction occurs when two species can be shown to have elicited a response for one another (Lawrence, 1968). This occurs in the case of a clionid which bored into a living oyster which responded by forming repair blisters. It also appears that partitions were constructed in response to a parasitic worm. Indirect association occurs when the action of

Table 5.3 Distribution of Body Fossils and Traces and Paleoecological Implications\*

Palaenontological Evidence	Cemented	EC10	WC2-8	WC1.9	Implications to this study
<u>Ostrea glabra</u> -articulated	A	X	X	X	c) <u>in situ</u>
-disarticulated	C	A	A	R	f) transported
-badly fragmented	R	R	A	A	f) oscillatory wave action
<u>Corvula sp.</u>	C	X	X	X	c) <u>Corvula sp.</u> - - muricid
<u>Membranipora</u> -form Cheilostomata	R	X	R	X	c) brackish water
<u>Oichnus simplex</u>	R	A	A	X	d) sedimentation rate not high
					<u>Ostrea</u> - naticid
					Tropical to sub-tropical shells exposed
<u>Oichnus paraboloides</u>	X	C	A	X	c) brackish water
<u>Entobia cretacea</u>	X	R	C	X	f) <u>Ostrea</u> -- muricid
<u>Entobia cretacea</u> & blisters	X	X	R	X	f) soft substrate
					f) brackish to normal marine
<u>Entobia sp. "a"</u>	X	R	R	X	c) <u>Ostrea-cliona</u>
<u>Entobia sp. "a"; cretacea</u>	X	R	X	X	c) lower intertidal zone
<u>Talpina</u>	R	A	C	X	c) brackish to normal marine
					<u>Ostrea</u> - - Phoronids
					sedimentation rate not high
					inter-tidal
					brackish
<u>Talpina</u> on broken edges, or with contrasting densities	X	C	R	X	f) reworked, bored surfaces exposed
<u>Zapfella</u>	X	X	R	X	<u>Ostrea</u> - - barnacle
					f) marine
					f) shell reduced by abrasion
Partitions	X	R	X	X	c) <u>Ostrea</u> - parasitic "worm"
					c) salinity >6‰
					c) temperature >10 C
ENVIRONMENT	Oyster Reef	Shell Concentrate	Sub-Tidal Channel	Tidal Channel or Flat	Tidally-dominated Delta

\*Symbols used:

- A=abundant C=common R=rare X=not found
- c) Implications concern cemented beds
- f) Implications concern unconsolidated sand
- direct relationship between organisms
- indirect relationship between organisms

one organism is seen on another. Borings by gastropods, sponges, phoronids and barnacles in oyster shells illustrate this relationship. The oysters were not necessarily alive but did provide a suitable substrate for boring. The third degree of interaction is not shown in the table. It involves the coexistence of two species which probably had little influence on one another. This type of relationship exists between Ostrea glabra and Corbula sp. Information contained in transported oyster fragments contains conflicting environmental implications (Table 5.3). This along with evidence of reworking discussed earlier indicates that this material has been exposed to contrasting paleoenvironments. Ostrea glabra valves were probably derived from oyster reefs where they were affected by organisms that thrived under brackish conditions. Valves were transported to higher salinity conditions. There they were exposed to marine borers. Transportation was probably intermittent with periods when shells were buried.

## CHAPTER 6

### SUMMARY AND CONCLUSIONS

#### Interpretation of Depositional Setting

The study area occurs in a deltaic context. A controversy exists concerning whether fluvial or tidal processes dominated deltaic construction (Shepherd and Hills, 1970; Rahmani, 1981). The in situ oyster beds and transported shell concentrate may provide some valuable clues to solving this problem. There appear to be two distinct fossil micro-environments represented. The overlying in situ oyster bank is characterized by Ostrea glabra, Corbula sp., muricids and possibly Stylochus inimicus. These fauna tend to thrive under very specific low salinity conditions. This indicates that the influx of fresh (river) water was a significant factor in this micro-environment. A deltaic interpretation is reasonable from a paleoecological perspective. The scarcity of epifaunal body fossils and traces suggests that waters were somewhat muddy and agitated (Stanton and Nelson, 1980). The unconsolidated unit consists of transported shell fragments that have been subjected to higher salinities approaching truly marine. Fauna that are indicative of this are: barnacles and muricids. The oyster bed units of the Cretaceous Bearpaw-Horseshoe Canyon formation transition at Drumheller appear to be analogous to those of the modern Georgia

coast studied by Wiedmann (1972). The overlying in situ oyster beds appear to be barren of Entobia indicating little cliona activity has occurred. They appear to represent a "reef structure". The large shell fragments of EC10 correspond to the "shell concentrate" described by Wiedmann. The rare occurrence of Entobia in shell concentrate suggests a moderate level of clionid activity. In the Willow Creek sites 2-8 Entobia is common suggesting higher levels of cliona activity. These sites may represent sub-tidal channel lag. This supports Rahmani (1981) in his hypothesis that coastline processes were tidally-dominated. Another line of reasoning is the low number of species that were represented in the oyster reef. Shepherd and Hills (1970) suggest that the in situ oysters now found in cemented beds existed in sheltered bays. However, the assemblages of boring fauna tend to be high in sheltered bays (Warme, 1975a) and this is not the case at Drumheller.

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