TAPHONOMY OF A PLIOCENE OPHIUROID MASS MORTALITY LAGERSTÄTTE IN THE TIRABUZÓN FORMATION, BAJA CALIFORNIA SUR

René Anne Shroat-Lewis

A Thesis Submitted to the
University of North Carolina at Wilmington in Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

Department of Geography and Geology

University of North Carolina at Wilmington

2007

Approved by

Advisory Committee

____________________ ____________________

____
Chair

Accepted by

____
Dean, Graduate School

This thesis has been prepared in a style and format

consistent with the journal

PALAIOS

TABLE OF CONTENTS

ABSTRACT

Preservation of fully articulated ophiuroids (ophiuroid Lagerstätte) is rare due to rapid disarticulation of their endoskeletons. Recently, material from a mass mortality bed(s) of well preserved ophiuroids was found in the Pliocene Tirabuzón Formation, 4 kilometers north of Santa Rosalía, Baja California Sur.

Unconsolidated sediment samples from the Tirabuzón Formation indicate a high abundance, yet low diversity, benthic foraminiferal assemblage. Three species are most abundant: (1) *Virgulina californensis*; (2) *Bolivina interjuncta*; and (3) *Uvigerina attenuata*. The high frequency of *Bolivina interjuncta* and *Uvigerina attenuata* throughout the formation suggests the Tirabuzón Formation was deposited in 200-500m water depth.

The ophiuroid fossil assemblage appears to be monotaxic and was identified as the genus *Ophiocnemis*. Few of the ophiuroids in these samples were found whole. Instead, an anomalous (152:1) ratio of arms to discs exists. The individual arms and discs display a high degree of articulation, i.e. arms with spines still attached and articulated jaw structures. The high degree of articulation found in the arms suggests: (1) rapid burial; (2) no decomposition prior to interment; and (3) lack of post mortem reworking and bioturbation.

To determine the possible cause of the abnormal ratio of arms to discs, live ophiuroids were subjected to simulated wave current coupled with turbidity, temperature, and/or salinity changes. Agitation in normal salinity/temperature seawater caused orientation difficulties and varied arm-curling responses. Changes in suspended sediment (0-235 mg/l) had no effect on the ophiuroids over a 180 minute period. Warm water

(>30° C) caused arm rigidity and cool water (<18° C) caused substrate attachment difficulties. Both hypersaline (>52 ppt) and hyposaline (<24 ppt) water produced: (1) arm rigidity; (2) attachment difficulties; (3) lethargy; and/or (4) death. Arm flexibility of live ophiuroids subjected to hypersaline water was restored post mortem, but live ophiuroids exposed to hyposaline water exhibited prolonged arm rigidity. Prolonged arm rigidity, high energy storm waves, and sorting of the elongate arms from the flat central discs may account for the abnormally high arm to disc ratio in the Tirabuzón samples.

ACKNOWLEDGMENTS

First and foremost I must extend a heart-felt thank you to the best advisor and friend a person could ever ask for, Tricia Kelley. Your genuine desire to ensure the success of your students truly helps foster a love for our science. You have changed my life forever and I am eternally grateful.

I would like to thank my committee members: Dr. Richard Laws, who taught me that even forams must be open and willing to change in order to improve their world; Dr. W. Burleigh Harris, the closet paleontologist and master cell-phone smasher, who I hope will always laugh when he thinks of Model #1 and our field-trip mascot, Bert the Pumpkin; Dr. Frederick Hotchkiss who saw promise in a nervous undergraduate at a taxonomic workshop and gave her excellent tools to work with. I would also like to extend sincere thanks to Mr. Roger Shew who gave so freely of his time. The hours we spent pondering the feasibility of my crazy ideas was absolutely invaluable. I am indebted to Dr. Paul Thayer who not only offered great insight into my project but spent hours of his own time tweaking my figures. Dr. Lynn Leonard graciously provided me with a tank for my actualistic experiments. Furthermore, I would like to thank Cathy Morris in the departmental office who supported me from the beginning until the end. Her effervescent spirit kept me going and I couldn't have asked for better company to cry with on the day of my oral exam.

Along this wild journey I have found a strength I did not know I had. I credit my family whose support and love has meant a lot to me. I hope that my success will inspire other family members to pursue higher education as well.

Lastly, I am indebted to those who provided financial support for this project: Marine & Paleobiological Research Institute, Geological Society of America Graduate Student Research Grants, Association of Applied Paleontological Sciences, Association of Women Geoscientists, University of North Carolina Wilmington Graduate Student Summer Research Grant, Victor A. Zullo Memorial Scholarship, and University of North Carolina Wilmington Department of Earth Sciences Research Grant.

DEDICATION

I would like to dedicate this thesis to my sons, William Christopher and Richard Wayne Lewis, the most precious gifts God has bestowed upon me. They have supported me every day and in every way. Life without them is impossible to imagine.

To my grandfather, William Frank Martin, who taught me to wonder.

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Overview

Indurated material from a Pliocene ophiuroid lagerstätte was discovered in place in 1995 in the Tirabuzón Formation, Baja California Sur (Fig. 1), by Eric Prokopi, an amateur collector (Eric Prokopi, pers. comm., 2006). Located 4 kilometers north of Santa Rosalía, the Tirabuzón Formation was originally named the Gloria Formation by Wilson in 1948. Corkscrew-like burrows near the top of the bluff give the formation its name. An early-middle Pliocene age was established by Carreño (1982) based on planktonic Foraminifera. Although several papers have been written on the vertebrate fauna and planktonic Foraminifera associated with this formation, search of the biological and geological literature indicates no previous work on the ophiuroids.

Ophiuroids, also known as brittle sea stars, belong to the phylum Echinodermata (from the Greek *echinos*, meaning spiny, and *derma*, meaning skin), which also includes such recognizable invertebrates as starfish, sea cucumbers and sea urchins. The word ophiuroid means “snake-like” and refers to the movement and appearance of the arms. Generally, echinoderms have a detailed fossil record with several extinct classes; ophiuroids are one exception. Today’s echinoderms constitute a medium-sized phylum with five living classes containing about 6000 living species (Boardman et al., 1987).

Like other echinoderms, ophiuroids exhibit radial five-sided (pentameral) symmetry, a calcium carbonate skeleton, a water vascular system, and the ability to regenerate. The arms of ophiuroids and starfish, called “rays,” are composed of specialized high-magnesium calcite ossicles surrounded by individual calcite plates. Under polarizing light these ossicles are birefringent (double-refractive) and behave as a

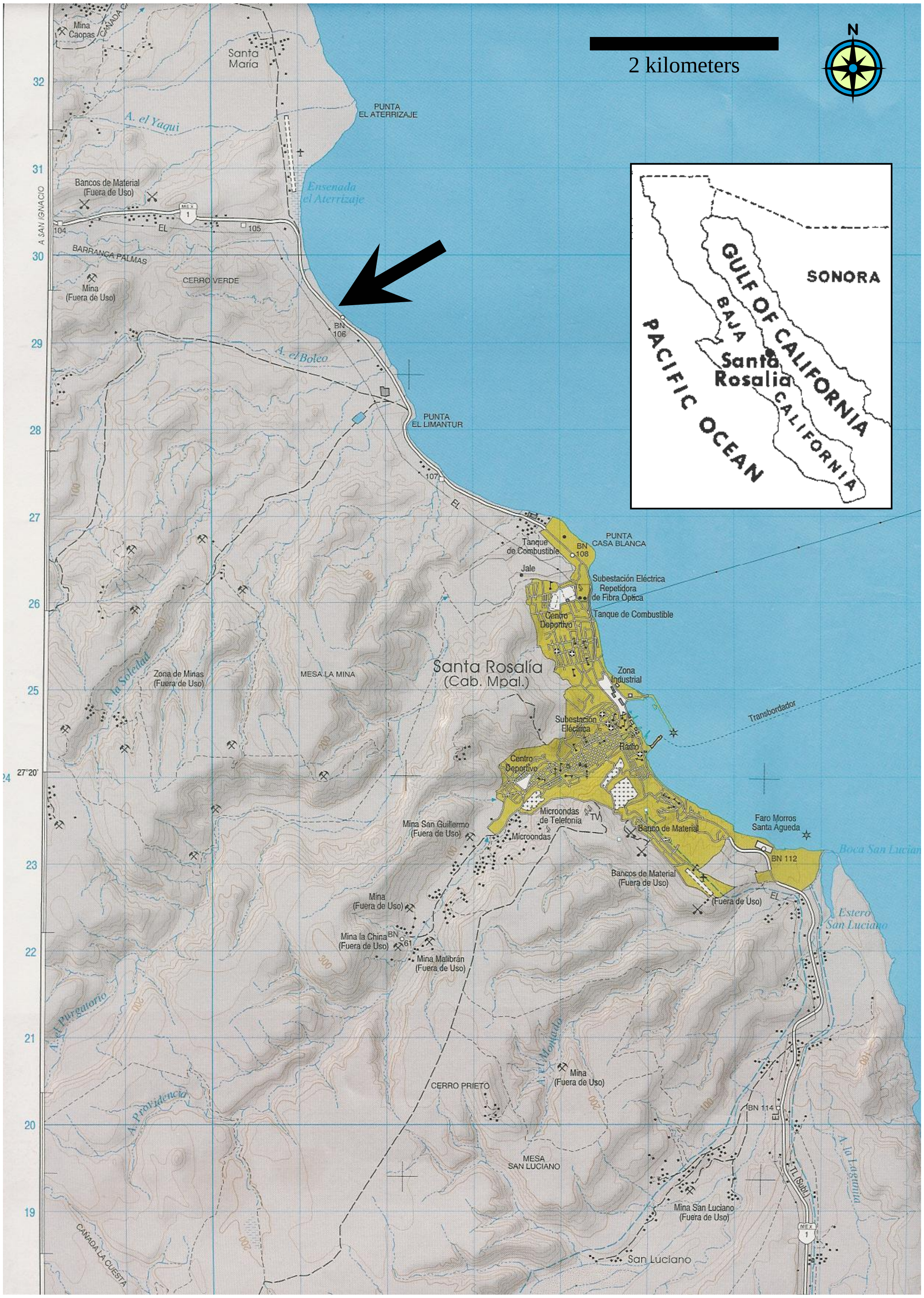


Figure 1—Location map of the study area. Arrow indicates location of the Tirabuzón Formation (Instituto Nacional de Estadística, 1993).

single crystal of calcite. Although the internal skeleton preserves well, rapid disarticulation of the ossicles and plates post mortem causes ophiuroids to be poorly represented in the fossil record. The soft tissue that connects the ossicles is highly susceptible to decay. Post mortem decomposition weakens this soft tissue, resulting in complete dissociation of ossicles into an accumulation of small, individual parts.

Statement of Intent

This study will incorporate paleontological data and theories with actualistic experiments in order to explain taphonomic conditions that promote an ophiuroid lagerstätte deposit; modern live ophiuroids will be used for comparison. Pliocene environmental conditions that may have contributed to the ophiuroid mass mortality event will be examined. The results will be used to interpret the depositional history of the ophiuroid mass mortality bed(s).

I propose the following hypotheses:

1. The ophiuroid mass mortality event occurred as a result of a strong storm, such as a hurricane.
2. Fresh water inundation and high turbidity associated with the storm caused a high-stress setting that promoted ophiuroid disc autotomization.
3. Disc autotomization and preferential sorting led to the anomalous ratio of ophiuroid discs to arms found in the ophiuroid lagerstätte samples from the Tirabuzón Formation.

BACKGROUND

Location and Setting of the Study Area

The Gulf of California, also known as the Sea of Cortez, is a small body of water that separates the Baja Peninsula from the mainland of Mexico. The current configuration of the Gulf evolved between the Miocene and Recent and is due to three phases of development: subduction, extension and transtension (Ledesma-Vázquez, 2002). At approximately 1,100 kilometers long and 80-210 kilometers wide, the Gulf is a long narrow marine basin that is open to the Pacific Ocean at the southern end and closed at the northwest end. The presence of large islands in the basin constricts the mid-section to an effective width of only 50 kilometers.

Originally named the Gloria Formation by I.F. Wilson in 1948, the Tirabuzón Formation, translated as "Corkscrew Hill," is exposed on the west side of Mexican Federal Highway 1, four kilometers north of the town of Santa Rosalía, Baja California Sur (Figs. 1–2). The paved road separates the outcrop from the Sea of Cortez. The Tirabuzón Formation unconformably overlies the Boleo Formation and is unconformably overlain by the Infierno Formation. Geologic maps by Wilson (1948) indicate that the Infierno Formation is not represented in the study area (Fig 3).

The outcrop, which constitutes the basis of this thesis, is approximately 36 meters in height and extends along the road for approximately 1 kilometer. Deposits of Quaternary volcanic rocks from the nearby Tres Vírgenes volcano blanket the nearby mesas and spread over the sides of the Tirabuzón Formation arroyos (Wilson, 1948). Abundantly fossiliferous, the Tirabuzón Formation consists mainly of poorly indurated argillaceous sandstone. Minor lenses of siltstone, claystone, and limestone also occur.

Figure 2— The Tirabuzón Formation extends from base to top of outcrop in photo.

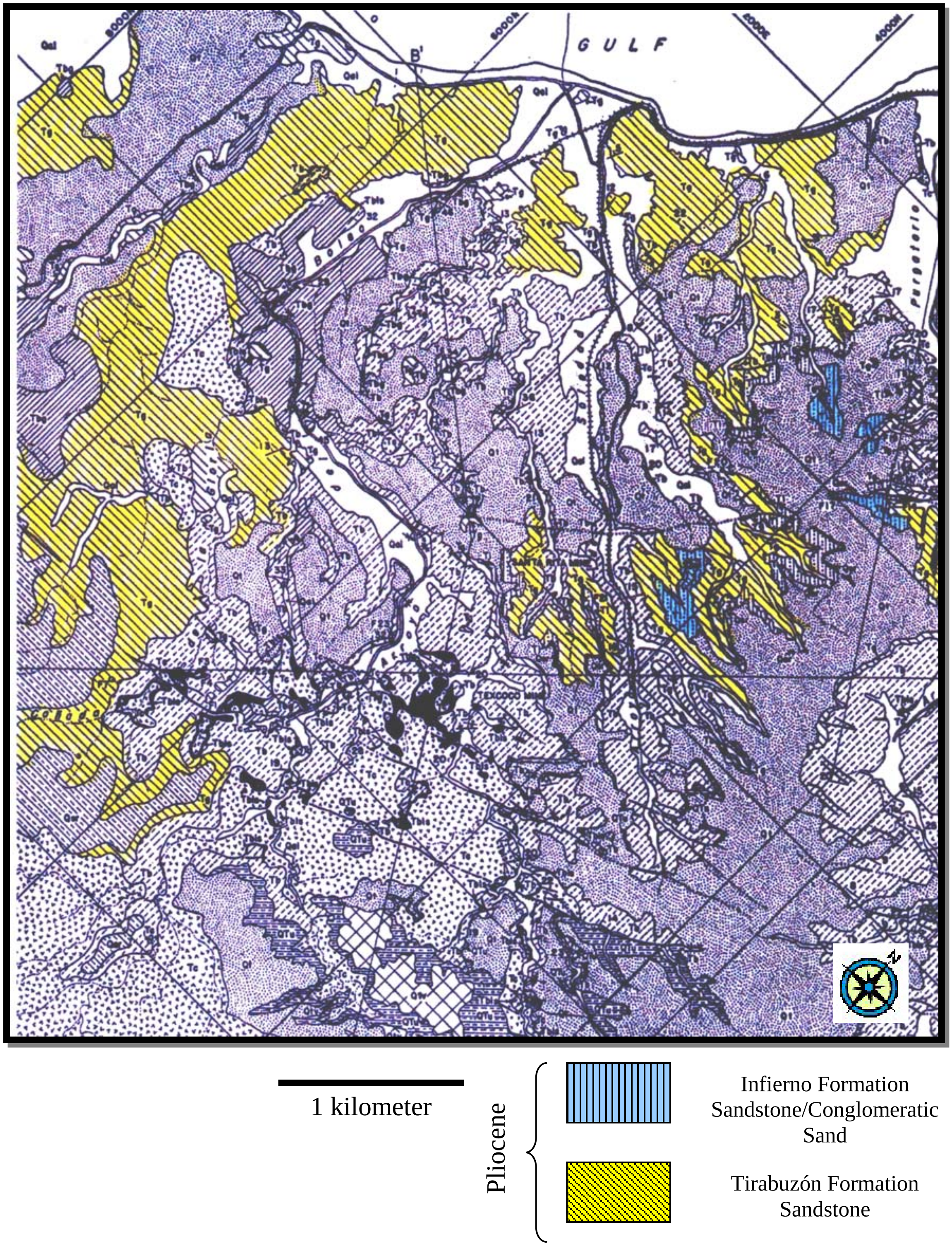


Figure 3—Geologic map of study area. Arrow indicates location of study site located at 27° 27.714'N, 112° 17.094'W (Wilson, 1948).

The rocks appear to be flat lying. The geometry of the Tirabuzón Formation exposure and the absence of the Infierno Formation indicate that material collected from the study area originated in the Tirabuzón Formation.

Ophiuroid Biology and Ecology

Ophiuroids have a fairly complex internal anatomy (Fig. 4). Their body is composed of coelomic cavities containing several organ systems. The nervous system includes a circumoral ring around the mouth in the central disc that joins with the radial nerve cord and runs on the underside of each arm in the ambulacral groove. All nerve processes occur in the arms as ophiuroids lack anything that resembles a brain (Cobb and Stubbs, 1981). Ophiuroids also have a water vascular system that opens to the exterior through a hydropore or madreporite. The water vascular system allows fluids to be transported through the arms allowing hydraulic extension of the tube feet. These tube feet are used for the detection and transfer of food to the mouth, movement, and sensory perception. Respiration occurs in bursae located at the base of each arm. After feeding, waste material is ejected through the mouth as ophiuroids lack an anus.

Ophiuroids have existed since the Ordovician and maintained an epifaunal environmental preference for millions of years (Aronson, 1989). A number of changes during the Mesozoic, most notably the rise in durophagous (shell-crushing) predators, caused a change in this environmental preference. Many ophiuroids became infaunal, burrowing several centimeters into the sediment in an attempt to seek shelter or hide from their predators (Aronson, 1989). Present-day ophiuroids are strictly marine benthic crawlers and range anywhere from shallow to deep-sea environments. Ophiuroids are quite common on abyssal plains and in oceanic trenches. Naturally gregarious,

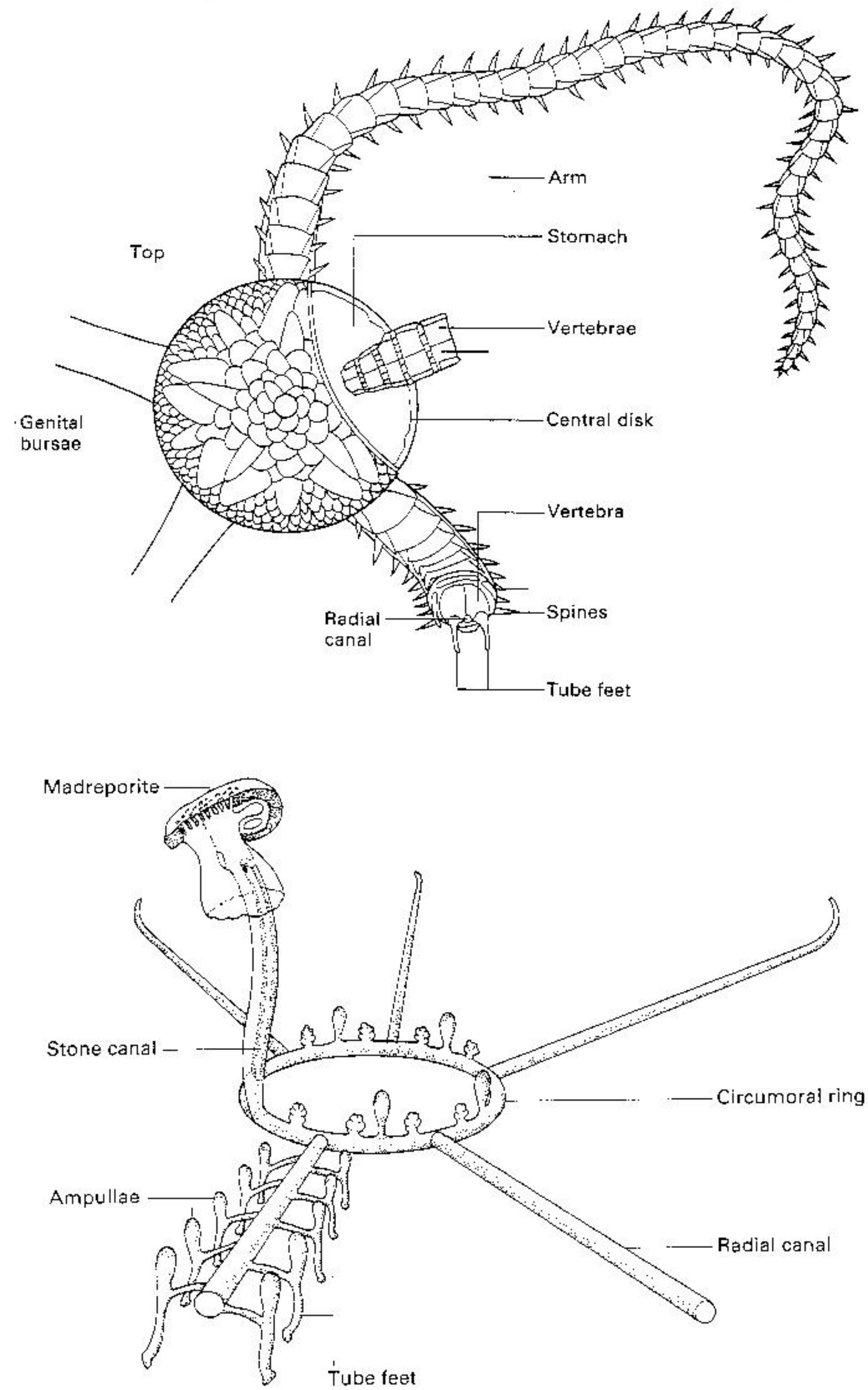


Figure 4— Ophiuroid morphology and internal anatomy. Modified from Boardman et al., 1987.

ophiuroids occur in large groups that often completely cover the ocean floor (Boardman et al., 1987).

Living ophiuroids require three conditions for growth and survival: (1) sedimentation rates must be very low because sediment clogs the water vascular system, ultimately causing suffocation; (2) enough food must be present in order to sustain life; and (3) predation pressure must be low (Aronson, 1989).

Ophiuroids prefer to live in clear water as their water vascular systems are sensitive to fine sediment. Even small amounts of sediment can be lethal as the ophiuroid ambulacral system clogs quite rapidly. The inability of ophiuroids to survive in high turbidity waters is their “Achilles heel” (Seilacher et al., 1985).

Ophiuroid respiration and feeding are accomplished through arm oscillation after extension outside of the protective burrow (Stancyk et al., 1994). Ophiuroids obtain energy through various methods of food gathering. Two distinct groups, carnivores and microphagous feeders, are most often recognized (Woodley, 1967). Carnivorous ophiuroids are usually larger in size and employ two methods to trap their prey: (1) active pursuit; and (2) arm loop capture, a process in which ophiuroids flex their arms around a large food particle and deliver it directly to the mouth. Microphagous ophiuroids use less active methods to gather food. Many are deposit feeders, gathering settled detritus directly from the sea floor, whereas others are suspension feeders that wave their arms above the sea floor, collecting food particles suspended in the water. Basket stars, which form “baskets” with their outstretched multi-branched arms, capture plankton from steady water currents that pass through these arms. The food is then passed down the sticky tube feet, located in the ambulacral groove, towards the mouth and stomach, located in the center of the disc.

One consequence of the practice of arm oscillation is frequent attack by predators that nip the distal third of the ophiuroid arm, causing sublethal arm damage (Makra and Keegan, 1999). In an attempt to distract predators, ophiuroids may cast off, or autotomize, entire body parts as an escape mechanism. These body parts regenerate easily (Hendler et al., 1995). Regeneration scars from this sublethal predation are recognized by color difference and/or discontinuity in arm thickness and are used for identification of predation (Makra and Keegan, 1999). Makra and Keegan (1999) also suggested that physical stress related to storm events or extreme environmental conditions may be a factor that leads to autotomization.

Ophiuroids store nutrients necessary for rapid regeneration of autotomized arms in their central disc. After autotomization, these nutrient stores enable survival without nutrient consumption until new arms regenerate, usually within 2 weeks to 2 months (Hendler et al., 1995). Individuals then return to normal feeding habits. Fielman et al. (1991) used actualistic experiments to study factors important for rapid regeneration. These experiments examined ophiuroid arm and disc regeneration patterns after the removal of 1–5 arms from the central disc. The results indicate that an increase in the number of arms removed causes an increase in regeneration time as stored nutrients are shared evenly among regenerating arms. Interestingly, regenerated arms show an increase in both length and total weight when compared to the original arm that was removed. Complete disc autotomy substantially decreased the rate of arm regeneration.

Although regeneration with one arm and no disc is possible, individuals with even partial discs regenerated arm tissue more rapidly than those without (Fielman et al., 1991).

Taphonomy

Within the past two decades an interdisciplinary branch of paleontology has gained importance in our understanding of the fossil record. Taphonomy, the science of the "laws of burial" (from the Greek *taphos*, meaning tomb, and *nomos*, meaning law), was originally recognized in 1947 by Russian paleontologist Ivan Efremov (Allison and Briggs, 1991). This multidisciplinary science involves aspects of biology, geology, and chemistry. It uses information contained in the fossil record to help establish processes affecting organism preservation from death, through decay and disintegration, until fossil discovery. Taphonomy also gives powerful insights into paleoenvironmental information, including clues that help geologists recognize paleoenvironmental changes and the effect of those transitions on the faunal population.

Defined as exceptional preservation of fossil materials, lagerstätte deposits are unusually rich either in faunal diversity or quality of preservation. Nebelsick (2004) noted that echinoderm Lagerstätte deposits are created in three principal ways: (1) smothering of organisms by mass flow deposits (obrution); (2) deposition in anoxic or hypersaline environments; and (3) storm-generated deposits (tempestites). Preservation of fully articulated ophiuroids (ophiuroid lagerstätte) is rare due to the rapid disarticulation of the ossicles that make up their endoskeleton. Post mortem disarticulation rates were investigated by Twitchett et al. (2005). At 6°C, dead ophiuroids begin disarticulation within 15 hours due to the rapid decay of labile connective tissue. Disarticulation rate of dead ophiuroids doubles with each 10°C rise in temperature (Twitchett et al., 2005). This high disarticulation rate infers that rapid burial must occur in order to preserve fully articulated specimens. Brett and Seilacher (1991) noted that lack of disarticulation in a dense accumulation of fossilized individuals can be a distinctive indication of an obrution, or "smothering" event. Faunal assemblages in obrution deposits often do not include organisms that are capable of active escape such as ophiuroids (Kranz, 1974). Only five centimeters of sediment cover is necessary to prevent ophiuroid escape (Goldring and Stephenson, 1972).

In this study I used actualistic experiments with the purpose of examining the effects of changes in temperature, salinity, and turbidity on live ophiuroids. My goal was to determine if temperature, salinity, and/or turbidity fluctuations associated with strong storms could have caused this mass mortality event and promoted the formation of the ophiuroid lagerstätte.

METHODS

Indurated Float Material Provided by MPRI

Fifteen pieces of indurated ophiuroid material from the Tirabuzón Formation were provided by Dr. Frederick Hotchkiss of the Marine & Paleobiological Research Institute (MPRI) located in Vineyard Haven, Massachusetts. The indurated ophiuroid material, originally collected by Eric Prokopi in 1995, was purchased by Dr. Frederick Hotchkiss from a commercial vendor on a popular internet auction site. According to Eric Prokopi, this material was collected from *in* situ lenses located high in the Tirabuzón Formation; all exposed indurated ophiuroid material was collected, and there was no evidence of other lenses of material (pers. comm., 2007).

Sample numbers MPRI0023–MPRI0037 were assigned to the pieces of indurated material by the MPRI. The 15 pieces range in size from 12 centimeters^2 to 66 centimeters^2.

Field Sampling Methods

Field work was conducted by René A. Shroat-Lewis (author) and Dr. Patricia H. Kelley in June 2006. Eric Prokopi, the amateur collector, was unable to provide information about the exact location where the original collection took place (pers. comm., 2006). For that reason, repeated searches in the numerous east-dipping arroyos along the one kilometer stretch of the Tirabuzón Formation outcrop were conducted in an attempt to determine the location of the ophiuroid bed(s) *in situ*. Although these searches were unsuccessful in locating an *in situ* exposure of the ophiuroid bed(s), 17 pieces of indurated float material from the ophiuroid bed(s) were collected near the top of one arroyo. Sample numbers TBI001–TBI017 were assigned to the indurated float samples collected in this arroyo located at 27° 21.714'N, 112° 17.094'W. Geographic coordinates of the arroyo were determined using a Garmin Geko® 101 Global Positioning System (GPS) unit. No other arroyos along the outcrop provided indurated ophiuroid float material. The 17 pieces of indurated ophiuroid float material collected from the Tirabuzón Formation range in size from 8 centimeters^2 to 258 centimeters^2.

During the course of exploration for *in situ* ophiuroid material, 19 unconsolidated sediment samples were collected from the Tirabuzón Formation in the same arroyo where the indurated float material was collected. Unconsolidated sediment samples of approximately 150 g were taken at intervals of about 1.5 meters from the base to the top of the accessible outcrop (Fig. 5). The outcrop surface was scraped clean prior to

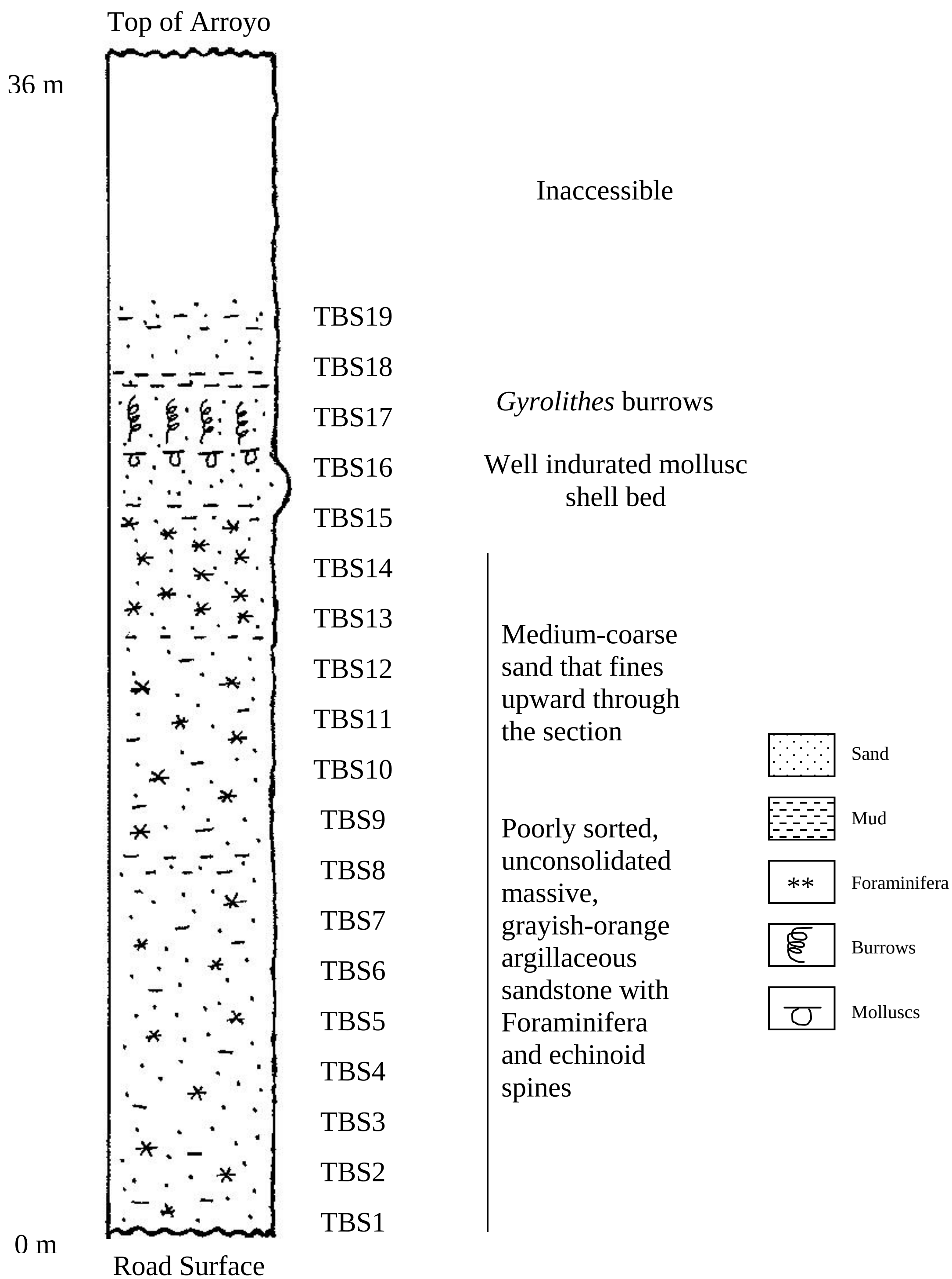


Figure 5—Composite stratigraphic column of arroyo located at coordinates 27° 21.714'N, 112° 17.094'W in the Tirabuzón Formation. Approximate collection locations of samples TBS1-TBS19 are indicated.

sampling to eliminate possible contamination. Unconsolidated sediment samples were placed into labeled sample bags numbered TBS1–TBS19.

Lithologic Methods

Approximately 40 g of sediment from unconsolidated sediment samples TBS1-TBS19 were placed into individual beakers along with 5 g of Calgon water softener (Sodium Hexametaphosphate) and 250 ml of water. Beakers were placed in a Cole/Parmer sonic bath for 15 minutes and mechanically disaggregated before being washed over a U.S. Standard No. 230 screen (63 μm) in order to remove the mud-sized fraction. Samples were placed in a Precision Economy Oven for 24 hours at a temperature setting of 1 for drying. After drying, sediment samples were sieved using a 125 μm screen and the coarser fraction used for analysis.

Dry-sieved samples were examined using a Nikon® type 104 binocular microscope. Percentages of quartz, feldspar, and accessory minerals were estimated through comparison to visual charts. Additional notes were made on degree of sorting, rounding, preservation of fossils, types of minerals, and presence of iron-staining. Grain size, sorting, and roundness were characterized using standard methods described by Folk (1974). Unconsolidated sediment colors were identified using the GSA rock color chart (The Rock Color Chart Committee, 1975) under ambient light conditions.

Petrographic Methods

Two additional pieces of indurated float material collected from the Tirabuzón Formation were sent to Spectrum Petrographics, Inc. for thin-section preparation. Samples were impregnated with blue dye and stained with alizarin red S to assist in the detection of calcite. Thin sections TBTS001 and TBTS002 were analyzed using a Zeiss photomicroscope. A 200 point count of each thin section was done to compare relative abundance of microcrystalline calcite matrix, sparry calcite cement, allochemical grains, and void space. A ribbon method of counting using a mechanical stage was used for each thin section to ensure the accuracy of relative abundance point counts. Data were normalized to 100% using the four categories (microcrystalline calcite matrix, sparry calcite cement, allochemical grains, and void space). The samples were classified using Folk's (1962) terminology. Photomicrographs of thin sections were taken using a Leica DM EP polarizing microscope fitted with a digital camera.

Paleontological and Taphonomic Methods

A representative microfossil fauna, consisting of at least 200 foraminifers, was randomly picked from each dry-sieved sediment sample (TBS1–TBS19) and placed on Gum Tragacanth coated slides. Previous work by Carreño (1982) identified planktonic Foraminifera from the Tirabuzón Formation; therefore, only benthic specimens were identified to species level whenever possible based on Natland (1950) and Phleger (1964).

Five pieces of indurated ophiuroid material were randomly selected from the 32 total pieces of indurated ophiuroid material; two of the pieces selected were provided by MPRI and three were collected during field sampling. Photographs of the five randomly selected pieces were taken using a Nikon® D100 digital camera. Ophiuroid arm direction on these five pieces was determined by placing the digital photograph on a 360° marking system, lining up a straight edge with the ophiuroid arm, and measuring direction. Each piece of indurated ophiuroid material was randomly placed on the 360° marking system due to lack of *in situ* orientation information.

Recorded ophiuroid arm orientations were symmetrically plotted on rose diagrams using Rose (V. 2.1.0) from Todd Thompson Software. The Rayleigh Test for Randomness of Circular Data was used to determine if preferred ophiuroid arm orientation existed in individual pieces of the indurated material. Pieces of the indurated ophiuroid material were not compared to each other due to lack of *in situ* orientation information.

Ophiuroid arm to disc ratios were determined for each piece of the indurated ophiuroid material. Total number of discs was determined by counting those visible on the non-weathered side of the piece. The estimated total number of arms was determined by randomly placing a 2x2 centimeter window and counting the number of arms visible in the window. When possible, ten non-overlapping placements of the window were conducted for each sample. Every attempt was made to ensure windows were placed far enough away from each other so as not to count the same arm twice. The average number of arms per 2x2 centimeter grid was calculated for each piece. Total area of the piece was approximated and an overall estimate of number of arms per sample was determined. An arm to disc ratio was calculated for each piece of ophiuroid material by dividing the estimated total number of arms in a sample by the number of discs in the same sample. Finally, an overall estimated arm to disc ratio was determined by averaging the arm to disc ratios of the 32 pieces of indurated ophiuroid material.

A semi-quantitative taphonomic scale that includes seven discrete stages of disarticulation was formulated by Kerr and Twitchett (2004) in order to measure various states of ophiuroid preservation (Table 1). This taphonomic scale assigns fully articulated and complete ophiuroids to a Stage 0 while completely disarticulated ophiuroids are designated a Stage 6. These seven stages were used to classify the indurated ophiuroid material.

Actualistic Methods

Forty-eight live ophiuroids of the species *Ophiothrix angulata*, common in the Gulf of Mexico, were purchased from Gulf Specimen Marine Laboratories. They were stored in a 10-gallon marine aquarium filled with fresh-filtered, 33 ppt, seawater (HSW), aerated, and kept at room temperature (~ 24°C). Foam "coral" branches provided by the Gulf Specimen Marine Laboratories were used as substrate in the aquarium.

To simulate storm/wave motion a round tank with a diameter of 30.5 centimeters was fitted with a 24V motor and round water agitator (Fig. 6). A glass bell-shaped bowl was inverted and placed in the center of the tank to prohibit ophiuroids from moving to the center, where water movement is substantially decreased. Conditions inside the experimental tank were varied by changing at least one of the following factors with each run: (1) presence of sediment; (2) salinity; (3) temperature; and/or (4) speed of rotation. Figure 7 is a flow chart depicting available choices. Only one parameter was varied with each experimental run.

Sediment used in the tank was sold commercially by Quikrete and marketed as "Play Sand." Screened, washed, and dried, this sediment was chosen to help reduce incidence of biological contamination. The sand is well sorted, medium grained, and subangular to subround. For each experimental run that included sediment, 640 g of sediment were placed into the tank before starting the motor. The experimental tank

Stage	Appearance of ophiuroid skeleton
0	Fully articulated and complete.
1	Loss of ventral plates: oral shields, tooth papillae and jaws.
2	Arms begin to break off at/near the disk. At least one arm remains attached.
3	No arms attached to disk. Disarticulated arms begin to fragment.
4	Disk begins to fragment. Arm fragmentation continues.
5	Disk is completely disarticulated. Few, small arm fragments remain.
6	Complete disarticulation.

Table 1– Semi-quantitative disarticulation scale, from Kerr and Twitchett (2004).

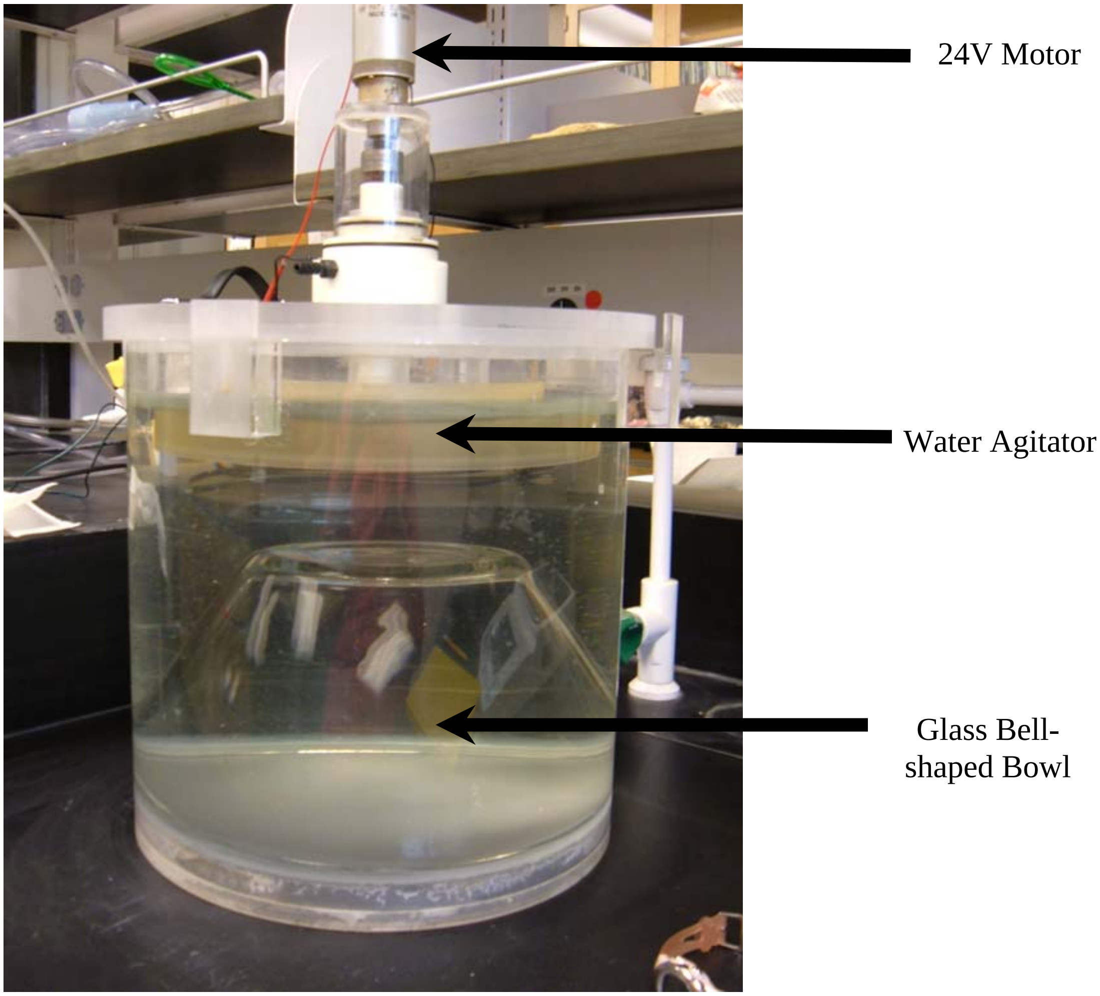


Figure 6—Experimental tank setup

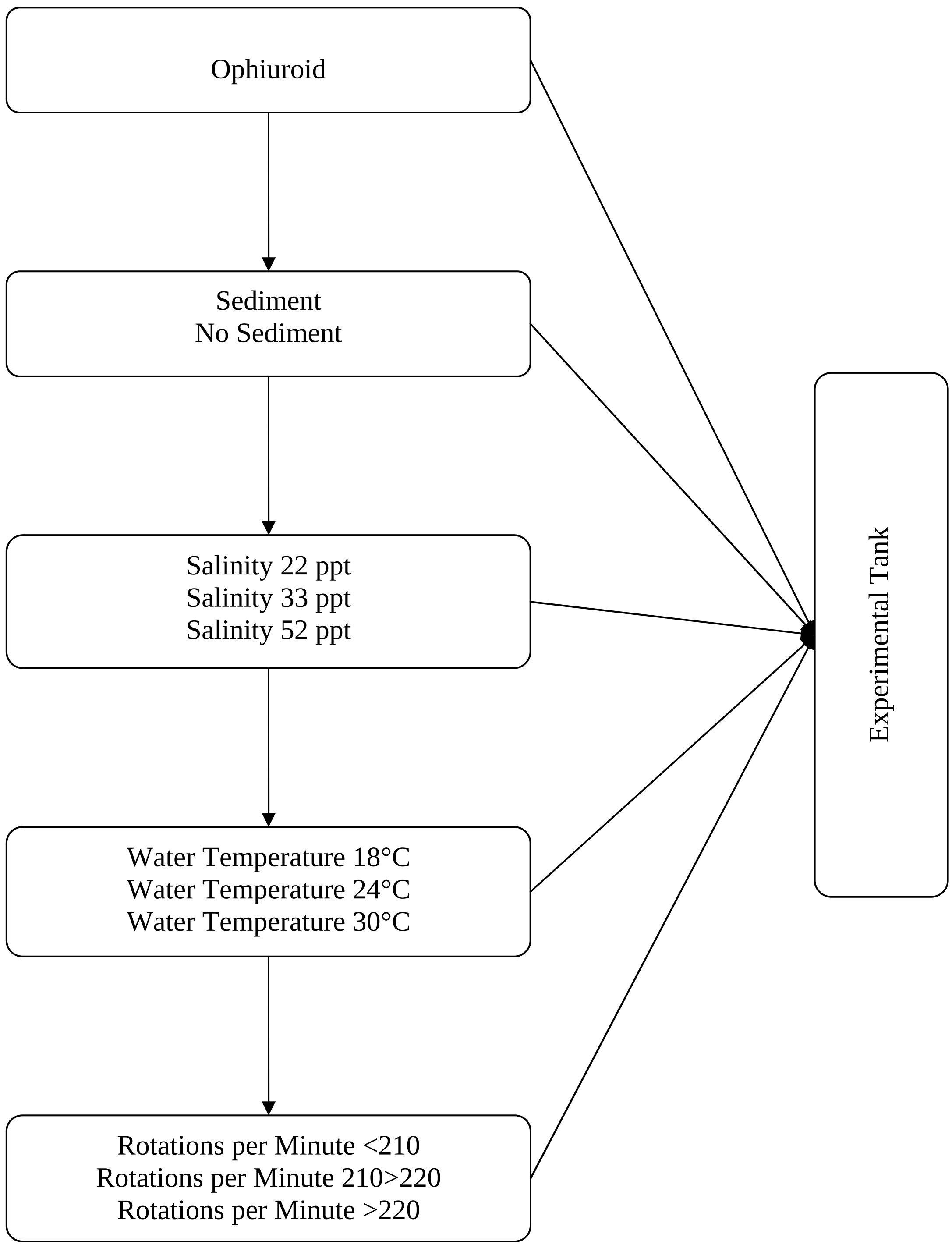


Figure 7—Flow chart indicating treatment methods employed in actualistic experiments. One item from each category was chosen as a condition in the experimental tank.

setup ran for two minutes before a live ophiuroid was released into the tank to ensure sediment was suspended in the current.

The amount of total suspended sediment was determined for each run of the experimental tank. Approximately 340 ml of water were removed while the experimental tank was running so as to capture the amount of suspended sediment. Samples were poured into a vacuum setup containing pre-weighed filter paper. Once the excess water was removed, the filter paper was placed in an oven for 48 hours to dry at a temperature setting of 1. After removal from the oven the filter paper was weighed again. The concentration of total suspended sediment (mg/l) was calculated by subtracting the weight of the filter paper (mg) from the weight of the filter paper plus sediment (mg) and dividing by the original sample volume (l).

Salinity was measured using an Aquatic Gardens Aquarium Hydrometer and Thermometer. Salinity of the water inside the experimental tank was increased to 52 ppt by the addition of Oceanic Natural Sea Salt Mix to fresh-filtered seawater (HSW). Salinity of the water was decreased to 18 ppt by the addition of fresh water.

Seawater temperature in the experimental tank was increased to 30°C by placement of an IKA EH4 basic suspended thermostat inside the tank. Seawater temperature in the experimental tank was reduced to 18°C by placement of quart-sized Ziploc® bags filled with crushed ice into the experimental tank. These bags were removed once the desired temperature was reached.

Rotations per minute of the water agitator were measured with a tachometer from Extech® Instruments. Rotations per minute were classified as either: (1) slow (<210 rpm); (2) medium (210 - 220 rpm); or (3) fast (>220 rpm).

Once components of the experimental tank setup were chosen (i.e. sediment, salinity, temperature, and rotations per minute) the motor was connected to a power source and was allowed to run for two minutes prior to the release of a live ophiuroid. The following measurements were recorded for each ophiuroid prior to release into the running tank: (1) weight; (2) longest-arm length; and (3) disc width. Once released the live ophiuroid was subjected to 180 minutes of motion. If an ophiuroid was able to bury itself in the sediment, the tank was shaken until the ophiuroid was uncovered and freely moving with the current. Only one live ophiuroid was used for each run.

At the end of each 180 minute run, the ophiuroid was removed from the experimental tank and placed in an individual holding tank for 24 hours. The individual holding tank contained aerated seawater with the same salinity and temperature as the experimental tank from which the ophiuroid had just been removed. The ophiuroid was closely observed for 4 hours for any signs of stress (i.e. autotomization, disarticulation). The ophiuroid was examined again after 24 hours for any further signs of stress. Ophiuroids that survived intact were then returned to the 10-gallon holding tank for later use.

Sympathetic Autotomization Analysis

Sympathetic autotomization is based on the supposition that like affects like. In this study, would arm autotomization by one ophiuroid cause imitation by another ophiuroid? To determine if sympathetic autotomization would occur, one arm of a live ophiuroid was compressed using a pair of tweezers until the arm was autotomized by the ophiuroid. After autotomization the injured ophiuroid was placed in a holding tank containing aerated, room temperature (24°C), 33 ppt salinity seawater. Two non-injured live ophiuroids were placed into the same holding tank with the injured ophiuroid. Ophiuroids were closely observed for two hours for signs of sympathetic autotomization. Ophiuroids were reexamined after 24 hours for signs of sympathetic autotomization.

Ophiuroid arm autotomization naturally occurs as a response to predatory attack. To determine if arm autotomization would occur in response to perceived danger, a live blue crab (*Callinectes sapidus*) was placed in a sealed individual plastic container drilled with numerous holes. The sealed individual plastic container was placed in a holding tank containing aerated, room temperature (24°C), 33 ppt salinity seawater. Three live ophiuroids were placed into the same holding tank as the live crab. The sealed plastic container prevented direct contact between the live blue crab and the live ophiuroids. Holes drilled in the plastic container allowed the transfer of water, oxygen, and any offensive/defensive chemicals produced by the live crab and/or the live ophiuroids. Ophiuroid behavior was closely observed for the first two hours in order to note reactions of the live ophiuroids to the predator. The live ophiuroids were again examined after 24 hours for evidence of autotomization.

Post Mortem Disarticulation Analysis

One ophiuroid that did not survive the 180 minute experimental tank run was placed in an individual clear holding tank containing non-aerated, room temperature (24°C), and 33 ppt salinity seawater. The clear holding tank was covered with a clear lid in order to prevent outside contamination and/or physical disturbance. Light was able to penetrate the clear container. The degree of post mortem disarticulation (spines, arms, and jaw structure) and the condition of connective tissue was assessed daily for 16 days.

RESULTS

Lithologic and Petrographic Data

Quartz constitutes the major portion of the detrital sand fraction in unconsolidated sediment samples TBS1–TBS19 from the Tirabuzón Formation . Most grains are angular to subround and medium to coarse grained. Feldspar and other accessory minerals are less common in the detrital sand fraction (Table 2). The pre-sieved unconsolidated sediment is grayish-orange (10YR 7/4) (The Rock Color Chart Committee, 1991) and generally fines upward through the section. Mud content gradually increases from the base towards the top of the unit with some fluctuations. Overall mud content in the section ranges between 21.3%, found in unconsolidated sediment sample TBS11, to 51.9%, found in unconsolidated sediment sample TBS18. Figure 8 shows the changes in composition and grain size for the measured section from the Tirabuzón Formation.

Sediment sample TBS16 represents the only indurated sediment sample collected from the same arroyo in the Tirabuzón Formation. Located 22.8 meters from the base of the measured section, this moderately indurated sediment sample was collected immediately below a thin shell bed. Attempted removal of mollusc shells was unsuccessful as they were extremely fragile. Dissolution of the calcium carbonate mollusc shells is the likely source for the cement binding this moderately indurated, yet moderately friable, sediment sample.

The indurated float samples collected near the top of the arroyo in the Tirabuzón Formation located at 27° 21' 714"N, 112° 17' 094"W are limestone. Based on the classification scheme of Folk (1962) the bioclast-rich indurated float material from the

	TBS 1	TBS 2	TBS 3	TBS 4	TBS 5	TBS 6	TBS 7	TBS 8	TBS 9	TBS 10	TBS 11	TBS 12	TBS 13	TBS 14	TBS 15	TBS 16	TBS 17	TBS 18	TBS 19
Description																			
Height from Base of measured section (m)	0	1.5	3.0	4.5	6.1	7.6	9.1	10.6	12.2	13.7	15.2	16.7	18.3	19.8	21.3	22.8	24.4	25.9	27.4
Induration	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	MI	U	U	U
Percent Quartz	84	76	83	72	80	79	85	93	59	78	87	94	89	66	71	40	6	53	92
Percent Feldspar	15	20	10	10	10	20	9	5	5	20	10	5	5	5	5	0	0	1	8
Percent Rock Fragments	0	0	4	15	8	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Percent Foraminfera (planktonic & Benthic)	0	3	2	2	0	0	5	3	35	0	3	0	6	28	23	59	93	45	0
Percent Other	1	1	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	1	1
Sedimentological Chraracteristics																			
Percent Sand	76.7	69.0	69.3	72.9	73.7	64.4	64.2	58.9	71.0	73.1	78.7	77.1	69.9	67.2	71.7	63.9	66.9	48.1	57.6
Percent Mud	23.3	31.0	30.7	27.1	26.3	35.6	35.8	41.1	29.0	26.9	21.3	22.9	30.1	32.8	28.7	36.1	33.1	51.9	42.4
Iron Staining	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	Yes	No	No	No	No	No	No	No
Sorting	VPS	VPS	VPS	EPS	VPS	VPS	EPS	VPS	VPS	VPS	VPS	MS	EPS	VPS	VPS	MS	VPS	MS	EPS
Roundness	SA	SR	SA	SA	SA	SA	A	SA	A	SR	SR	SA	SA	A	SA	SA	SA	SA	SA

Index: U = Unconsolidated, MI = Moderately Indurated, VPS = Very Poorly Sorted, MS = Moderately Sorted, EPS = Extremely Poorly Sorted, A = Angular, SA = Subangular, SR = Subrounded

Table 2—Lithology of sediment samples TBS1-TBS19 collected from the measured section of the Tirabuzón Formation.

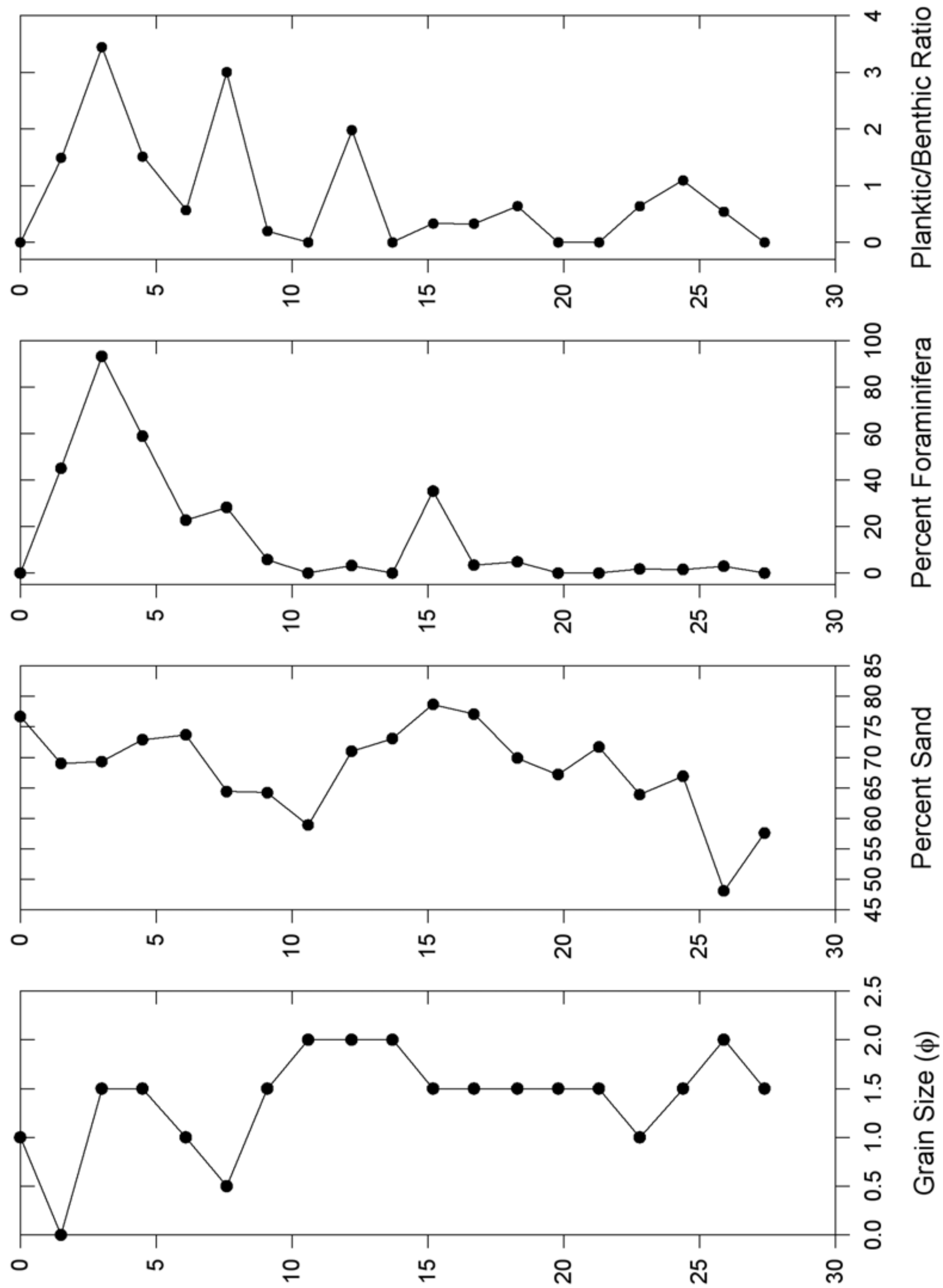


Figure 8—Visual representation of grain size, percent sand, percent Foraminifera, and planktic/benthic ratio for sediment samples TBS1-TBS19 from the measured section of the Tirabuzón Formation.

Tirabuzón Formation can be either an ophiuroid poorly-washed biosparrudite or biomicrudite (Table 3). Dunham's (1962) classification of carbonate rocks would name this an ophiuroid-bearing packstone.

Petrographic examination of thin sections made from two pieces of the indurated float material establishes that ophiuroid bioclasts are the primary component in the indurated float samples although trace amounts of quartz, micrite, and calcite spar are present as well (Fig. 9). The thin sections illustrate the high degree of ophiuroid arm articulation. Staining of the thin sections with Alizarin Red S permitted the calcite ophiuroid bioclasts to be identified.

Two types of initial porosity, interparticle and intraparticle, are observed. The well developed pores exceed 10 percent volume of the limestone. Interparticle porosity is slightly reduced by microcrystalline calcite (micrite) giving it a "dusty" appearance. Intraparticle porosity is reduced by micrite growth of equant calcite crystals that fills fine pores of the ophiuroid vertebrae and spines, thereby allowing them to remain visible in thin section. Single-crystal syntaxial cement surrounds some of the ophiuroid ossicles. Porosity reduction due to mechanical compaction was not observed.

Paleontological and Taphonomic Data

Eleven species of benthic Foraminifera were identified in 13 of the 19 sediment samples (TBS1- TBS19) taken from the Tirabuzón Formation (Table 4). Test preservation of the Foraminifera ranged from poor to excellent and many specimens were stained from the high iron content in the sediment. Poor foraminiferal test preservation suggests that partial dissolution of Foraminifera tests has occurred. Euhedral rhomb growth on the outer surface of some of the foraminifer tests may be due to this

Thin Section	TBTS001	TBTS002
Percent Micrite	8	10.5
Percent Spar	13	6
Percent Allochem	66.5	73
Percent Void Space	12.5	10.5
Total Percent	100	100
Rock Name	Poorly-Washed Biosparrudite	Poorly-Washed Biomicrudite

Table 3—Thin section data and Folk (1962) classification of indurated ophiuroid samples collected near the top of the Tirabuzón Formation.

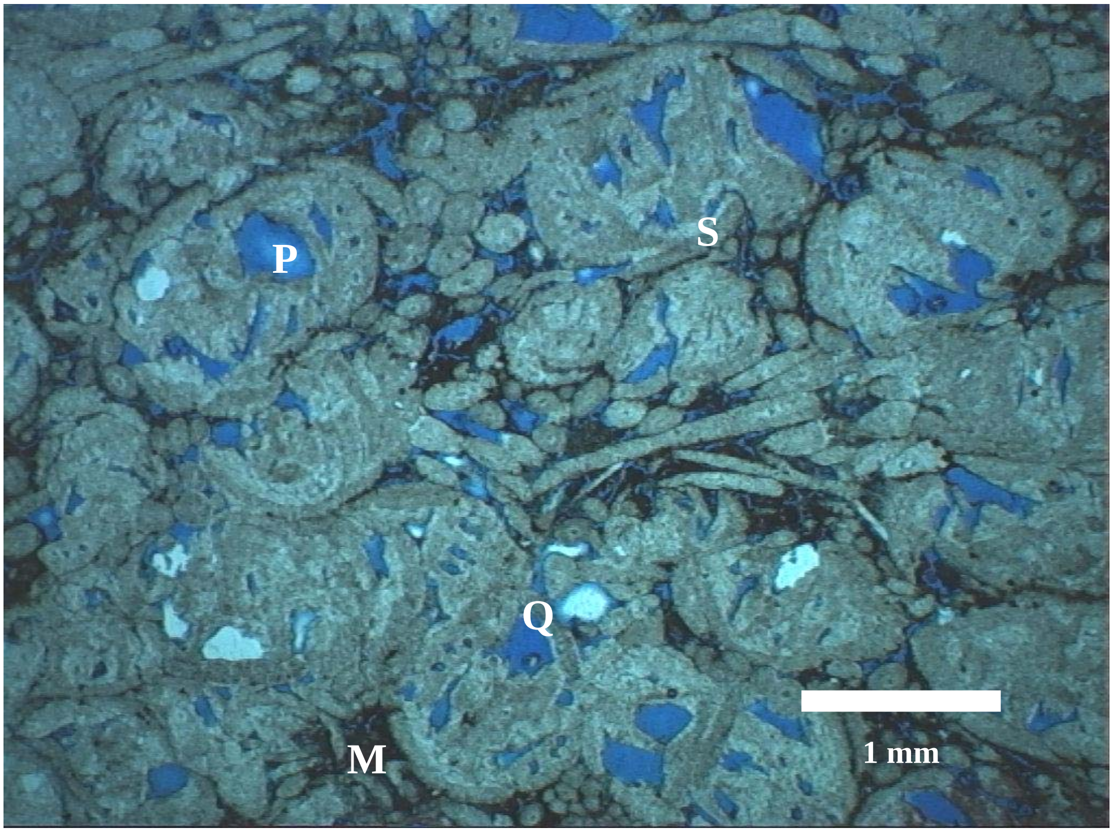


Figure 9—Photomicrograph of thin section, ophiuroid Lagerstätte, collected near the top of the Tirabuzón Formation. Note presence of cuts through both the long and short axis of the ophiuroid spines. White represents quartz (Q), blue represents porosity (P), dark areas represent micrite (M), light gray represents spar (S).

microfossil dissolution.

Of the 13 samples of unconsolidated sediment containing Foraminifera, only samples TBS16 and TBS17 had a higher incidence of number of Foraminifera to terrigenous grains. Sample TBS17, in particular, was of great interest. After wet sieving, 26.7g (62%) of the original 39.9 g sample remained. This remaining 62% contained a ratio of 14:1 planktonic Foraminifera to terrigenous grains (Fig. 10). Few nanofossils were observed in the mud fraction of the unconsolidated sediment sample. The high percentage of planktonic Foraminifera, which are typically found in the pelagic zone (open-ocean), coupled with the presence of nanofossils in the mud fraction classifies this unconsolidated sediment sample to be a deep-sea calcareous ooze. In comparison, 11 of the remaining 12 unconsolidated sediment samples have a higher incidence of terrigenous grains to planktonic Foraminifera; the range varies from 62:1 to 1.2:1 with an average of 6:1.

Continued comparison of terrigenous grains to Foraminifera shows a dramatic change between unconsolidated sediment samples TBS8 and TBS10. Sample TBS8 has a ratio of 28:1 terrigenous grains to Foraminifera; sample TBS9 has a ratio of 2:1 terrigenous grains to Foraminifera; and sample TBS10 contains no Foraminifera (Fig. 10). A steady increase in the number of Foraminifera coupled with a decrease in the number of terrigenous grains begins at sample TBS11 and continues up section to TBS19 (Fig.10).

The fossil assemblage found in the indurated ophiuroid material appears to be monotaxic with ophiuroids as the sole constituent. The dense clustering of ophiuroids in

	TBS 2	TBS 3	TBS 4	TBS 6	TBS 7	TBS 8	TBS 9	TBS 11	TBS 13	TBS 14	TBS 15	TBS 16	TBS 17	TBS 18	TBS 19	Depth Range
Megafauna																
Echinoderm (spines)	X	X	X		X	X	X	X		X	X	X	X	X	X	
Microfauna																
Benthic Foraminfera																
Bolivina pseudobeyrichi	X	X							X							400 – 1300m
Cibicides basiloba	X	X	X	X		X				X						40 – 900m
Nonionella stella	X	X	X	X		X		X	X	X	X	X	X	X		12 – 950m
Bolivina pacifica	X	X		X		X	X		X	X	X					90 – 950m
Globobulimina pacifica	X	X		X							X					128 – 3050m
Textularia schencki	X		X				X	X	X	X	X	X	X			11 – 350m
Bolivina interjuncta	X	X	X	X		X	X	X		X			X			270 – 1000m
Uvigerina attenuata		X		X		X	X							X		275 – 1000m
Elphidium articulatum							X	X								11 – 350m
Virgulina californensis	X						X									
Rotalia sp.	X							X	X	X	X	X	X	X	X	
Planktonic Foraminfera	X	X	X		X	X	X	X	X	X	X	X	X	X	X	
Ostracods			X						X				X			

Table 4–Table of taxa identified in unconsolidated sediment samples TBS1-TBS19 collected from the measured section of the Tirabuzón Formation.

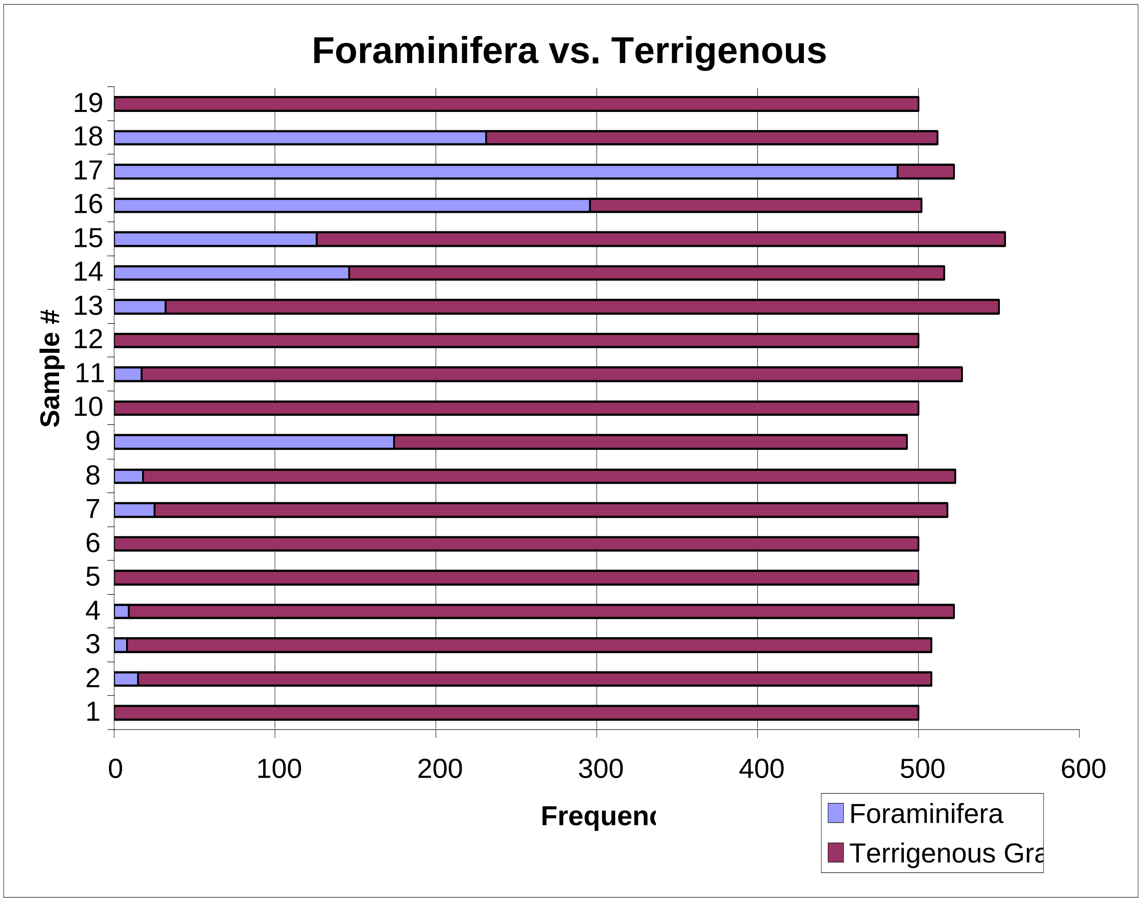


Figure 10—Ratio of Foraminifera to terrigenous grains in sediment samples from the measured section of the Tirabuzón Formation.

the indurated float material makes it difficult to determine exactly how many individuals are represented. Nearly equal amounts of the ophiuroids are preserved in normal (aboral surface up) and inverted (oral side up) orientations.

Ophiuroids were identified as *Ophiocnemis* using Fell (1960) and Smith et al. (1995). Diagnostic characteristics included: (1) broad, triangular radial shields; (2) an articular pit on the radial shield and a ball-like condyle on the genital plate; (3) aboral plating distinct from arm plating; (4) vertebrae united and fused throughout; (5) single large dorsal plates; (6) lateral arm plates at base of the arm confined to oral surface; (7) lateral arm spines well-developed, erect, and extending outwards from arms; (8) cylindrical primary arm spine shape; (9) oral papillae absent; and (10) lower surface of disc covered by fine scales.

Rounded positive relief features were found on several pieces of the indurated ophiuroid material. Less than one centimeter in height, these raised-relief features may be sole casts. Other pieces of the indurated material display a slight cup-shape. These pieces of indurated material may be the result of filling of impressions made in the sediment by the impact of objects in the current or by wave scouring of the seafloor.

Five of the 32 pieces of indurated ophiuroid material provided by MPRI and/or collected from the Tirabuzón Formation were examined for preferred arm orientation. Lack of *in situ* orientation information for these five pieces prevented comparison with each other. When examined individually, arm orientation on the five selected samples of indurated ophiuroid material appears polymodal, with three predominant directions. The Rayleigh test was used to evaluate the significance (at 0.05) of the vector mean. The calculated vector magnitude was greater than the critical value for the number of observations in three of the five individual pieces examined (Table 5, Fig. 12). Based upon these findings the sample is considered to be from a population with a preferred orientation (Lindholm, 1987).

As previously noted, ophiuroids exhibit pentameral symmetry with five arms joined to the oral side of the central body disc. The samples of indurated material from the Tirabuzón Formation indicate an anomalous ratio of arms to discs. An estimate of 10,042 arms was calculated from the 32 pieces of indurated ophiuroid material studied. Additionally, 66 ophiuroid discs (equivalent to jaw structures) were visible on the non-weathered surface of the material. The data suggest a ratio of 152 (complete to near complete) arms for each disc exists (Table 6).

None of the ophiuroids in the indurated material from the Tirabuzón Formation appears to be complete. Instead, ophiuroid arms in these samples appear to have been broken off from the central discs. Although separated from each other, the arms and jaw structures do exhibit exceptional preservation on their own. The four plates that surround the vertebral ossicles in the arms, along with arm spines that extend perpendicular from the vertebrae, remain articulated (Fig. 13). The 66 jaw structures (discs) also appear to be articulated. No evidence of abrasion on skeletal elements was observed. Most of the ophiuroid discs observed in the samples still had at least one full arm attached. These observations suggest that the ophiuroids in the indurated ophiuroid samples from the Tirabuzón Formation should be assigned to either stage two or three of Kerr and Twitchett (2004).

Actualistic Data

Thirty-five separate runs of the experimental tank setup using 35 live ophiuroids

Sample Number	MPRI0026	MPRI0024	TBI014	TBI016	TBI015
Number of Points	78	97	95	52	86
Class Interval (size)	30	30	30	30	30
Vector Mean	-28.21	2.06	18.26	-25.96	17.94
Angular Deviation	±66.80	±68.77	±61.35	±64.58	±69.44
Vector Magnitude	24.99	27.13	40.54	18.96	22.84
Preferred Orientation using the Rayleigh Test	No	Yes	Yes	No	Yes

Table 5—Preferred orientation data calculated by Rose 2.1.0 software program (Todd Thompson Software).

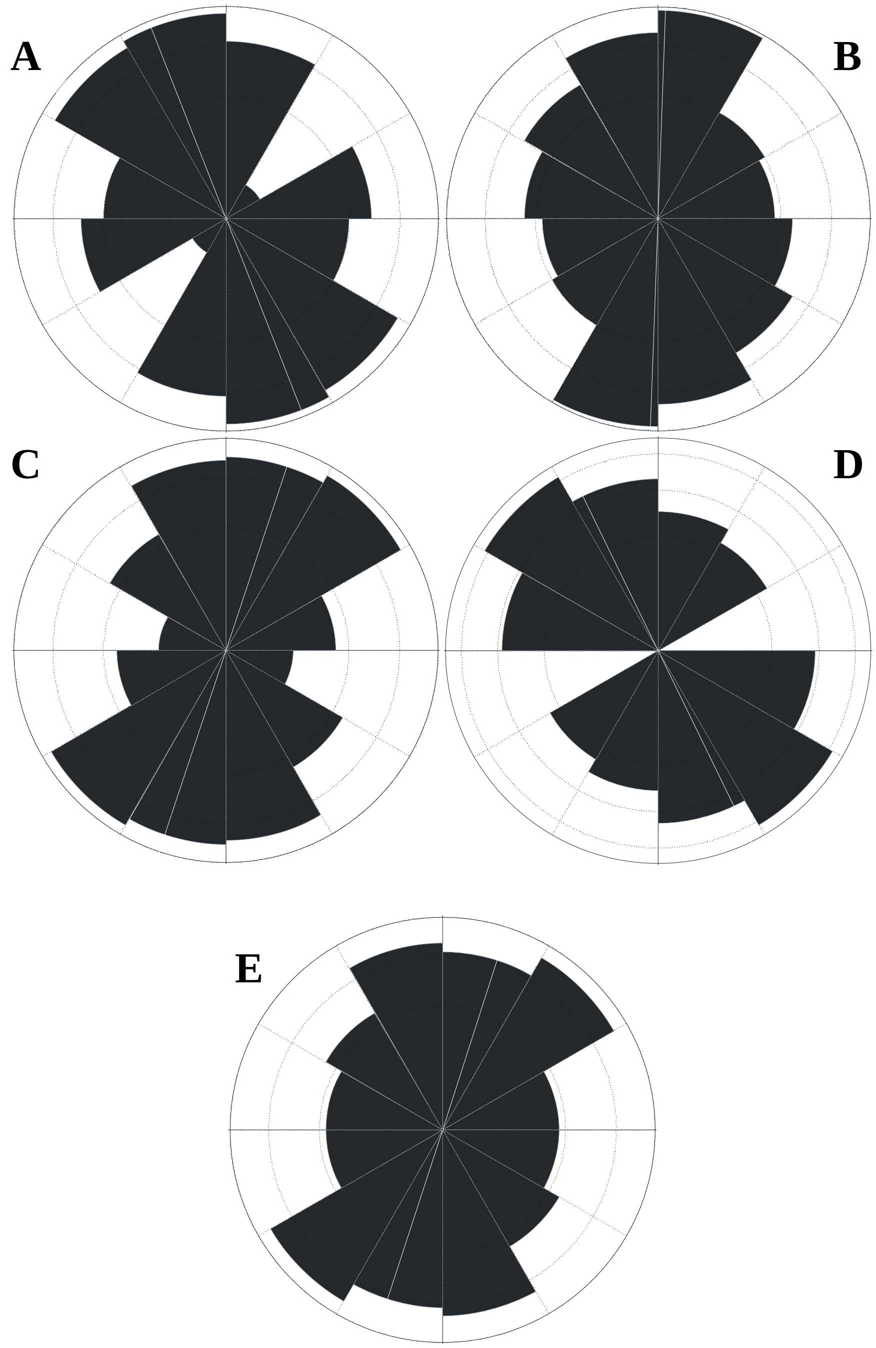
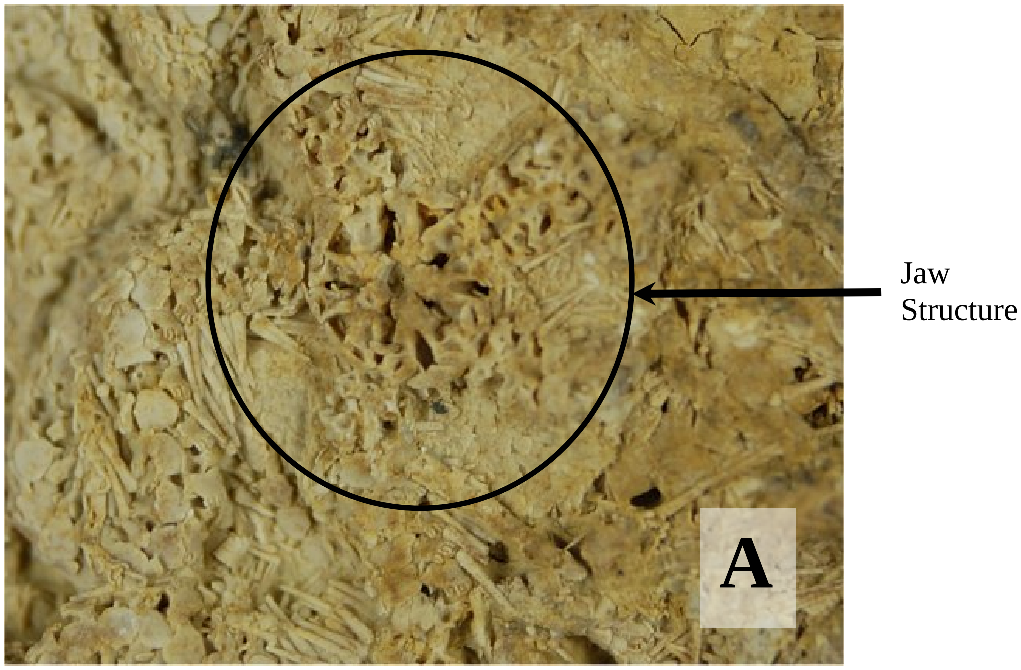


Figure 11—Rose diagrams of arm orientation data from indurated ophiuroid samples: (A) MPRI0026; (B) MPRI0024; (C) TBI014; (D) TBI016; and (E) TBI015.

Sample Number	Size (centimeters^2)	Average Estimated Number of Arms (1x1 centimeters^2)	Estimated Arms per Piece	Number of Disks Counted	Estimated Arm/Disk Ratio
TBI-001	252	7.4	1858.5	14	132.8
TBI-002	70	7.4	519.8	4	129.9
TBI-003	36	TW	TW	TW	TW
TBI-004	72	TW	TW	TW	TW
TBI-005	9	7.8	69.8	0	
TBI-006	21	TW	TW	TW	TW
TBI-007	9	TW	TW	TW	TW
TBI-008	258	6.1	1573.8	8	196.7
TBI-009	27	6.6	178.9	1	178.9
TBI-010	8	TW	TW	TW	TW
TBI-011	148.5	7.8	1150.9	4	287.7
TBI-012	153	6.7	1017.5	2	508.7
TBI-013	20	6.3	126.7	1	126.7
TBI-014	42	7.2	301.0	6	50.2
TBI-015	36	TW	TW	TW	TW
TBI-016	60	7.5	448.1	3	149.4
TBI-017	12	TW	TW	TW	TW
MPRI0023	42	8.3	350.0	1	350.0
MPRI0024	24	8.5	205.0	2	102.5
MPRI0025	28	5.6	156.3	4	39.1
MPRI0026	16	5.5	88	0	
MPRI0027	32	9.7	309.3	0	
MPRI0028	20	9.4	187.0	3	62.3
MPRI0029	15	7.3	108.8	0	
MPRI0030	36	TW	TW	TW	TW
MPRI0031	21	7.4	156.2	1	156.2
MPRI0032	30	10.4	312.5	5	62.5
MPRI0033	20	6.3	125	0	
MPRI0034	15	9.3	185.8	0	
MPRI0035	12	9.4	1125.5	0	
MPRI0036	12	7.6	91.5	0	
MPRI0037	66	6.9	457.1	7	65.3
Total Number of Indurated Samples	32				
Estimated Total Number of Arms	10,042				
Total Number of Disks Counted	66				
Average Estimated Number of Arms to Disks	152				

Table 6—Estimated arm to disc ratios. TW=Too weathered for assessment.



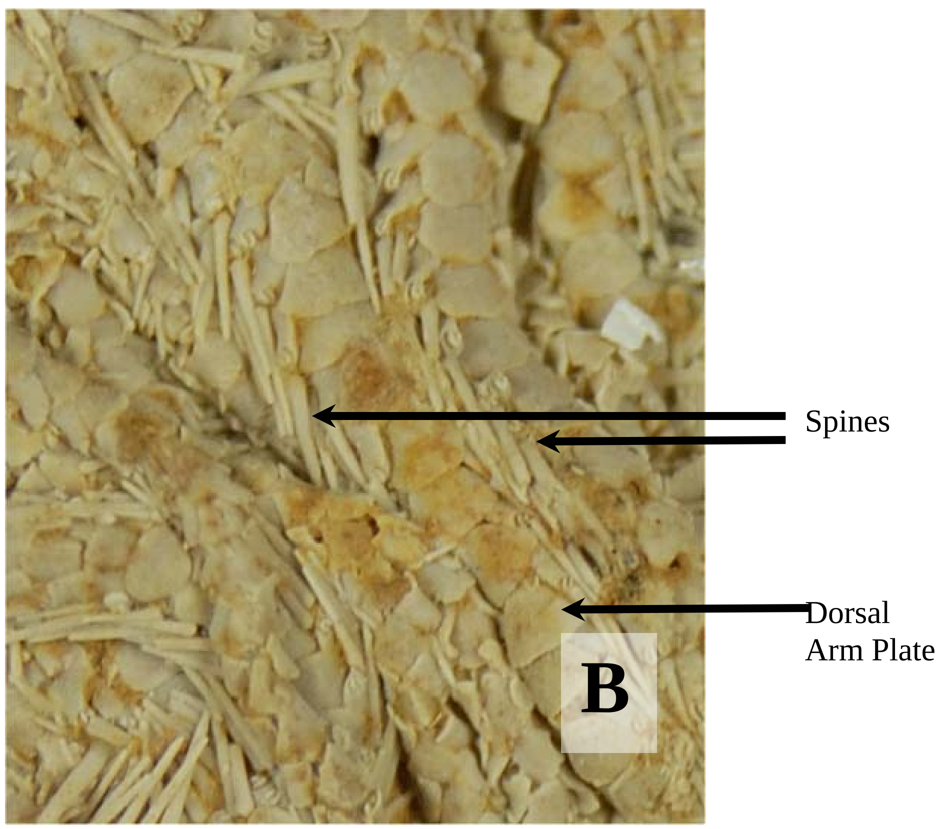


Figure 12—Articulation of ophiuroids within the indurated ophiuroid material collected near the top of the Tirabuzón Formation. (A) Jaw structure and (B) leg articulation.

were conducted. Once released into the running experimental tank containing fresh-filtered seawater (HSW), each live ophiuroid flailed its arms in an attempt to grab on to the substrate. After approximately 30 minutes of unsuccessful attachment attempts the live ophiuroid changed body posture, resembling an upside down jellyfish, with oral side of the disc facing upward and all five arms raised above the disc. Ultimately, the ophiuroid curled into a ball-shaped configuration with the arms curled beneath the oral surface, possibly as an attempt to protect the jaw structure. This ball-shaped posture caused the live ophiuroid to remain closer to the bottom of the running experimental tank where it tumbled along the substrate. After approximately 30 minutes the ophiuroid extended two or three of its arms for one minute or less in an attempt to grab onto the substrate. After unsuccessful attempts at attachment, the ophiuroid returned to the ball-shaped posture. After 90 minutes the ophiuroid remained in this ball-shaped posture and rarely extended its arms.

The amount of total suspended sediment in the running experimental tank was calculated for each experimental run and found to range from 0 mg/l to 235 mg/l depending upon speed of seawater rotation within the tank. The presence or absence of sediment in the running experimental tank appeared to have no effect on the 35 live ophiuroids used in the actualistic experiments, including timing of curling posture.

On the other hand, changes in seawater temperature appeared to have an effect on the curling behavior of the live ophiuroids. In warmer seawater (30° C) and much cooler seawater (18°C) the live ophiuroids kept an open posture (all arms extended outwards from the central disc) for much longer. The ophiuroid arms were more rigid than in the room temperature (24°C) seawater, which may explain why it took longer to adopt the curled posture.

Changes in seawater salinity produced similar results. Both lower salinity (22 ppt) and higher salinity (53 ppt) caused arm rigidity. However, curling of the arms into a ball-shaped posture occurred more rapidly than in 33 ppt fresh filtered seawater (HSW).

After placement in the individual holding tank each ophiuroid behaved slightly differently. Most of the live ophiuroids had difficulty righting themselves correctly, i.e. oral side down. A few ophiuroids remained curled in the ball-shaped posture for hours while others uncurled almost immediately and crawled to the corners of the individual holding tank.

Once removed from the running experimental tank that contained warmer (30°C) seawater the ophiuroids were lethargic, could not right themselves, and lost arm spines much easier. Additionally, the ophiuroid tube feet were unable to cling to the substrate. After removal from cooler seawater (18° C), the ophiuroids had difficulty attaching to the substrate and continued to be lethargic even after 24 hours.

After placement in the individual holding tank only two of the 35 ophiuroids used in the actualistic experiments displayed autotomization. The first ophiuroid to autotomize had undergone the 180 minute testing method in 33 ppt, 24°C, fresh-filtered seawater (HSW). Partial autotomization of one arm began 30 minutes after placement in the individual holding tank. Initially, one centimeter of one arm was lost from the total arm length of 2.49 centimeters. The autotomized portion of the ophiuroid arm continued to twitch for several hours after detachment. Over the next couple of hours the same arm that autotomized continued to break apart into smaller pieces. During this period the other arms remained intact. When only 0.4 centimeters of the autotomized arm remained attached to the central disc, initiation of autotomization in the remaining four arms followed in the same manner. Within 48 hours the five ophiuroid arms had completely disarticulated into 42 separate pieces and the ophiuroid perished. The disarticulated arm pieces were scattered around the bottom of the holding tank although there was no externally created physical disturbance, suggesting that the ophiuroid continued to move around the tank during autotomization and possibly until the time of death.

The second ophiuroid to autotomize was removed from the running experimental tank containing low salinity (22 ppt), 28°C, seawater after 180 minutes and placed into an individual holding tank that contained seawater with the same salinity and temperature as the tank from which it had been removed. Unlike the previous ophiuroid that displayed autotomization, concurrent autotomization of all five arms began within four hours of removal from the running experimental tank. Within 36 hours the ophiuroid had autotomized portions of all five arms and only 0.3 centimeters of each 1.89 centimeters arm remained attached to the disc at the time of death.

Overall, six of the 35 live ophiuroids that were used in the actualistic experiments perished as follows:

1. The first ophiuroid died after 180 minutes in the running experimental tank setup with 33 ppt, 24°C seawater. This ophiuroid was later used for investigation of post mortem disarticulation.
2. Two ophiuroids died after varied rates of autotomization of all five arms as described above.

3. Death occurred within 24 hours for a live ophiuroid that had been placed in the running experimental tank containing higher (52 ppt) salinity seawater. Post mortem examination of the dead ophiuroid subjected to the high salinity seawater revealed that even post mortem the arms remained flexible and extended outward from the central disc. The arm spines also remained flexible and attached to the arms. Slight pressure from tweezers did not affect the arm.
4. Two ophiuroids used in separate runs of the experimental tank containing lower salinity (22 ppt) seawater died. Post mortem examination of the two dead ophiuroids that were individually subjected to the lower salinity seawater revealed that the arms were extremely rigid even post mortem. The arm spines were stiff and radiated outward, perpendicular to the arms. When subjected to slight pressure by tweezers the arms broke apart easily.

Sympathetic Autotomization Observations

No evidence of sympathetic autotomization was noted in the experiment with the injured ophiuroid. After forced autotomization of one arm with tweezers was completed the injured live ophiuroid was released into a holding tank with two non-injured live ophiuroids. Much activity by the two non-injured ophiuroids occurred in the first 20 minutes after release of the injured live ophiuroid into the same holding tank. Initially the two non-injured ophiuroids rapidly moved away from the injured ophiuroid towards the far side of the tank. The two non-injured ophiuroids climbed the sides of the tank towards the water’s surface. After 20 minutes the non-injured ophiuroids moved closer to the injured ophiuroid. One non-injured ophiuroid climbed on top of the injured live ophiuroid and remained in that position for a little over 2 hours.

Three live ophiuroids, placed in the holding tank with the sealed plastic container holding the blue crab (*Callinectes sapidus*), showed no evidence of autotomization in response to perceived danger. In fact, the three ophiuroids climbed repeatedly over the top and along the outside of the sealed plastic container that held the blue crab.

Post mortem Disarticulation Observations

An ophiuroid that did not survive a 180 minute experimental tank run in 33 ppt, 24°C seawater was examined for 16 days post mortem. After five days post mortem the ophiuroid skeleton was still intact but the arms began to lose structure and became jelly-like. Dead ophiuroid disarticulation began on day six when short portions (<1 centimeter) of one ophiuroid arm disarticulated. The arm spines were still attached to the disarticulated pieces of the arms and the jaw structure was unaffected. By day seven the arms disarticulated easily as the tissue holding the arm together decayed. However, the spines remained attached and the tube feet were still recognizable. Ossicle disarticulation was noted on day 10. Total disarticulation of arms was completed by day 14.

DISCUSSION

Environmental Interpretation

Unconsolidated sediment samples from the Tirabuzón Formation contain a high abundance, yet low diversity, benthic foraminiferal assemblage. Eleven species of benthic Foraminifera were found in the unconsolidated sediment samples. Stratigraphic ranges of these 11 species span from the Upper Cretaceous to the Holocene. Three species of Foraminifera were most abundant in the unconsolidated sediment samples: (1) *Virgulina californensis*, which is most abundant in the Miocene; (2) *Bolivina interjuncta,* which is most abundant from the late Miocene through the late Pliocene; and (3) *Uvigerina attenuata,* which is most abundant in the middle Pliocene (Natland, 1950). Based upon the benthic Foraminifera, the Tirabuzón Formation is assigned to a late Miocene-middle Pliocene age. Although varying percentages of benthic Foraminifera indicate slightly changing environments, the high frequency of *Bolivina interjuncta* and *Uvigerina attenuata* suggest these unconsolidated sediment samples were deposited in 200-500 meters of water depth (Natland, 1950). This interpretation is in agreement with current work by Carreño and Smith (2007).

On the basis of petrographic examination and the high abundance of ophiuroid ossicles, the indurated limestone float from the Tirabuzón Formation is interpreted to have been deposited in an environment with clear, shallow water, low turbidity, and normal marine salinity. The high frequency of echinoid spines and mollusc fragments in all but two of the sediment samples (Table 4) indicates that most of the Tirabuzón Formation was likely deposited in the sublittoral zone (<200 meters depth) (Boardman, et al., 1987).

Geologic maps and position of the indurated float material in the arroyo suggest that the source of the indurated float material occurs stratigraphically higher in the section than where the unconsolidated sediment samples were collected. The difference in depositional water depth between the ophiuroid bed(s) and unconsolidated sediment samples can most likely be attributed to the continued relative fall of sea level. Analysis of the formations that overly the Tirabuzón Formation supports the premise that sea level was falling. The Infierno Formation, consisting of sandstone and conglomeratic sand (Carreño and Smith, 2007), was deposited in shallower water than the Tirabuzón Formation. Above the Infierno Formation lies the Pleistocene Santa Rosalía Formation. This formation grades from a marine sandstone into consolidated non-marine sediments (Carreño and Smith, 2007).

Paleoecological Interpretation

The indurated ophiuroid material from the Tirabuzón Formation exhibits a very dense, monotaxic assemblage. The same conditions were noted for an ophiuroid bed from Ohio by Kessling and Le Vasseur (1971). The only other fossils found in the Ohio ophiuroid bed included one short crinoidal stem and one fragment of a crinoid arm. Kessling and Le Vasseur (1971) suggest that high density and low diversity in this fossil assemblage may be attributed to the feeding effectiveness of the dense ophiuroid community which consumed larval forms of potential food-supply competitors before they had the opportunity to settle. Huge quantities of food would be necessary for the dense population of ophiuroids to survive. Kessling and Le Vasseur (1971) quote Reese (1966) as stating that dense populations of ophiuroids are often found associated with tidal currents where there exists a steady flow of suspended food.

Taphonomic Interpretation

Kerr and Twitchett (2004) noted that the degree of disarticulation observed in fossilized ophiuroids is not directly related to the nature and distance of transportation. Although substantial transportation may have occurred, full articulation is still possible if the ophiuroids were alive or recently dead when transportation occurred. Kidwell and

Baumiller (1990) noted that disarticulation of the fragile skeletons occurs more rapidly if echinoderms are subjected to physical disturbance or higher temperatures. In the present experiment it was shown that at 24° C the arm connective tissue began to lose structure within five days post mortem and disarticulation of the spines and ossicles began within six days. Disarticulation of the jaw structure was not observed even 15 days post mortem. The detached ophiuroid arms found in the indurated material from the Tirabuzón Formation display a high level of articulation and the skeletal elements lack evidence of abrasion indicating that little, if any, transportation occurred once necrolysis began.

Kerr and Twitchett (2004) noted that in order to retain a high degree of articulation the speed of interment is important for preservation of organisms with multi-element skeletons. In the warmer waters of the Pliocene Gulf of California (Natland, 1950) the ophiuroid's connective tissue would have decayed rapidly and the individual ossicles would have scattered under normal conditions. A blanket of sediment covering the ophiuroids would protect them from physical or biological disturbance during necrolysis. Without rapid burial the high degree of articulation found in the Tirabuzón Formation indurated material would not be possible. This degree of articulation provides strong evidence that rapid interment with limited residence time on the sea floor occurred.

The high degree of articulation found in the detached arms also suggests the site of this mass mortality event remained undisturbed following deposition. Disturbance by either the redistribution of sediment through reworking or by the turning or mixing of the sediment by living organisms (bioturbation) would have broken apart the ophiuroid skeletons, thereby reducing the degree of articulation. These factors combined suggest that the ophiuroids found in the indurated material from the Tirabuzón Formation: (1) did not undergo decomposition prior to interment; (2) were rapidly buried based upon the preservational characteristics of the indurated samples; and (3) neither reworking nor bioturbation occurred post mortem. In addition, the almost identical degree of disarticulation throughout the ophiuroid bed(s) indicates it was a single living population rather than a time averaged population.

Origin of Ophiuroid Lagerstätte Deposits

As stated earlier, Nebelsick (2004) noted that echinoderm Lagerstätte deposits are created in three principal ways: (1) smothering of organisms by mass flow deposits (obrution); (2) deposition in oxygen deficient (anoxic) or hypersaline environments; and (3) storm-generated deposits (tempestites). If the ophiuroid deposit located in the Tirabuzón Formation was an obrution deposit the live ophiuroids would have been caught up in the mass flow and buried. As the ophiuroids tumbled in the flow of sediment the arms would curl in an attempt to protect the central disc, based on the actualistic experiments conducted in this study. Once settled, if the blanket of sediment was >5 centimeters thick the ophiuroids may not have been able to escape. Additionally, uncurling of the ophiuroids arms would be difficult due to the weight and compaction of the overlying sediment. Preferential direction of the arms would likely not exist. Additionally, a copious amount of sediment would be included with the ophiuroids in the obrution deposit. Petrographic examination of the indurated material from the Tirabuzón Formation revealed that little sediment was present. Therefore, the evidence strongly suggests that an obrution deposit was unlikely.

Anoxic events occur when the oceans become deprived of oxygen due to a rise in water temperature and an increase in atmospheric CO_2 levels. They can also occur as a result of the reduced flow of water. The accumulation of dead plants and organisms resulting from anoxic events creates organic rich black shales. No organic rich shales are associated with the Tirabuzón Formation. The continued opening of the Sea of Cortez would have promoted the circulation of fresh seawater. The flow of normal marine seawater would also prevent the occurrence of hypersaline conditions. Therefore, it is unlikely that the ophiuroids perished as a result of either anoxic or hypersaline conditions.

On the other hand, if the living population of Baja ophiuroids inhabited an area associated with a shallow tidal current and deposition occurred during a storm event, a hyposaline situation might be likely as fresh water runoff from the storm could lower the salinity of the water relatively close to shore. Ravelo et al. (2006) investigated Pliocene sea surface temperatures in the equatorial Pacific Ocean using foraminiferal assemblages derived from Ocean Drilling Program sediment cores. Oxygen isotope signatures derived from Foraminifera tests provide evidence that Pliocene North American temperate regions were significantly warmer than today. These warmer temperatures weakened westerly trade winds, thereby allowing warmer water to flow eastward. The build-up of warmer water, also known as El-Niño Southern Oscillation, produced strong tropical storms. Heavy rainfall from these massive storms would cause an increase in sediment load carried by rivers flowing to the sea. The inundation of fresh water from high rainfall coupled with increased sediment load may have periodically altered the salinity and turbidity in this area. Given that rapid sediment influx and burial are cited as factors that promote the preservation of articulated, multi-element skeletons such as ophiuroids (Brett and Baird, 1986), these sudden changes could account for the ophiuroid Lagerstätte.

Strong bottom currents and high energy waves are associated with strong storms. Strong currents that scour the sea floor could transport dense populations of ophiuroids to a location where the current waned. The entrained ophiuroids would tumble repeatedly in these energetic conditions, causing entanglement of the ophiuroid limbs. As noted in the actualistic experiments of this study, the ophiuroids exposed to hyposaline water experienced: (1) rigidity of the arms; (2) inability to attach to the substrate; (3) lethargic disposition; and/or (4) death. When squeezed with tweezers, the arms of the ophiuroids subjected to low salinity water broke very easily. Thus, breakage of the rigid appendages from the central disc would likely occur as a result of influx of fresh water during the storm event. Additionally, the cup-shaped positive-relief features noted on some of the indurated float material collected from the Tirabuzón Formation could be due to ophiuroids filling in scour marks created by the strong waves and currents.

The hydrodynamic properties of both complete ophiuroids and disarticulated portions would be much different. Sorting of the more lightweight, elongate arms from the flat-sided central discs would occur as a result of the intense current action. The elongate arms would align perpendicular with wave direction or parallel to the current direction; preferential direction would be expected (Brett and Baird, 1986). Ophiuroids that did not suffer arm loss would continue to remain unstable on the seafloor and churn in the waves. On the other hand, the discs that had lost arms would be more stable in the moving sediment if positioned flat on the seafloor. Sorting of the elongate arms from the flat central discs could account for the abnormal arm to disc ratio in the Tirabuzón samples.

Summary

At the beginning of this thesis I proposed three hypotheses for the formation of this ophiuroid Lagerstätte:

1. The ophiuroid mass mortality event occurred as a result of a strong storm, such as a hurricane.
2. Fresh water inundation and high turbidity associated with the storm caused a high-stress setting, which promoted ophiuroid disc autotomization.
3. Disc autotomization and preferential sorting led to the anomalous ratio of ophiuroid discs to arms found in the indurated samples from the Tirabuzón Formation.

It can be concluded that the first of the three hypotheses appears to be valid. The following lines of evidence suggest that this ophiuroid Lagerstätte is the result of a storm deposit and fresh water inundation: (1) depositional environment of the indurated material; (2) interpretation of El Niño conditions during the Pliocene that would have promoted storm activity; (3) preferred orientation of the arms in the indurated material; and (4) arm rigidity and breakage in response to hyposaline water in the actualistic experiments.

On the other hand, the second hypothesis, that fresh water inundation and turbidity would cause the ophiuroids to autotomize their discs, was shown to be an invalid hypothesis based on results from the actualistic experiments. Although exposed to stressful conditions, at no time during any of the actualistic experiments did an ophiuroid autotomize a central disc. The anomalous ratio of arms to discs appears to be a result of exposure to fresh water, which caused the arms of the ophiuroid to become quite fragile. Additionally, the ophiuroids did not appear to be affected by up to 235 mg/l of suspended sediment.

Finally, evidence suggests the third hypothesis is partially valid. Although the ophiuroids did not autotomize their central discs, breakage of the ophiuroid arms as a result of exposure to hyposaline water likely accounts for the anomalous ratio of arms to discs. Strong waves and bottom currents associated with a storm event coupled with the different hydrodynamic properties of the flat ophiuroid discs and elongate arms would cause preferential sorting.

CONCLUSIONS

1. The unconsolidated sediment in the Tirabuzón Formation was deposited during a period of relative sea level rise and at a depth of 200-500 m. The maximum flooding surface occurs near sample TB-17. Sea-level apparently declined higher in the section, resulting in the shallow marine and non-marine deposits of the overlying Infierno and Santa Rosalía formations.
2. The indurated ophiuroid material collected from the Tirabuzón Formation is interpreted to have been deposited in an environment with clear, shallow water, and a normal marine setting.
3. The fossil assemblage appears to be monotaxic. Ophiuroids were identified as *Ophiocnemis* sp.
4. The ophiuroids in the Tirabuzón Formation are well preserved and assigned to stages two and/or three using the taphonomic scale proposed by Kerr and

Twitchett (2004). Although most arms are detached from the central disc, individual arms remain fully articulated.

5. The high degree of articulation of the ophiuroid skeletons contained within the indurated material from the Tirabuzón Formation suggests: (1) the ophiuroids did not undergo decomposition prior to interment; (2) rapid burial is strongly implied based upon the preservational characteristics of the indurated material; and (3) neither reworking nor bioturbation occurred post mortem.
6. During the actualistic experiments, exposure to both high salinity seawater (53 ppt) and low salinity seawater (22 ppt) caused ophiuroid arm rigidity and rapid curling of the arms. Post mortem examination of the ophiuroids subjected to high salinity seawater (53 ppt) showed that the arms remained flexible. Post mortem examination of ophiuroids subjected to low salinity seawater (22 ppt) showed that the arms remained extremely rigid. Slight pressure applied to the arms caused the arms to break.
7. The ophiuroid Lagerstätte deposit is interpreted as a storm deposit based on the following evidence: 1) high concentration of ophiuroid skeletons; 2) deposition within a shallow water, near shore setting, 3) appearance of preferred orientation of arms and 4) response of ophiuroids to the actualistic experiments.
8. Neither sympathetic autotomization nor autotomization as a result of perceived danger appears to have played a role in this ophiuroid Lagerstätte.

LITERATURE CITED

Allison, P.A., and Briggs, D.E.G., 1991, Taphonomy: releasing the data locked in the fossil record: Plenum Press, New York, 560 p.

Aronson, R.B., 1989, Brittlestar beds: low-predation anachronisms in the British Isles: Ecology, v. 7, p. 856-865.

Boardman, R.S., Cheetham, A.H., and Rowell, A.J., 1987, Fossil Invertebrates: Blackwell Science, Cambridge, MA, 713 p.

Brett, C.E., and Baird, G.C., 1986, Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation: Palaios, v. 1, p. 207-227.

Brett, C.E., and Seilacher, A., 1991, Fossil lagerstätten: a taphonomic consequence of event sedimentation: *in* Einsele, G., Ricken, W., and Seilacher, A., eds., Cycles and Events in Stratigraphy: Springer-Verlag, Berlin, p. 283-297.

Carreño, A.L., 1982, Biostratigraphy at the Loma del Tirabuzón (Corkscrew Hill), Santa Rosalía, Baja California Sur, Mexico: Proceedings – North American Paleontological Convention, v. 3, p. 67-69.

Carreño, A.L., and Smith, J.T., 2007, Stratigraphy and correlations for the ancient Gulf of California and Baja California peninsula, Mexico: Bulletins of American Paleontology, No. 371, 146 p.

Cobb J.L.S., and Stubbs T.R., 1981, The giant neurone system in Ophiuroids. I. The general morphology of the radial nerve cords and the circumoral nerve ring: Cell and Tissue Research, v. 219, p. 197-207.

Fell, H.B., 1960, Synoptic Keys to the Genera of Ophiuroidea: Zoology Publications from Victoria University of Wellington, No. 26, 44 p.

Fielman, K.T., Stancyk, S.E., Dobson, W.E., and Jerome Clements, L.E., 1991, Effects of disc and arm loss on regeneration by *Microphiopholis gracillima* (Echinodermata: Ophiuroidea) in nutrient-free seawater: Marine Biology, v. 111, p. 121-127.

Folk, R.L., 1962, Spectral subdivision of limestone types: *in* Ham, W.E., ed., Classification of Carbonate Rocks – a symposium: American Association of Petroleum Geologists Memoir 1, Tulsa, p. 62-84.

Folk, R.L., 1974, Petrology of Sedimentary Rocks: Hemphill Publishing Co., Austin, 182 p.

Goldring, R., and Stephenson, D.G., 1972, The depositional environment of three Starfish Beds: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 1972, p. 611-624.

Hendler, G., Miller, J.E., Pawson, D.L., and Kier, P.M., 1995, Sea stars, sea urchins and allies: echinoderms of Florida and the Caribbean: Smithsonian Institution, Washington, DC, 392 p.

Instituto Nacional de Estadística, 1993, Santa Rosalia G12A36, 1:50,000, Aguascalientes, Mexico.

Kerr, T.J.V., and Twitchett, R.J., 2004, Experimental decay and disarticulation of *Ophiura texturata*: implications for the fossil record of ophiuroids: *in* Heinzeller, T., and Nebelsick, J.H. eds., Echinoderms: München: A.A. Balkema Publishers, London, p. 439-446.

Kesling, R.V., and Le Vasseur, D., 1971, *Strataster ohioensis*, a new Early Mississippian brittle-star, and the paleoecology of its community: University of Michigan Museum of Paleontology Contributions, Ann Arbor, v. 23, p. 305-341.

Kidwell, S.M., and Baumiller, T., 1990, Experimental disintegration of regular echinoids: roles of temperature, oxygen, and decay thresholds: Paleobiology, v. 16, p. 247-271.

Kranz, P., 1974, Anastrophic burial of bivalves and its paleoecologic significance: Journal of Geology, v. 82, p. 237-265.

Ledesma-Vázquez, J., 2002, A gap in the Pliocene invasion of seawater to the Gulf of California: Revista Mexicana de Ciencias Geológicas, v. 19, p. 145-151.

Lindholm, Roy C., 1987, A practical approach to sedimentology: Allen and Unwin, London, 276 p.

Makra, A., and Keegan, B.F., 1999, Biology and environment: Proceedings of the Royal Irish Academy: v. 99B, p. 95-102.

Natland, M.N., 1950, Report of the Pliocene and Pleistocene Foraminifera *in*: 1940 E.W. Scripps cruise to the Gulf of California. Geological Society of America Memoir 43, part IV, p. 1-53.

Nebelsick, J.H., 2004, Taphonomy of Echinoderms: introduction and outlook: *in* Heinzeller, T., and Nebelsick, J.H. eds., Echinoderms: München: A.A. Balkema Publishers, London, p. 471-477.

Phleger, F.B., 1964, Patterns of living benthonic Foraminifera, Gulf of California. *in*: van Andel, Tj.H., and Shor, Jr., G.G. eds. Marine geology of the Gulf of California, a symposium: American Association of Petroleum Geologists Memoir 3, Tulsa, p. 377-394.

Ravelo, A.C., Dekens, P.S., and McCarthy, M., 2006, Evidence for El Niño-like conditions during the Pliocene: GSA Today, v. 16, p. 4-11.

Reese, E.S., 1966, The complex behavior of echinoderms: *in* Boolootian, R.A., Physiology of Echinodermata, Interscience Publishers, New York, p. 157-218.

Seilacher, A., Reif, W.E., Westphal, F., Riding, R., Clarkson, E.N.K., and Whittington, H.B., 1985, Sedimentological, ecological and temporal patterns of fossil Lagerstätten: Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, v. 311, p. 5-24.

Smith, A.B., Paterson, G.L.J., and Lafay, B., 1995, Ophiuroid phylogeny and higher taxonomy: morphological, molecular and palaeontological perspectives: Zoological Journal of the Linnean Society, v. 114, p. 213-243.

Stancyk, S.E., Golde, H.M., Pape-Lindstrom, P.A., and Dobson, W.E., 1994, Born to lose. I. Measures of tissue loss and regeneration by the Brittlestar *Microphiopholis gracillima* (Echinodermata: Ophiuroidea): Marine Biology, v.118, p. 451-462.

The Rock Color Chart Committee, 1991, Rock Color Chart: Munsell Color, distributed by the Geological Society of America, New York, 11 p.

Twitchett, R.J., Feinberg, J.M., O’Connor, D.D., Alvarez, W., and McCollum, L.B., 2005, Early Triassic ophiuroids: their paleoecology, taphonomy, and distribution: Palaios, v. 20, p. 213-223.

Wilson, Ivan F., 1948, Buried topography, initial structures, and sedimentation in Santa Rosalía area, Baja California, Mexico: Bulletin of the American Association of Petroleum Geologists, v. 32, p. 1762-1807.

Woodley, J.D., 1967, Problems in the ophiuroid water-vascular system: *in* N. Millot, ed., Echinoderm Biology: Symposia of the Zoological Society of London No. 20, Academic Press, New York, p. 75-103.

BIOGRAPHICAL SKETCH

René Anne Shroat-Lewis was born in New York City in August, 1964. Her family moved to West Palm Beach, Florida while she was an infant. Raised by her grandparents, William and Irene Martin, René had a very happy childhood. Some of her favorite memories are of fishing with her grandparents in a small town called Jensen Beach, Florida.

René graduated in 1981 from John I. Leonard High School and joined the United States Navy as a Gunners Mate. While in the Navy, she married and had two children, William and Richard. After serving 4 years active duty, René was Honorably Discharged and lived throughout southern California, including Long Beach, San Diego, and Camarillo.

In 1997, René decided to make a change in her life and started taking a few classes at the local community college. René eventually left her position as a housing officer and returned to school full-time. She moved to Wilmington, North Carolina to be closer to her family. While attending Cape Fear Community College she met Dr. Patricia H. Kelley and caught the paleontology bug. René, the first person in her family to attend university, earned her Bachelor of Science in Geology from the University of North Carolina Wilmington in 2005.

René's research interests include all things marine, though echinoderms remain her passion. In the fall of 2005, she began the Masters in Geology program at the University of North Carolina Wilmington, focusing on ophiuroid taphonomy.

René is the recipient of many distinguished awards including: The Association for Women Geoscientists Winifred Goldring Award; The Association for Women

Geoscientists Chrysalis Scholarship; the Association for Applied Paleontological Sciences James R. Welch Scholarship: and University of North Carolina Wilmington Department of Earth Sciences Victor A. Zullo Memorial Research Award, to name but a few.

René is a member of the Geological Society of America, Association for Women Geoscientists, The Paleontological Society, and Sigma Xi.

In her spare time, René is an avid scrapbook/life artist. To date she has completed over 25 personal scrapbooks with many more in the works. She loves spending time with her friends and believes that scrapbooking is the new “quilting bee.” She also enjoys traveling, riding roller coasters and watching chick-flicks. However, nothing compares to the amount of joy she gets from spending time with her sons, who luckily, also love traveling and riding roller coasters (although they’re not really fans of chick-flicks).

After completing her Master’s thesis, René moved to Knoxville, Tennessee to begin a doctoral degree in the Department of Earth and Planetary Sciences at the University of Tennessee. Eventually she would like to teach geology at the university level.