LATE CRETACEOUS SPONGE BORINGS -
INDICATORS OF SALINITY AND SEDIMENTATION
DRUMHELLER, ALBERTA

LICENCE TO McMASTER UNIVERSITY

This THESIS has been written
[Thesis, Project Report, etc.]

by MARK CHRISTOPHER BIRCHARD for
[Full Name(s)]
Undergraduate course number GEO. 4K6 at McMaster
University under the supervision/direction of
DR. MICHAEL J. RISK.

In the interest of furthering teaching and research, I/we hereby grant to McMaster University:

1. The ownership of 3 copy(ies) of this work;
2. A non-exclusive licence to make copies of this work, (or any part thereof) the copyright of which is vested in me/us, for the full term of the copyright, or for so long as may be legally permitted. Such copies shall only be made in response to a written request from the Library or any University or similar institution.

I/we further acknowledge that this work (or a surrogate copy thereof) may be consulted without restriction by any interested person.

Michael Risk
Signature of Witness,
Supervisor

Mark Birchard
Signature of Student

April 29/87
date

(This Licence to be bound with the work)

LATE CRETACEOUS SPONGE BORINGS -
INDICATORS OF SALINITY AND SEDIMENTATION
DRUMHELLER, ALBERTA

by

MARK CHRISTOPHER BIRCHARD

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

McMaster University
April 1987

BACHELOR OF SCIENCE (1987)
(GEOLOGY)

McMASTER UNIVERSITY
HAMILTON, ONTARIO

TITLE :	Late Cretaceous sponge borings - indicators of salinity and sedimentation, Drumheller, Alberta
AUTHOR :	Mark Christopher Birchard
SUPERVISOR :	Dr. Michael J. Risk
NUMBER OF PAGES :	viii, 47

ABSTRACT

A detailed study of sponge boring morphotypes within the molluscan fauna of Upper Cretaceous estuarine sediments near Drumheller, Alberta provides information relevant to the depositional environment. Problems with regard to utilizing *Entobia* as a paleoenvironmental indicator and as an indicator of salinity do not appear to be insurmountable.

Distributions and characteristics of associated marine organisms (phoronid worms, gastropods and encrusting bryozoa) suggest that sponge colonies were affected by salinity and sedimentation. Boring networks in *Ostrea glabra* suggest that more than one species of sponge were present. Sponge distribution patterns, changes in papilla and chamber sizes and preferential occurrence of sponge borings on certain shell thicknesses provide good evidence for responses to salinity and sedimentation.

ACKNOWLEDGEMENTS

I would like to thank a number of people for assisting in the production and development of this thesis. First and foremost I thank Dr. Mike Risk for supervising this thesis, providing constructive criticism and suggestions, and for developing my interest in palaeontology during my stay at McMaster. Thanks are also due to Alec Aitken, especially, and the rest of the palaeontology research group at McMaster for lending assistance in a variety of ways.

I would like to acknowledge the generosity of Dave Eberth and staff at the Tyrrell Museum of Paleontology, plus special thanks to Karen for field assistance on more than one hot, summer afternoon. Thanks also to Jack Whorwood for his photographic expertise.

Finally, thanks to my colleagues for many `more than interesting' late night `brainstorming sessions' at the Rathskellar. Good friends are hard to come by !

TABLE OF CONTENTS

Page

CHAPTER 1 INTRODUCTION

Study area 1
Stratigraphy and Interpretations 3

CHAPTER 2 TECHNIQUES

Sampling 9
The Search for Spicules 11

CHAPTER 3 SPONGE BORINGS AS PALEOENVIRONMENTAL INDICATORS

Macroborings - Importance as Trace Fossils 14
Paleoenvironmental Studies 14
Implications of Trace Importance to this Study 15

CHAPTER 4 PALEOECOLOGIC INFORMATION

Evidence from *Ostrea glabra* 20
Evidence from *Oichnus* 21
Evidence from *Talpina* and bryozoa 23
Evidence from boring sponges 25
  Entobia distributions 29
  Size data and analysis 30
    A: Papillae 30
    B: Chambers 32
  Evidence from shell thickness 37

CHAPTER 5 CONCLUSIONS 40

REFERENCES 43

LIST OF TABLES

Page

Table 4.1 Papillae measurement data for _Entobia_ 33

Table 4.2 _Entobia_ _cretacea_ type 1 chamber analysis Short and long axis dimensions 37

LIST OF FIGURES

		Page
Figure 1	Location of study area	2
Figure 2	Fence diagram of Willow Creek area	4
Figure 3	Paleogeographic map showing extent of Early Maastrichtian seas	5
Figure 4	Depositional paleoenvironments of the Bearpaw - Horseshoe Canyon transition	8
Figure 5	Isopach map of Unit E4 showing facies transition and distribution of oyster beds	25
Figure 6	Type ichnospecies of _Entobia_	26
Figure 7	_Entobia_ boring types in _Ostrea glabra_, Drumheller, Alberta	28
Figure 8	Mean papillae sizes of _Entobia_ at Willow Creek	33
Figure 9	Comparison of _Entobia_ chamber dimensions	34
Figure 10	Type 1 chamber dimensions of _Entobia cretacea_	36
Figure 11	Frequency plot of thickness of _Ostrea_ valves where bored by _Entobia_	38

LIST OF PLATES

Plate I	*Entobia* and *Talpina* borings from section WC-8
Plate II	Sampling site WC-7
Plate III	Borings in *Ostrea glabra* from consolidated sands at WC-5
Plate IV	Willow Creek section
Plate V	X-radiographs of *Entobia* boring networks
Plate VI	SEM of natural casts of *Entobia* boring networks
Plate VII	Juvenile oysters on *Ostrea glabra*
Plate VIII	*Entobia cretacea* and *Entobia* type 'a' chambers

CHAPTER 1

INTRODUCTION

Studies of borings produced by clionid sponges indicate that identification and subsequent mapping of clionid distribution patterns may be a valuable component of some paleoenvironmental studies (Lawrence, 1967 ; Hopkins, 1956). A detailed study of 'clionid' boring morphotypes within the molluscan fauna of Upper Cretaceous sediments near Drumheller, Alberta may provide information relevant to the depositional environment.

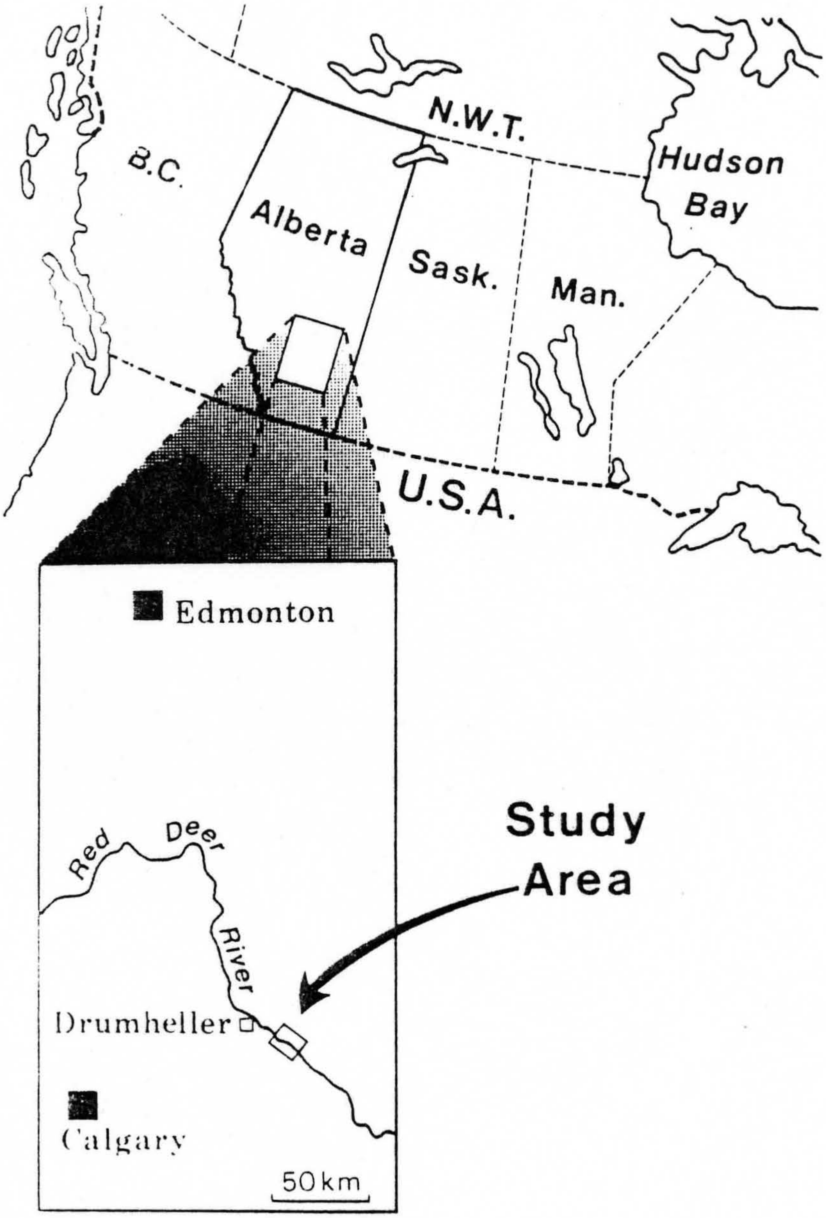
At the Willow Creek section southeast of Drumheller, Alberta, sedimentologic studies suggest an estuarine-deltaic environment (Shepheard and Hills, 1970; Rahmani, 1983). The associated oyster assemblage possesses well preserved macroborings of sponges, gastropods and phoronid worms.

This study will test the hypothesis that salinity is the primary factor which influences boring sponge distributions within the unconsolidated sands of these Upper Cretaceous oyster beds.

Study Area :

A superb section of Upper Cretaceous sediments occurs approximately twelve kilometres southeast of Drumheller, in the 'badlands' of Alberta, along the Red Deer River (Figure 1). Both vertical and horizontal exposure of strata are excellent.

Figure 1. Location of study area (after Rahmani, 1983).


N.W.T.
B.C.
Alberta
Sask.
Man.
Hudson Bay
U.S.A.
Edmonton
Red Deer River
Drumheller
Calgary
50 km
Study Area

Stratigraphy and Interpretations :

The Willow Creek section, near Drumheller, has been studied in considerable detail by geologists because of its accessibility and excellent exposure (Figure 2). Several recent studies suggest that these clastic sediments represent a prograding deltaic sequence (Shepheard and Hills, 1970; Rahmani, 1983). The oyster bearing unit occurs within the lowermost Horseshoe Canyon Formation, a shallow marine deposit which is directly underlain by marine sediments characteristic of the Bearpaw Formation. At Willow Creek, the Horseshoe Canyon Formation grades upwards into continental sediments. This sequence of marine, transitional marine and continental sediments is strong evidence for a regression of epicontinental seas in the Western Interior Seaway of North America during late Campanian - early Maastrichtian time (Figure 3).

Stratigraphic unit descriptions developed by Shepheard and Hills (1970), along with section location names as modified by Rahmani (1983), were adopted as a basis for this study.

A prominent oyster bed up to four metres thick occurs at the Willow Creek section. This bed roughly trends northeast to southwest and pinches out approximately one kilometre to the southeast of the mouth of Willow Creek. _Ostrea glabra_ shells occur within unconsolidated sediments both as disarticulated fragments and as distinct 'lenses' of articulated specimens. Glauconite and organic matter are abundant in these sediments,

Figure 2. Fence diagram showing units and facies in the Willow Creek area (after Rahmani, 1983).

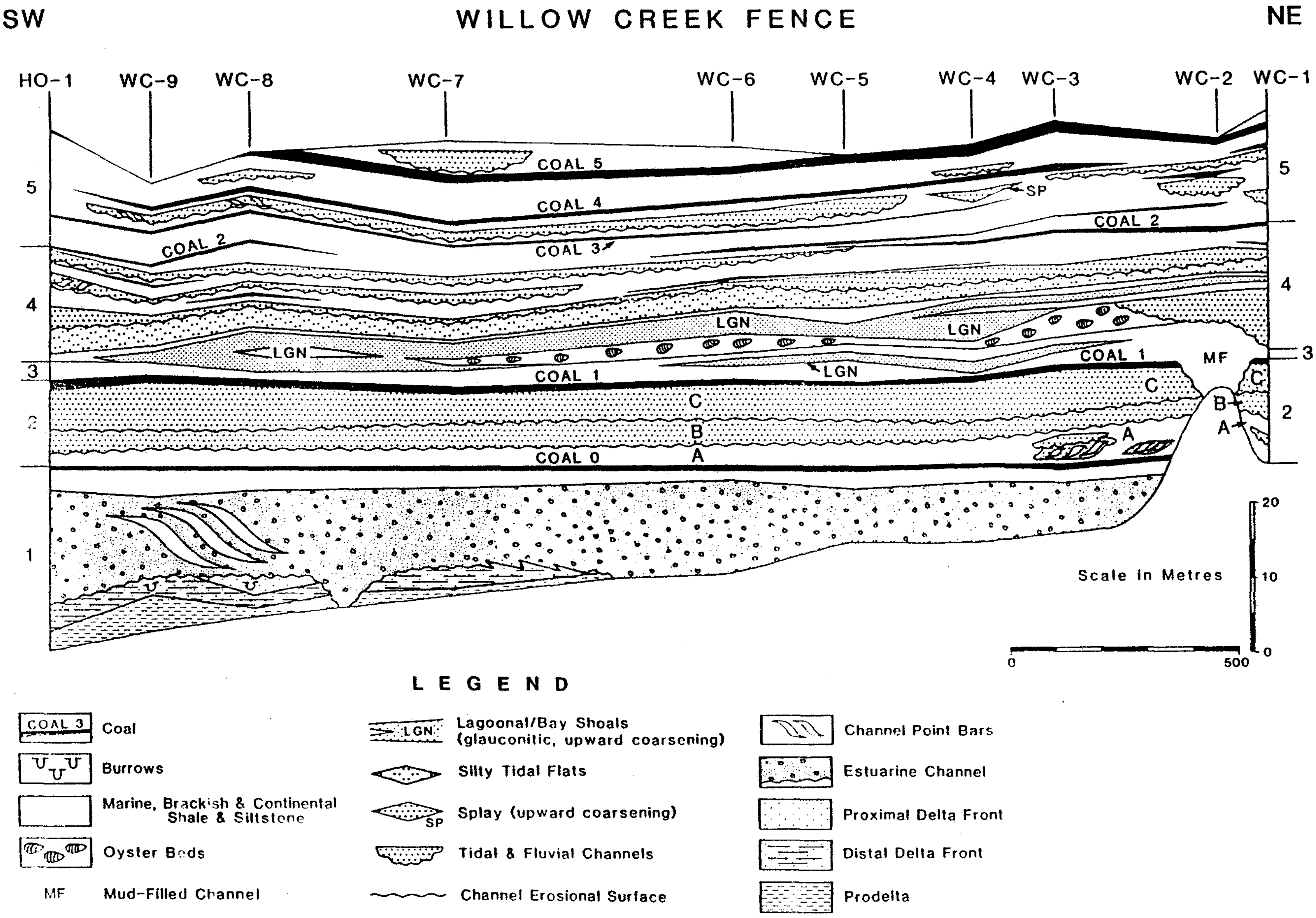
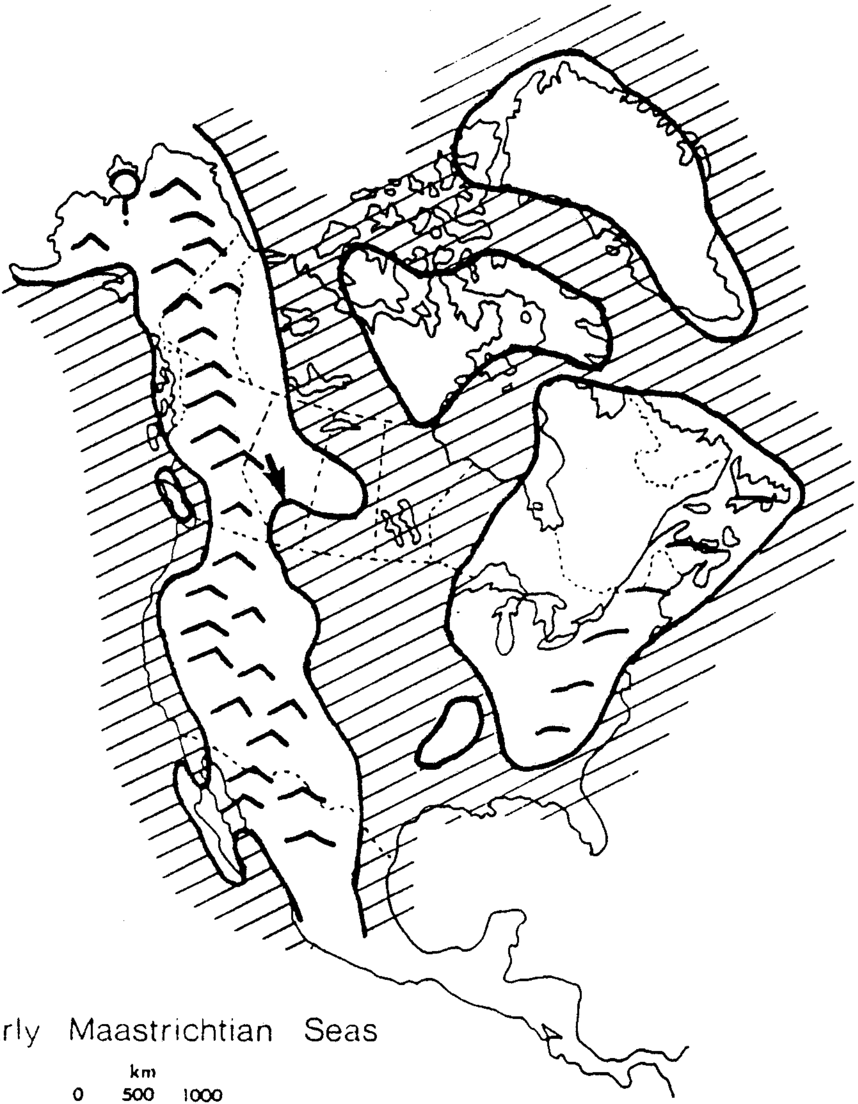

SW
WILLOW CREEK FENCE
NE
HO-1
WC-9
WC-8
WC-7
WC-6
WC-5
WC-4
WC-3
WC-2
WC-1
COAL 5
COAL 4
SP
COAL 2
COAL 3
COAL 2
LGN
LGN
LGN
LGN
COAL 1
COAL 1
MF
C
B
A
COAL 0
5
4
3
2
1
5
4
3
2
Scale in Metres
20
10
0
0
500
LEGEND
COAL 3
Coal
Burrows
Marine, Brackish & Continental Shale & Siltstone
Oyster Beds
MF
Mud-Filled Channel
LGN
Lagoonal/Bay Shoals (glauconitic, upward coarsening)
Silty Tidal Flats
SP
Splay (upward coarsening)
Tidal & Fluvial Channels
Channel Erosional Surface
Channel Point Bars
Estuarine Channel
Proximal Delta Front
Distal Delta Front
Prodelta

Figure 3. Paleogeographic map showing extent of Early Maastrichtian seas (after Rahmani, 1983). Arrow indicates study area.



Early Maastrichtian Seas

km
0 500 1000

indicating the presence of both marine and terrestrial influences. Faunal evidence from the unconsolidated sands suggests that sponges, gastropods, phoronid worms (Plate I) and encrusting bryozoa were present. Kemp (1983) also observed evidence of borings attributable to marine acrothoracians, and partitions in oyster shells possibly produced in response to a parasitic flatworm, Stylochus inimicus. The unconsolidated shell bed moves up in stratigraphic position to the west and changes accordingly from a sandy to a shaly facies (Shepheard and Hills, 1970).

Overlying these sediments in some locations are massive carbonate cemented sands containing many complete or nearly complete Ostrea shells (Plate II). These cemented sands are generally 20 centimetres to three metres thick and occur as laterally discontinuous patches of essentially in situ shells. Again, glauconite and organic matter are abundant. Evidence of gastropods, phoronid worms and encrusting bryozoa are found in shells collected from these sands. Sponge borings were observed in shells from consolidated sands at one location; however, these are rare in this part of the unit (Plate III). The oyster beds occur within Unit E4 of Rahmani's stratigraphic framework (Figure 2).

Shepheard and Hills (1970) propose that the deltaic complex responsible for deposition of the sediments was river dominated, and hence can be compared with the modern-day Mississippi Delta setting. Accordingly, oysters and sands of Unit E4 are

Plate I *Entobia* and *Talpina* borings from WC-8

Lower valves of *Ostrea glabra* show variability in chamber exposure, boring densities and location of borings.

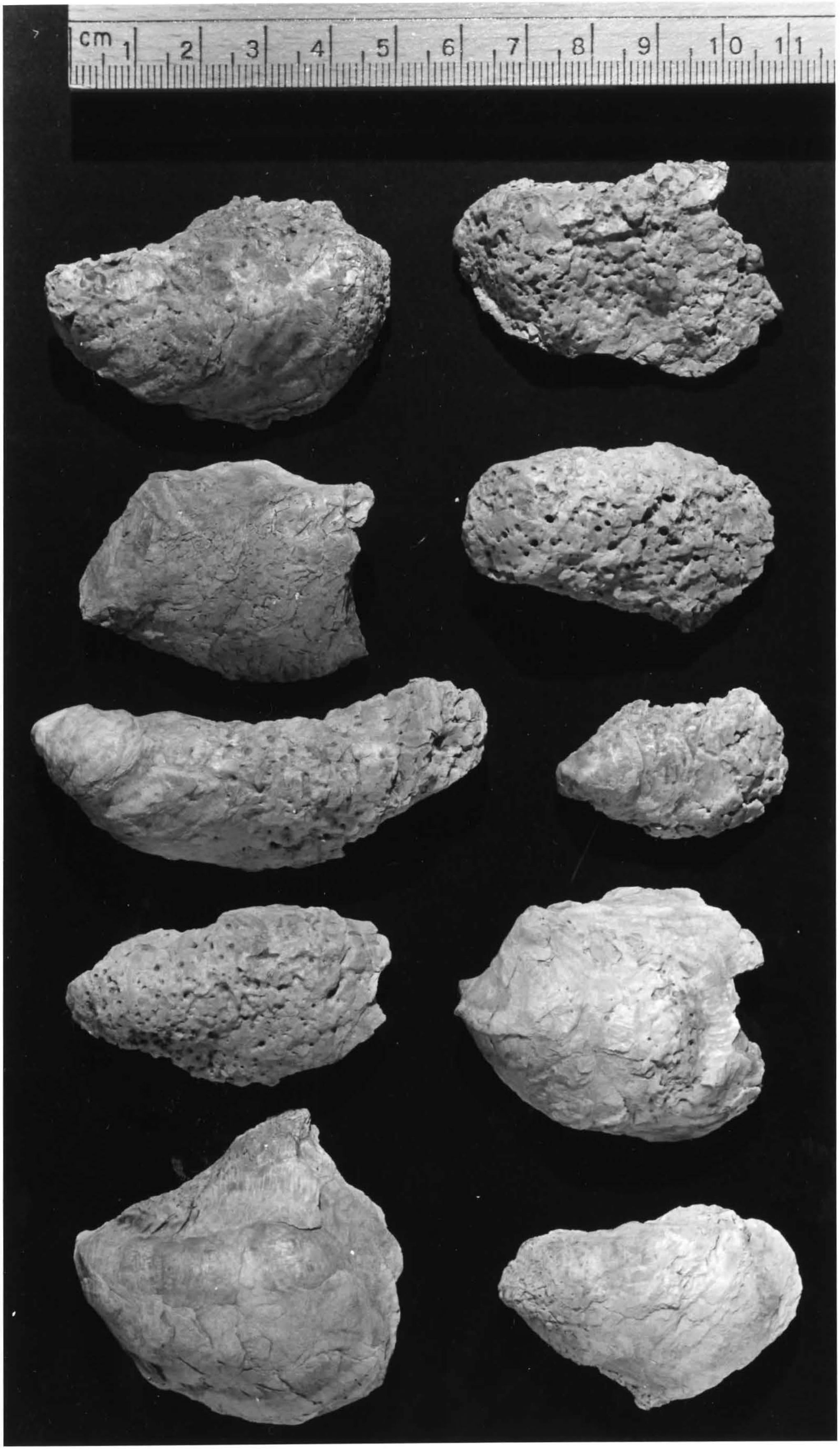
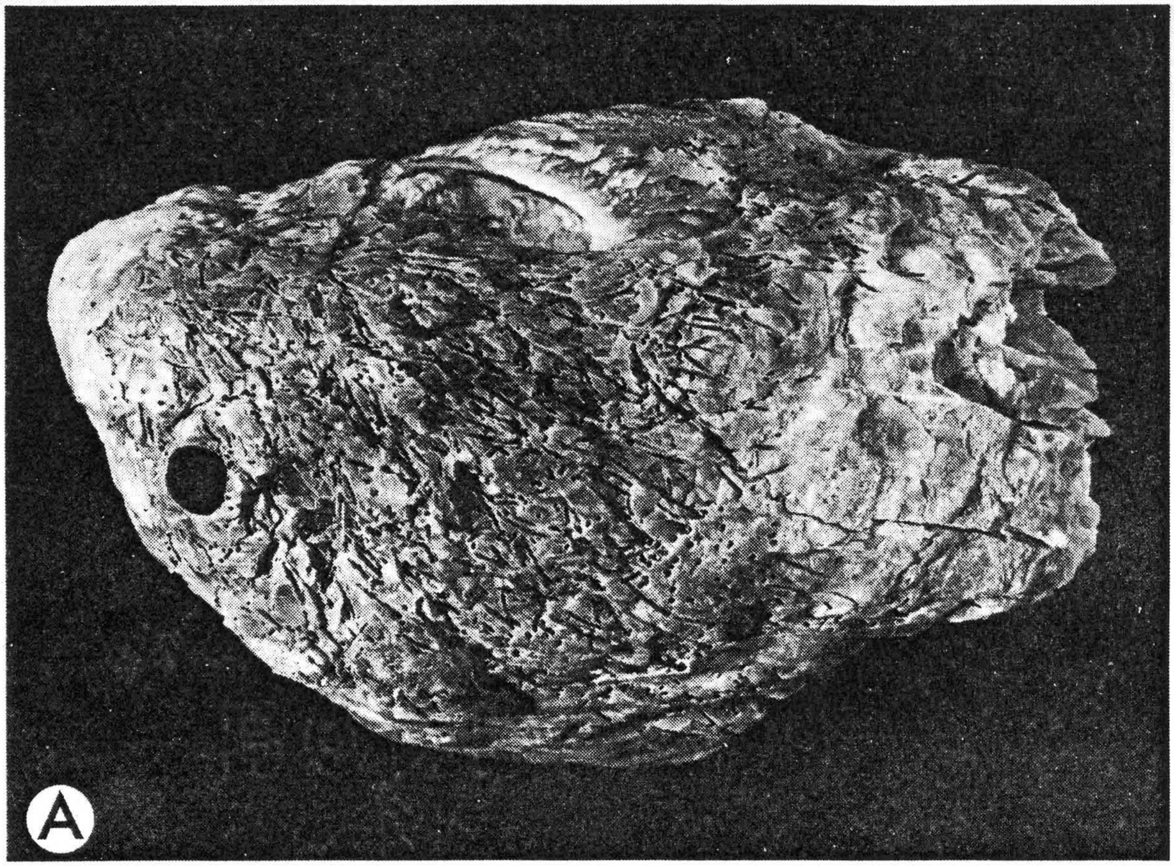

cm
1
2
3
4
5
6
7
8
9
10
11

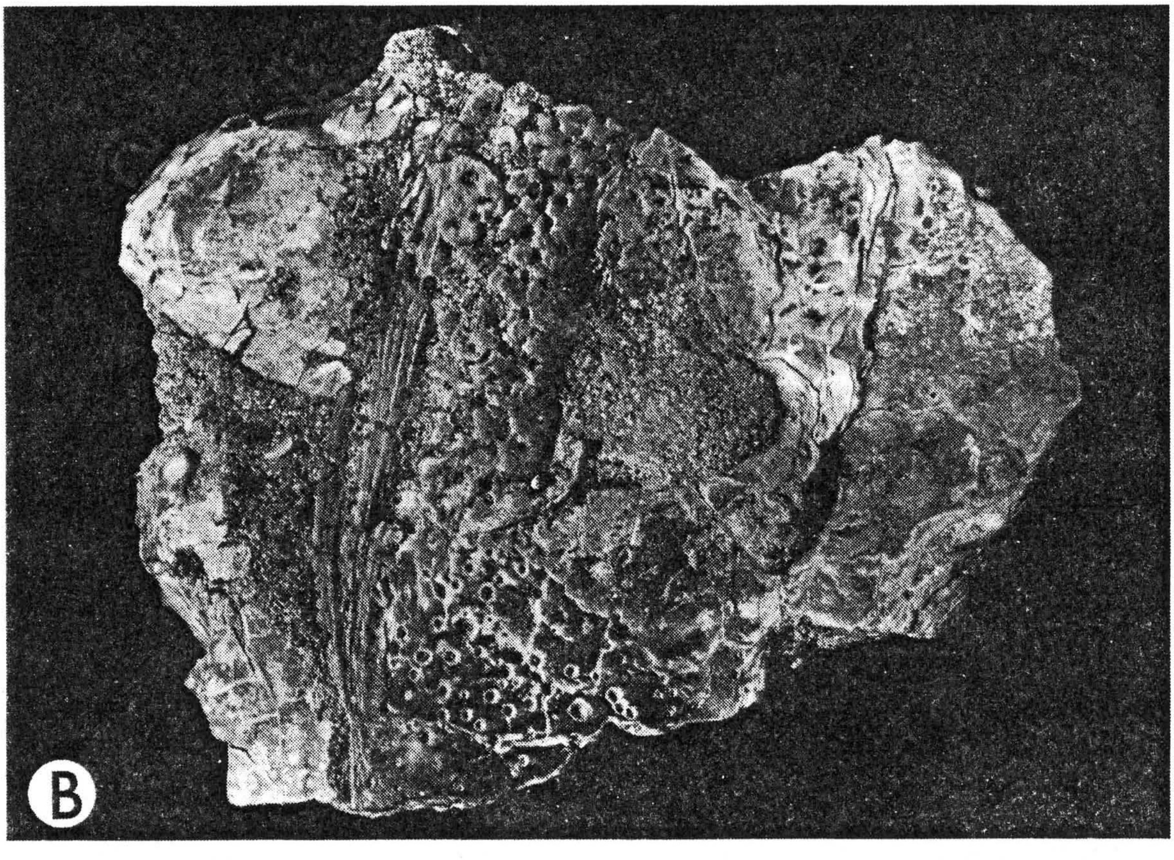
Plate II Sampling site WC-7

Fig. A: Section WC-7 showing thick accumulation of oyster sands. Resistant consolidated sands mark the top of the oyster bed.

Fig. B: $CaCO_3$-cemented oyster sands. Glauconite and organics are abundant.

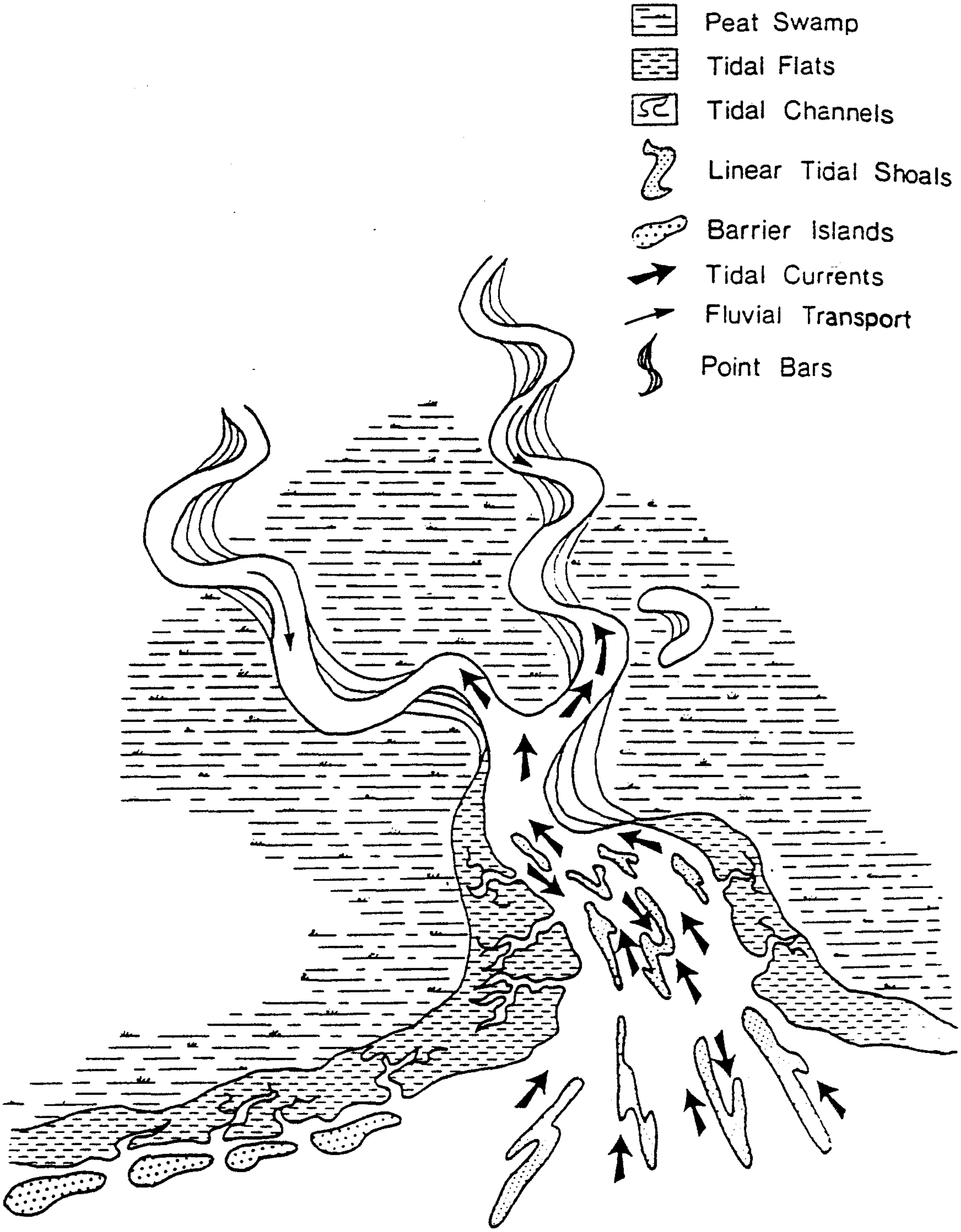
Plate III	Borings in Ostrea glabra from consolidated sands at WC-5
Fig. A:	Thick lower valve with dense Talpina borings. Talpina enter perpendicular to the substrate and then parallel the substrate surface. Large, incomplete Oichnus simplex at umbonal region of valve. Shell is 5.5 cm in length.
Fig. B:	Exposed Entobia chambers on inner surface of oyster shell. Glauconitic sands comprise boring infill material. Shell fragment is 5 cm long.


A


B

interpreted as deposits occurring within a sheltered, open bay seaward of the delta . Rahmani, however, proposes that the sequence better approximates a prograding delta complex in an embayment where tidal influences dominated over wave and river processes, and is therefore analogous to the modern Ord River Delta setting (Figure 4). With this interpretation, oyster deposits represent a transition from barrier island to back-barrier and open bay lagoonal environments. Oyster shell fragments at the base of Unit E4 represent migrating tidal channel lag deposits while 'lenses' of articulated and interspersed disarticulated shells are evidence of storm effects acting upon the barrier system. Both depositional interpretations represent complex and possibly actively changing shallow marine environments.

Figure 4. Depositional paleoenvironments of the Bearpaw-Horseshoe Canyon transition, Drumheller, Alberta (after Rahmani, 1983).


Peat Swamp
Tidal Flats
Tidal Channels
Linear Tidal Shoals
Barrier Islands
Tidal Currents
Fluvial Transport
Point Bars

CHAPTER 2

TECHNIQUES

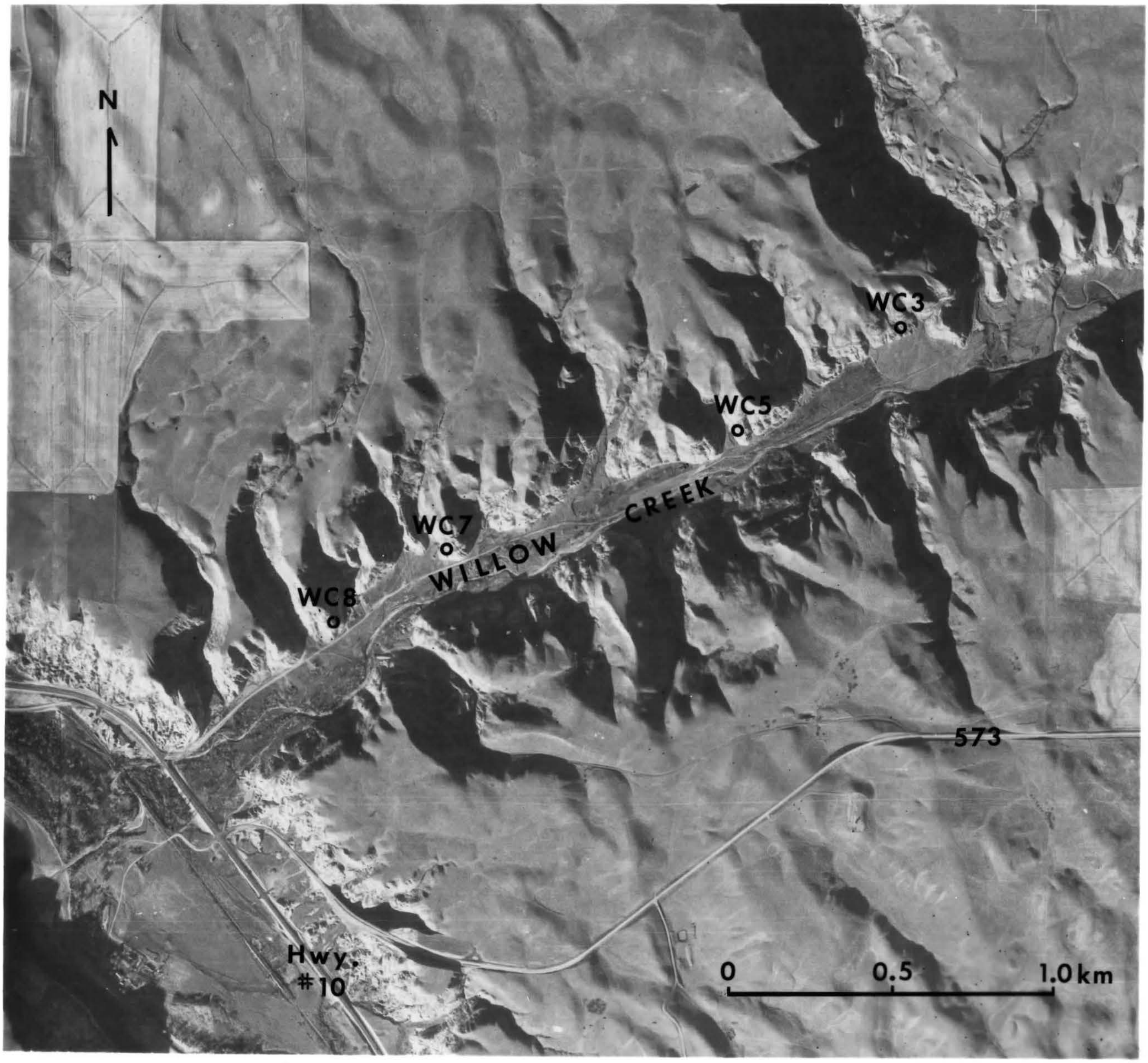
Sampling :

Four sampling locations were selected so as to best represent a possible 'marine' to potentially 'nonmarine' transition. These sites represent two positions near both the eastern and westernmost pinchouts of the oyster beds (WC-3 and WC-8 respectively) as well as two intermediate locations (WC-5 and WC-7) (Plate IV). Selected sampling locations closely approximate the stratigraphic section locations described by Rahmani (1983).

Approximately 100 bored *Ostrea* valves were collected from unconsolidated sediments at each of the locations. Details regarding collection location within the stratigraphic sequence were noted along with other pertinent sedimentologic and palaeontologic information. Approximately another 100 random samples were collected from the surface at each location for general observations regarding weathering effects, abrasion, boring morphotypes, etc.

After collection, samples were washed, etched for a few seconds in dilute HCl and then, where necessary, cleaned in an ultrasonic bath to remove fine sediments. Samples were then separated into left and right valves and on the basis of presence of macroborings on inner, outer or both surfaces of the shell. A number of individual valves and articulated shells were fragmented, but this apparently is due to weathering at the

Plate IV. Willow Creek section.
Air photo locations of sampling sites.


N
WC3
WC5
WC7
WC8
WILLOW
CREEK
573
Hwy.
#10
0
0.5
1.0 km

outcrop.

Observed macroborings include those of muricid gastropods (*Oichnus*), phoronid worms (*Talpina*) and sponges (*Entobia*). The ichnogenus *Entobia* represents those borings which are attributable to sponges of the family Clionidae (Bromley, 1970). Kemp (1983) suggested that three boring morphotypes of *Entobia* existed at the Willow Creek section. Morphotypes in this study were initially defined using the criteria of Kemp (1983). For shells with sponge borings that appeared to have occurred pre mortem, sizes of sponge papillae, chambers and rootstocks were obtained using a binocular dissecting microscope with an ocular micrometre.

X-radiography was used in an attempt to provide additional data on chamber dimensions where the chambers remained unexposed. However, shell thicknesses and extensive three-dimensional development of chambers made imaging very difficult and only limited information was produced (Plate V).

Position of the borings on the shell surface (i.e. near the umbo, margins, etc.), associations with other boring organisms and approximate boring densities were also noted. For these same *Entobia* bored shells, the shell thickness at the bore location was measured using a dial calipers. Several thicknesses were collected for a single shell if borings were widespread on that shell surface.

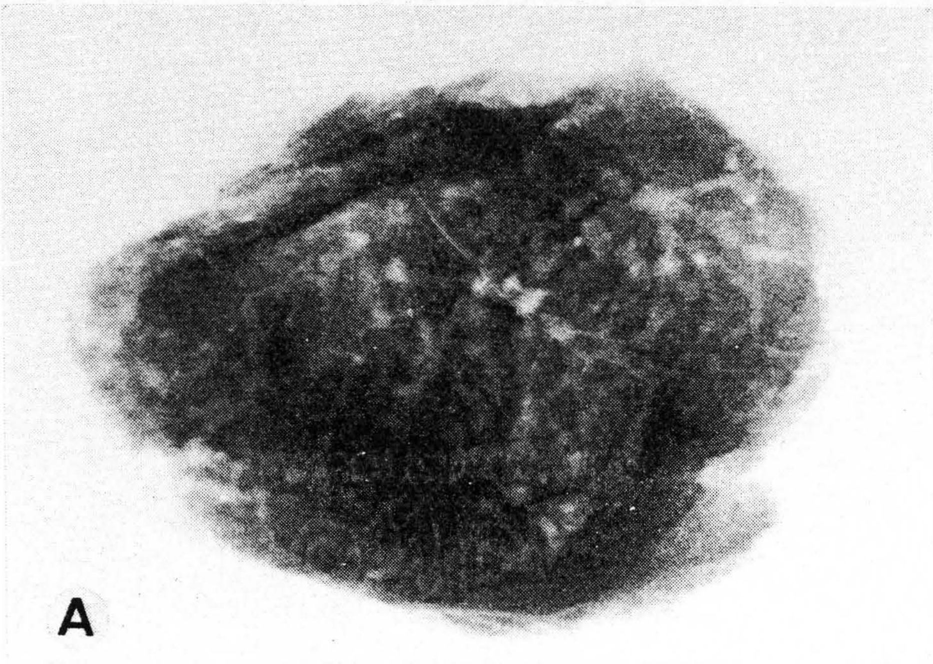
Data collected for gastropod borings consisted of the size and position of the borehole on the left or right valve,

Plate V X-radiographs of *Entobia* boring networks

Fig. A: Chambers of *Entobia cretacea* showing characteristic ‘string-of-beads’ pattern. Shell is 4.5 cm in length.

Fig. B: Intricate branching patterns of *Entobia cretacea*. Shell fragment is 3 cm in length.

Fig. C: Thick *Ostrea* valve giving poor resolution to *Entobia* chambers. Branching patterns are poorly developed here. Shell is 4 cm long.



A

B

C

initiation from the inner or outer surface and whether the boring was complete or incomplete. Talpina borings were widespread at the Willow Creek section although little variability occurred in size of borings or ranges in boring density between the four sampling locations. Relative abundance of Talpina borings was also noted.

The Search for Spicules :

The taxonomy of Recent clionids is based primarily upon spicule types and secondarily upon features like perforation size and the nature of the excavated galleries (Old, 1941). In fossil sponge borings, preservation of spicules is rare. This occurs because during fossilization opaline silica may dissolve and be replaced by calcium carbonate, or vice versa, and either may be replaced by iron compounds (de Laubenfels, 1955). Hence, palaeontologists often study the cavities as trace fossil evidence of ancient 'clionid' presence. Being a diehard optimist, the author underwent the task of at least attempting to look for some preserved spicules. Since the networks of boring chambers are well preserved in many Ostrea shells, it would seem reasonable to assume that part of the siliceous skeleton might become preserved inside.

Several Ostrea valves possessing intricate boring networks of the various Entobia morphotypes were selected for dissolution. These included shells which had not been initially cleaned, as well as other samples which contained abundant sediment infill in the boring networks. Samples were first left to dissolve in hot, dilute nitric acid for approximately twelve hours to remove the shelly substrate and any other organic materials. Residual materials plus liquid were then further diluted, excess liquids were separated and both residuum and liquid were scanned separately for the presence of siliceous materials using a binocular microscope. The residuum was mostly fine sediment.

Recent sponge spicules are composed of opaline silica and have a density of approximately 2.02 g/c.c. A sodium polytungstate solution was prepared and subsequent centrifugation of residual sediments in this solution caused separation of silica from remaining clastic sediments. Sodium polytungstate is a non-toxic chemical (spec. grav. >1.0 - 3.1) highly recommended as a safe way to carry out heavy mineral separations. Almost complete recovery of the sodium polytungstate solution can be obtained.

Removal of less dense materials using a pipette provided interesting results. Firstly, it was observed that fibrous materials 0.1 mm wide and up to 3.0 mm in length were commonly found. These occurred individually or as aggregated masses. These however, did not closely resemble modern siliceous spicules but rather appear to be silicified plant tissues preserved within sediments which fill borings. Secondly, a few extensively bored _Ostrea_ valves, upon dissolution, revealed natural casts of the _Entobia_ borings. These casts preserve the highly characteristic ornament of `scalloping' found in sponge borings. This occurs as a result of the method of boring by removal of silt sized chips.

Secondly, branching rootstocks (Groot, 1977) were commonly found and these were infrequently connected with chambers (Plate VI). Volz (1939 in Bromley, 1970) indicated that a characteristic of borings of different species of sponge was a variability in their advancing edges. This may be either a few long, thin branches straggling out in exploratory fashion from the older part of the boring, or as in other species, a rapid swelling of branches advancing as a 'closed front'. The most intricate rootstock branches were observed from dissolved shells characterized by one boring form (*Entobia* type 'a'), while longer branches with infrequent bifurcations were found associated with another boring form (*Entobia cretacea*). These boring types will be described later. These differences in rootstocks and advancing edges, although only supported by limited data, provides initial evidence for more than one species of sponge.

Plate VI SEM of natural casts of *Entobia* boring networks.

Fig. A: *Entobia* cast with part of a chamber (near bottom of photo) and branching rootlets.

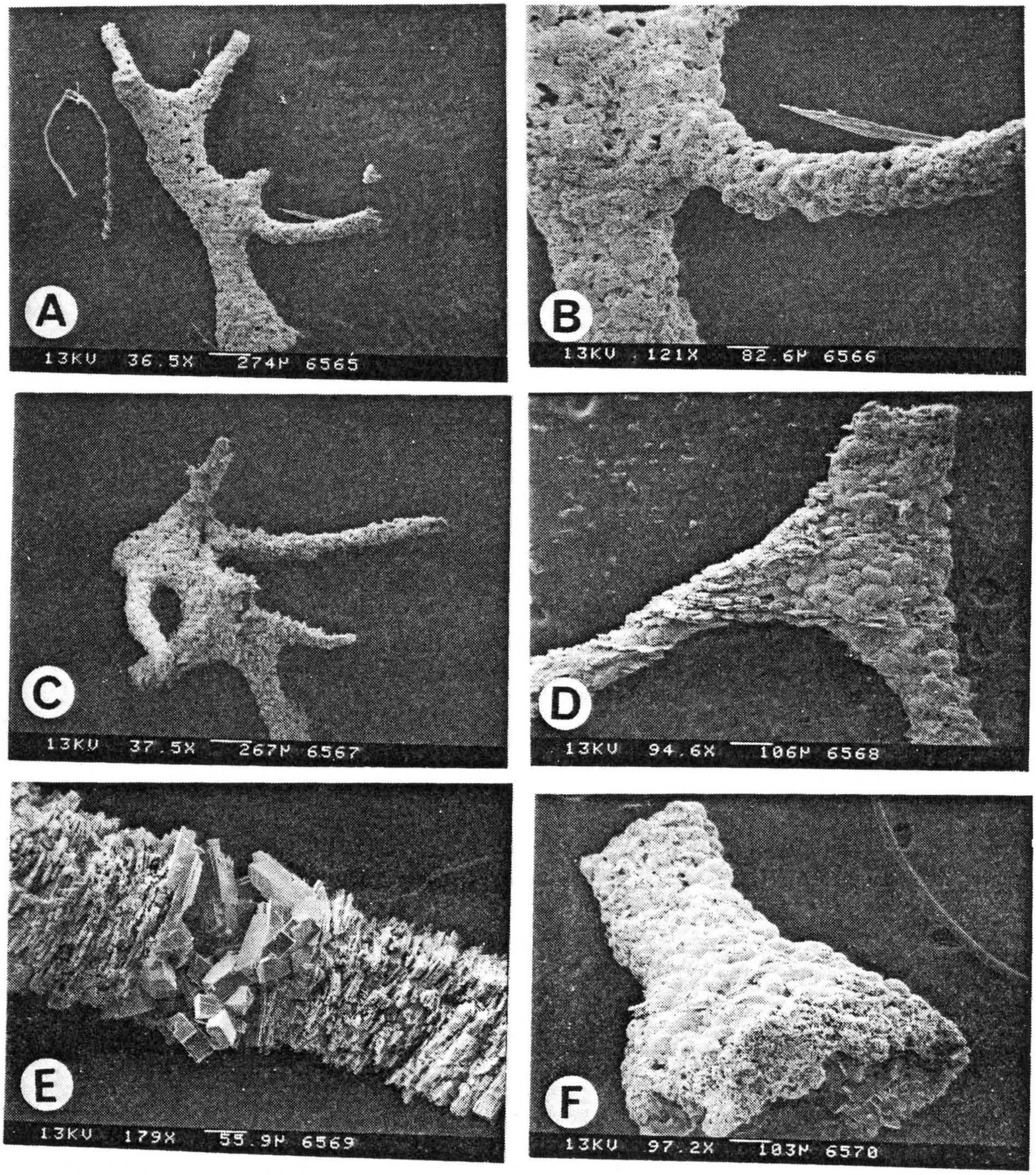
Fig. B: Close up of Fig. A showing scalloped texture characteristic of sponge borings. Each scallop represents removal of a silt sized chip.

Fig. C: Intricate branching rootlet network. Rootlets from separate exploratory branches rarely interconnect. Leaching has destroyed much of the scalloped texture.

Fig. D: Well preserved scalloping.

Fig. E: Leaching and mineral replacement in natural cast.

Fig. F: Rootlet and base of *Entobia* chamber.


A
13KV 36.5X 274µ 6565
B
13KV 121X 82.6µ 6566
C
13KV 37.5X 267µ 6567
D
13KV 94.6X 106µ 6568
E
13KV 179X 55.9µ 6569
F
13KV 97.2X 103µ 6570

CHAPTER 3

SPONGE BORINGS AS PALEOENVIRONMENTAL INDICATORS

Macroborings - importance as trace fossils :

Borings are trace fossils produced by an organism penetrating a hard substrate (Bromley, 1970). In many instances in the fossil record, body fossils of the borer are not preserved and therefore traces may be the sole evidence of the presence of the instigator and its relationship with a shelled host (McHuron, 1972). Palaeontologic interest in borings is twofold, they may give information on both the boring organism and the shell bearing animal (Boekschoten, 1966).

Post-mortem events which can seriously hamper the recognition and analysis of fossil communities include :

1) information losses through nonpreservation, and
2) losses through transport.

Paleoecologists must first be taphonomists, because studies of life environmental histories require a prior knowledge of post mortem events (Lawrence, 1968).

Paleoenvironmental studies :

Near Drumheller, Alberta, little work has been done on the paleoecology of oyster assemblages in the Horseshoe Canyon Formation. Contrastingly, studies initially carried out by Waage (1961) and followed up by Feldmann and Palubniak (1973) on a Maastrichtian oyster assemblage in the Fox Hills formation of

North Dakota dealt specifically with characteristics of the oyster biocoenose.

Information regarding the degree of disarticulation of *Crassostrea* shells inferred relative amounts of shell transport, which in turn was associated with marine energy conditions. Preburial abrasion of shells was distinguished from shell breakage due to weathering by the presence of limonite staining on broken edges. Limonite stains apparently occurred shortly after burial. Therefore, broken edges with limonite stains represent preburial abrasion. Large shell samples were also analyzed in terms of the relative proportions of left vs. right valves. This data, along with orientations of elongate shells allowed for possible inferences related to hydraulic sorting (Feldmann and Palubniak, 1973).

This study deals with borings of endolithic organisms. The traces produced by these excavators possess two attributes that render them potentially useful in paleoenvironmental analysis :

1) The borings are diagenetically relatively indestructable and are commonly better preserved in the fossil record than are skeletons of the organisms that produced them

2) They are genuinely in situ relative to their substrate, and it is generally obvious from abrasion and boring infill material if such a substrate has been reworked subsequent to boring (Bromley, 1978).

Implications of trace fossil importance to this study :

Several inferences can be made about the Willow Creek oyster bed (especially within unconsolidated sands) by considering the assemblage of organisms present, their tolerance to sedimentation, method and purpose of boring organisms as well as other ecological implications.

Oyster beds serve as habitat for fauna which utilize the hard substrate of the oyster shells. Boring organisms in particular may penetrate such substrates for three possible reasons :

1) protection against predators.

2) to support organisms in their proper orientation to perform life functions.

3) to obtain nutrients from the substrate itself, or to feed on the organism which is protected by the substrate.

Three factors appear to have a direct influence upon the distribution of many marine organisms - temperature, substrate and salinity (Wells, 1961). In this study, it is assumed that the temperature effect upon boring organisms is essentially constant, and that the only variability which may occur would be to species exposed to prolonged periods of shallow water. Substrate type is also constant, being represented by the oyster shell itself. The third factor, salinity, becomes important in estuarine areas where fresh waters flow into and mix with seawater. Where oyster beds range far up an estuary, they provide an opportunity to observe the distributional limits of species within this single substrate type where salinity is the chief affecting variable.

Boring sponges are unable to withstand extended periods of reduced salinities. Laubenfels (1947) thought that clionid boring may be an adaptation for surviving periods of low salinity, but offered no supporting evidence.

Modern studies have been directed towards environmental fluctuations and faunal distributions. Hopkins (1956) defined six zones within estuarine waters of Louisiana, each of which represents a presence, absence or relative abundance of various sponge species. In his study, Hopkins was able to show that identification of various species of _Cliona_ was important because they differed in their salinity tolerances. _Cliona celata_ and _Cliona truitti_, especially, were excellent indicators of the salinity regime at this location (Hopkins, 1956). The former species appears characteristic of lowered salinities, while the latter is indicative of higher or near normal salinity. Sponge distribution apparently corresponds with the ability of the sponge species to endure periods of lowered salinity (Hopkins, 1956).

Old (1941) proposed a relation between salinity and sponge papillae sizes. Distributions of identified species along the Atlantic Coast of North America suggest that papillae sizes were found to be larger for distinctly marine species of boring sponges as compared to species inhabiting reduced salinity waters which were observed to have smaller papillae. This conclusion appears also to have been supported by Hopkins' study (1956) in which small papillae of the sponge _Cliona truitti_ are predominant in zones 1 and 2, both of which are characterized by reduced salinities. Hopkins' zone 5, in contrast, represents the more marine area and is dominated by the sponge *Cliona celata* which possesses comparatively larger papillae sizes. Intermediate zones are inhabited by both sponge species, yet are characterized by the dominant species.

In contrast, variations in sponge distribution patterns can also occur. Distribution of *Cliona* species in Newport River and in many South Carolina estuaries (Hopkins, 1956) differs from the pattern found in Louisiana (Wells, 1961). It appears that the relative stability of the salinity regime is important in determining the pattern of distribution found in estuarine areas (Wells, 1959).

Hartman (1958) reviewed available literature, and along with his own experimental work, showed that *Cliona celata* and *Cliona vastifica* are capable of functioning in environments of reduced salinity for short periods of time. *Cliona vastifica* however, can function in lower salinities than can *Cliona celata*.

There has been limited study to date on ancient fossil assemblages which have specifically dealt with sponge borings. This is in part due to taxonomic difficulties which occur as a result of the lack of preservation of the siliceous spicules. Lawrence (1967) suggested various criteria which may be used to infer important relationships of 'clionid' assemblages to their paleoenvironment. Specifically, Lawrence proposed that " two perforation and gallery form groups can be recognized in both

Recent and ancient settings ". Identification of these boring types and mapping of distribution patterns may in some cases provide valuable information to paleoenvironmental studies. Both clionid gallery forms were recognized by Lawrence in a late Oligocene channel deposit at Belgrade, North Carolina. There, the two form groups appear not to have been randomly distributed through the channel deposit. As well, Lawrence's observations show that the distribution patterns of these two boring types could possibly have occurred as a result of environmental influences. A regression could have brought lowered salinities and increased environmental fluctuations into the channel area, thereby affecting the distribution of the clionid species.

CHAPTER 4

PALEOECOLOGIC INFORMATION

Evidence from Ostrea glabra :

The oyster assemblage at Willow Creek appears to have been deposited in a shallow, back barrier lagoon or sheltered bay. The degree of disarticulation of valves is a reliable indicator of relative amount of transport (Boucot et. al, 1958 in Feldmann and Palubniak, 1973). Oyster shells in unconsolidated sands have not been transported a great distance and generally appear to be in situ.

Articulated lenses of Ostrea are common. The effect of transport of shells over a coarse bottom, particularly sand or other shells, has caused some disarticulation and abrasion (Feldmann and Palubniak, 1973). It is evident that few borings were initiated on broken surfaces. Therefore, borings on other parts of the shell occurred pre-mortem and before any transport. Storm deposits of disarticulated valves can be observed in sections at Willow Creek.

At WC3, WC5 and WC7 most of the Ostrea shells are quite `flat', indicating lateral growth increasing the surface area of the shell in contact with the substate and not increasing the depth of the lower valve. These oysters would have existed in areas of low sedimentation where their feeding margins were not in jeopardy of being smothered (Feldmann and Palubniak, 1973).

At WC-8, some `flat' valves are present, but most shells appear to be more upward curved. These shells may indicate an area of more rapid sedimentation where the oysters were required to keep their feeding margin above the substate (Feldmann and Palubniak, 1973). These curved shells also have a wide attachment area which indicates attachment to other oyster shells. Clustering of oysters and competition for food could also cause an increase in depth of the lower valve, however, it is more common for this to occur as a response to sedimentation.

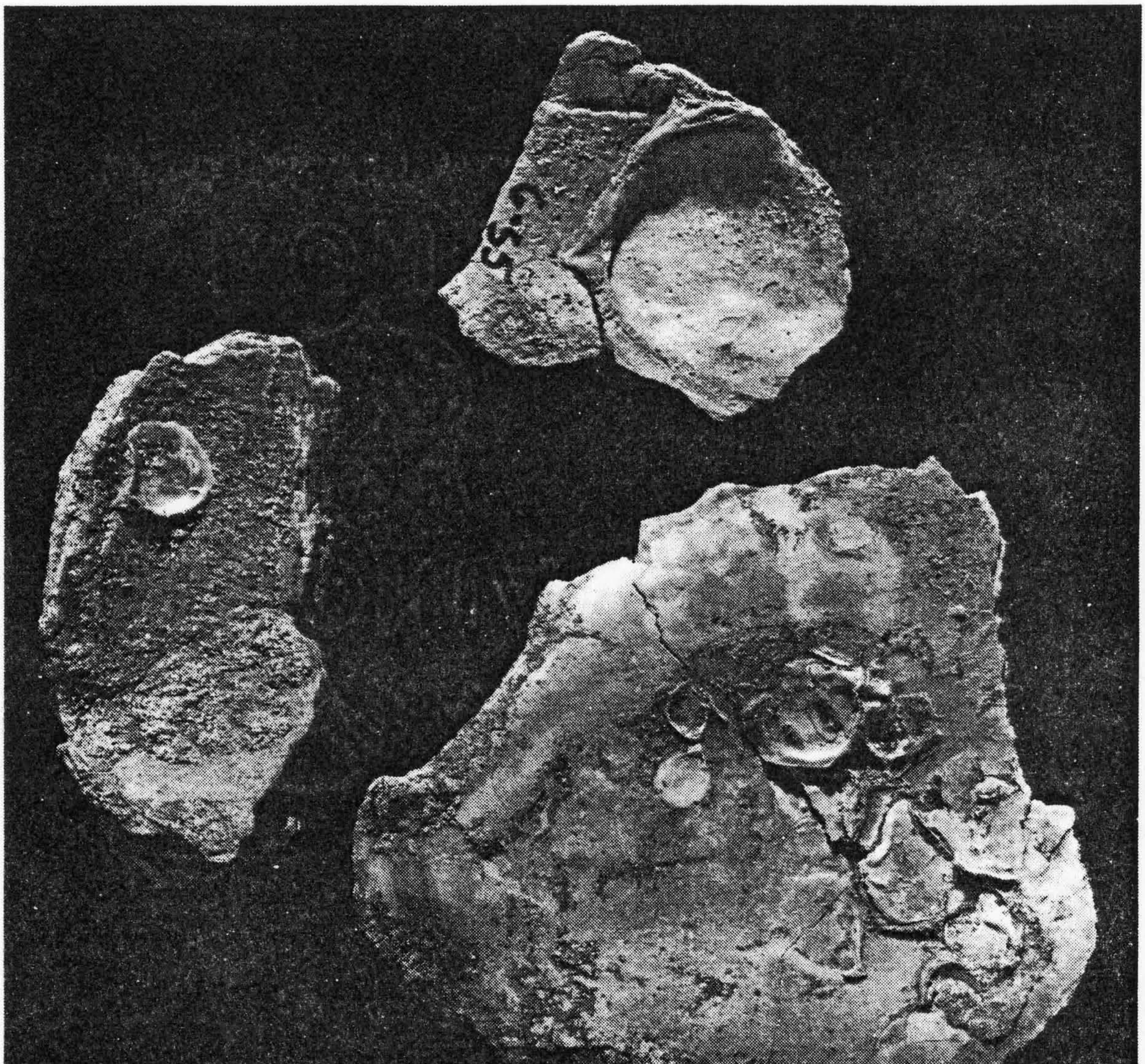
Oysters have pelagic larvae which, upon finding a suitable substrate, cement their left valve to the bottom (Yonge, 1960). Of the collected samples at Willow Creek, <5% of Ostrea valves have spat attached to them. Attachment usually occurs on the outer surfaces of oyster valves. At WC-8, few oyster spat were observed attached to other valves (Plate 7), suggesting that oyster larvae attached themselves directly to a clean sand bottom rather than to the oysters themselves. Fewer oyster spat were observed at WC-8, as compared to the other sampling locations. WC-8 may be further from the reproducing oyster bank, or conditions there were unfavourable for oyster reproduction.

Evidence from Oichnus :

Evidence of predation by gastropods is common in Ostrea valves at Willow Creek. On the basis of borehole roundness, taper and size, Kemp (1983) suggests that two borehole forms indicate the presence of both naticid (Oichnus paraboloides) and muricid (Oichnus simplex) predators. I did not observe any

Plate VII Juvenile oysters on _Ostrea glabra_

Large right valve has evidence of encrusting bryozoa and 17 juvenile oysters attaching to the inner surface. Bryozoa postdate juvenile oyster attachment.


G35

borings attributable to naticid gastropods.

96 Oichnus borings were found in Ostrea valves. 39% of these were found in left valves while 61% were located in right vales. Of both right and left valves, >90% of the borings were initiated from the outer surface of the shell. This provides strong evidence for borings occurring pre-mortem. In terms of predation rates, approximately 7% of all borings were complete, 9% showed complete penetration of the right valves while only 5% of borings successfully penetrated the much thicker left valves.

Relative abundances of Oichnus at the four section locations could not be determined due to field sampling procedures. Casual observation and comparison with abundances of other boring types suggest however that Oichnus are more common at the easternmost sections. Oichnus borings are rare at WC-8, while Entobia is abundant. At WC-7, Oichnus becomes the dominant boring species with Entobia being commonly found. This sharp transition of boring abundance may prove significant, since it has been shown that some genera of muricids (for example, Murex), can tolerate lower salinity waters than can naticids (Caspers, 1957 in Kemp, 1983). Muricids are epifaunal gastropods and the increasing abundance, from WC-8 to WC-7, may represent a sudden transition to a harder substrate. This seems probable in lieu of evidence from Ostrea valve curvatures which also suggest the presence of a harder substrate in eastern locations.

Oichnus simplex borings were very rarely found associated with Entobia boring networks. Where they did occur together, the

Oichnus borings were very small and likely represented borings produced by juvenile gastropods. *Oichnus simplex* borings are generally not observed in close proximity to sponge borings. Never were *Oichnus* and *Entobia* boreholes superimposed on a shell surface.

Kemp (1983) does not discuss this trace association and shows only one example of incomplete *Oichnus paraboloides* borings occurring with nearby *Entobia cretacea* on an abraded shell fragment. This is the only negative association which exists between trace producers at Willow Creek. *Talpina* and encrusting bryozoa are both found with *Oichnus* and *Entobia*.

The absence of gastropod borings with sponges suggests that the sponge was 'toxic' to the boring gastropod. Perhaps either a toxic chemical in the sponge tissue, or the presence of sharp, non-digestible spicules deterred gastropods from feeding on sponge infested oysters. Either of these possibilities seems reasonable, since an extensive sponge boring network would reduce the shells thickness and stability, therefore providing easier access to internal oyster body parts by predaceous gastropods. If spicules alone deterred gastropod predation, it would be expected that gastropods would initiate boring, reach the sponge colony and then cease boring, thereby leaving an incomplete borehole. Incomplete gastropod boreholes are not found superimposed on sponge borings. Therefore, sponges probably had developed a chemical toxicity by the Upper Cretaceous.

Evidence from Talpina and bryozoa :

Borings produced by phoronid worms (Kemp, 1983) may occur on Ostrea valves along with Entobia, Oichnus and encrusting bryozoa. Kemp (1983) observed that Talpina were ubiquitous in the Willow Creek section, particularly at Rahmani's EC-10 site located approximately one kilometre south of WC-8 at the southern pinch out of the oyster beds. In this study, Talpina represent approximately 50% of all borings in Ostrea valves at WC-8, while representing approximately 25% of bored shells at WC-7, WC-5 and WC-3. This decrease in abundance towards WC-3 may be due to the change from a shaly to a sandy substrate.

Phoronids generally dwell in the upper littoral zone and may live in brackish water (Hyman, 1959). As filter feeding organisms, like sponges, they cannot tolerate high rates of sedimentation. Many of the Talpina borings are concentrated at shell margins, indicating that boring took place along surfaces of Ostrea valves that were not covered by sediment.

Encrusting bryozoa are infrequent at all Willow Creek sections and are found along with Entobia, Talpina and Oichnus. Oyster spat were commonly observed on shell surfaces with bryozoa. Both juvenile oysters and bryozoa require non-turbid, sediment-free environments for survival. The comparatively rarer occurrence of bryozoa, with respect to other fauna, at Willow Creek may suggest that either;

1) water conditions were generally too turbid for the bryozoa to become prolific, or

2) bryozoa were not well preserved.

Characteristics of macroborings and related organisms suggest that variations occur between sections. These may possibly occur as a response to either salinity fluctuations or a change in substrate. This substrate change corresponds closely with the facies transition which occurs near the WC-7 section (Figure 5).

Evidence from boring sponges :

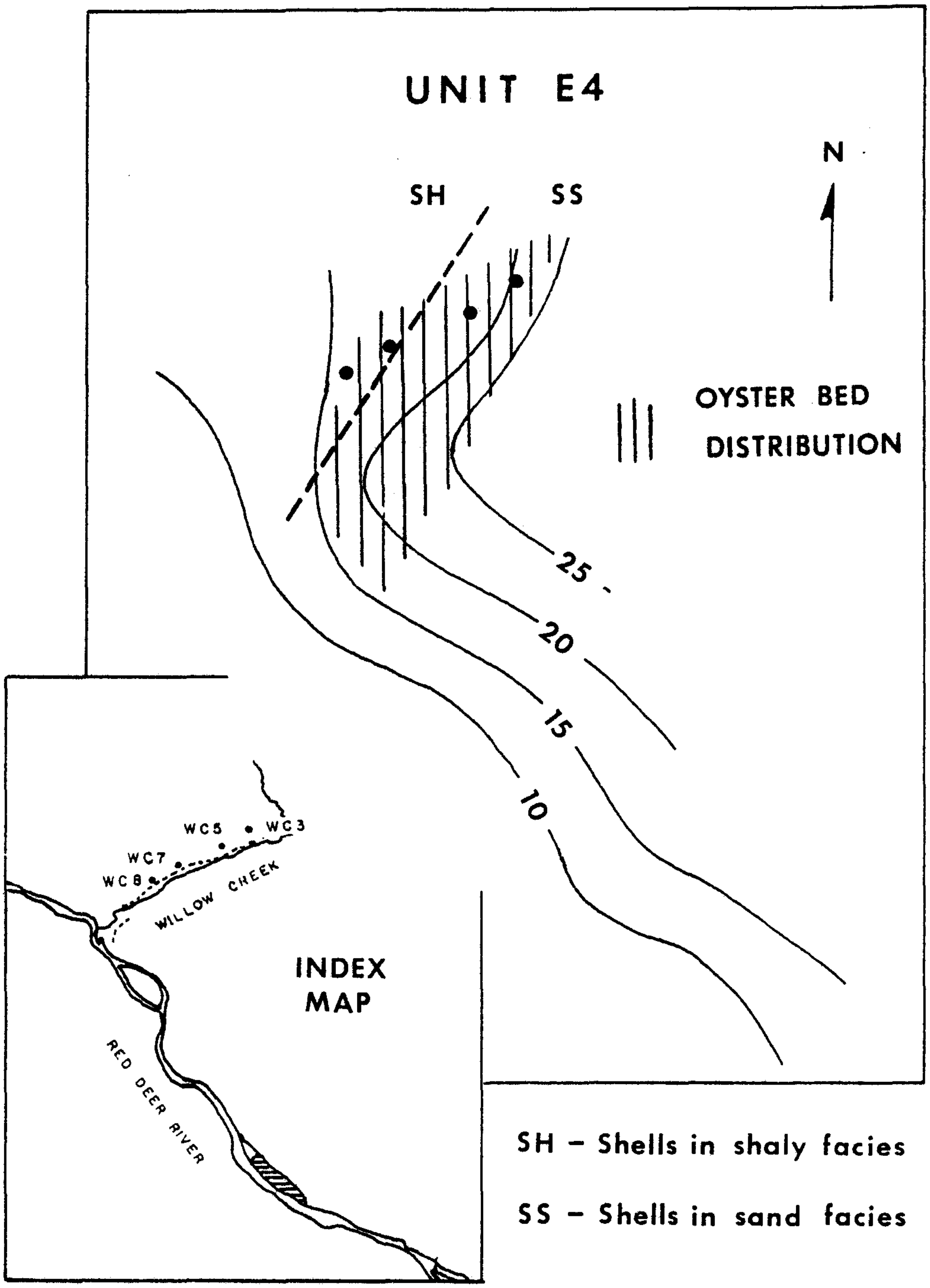
Many Mesozoic sponge borings show a considerable resemblance to Recent ones and would appear to be the work of the Clionidae. Entobia Bronn is the only ichnogeneric name which can be used to refer to such boring types (Bromley, 1970). A diagnosis for borings of the ichnogenus Entobia is:

'shallow excavations in calcium carbonate consisting of closely spaced, interconnected, spherical, ellipsoidal or cylindrical chambers. Diameters commonly 0.2 to 20mm, sometimes fused into crysts up to 40mm. Minute perforations connecting to subsurface chambers may be the sole surface manifestation, although chambers may be exposed' (Figure 6) (Kemp, 1983).

Kemp (1983) subdivided sponge chamber excavations, in Willow Creek oysters, into two types. These were based primarily upon long axis orientations of chambers with respect to the shell surface. Type 'a' chambers are somewhat ellipsoidal in shape with long axes of chambers oriented generally parallel to the shell surface. Type 'd' chambers have a more cylindrical form with long axes perpendicular to and extending a considerable

Figure 5. Isopach map of Unit E4 (modified from Shepheard and Hills, 1970). Unit E4 defined by Shepheard and Hills is thinner than that described by Rahmani. Thicknesses are in feet.

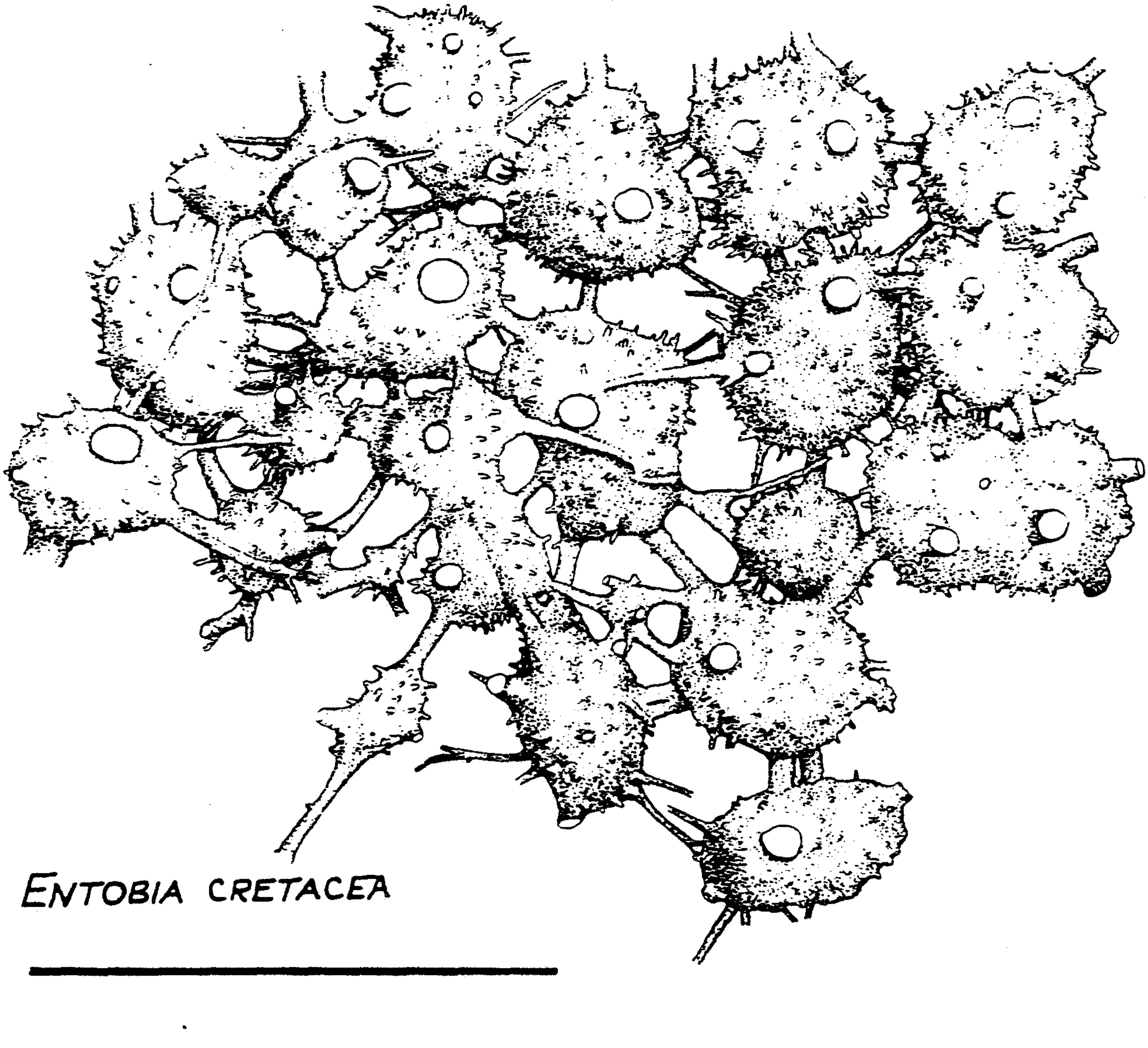
Dashed line represents transition of unconsolidated sediments from a sand to a shale facies.



SH – Shells in shaly facies

SS – Shells in sand facies

Figure 6. The type ichnospecies of Entobia seen in a natural cast of the boring in flint. The substrate, dissolved to expose the boring was an inoceramid bivalve shell, Cretaceous chalk, England. Scale bar 1 cm. (after Ekdale et al., 1984).



ENTOBIA CRETACEA

depth into the shell (Plate VIII). As a recommendation for taxonomic use, and for the sake of simplicity in this study, 'a' chambers will be referred to as type 1 chambers and 'd' chambers type 2.

Of three possible morphotypes present, some of the borings attributable to sponges closely resemble Entobia cretacea (Portlock, 1842 in Bromley, 1970, p.78). The boring pattern is frequently branching and resembles a well developed camerate or 'string-of-beads' form (Figure 7). In this form type 1 chambers dominate and the boring morphology closely resembles Cliona vastifica - like forms of Lawrence (1969).

Borings in which branching patterns are not well developed and in which type 2 chambers dominate were classified as ichnospecies Entobia sp. 'a'. In this form, chambers appear generally independent of other chambers. Finally, an intermediate form with characteristics of both Entobia cretacea and Entobia sp. 'a' was described as Entobia sp. cretacea 'a' (Kemp, 1983).

By comparing papillae sizes and chamber forms, some taxonomic modifications can be proposed. Bromley states that in a given matrix and environment, the size at least of the surface pores of a given species is fairly constant (Bromley, 1970). Statistical analysis of papillae sizes of the three boring morphotypes shows that the mean papillae size of Entobia sp. cretacea 'a' is significantly different from Entobia cretacea, but is not different from Entobia sp.'a'. Entobia sp.'a' in turn is also significantly different from Entobia cretacea. Thus, both the

Plate VIII *Entobia cretacea* and *Entobia* type 'a' chambers

Fig. A: *Entobia* type 2 chambers

Fig. B: Type 2 chamber with long axis oriented perpendicular to the shell surface. Scalloped texture has not been preserved.

Fig. C: Shallow type 1 chamber of *Entobia cretacea* with scalloped surface.

Fig. D: Interconnected type 1 chambers with rootlets extending into the shell substrate.

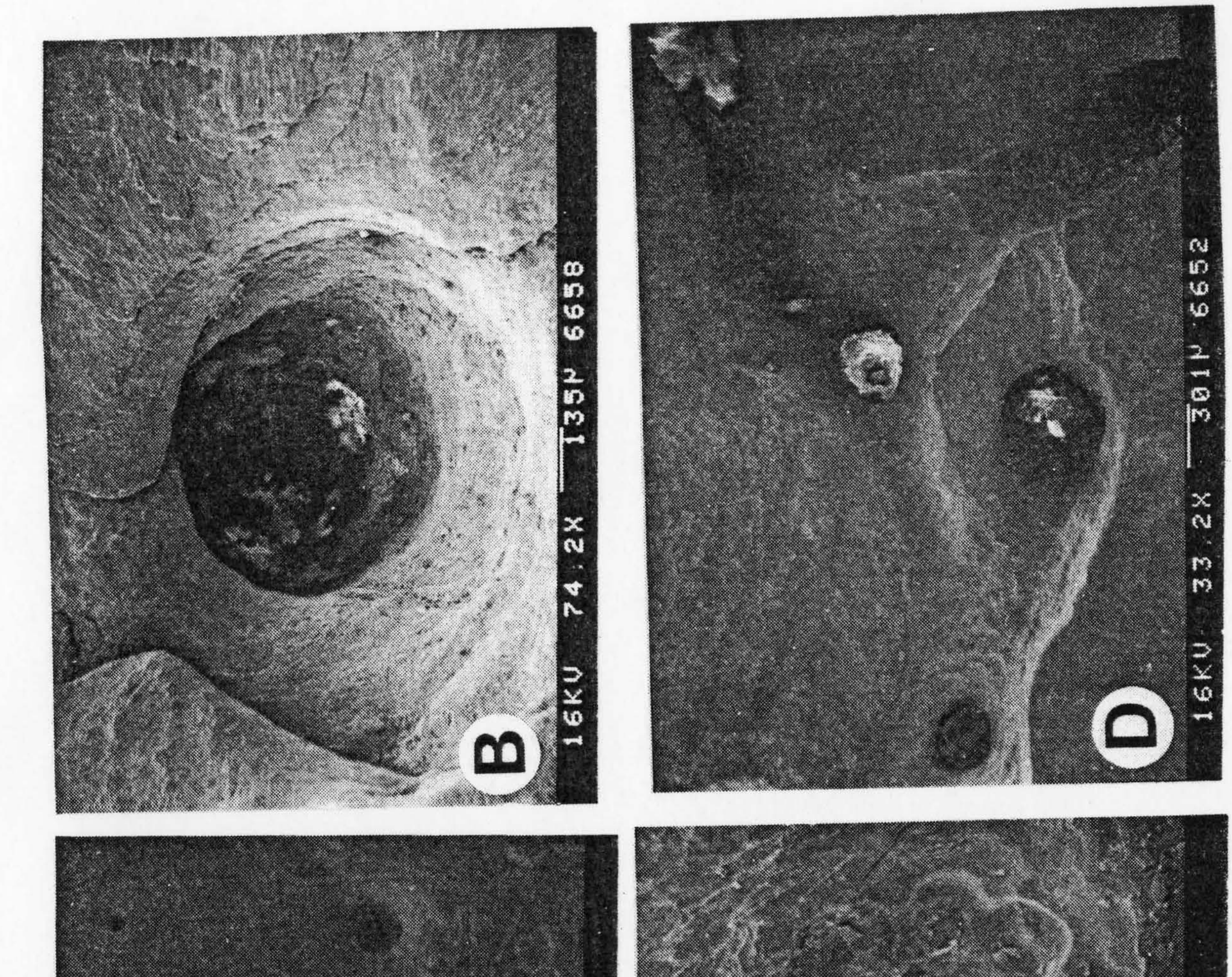
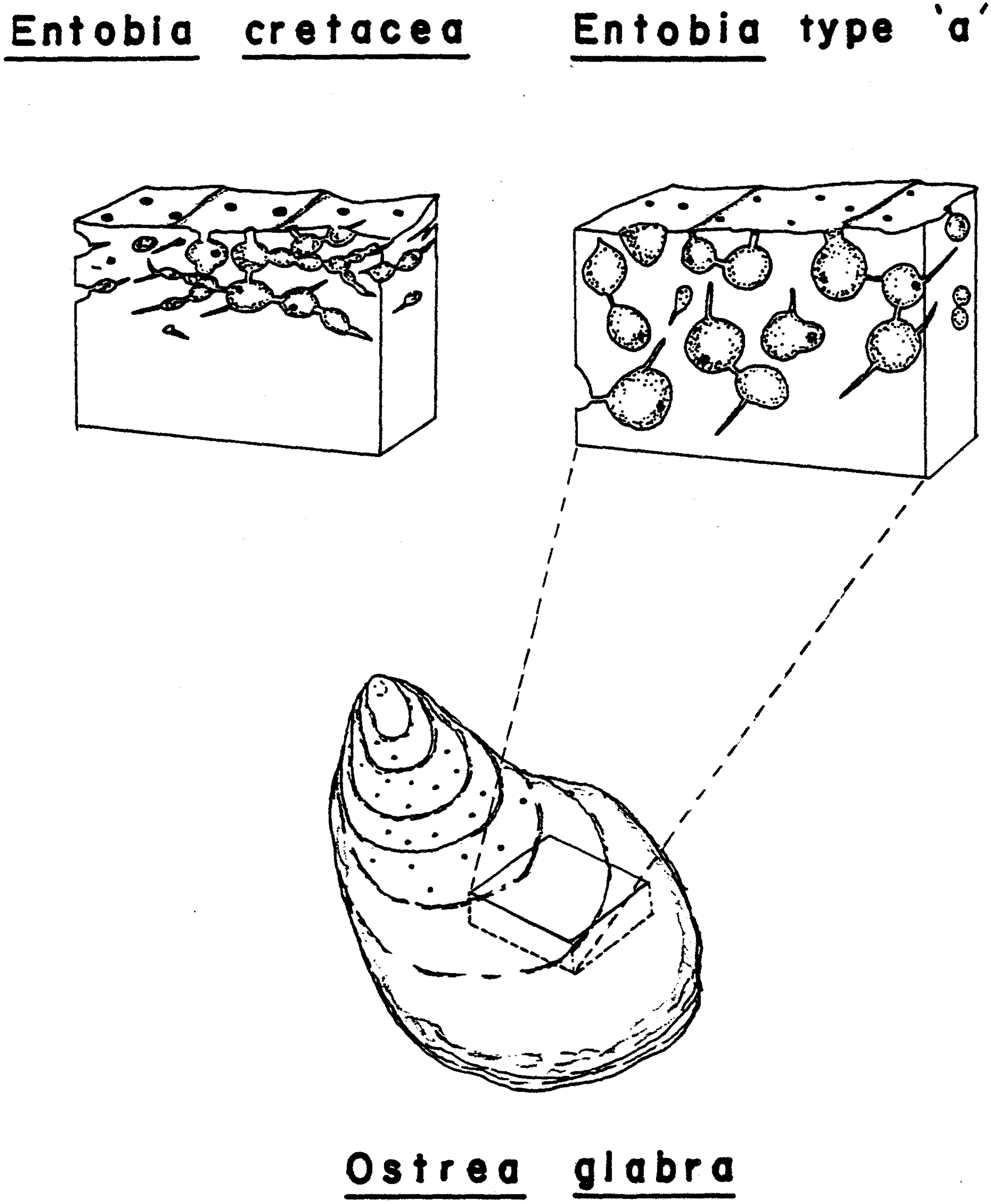

A
16KU 29.1X 344µ 6661
B
16KU 74.2X 135µ 6658
C
13KU 219X 45.7µ 6573
D
16KU 33.2X 301µ 6652

Figure 7. *Entobia* boring types in Upper Cretaceous *Ostrea glabra* shells, Drumheller, Alberta.


Entobia cretacea
Entobia type 'a'
Ostrea glabra

intermediate form, *Entobia* sp.*cretacea* `a', and *Entobia* sp.`a' have been combined in this study and have been termed *Entobia* type `a'. This is more reasonable in terms of borings produced by different sponge species.

Entobia distributions at Willow Creek :

Entobia borings are most commonly observed on the exterior surfaces of *Ostrea* valves. *Entobia cretacea* are found in both thick and thin shells, and chambers are commonly exposed. This is because chambers of *Entobia cretacea* occur parallel to the shell surface causing shell strength to be reduced. Shell abrasion causes chambers to become exposed. *Entobia* type `a' are commonly found on the thick umbonal region of left valves (Kemp, 1983), and as with *Entobia cretacea*, are commonly found along shell margins.

The position of *Entobia* on the shell is a response to larval settlement and the area of shell which is not covered by substrate. Nestler (1960 in Boeckschoten, 1966) described crowding of juvenile *Cliona* colonies on the most convex part of the left valve of the Upper Cretaceous oyster, *Pycnodonte*. There, larvae would be least hindered by bottom currents. Boeckschoten however, suggests that water currents produced by the oyster (necessary for respiration and food intake) attract larval sponges.

Hartman (1958) analyzed settling behaviour in sponges and suggested that *Cliona celata* settled preferentially on living thick shelled molluscs. Again, this may be associated with the water currents created by living molluscs (Lawrence, 1969). The occurrence of borings along shell margins, a lack of borings initiated on broken edges and on inner surfaces supports the assumption that borings occurred prior to death and transport of the oyster.

Abundances of *Entobia* borings change markedly between sampling sites. The WC-8 site is characterized by a dominance of *Entobia* type 'a' (90% of bored sponge samples) while *Entobia cretacea* represents the remaining 10%. In contrast, the other sampling sites are markedly different from the WC-8 location, but are similar to each other. At WC-7, WC-5 and WC-3, *Entobia cretacea* comprises 75% of borings. *Entobia* type 'a' are infrequently found.

Size data and analysis :

A: Papillae

Colonial sponges live within the intricate network of galleries bored into carbonate materials. The sponge maintains water currents, from which it filters its food, through perforations in the substratum surface, the papillae. Old (1941), Hopkins (1956), Hartman (1957) and Lawrence (1969) have discussed the possible importance of papillae to paleoenvironmental studies.

Although in many species, the exhalent papillae are noticeably larger than the inhalent papillae (Bromley, 1970), it was impossible in this study to distinguish the two. Measurements of papillae were obtained from premortem- bored, *in situ* shells at each of the sampling locations (Table 1). Enlargement of surface perforations and chambers (Boeckschoten, 1966) did not appear to be significant at Drumheller.

A plot of mean papilla size, of *Entobia cretacea* and *Entobia* type 'a', shows an increase in papillae size from WC-8 to WC-3 (Figure 8). 95% confidence intervals have been included. The data suggest that a response to salinity gradients may occur in *Entobia* species at Willow Creek.

With regard to previous studies of clionid distributions an increase of papilla sizes could infer an increase in salinity (or decreased frequence of lowered salinities; Hopkins, 1956) from WC-8 to WC-3. The shell collection sites are separated by less than 3 km, which is a small fraction of the lateral extent of some estuaries.

B: Chambers

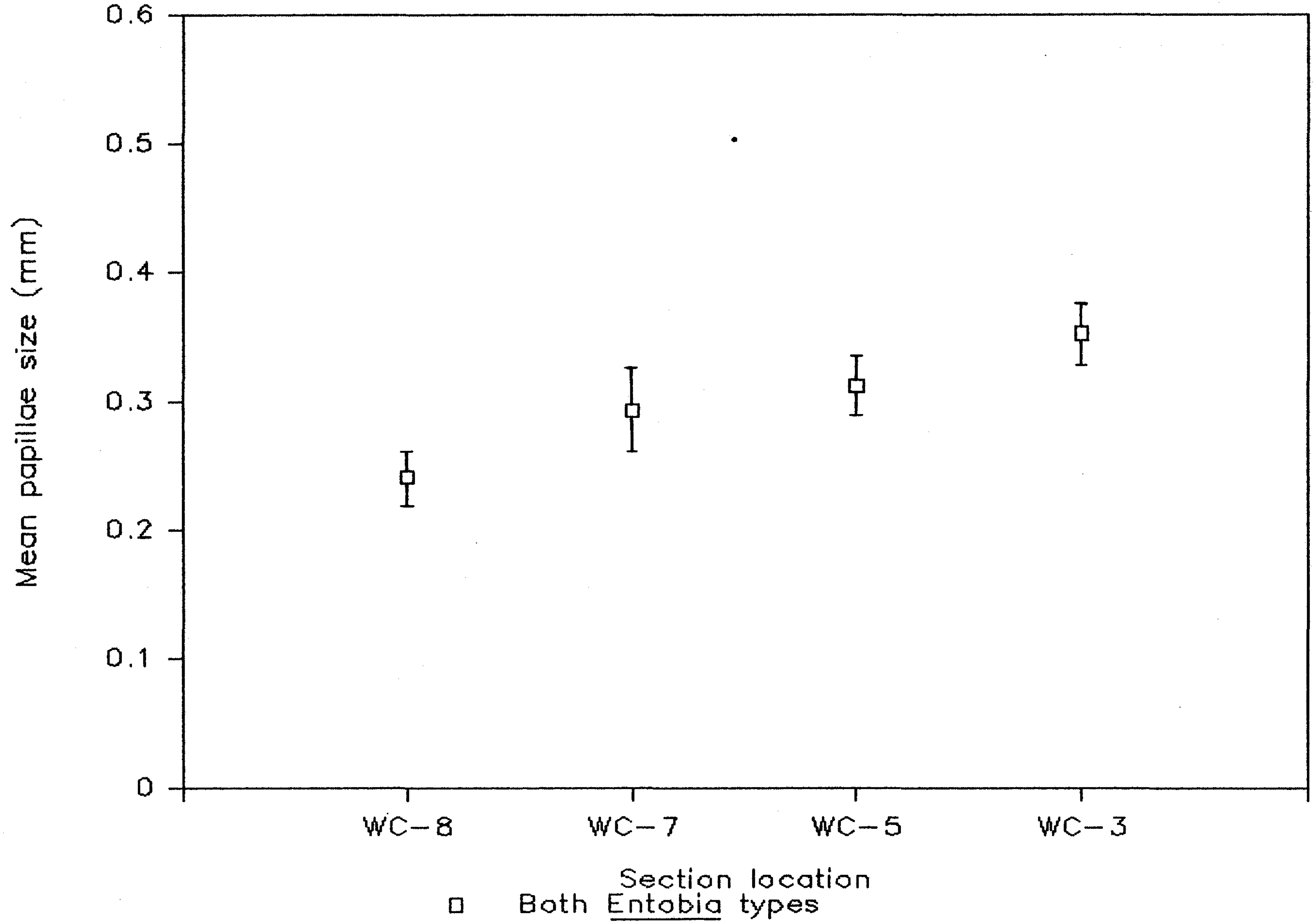
Type 1 chambers of *Entobia cretacea* and type 2 chambers of *Entobia* type 'a' vary in size. Short and long axis dimensions of chambers can't be used to designate the *Entobia* boring type, due to the overlap in sizes (Figure 9). Rather, trends in short and long axis dimensions of both boring types indicate that chambers decrease in size along branching networks. Depth of boring into the substrate and development of branching networks are therefore the best criteria for designating boring type.

Entobia : PAPILLAE MEASUREMENT DATA

Table
4.1

Section	Type	Mean papillae size (mm)	Std.devn	Number
WC-8	All	0.241	0.022	69
WC-7		0.293	0.129	70
WC-5		0.312	0.112	84
WC-3		0.353	0.047	19
WC-8	Type `a'	0.241	0.022	69
WC-7				
WC-5		0.208	0.095	17
WC-3		0.313	0.053	3
WC-8				
WC-7	E. cret.	0.293	0.129	70
WC-5		0.339	0.099	67
WC-3		0.359	0.043	16

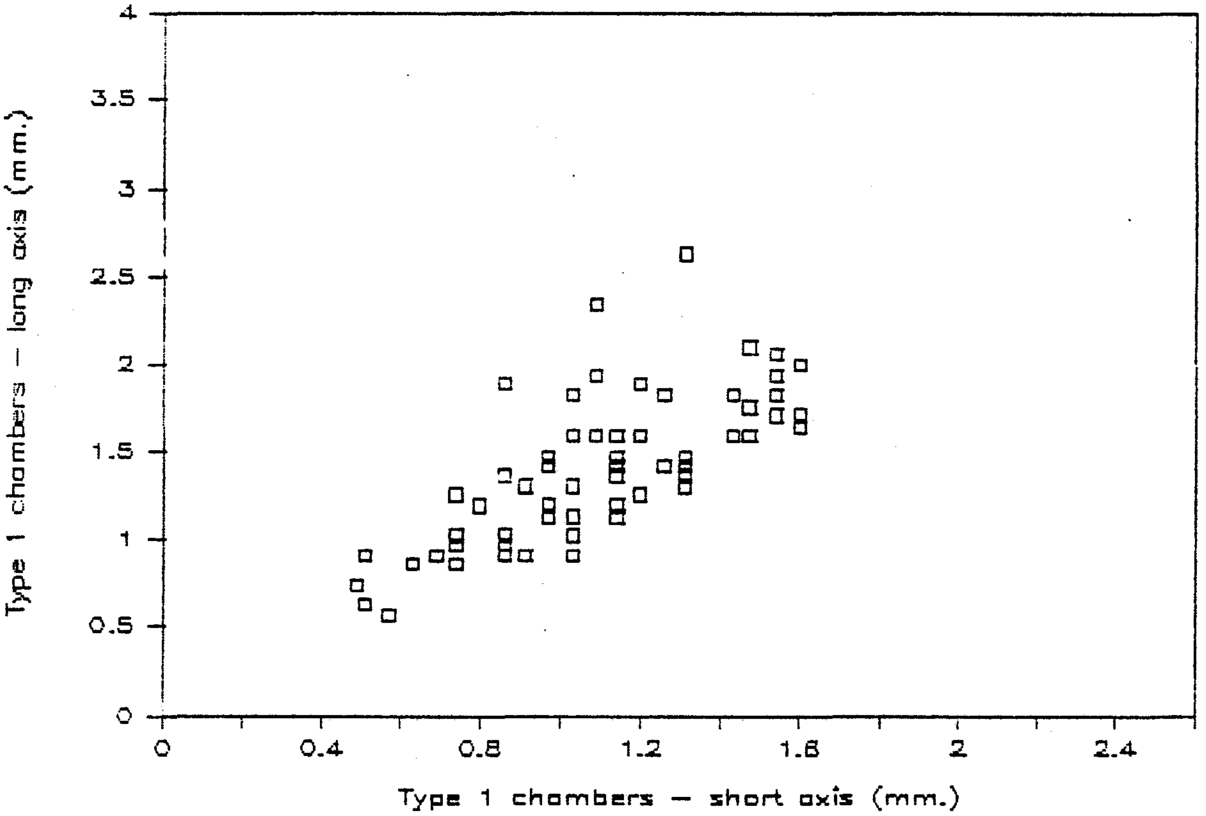
Figure 8. Graph of mean papillae sizes for _Entobia_ at Willow Creek sampling locations. 95 % confidence intervals included.



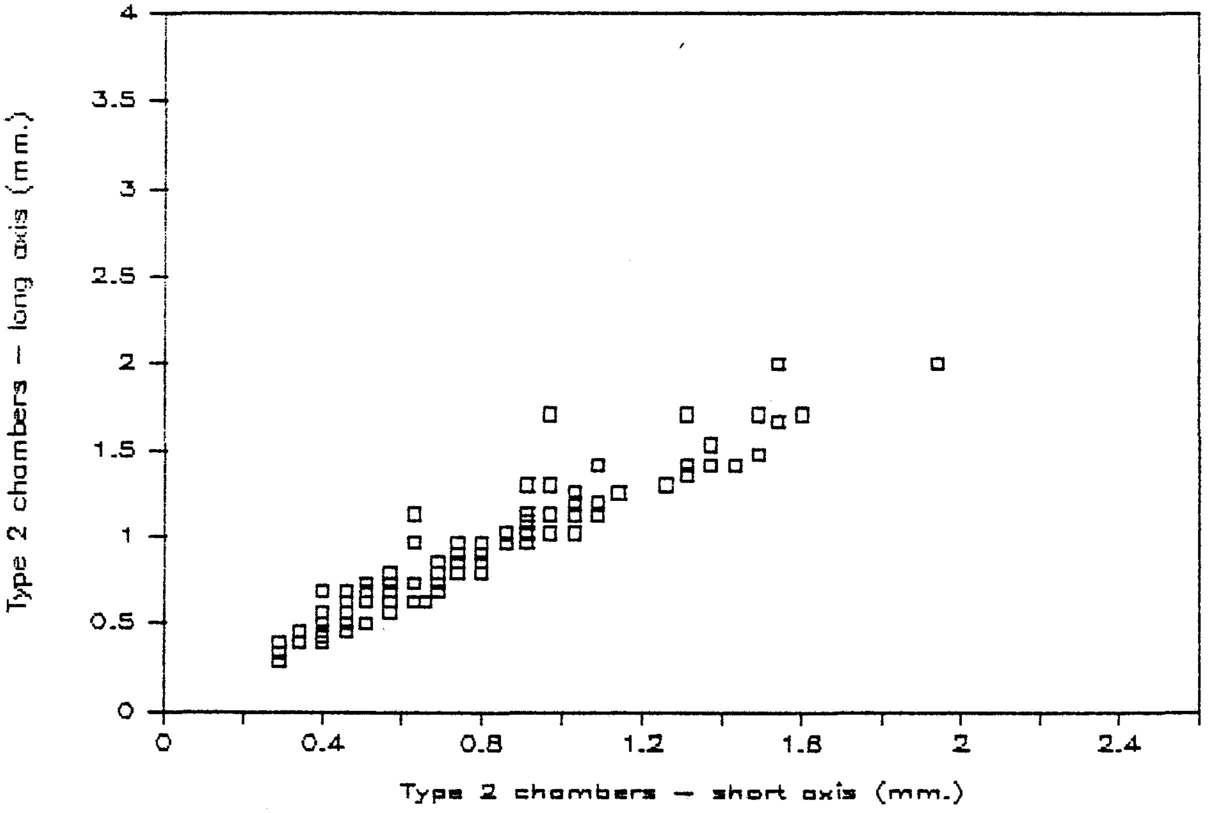
Mean papillae size (mm)
0.6
0.5
0.4
0.3
0.2
0.1
0
WC-8
WC-7
WC-5
WC-3
Section location
□ Both Entobia types

Figure 9. Comparison of dominant type chamber dimensions for _Entobia_ boring forms.

Entobia cretacea – chamber dimensions



Entobia type 'a' – chamber dimensions



Although *Entobia* type 'a' is the predominant boring morphology in *Ostrea* shells at WC-8, sparse *Entobia cretacea* are in fact present. Type 1 chamber measurements from *Entobia cretacea* at WC-8 are significantly smaller in size (Table 2) than type 1 chambers of *Entobia cretacea* at the other localities (Figure 10). This variation in chamber size suggests that different conditions may have affected the sponges which produced the type 1 chambers typical of *Entobia cretacea*.

Since the shell substrate is similar at both locations, and in light of evidence already presented, it would not seem reasonable to conclude that chamber networks at WC-3, WC-5 and WC-7 represent older boring networks while smaller chambers at WC-8 represent younger borings. As shown by the trend in papillae sizes, a salinity gradient may occur in this estuarine environment. Salinity fluctuations may inhibit the ability of the *Entobia cretacea* boring species to attain maximum chamber dimensions.

An influence of sedimentation could also affect chamber sizes. The possible effects of sedimentation has already been suggested to account for the upward growing *Ostrea* valves present at WC-8. Larger papillae of *Entobia cretacea* may have taken in more sediment than the smaller papillae of *Entobia* type 'a'. Energy requirements for *Entobia cretacea* sponges would have been increased when stressed by sedimentation and in response the sponge bored smaller chambers.

Entobia cretacea : TYPE 1 CHAMBER ANALYSIS

Table
4.2

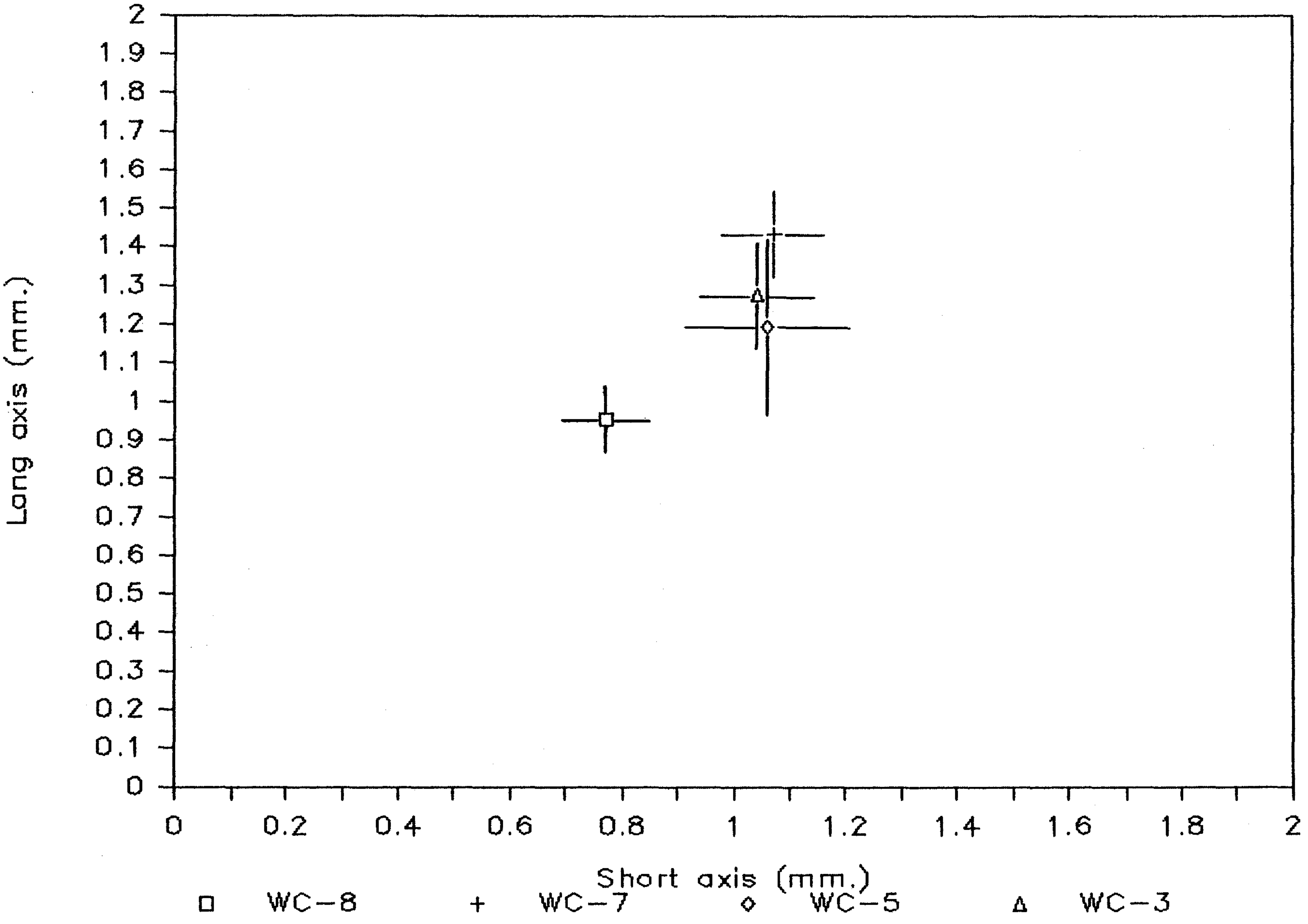
Short axes :

Section	Mean size (mm.)	Standard devn.	Number
WC-8	0.771	0.338	74
WC-7	1.072	0.34	53
WC-5	1.059	0.361	25
WC-3	1.042	0.235	21
All	1.075	0.303	99

Long axes :

Section	Mean size (mm.)	Standard devn.	Number
WC-8	0.954	0.397	74
WC-7	1.434	0.433	53
WC-5	1.193	0.572	25
WC-3	1.278	0.3	21
All	1.371	0.422	99

Figure 10. Type 1 chamber dimensions of _Entobia_ _cretacea_ borings.


Long axis (mm.)
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
Short axis (mm.)
□ WC-8
+ WC-7
◇ WC-5
△ WC-3

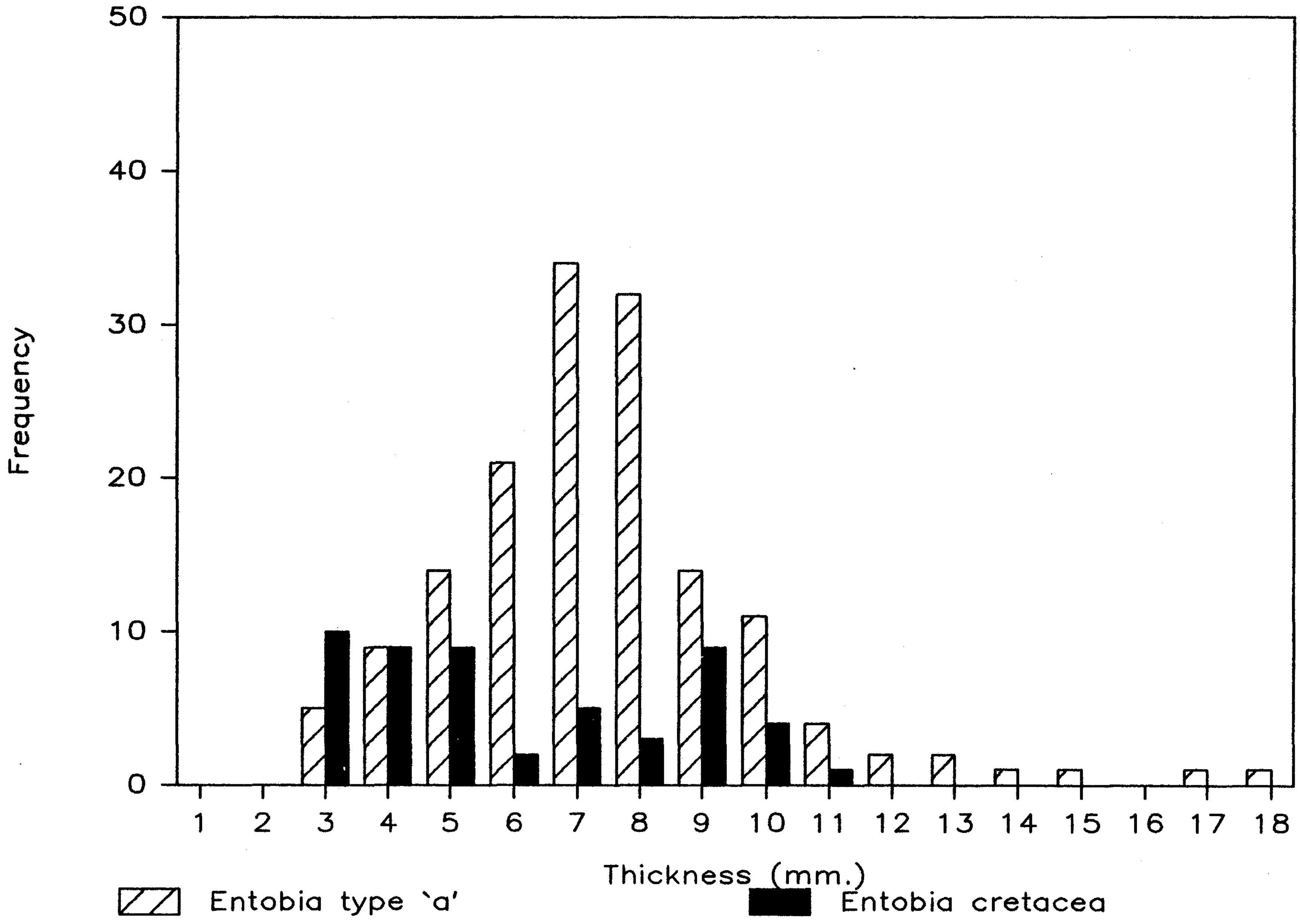
Evidence from shell thickness:

Measurements of *Ostrea* shell thickness, at positions of *Entobia* borings, were collected for *in situ* borings. Several thicknesses were obtained for a single shell if the boring colony was widespread upon the shell surface. Plots of size frequency vs. shell thickness for both *Entobia cretacea* and *Entobia* type 'a' show that *Entobia* type 'a' borings appear to be more selective with respect to their occurrence at a specific shell thickness (Figure 11). *Entobia* type 'a' borings dominantly occur in shells which are 6-8 mm thick.

This may suggest that there is an availability of thick shells to *Entobia* type 'a' borers. Since 90% of *Entobia* type 'a' borings occur at WC-8, this response may be related to the thicker, upward-curving *Ostrea* shells which occur there. The scarcity of juvenile oysters at WC-8 supports the suggestion that the shells at WC-8 are 'older' shells. The reproducing oyster banks may therefore be located further seaward in a more favourable marine environment.

Entobia type 'a' sponges could preferentially have settled on living, thick shelled molluscs. This might be a protective response to bottom currents (Hartman, 1958), increased sedimentation or increased grazing pressures. There is no evidence for an effect due to bottom currents or increased grazing pressure, but evidence provided from associated organisms (*Ostrea* and bryozoa) could support a response to sedimentation.

Figure 11. Frequency plot of thickness of _Ostrea_ valves where bored by _Entobia_


50
40
30
20
10
0
Frequency
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Thickness (mm.)
Entobia type `a'
Entobia cretacea

CHAPTER 5

CONCLUSIONS

Faunal evidence in the oyster-bearing, unconsolidated sands suggest that a subtidal community existed on a hard substrate. Distributions and characteristics of associated marine organisms within the oyster community (phoronid worms, gastropods and encrusting bryozoa) suggest that sponge colonies may have been directly affected by salinity and sedimentation.

Within the oyster community, evidence for sponge borings in *Ostrea* shells by more than one sponge species includes:

1) two distinct boring morphologies (*Entobia cretacea* and *Entobia* type `a') in which differences in the advancing edges and rootstocks occur (Volz, 1939).

2) the presence of both boring forms on a single *Ostrea* valve.

3) a preferential occurrence of *Entobia* type `a' forms on shells of moderate thickness (6-8 mm) while *Entobia cretacea* can be found in shells of varying thickness.

These sponges had apparently developed a chemical toxicity by Upper Cretaceous time as evidenced by a negative association with boring gastropods.

The intensity of boring and surface coverage makes sponge borings useful taphonomic indicators. Problems with regard to utilizing *Entobia* as a paleoenvironmental indicator and as an indicator of salinity do not appear to be insurmountable.

Evidence for periods of lowered salinity within the estuary include:

1) the distribution of boring sponges. *Entobia* type 'a' is dominant at WC-8, while *Entobia cretacea* is the dominant form at WC-5 and WC-3. *Entobia* type 'a' may be better able to withstand periodic influx of fresh water.

2) an increase in mean papilla size occurs from WC-8 to WC-3. This observation is supported by modern studies of estuarine clionid sponge distributions where marine sponges have larger papillae than brackish sponges. Thus, WC-3 represents a more marine location than WC-8.

3) a decrease in type 1 chamber sizes of *Entobia cretacea* occurs at WC-8, as compared to the other locations. This suggests that the sponge which produces *Entobia cretacea* borings may have been affected by adverse conditions at WC-8, possibly salinity fluctuations.

Evidence that a response to sedimentation and a correlative facies change at WC-7 from a shaly facies (WC-8) to a sandy facies (WC-5 and WC-3) includes:

1) upward curving *Ostrea* shells at WC-8. These likely grew upwards to keep their feeding margins above the sediment interface. Laterally growing shells at WC-7, WC-5 and WC-3 occur on a harder sandy substrate and grow to increase the area of their feeding margin.

2) few juvenile oysters occur at WC-8. This might indicate that the reproducing oyster bank is in a more marine position, less affected by sedimentation.

3) comparatively fewer _Oichnus simplex_ occur at WC-8 than at other locations. This may be due to the available substrate at each location.

4) _Talpina_ is dominant at WC-8, and decreases in abundance to WC-7, WC-5 and WC-3. This observation may also be due to the available substrates.

5) _Entobia_ type 'a' are the dominant sponge borings at WC-8. This sponge bores in thicker shells than its counterpart, _Entobia cretacea_, which is non-selective of shell thickness. This may be a response to available shell substrate, or increased turbidity such that deeper boring networks are required.

REFERENCES

Basan, P.B. (1978) Trace fossil concepts, S.E.P.M. short course no. 5, Oklahoma City.

Boeckschoten, G.J. (1966) Shell borings of sessile epibiontic organisms as palaeoecological guides. Palaeogeog. Palaeoclim. Palaeoecol. 2 p. 333-379.

Boeckschoten, G.J. (1967) Palaeoecology of some Mollusca from the Tielrode sands (Pliocene, Belgium). Palaeogeog. Palaeoclim. Palaeoecol. 2 p. 311-362.

Bromley, R.G. (1970) Borings as trace fossils and *Entobia cretacea* Portlock, as an example. In Trace Fossils (ed. by T.P. Crimes and J.C. Harper) p. 49-90. Seel House Press, Liverpool.

Bromley, R.G. (1978) Bioerosion of Bermuda Reefs. Palaeogeog. Palaeoclim. Palaeoecol. 23 p. 169-197.

Carriker, M.R. and E.L. Yochelson (1968) Recent gastropod boreholes and Ordovician cylindrical borings. U.S.G.S. Prof. Paper 595, 26p.

Cobb, W.R. (1969) Penetration of calcium carbonate substrates by the boring sponge, *Cliona*, Amer Zool. 9 p. 783-790.

Ekdale, A.A., R.G. Bromley and S.G. Pemberton (1984) Ichnology - Trace fossils in sedimentology and stratigraphy S.E.P.M short course, no. 15

Feldmann, R.M. and D.S. Palubniak (1973) Paleoecology of Maastrichtian Oyster Assemblages in the Fox Hills Formation. *In* The Cretaceous System in the Western Interior of North America (ed. by W.G.E. Caldwell). G.A.C. Spec. Paper 13, p. 211-233.

Groot, R.A. de (1977) Boring sponges (Clionidae) and their trace fossils from the coast near Rovinj (Yugoslavia). Geologie en Mijnbouw 56 (2), p. 168-181.

Guida, V.G. (1976) Sponge predation in the oyster reef community as demonstrated with *Cliona celata* Grant. J. Exp. Mar. Biol. Ecol. 25, p. 109-122.

Hantzschel, W. (1975) Borings. *In* Treatise on Invertebrate Palaeontology, 2nd Edn. (ed. by C. Teichert) part W, p. 122-139.

Hartman, W.D. (1957) Ecological niche differentiation in the boring sponges (Clionidae). Evolution 11, p. 294-297.

Hartman, W.D. (1958) Natural history of the marine sponges of Southern New England. Yale Univ., Peabody Mus. Nat. Hist., Bull. 12, 155 p.

Hartman, W.D., J.W. Wendt and F. Weidenmayer 1980. Living and Fossil Sponges, Sedimenta VIII (Notes for a short course).

Hopkins, S.H. (1956) Notes on boring sponges in Gulf Coast estuaries and their relation to salinity. Bull. Mar. Sci. 6, p. 44-58.

Hopkins, S.H. (1956) The boring sponges which attack South Carolina oysters, with notes on some associated organisms. Contr. Bears Bluff Lab 23, 30p.

Hopkins, S.H. (1957) Oysters. In Treatise on Marine Ecology and Paleoecology (ed. by J.W. Hedgepeth) p. 1129. G.S.A. Memoir 67, v. 1.

Hopkins, S.H. (1962) Distribution of species Cliona on eastern shore of Virginia in relation to salinity. Chesapeake Sci. 3 p. 121-124.

Irish, E.J.W. (1970) The Edmonton Group of South Central Alberta. Bull. of Can. Petrol. Geol. 18, no. 2.

Kauffman, E.G. (1977) Cretaceous. In Treatise on Invertebrate Paleontology pt. A, p. 418-487.

Kemp, K.M. (1983) Macroborings in Cretaceous oysters from Drumheller, Alberta : taphonomy and paleoecology (Unpubl. B.Sc. thesis) McMaster Univ., Hamilton, Ontario.

Ladd, H.S. (1957) Paleoecological Evidence. In Treatise on Marine Ecology and Paleoecology (ed. by J.W. Hedgepeth) G.S.A. Memoir 67, v. 2, p. 31-66.

Laubenfels, M.W. de (1955) Porifera. In Treatise on Invertebrate Paleontology , part E.

Lawrence. D.R. (1968) Taphonomy and information losses in fossil communities. Bull. Geol. Soc. Amer. 79 p. 1315-1330.

Lawrence, D.R. (1969) The use of clionid sponges in paleoenvironmental analysis. J. Palaeontology 43 p. 539-543.

Old, M.C. (1941) The taxonomy and distribution of the boring sponges (Clionidae) along the Atlantic Coast of North America. Chesapeake Bill. Lab. 44, 30p.

Rahmani, R.A. (1983) Facies relationships and paleoenvironments of a Late Cretaceous tide dominated delta, Drumheller, Alberta. Can. Soc. Petrol. Geol. field guide, no.6, 52p.

Reiswig, H.M. (1971) In situ pumping activities of tropical Demospongiae. Marine Biology 9, p. 38-50.

Rutzler, K. (1971) Bredin-Archbold Smithsonian Biological Survey of Dominica, Burrowing sponges, genus Siphonodictyon Berquist. from the Caribbean. Smithsonian Contr. to Zool., 77.

Rutzler, K. (1975) The role of burrowing sponges in bioerosion. Oecologia (Berl.) 19, p. 203-216.

Rutzler, K. and G. Rieger (1973) Sponge burrowing: Fine structure of Cliona lampa penetrating calcareous substrata Marine Biol. 21, p. 144-162.

Shepheard, W.W. and L.V. Hills (1970) Depositional environments Bearpaw - Horsehoe Canyon (Upper Cretaceous) transition zone, Drumheller, Alberta. Bull. Can. Pet. Geol. 18, no. 2, p. 166-215.

Sohl. N.F. (1969) The fossil record of shell boring by snails. Amer. Zoologist 9, p. 725-734.

Stanton, R.J. and P.C. Nelson (1980) Reconstruction of the trophic web in Paleontology: Community structure in the Stone City Formation (Middle Eocene, Texas). J. Paleont. 54, p. 118-135.

Stanton, R.J., E.N. Powell and P.C. Nelson (1981) The role of carnivorous gastropods in the trophic analysis of a fossil community. Malacologia 20, p. 451-469.

Waage, K.M. (1961) The Fox Hills Formation in its type area, Central South Dakota. Wyoming Geol. Assoc. Guidebook 16th Annual Field Conf. p. 229.

Warburton, F.E. (1958) The manner in which the sponge Cliona bores in calcareous substrates. Can. J. Zool. 36, p. 555-562.

Warme, J.E. (1975) Borings as trace fossils, and the processes of marine bioerosion. In The Study of Trace Fossils (ed. by R.W. Frey) Springer-Verlag, N.Y.

Warme, J.E. and N.F. Marshall (1969) Marine borers in calcareous terrigenous rocks off the Pacific Coast. Amer. Zool. 9, p. 765-774.

Wells, H.W. (1959) Boring sponges (Clionidae) of Newport River, N. Carolina, J. Elisha Mitchell Sci. Soc. 75, p. 168-173.

Wells, H.W. (1961) The fauna of oyster beds, with special reference to the salinity factor. Ecol. Monogr. 31, p. 239-266.

Wiedemann, H.U. (1972) Shell deposits and shell preservation in Quaternary and Tertiary estuarine sediments in Georgia, U.S.A. Sediment Geol. 7, p. 103.

Williams, H.G. and C. Stelck (1975) Speculations on the paleogeography of North America, p. 1-20. In The Cretaceous system in the Western Interior of North America (ed. by W.G.E. Caldwell) G.A.C Spec. Paper no. 13.