

ECOLOGY AND STRATIGRAPHY OF THE ECHINOIDS OF THE
OCALA LIMESTONE (LATE EOCENE)

MELVIN CROFT

CHEVRON USA, INC., NEW ORLEANS, LOUISIANA

and

GRAIG D. SHAAK

FLORIDA STATE MUSEUM, GAINESVILLE, FLORIDA

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I. ABSTRACT

The Ocala Limestone (Late Eocene) of Florida may be zoned using echinoids. In addition to biostratigraphic zonation, three separate echinoid communities may be recognized utilizing species differing in specimen size and substrate affinity. The communities present are: 1) a community of large echinoids, which are sand-dwellers; 2) a community characterized by mud-dwelling echinoids, as well as a few small species with affinities for a sandy substrate; and 3) a community of sand-dwelling echinoids of large size, the composition of which is different from that of community 1. The stratigraphic distribution of these three communities reflect physical changes in the environment of deposition, which may be explained by several hypotheses, but probably reflect a transgressive-regressive sequence.

II. INTRODUCTION

The echinoid fauna of the Ocala Limestone in northwestern peninsular Florida (Text-fig. 1) is abundant and diverse, yet

few studies have dealt with this fauna. The majority of previous works have been taxonomic, and none has concentrated exclusively on the ecology of the echinoid fauna. The purpose of this study is to explain the temporal distribution of echinoids within the Ocala Limestone.

The Ocala Limestone has been stratigraphically zoned in a variety of ways (Vernon, 1951; Puri, 1957; Cheetham, 1963; McCullough, 1969; Hoganson, 1972; Hunter, 1976; and Zachos and Shaak, 1978). The zonation proposed by Zachos and Shaak (1978), based on echinoids, is used in this study (Text-fig. 2).

The flat-lying Ocala Limestone crops out in two areas in Florida: northwestern peninsular Florida and the northern central panhandle. This study is limited to outcrops of peninsular Florida, which occur around the Ocala High. The outcrop pattern of the Ocala Limestone in this area exhibits an elongated northwest-southeast trending pattern, approximately 200 km long and 80 km wide. A structural high, flanked by younger deposits, is situated in the center of the Ocala outcrop pattern (Text-fig. 1).

EDITORIAL COMMITTEE FOR THIS PAPER:

DAVID J. BOTTJER, University of Southern California, Los Angeles, California
JOSEPH GHIOLD, Louisiana State University, Baton Rouge, Louisiana
PORTER KIER, U. S. National Museum, Washington, D.C.

Rock types of the Ocala Limestone include grainstones, packstones, and wackestones. These massive limestones are pure, cream to white, varying from soft, chalky, and friable, to hard and crystalline. Bedding in the Ocala is seldom apparent and portions are dolomitized. The Ocala is approximately 120 meters thick in northwestern peninsular Florida.

The Ocala Limestone is included in the Jackson Stage (Late Eocene) and Croft (1980) has correlated the formation, based on echinoids, with the P16 Foraminiferal Zone of Blow (1969). In northwestern peninsular Florida the Ocala Limestone lies unconformably above the Avon Park Limestone (Middle Eocene) and is overlain unconformably by the Suwannee Limestone (Oligocene).

The Ocala Limestone in northwestern peninsular Florida contains a diverse and abundant fauna. Irregular echinoids, gastropods, pelecypods, bryozoans, starfish (ossicles), ostracods, and foraminifera are common. Cheetham (1963) described 36 species of cheilostome bryozoa from the Ocala Limestone. Meeder (1976) reported 77 molluscan species from the Inglis Formation (Late Eocene). Puri (1957) reported a total of 142 foraminiferal species and 40 ostracod species from the Ocala. The most comprehensive summaries on the Ocala echinoids can be found in Cooke (1959), Fischer (1951), and Croft (1980). Thirty-two irregular echinoid species representing 16 genera are present in the Ocala Limestone. Four of these species were reported as new by Croft (1980).

Most modern irregular echinoids are extremely sensitive to the type of substrate in which they burrow and comparison of the functional morphology of fossil and modern echinoids can link each echinoid species to the type of substrate in which it most likely lived. Each of the 32 irregular echinoid species (Text-fig. 3) found in the Ocala Limestone are determined to have been sand-dwellers or mud-dwellers. The sand-dwelling echinoids are primarily restricted to the lower and upper Ocala, whereas the middle Ocala is characterized by a higher percentage of mud-dwelling echinoids and, more importantly, by lack of the large sand-dwelling echinoids. This observation indicates that substrate composition changed during deposition of the

Ocala from sandy to muddy, then back to sandy substrate. Such a change in bottom conditions is probably the result of varying water depths, indicative of a transgressive-regressive sequence.

III. BIOSTRATIGRAPHY

Ideally, planktonic organisms should be used to establish biostratigraphic zones in sedimentary beds. However, there are few planktonic organisms preserved in the Ocala Limestone; consequently, biostratigraphic zonation must be based on benthic organisms. Irregular echinoids may be used to zone the Ocala easily due to: 1) the relative abundance of irregular echinoids; 2) distinct breaks in the echinoid stratigraphic distribution; and 3) the ease of echinoid identification in the field.

Most echinoids species are adapted for specific substrate conditions, and consequently their stratigraphic distribution is strongly controlled by the lithofacies. The stratigraphic distribution of most echinoid species in the Ocala is a function of the substrate composition, and reflects an ecological zonation rather than a true time-evolutionary zonation. But there are exceptions. Zachos and Shaak (1978) proposed a zonation of the Ocala Limestone based on three species of *Oligopygus* (Echinoidea): *O. phelani* Kier, *O. haldemani* (Conrad) and *O. wetherbyi* de Loriol (Text-fig. 2). The stratigraphic distribution of these species of *Oligopygus* seems to be controlled little, if any, by the changing substrate types inferred for the Ocala during deposition; consequently, they probably represent a time evolutionary sequence (see Paleogeology section).

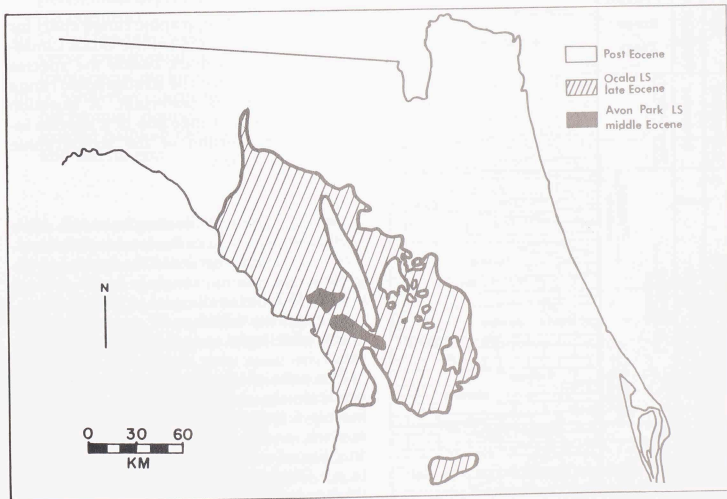
Due to the obvious ecologic control over most echinoid species of the Ocala Limestone, it is surprising that these three species seem to have been relatively unaffected by ecologic changes. However, changes in relative abundance suggest that the number of individuals (of *Oligopygus*) may have been affected by changing substrate conditions. Specimens of *O. phelani*, the first member of this lineage, are not abundant, perhaps because the species had not yet established itself in the community. A subsequent increase in specimens at the first occurrence of *O. haldemani* indicates the genus had begun to establish it-

self. *Oligopygus* reaches its lowest abundance in the middle Ocala, but increases again in the upper Ocala. This suggests that the muddy substrate conditions present at the time of deposition of the middle Ocala may have affected the ability of *O. haldemani* to compete, but obviously not to the same degree as most other echinoids found in the Ocala. The apparent ability of *Oligopygus* to withstand more hostile ecological conditions than other echinoids at that time make it an excellent zonal marker.

The three *Oligopygus* species divide the Ocala into three interval and two concurrent range zones (Text-fig. 2). There is little overlap in the ranges of these three species. The interval of rock containing both *O. phelani* and *O. haldemani* is generally only about one meter thick or less. The thickness of the interval of rock containing both *O. haldemani* and *O. wetherbyi* is uncertain, but is certainly no more than one or two meters. The intervals of rock containing the concurrent range zones are

rarely seen in outcrop, and for practical purposes only three interval range zones are used in this study: the *O. phelani*, *O. haldemani*; and *O. wetherbyi* biozones.

These three species of *Oligopygus* in the Ocala Limestone exhibit an evolutionary trend that can be traced easily. There are three morphological features that change with time; the shape of the peristomial depression, the position of the periproct, and test size; the latter increasing through time (see Table 1). *Oligopygus phelani*, found in the lower third of the Ocala, has a small, circular peristomial depression and the periproct is inframarginal (Text-fig. 4 A). *Oligopygus haldemani* found in the middle third of the Ocala, exhibits a transverse peristomial depression and the periproct is inframarginal (Text-fig. 4 B). *Oligopygus wetherbyi* from the upper third of the Ocala has a transverse peristomial depression as in *O. haldemani*, but the periproct is located about one half the distance to the peristome (Text-fig. 4 C).



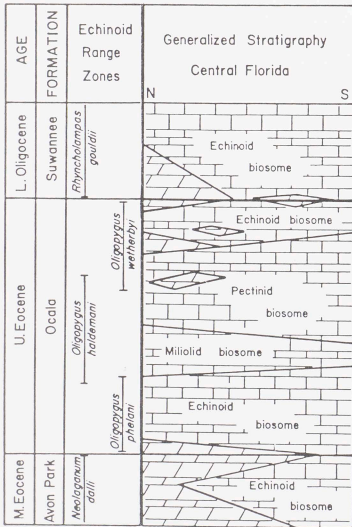
Text figure 1. Surface exposures of the Ocala Limestone in northwestern peninsular Florida (after Puri and Vernon, 1964).

IV. PALEOECOLOGY

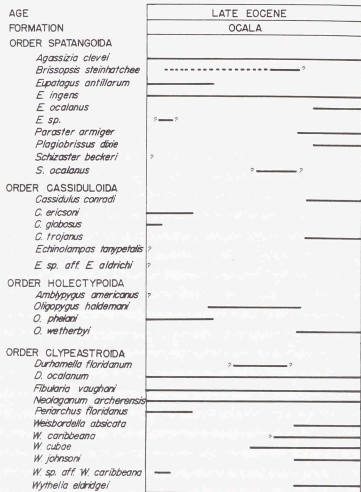
Paleoecological interpretations are based on fossil assemblages in the study strata. Biostratigraphic and taphonomic alteration of fossil assemblages must be recognized and interpreted before sound interpretations of the depositional environment can be determined (Fagerstrom, 1964). Biostratigraphic alteration is that resulting from predators, scavengers, and bottom currents. Taphonomic alteration includes replacement, leaching, and crushing of tests.

Factors that were evaluated to determine the amount, if any, of biostratigraphic alteration of the Ocala Limestone echinoid fauna are (1) size-frequency distributions, (2) ratio of whole to fragmental tests, (3) orientation of fossils, and (4) preservation of fossils.

Size-frequency distributions for echinoid populations of the Ocala are difficult to



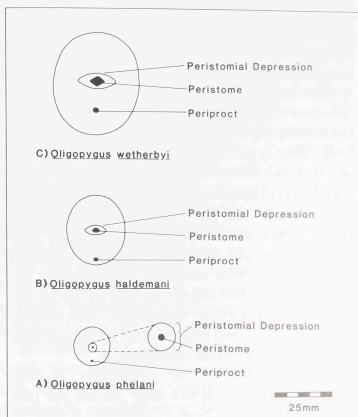
Text figure 2. Echinoid bistratigraphic zonation of the Ocala Limestone (Zachos and Shaak, 1978).



Text figure 3. Stratigraphic range chart for the irregular echinoids of the Ocala Limestone. A question mark beside the species name indicates that the stratigraphic range of that species is uncertain. A question mark beside the range line of a species indicates that portion of the stratigraphic range is uncertain.

quantify, as much collecting has to be done from spoil piles and float material; however, a typical echinoid assemblage includes specimens ranging from several mm to 100 mm in diameter. This observation suggests that few, if any, specimens were selectively removed by bottom currents.

The ratio of whole to fragmented tests is qualitatively estimated to be approximately 5:1, but this ratio varies between species, and is partially a function of test fragility of each species, as some species (e.g., *Oligopygus wetherbyi*) have much thicker tests than others (e.g., *Paraster armiger*). The tests of most echinoid species are seldom crushed, but the tests of *Periarachus floridanus* (Fischer) are nearly always broken, probably due to their large,



Text figure 4. Morphological variations in *Oligopygus* from the Ocala Limestone.

- O. phelani* – small test size, circular peristomial depression, and inframarginal periproct.
- O. haldemani* – medium test size, transverse peristomial depression, and inframarginal periproct.
- O. wetherbyi* – large test size, transverse peristomial depression, and periproct located halfway between the peristome and test margin.

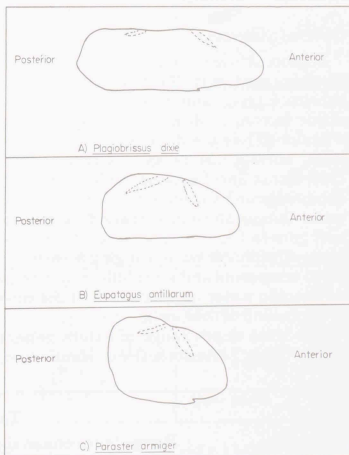
thin, flat construction. Tests of sand-dwelling echinoids of small size are often broken, a result of their fragile tests.

The effect of predation and scavenging on the whole to fragmented test ratio is not entirely known. Many different organisms, such as starfish, crabs, large fish, mammals, and gastropods prey upon echinoids and the remains of starfish (ossicles), crabs, and gastropods are common in the Ocala Limestone. Moore (1956) reported that three species of *Cassia*, a helmet conch, feed upon modern spatangoids. The gastropods bore through the echinoid test, producing a conspicuous round hole. Many Ocala Limestone echinoids display borings typical of preying gastropods.

The effect upon echinoids by preying starfish, crabs, fish, and mammals is un-

certain, but the predator probably crushes the echinoid test to feed upon it. Predation by gastropods would have little effect on the whole to fragmented test ratio, but predation by starfish, crabs, fish, and mammals would certainly decrease the ratio. The relatively high, whole to fragmented test ratio indicates minimal biostratigraphic alteration.

Generally, there is no preferred orientation of echinoid tests in the Ocala Limestone, indicating no selective deposition. Few echinoids are in life position. This observation indicates the presence of bottom currents strong enough to transport echinoid tests, but only for short distances. The test surfaces of most Ocala echinoids show little evidence of significant preburial transportation. Echinoid tests are generally fragile, and any significant preburial transportation would certainly destroy them. However, slightly crushed tests or pits and scratches on the outer surface in-



Text figure 5. Lateral views of a) *Plagiobrissus dixie*, b) *Eupatagus antillarum*, and c) *Paraster armiger*. The higher the posterior end of the test with respect to the anterior end, the deeper the echinoid burrows into the substrate (Nichols, 1959).

dicates that many of the echinoids have undergone minor preburial transportation. Specimens from the middle Ocala are less commonly broken than those found in the lower and upper Ocala.

With few exceptions, taphonomic alteration of the Ocala echinoid fauna is minimal. Most of the echinoids have been permineralized by calcite, and it is doubtful that any single population was selectively replaced. Areas of intense solution and dolomitization (diagenesis) reflect taphonomic alteration. In such areas, leaching and recrystallization, respectively, have obliterated most fossils. Most of the fossils found in the dolomitized rocks are preserved as molds.

The preceding qualitative evaluation indicates that the Ocala Limestone echinoid fauna lived, died, and was preserved at or near the site of deposition. Many specimens were probably moved short distances within the area of deposition, as indicated by abraded and broken tests, especially those of the large sand-dweller, *Periarchus floridanus*.

General Statement

Echinoids are stenotypic, vagrant, benthic organisms. Salinity, temperature, substrate type, and water depth are the major factors controlling their spatial distribution. They are dependent upon a constant, normal marine salinity (Booolootian, 1966; Ernst and Seibertz, 1977). Although echinoids can be used to make generalized water temperature interpretations, the extant genera found in the Ocala Limestone presently inhabit water ranging from tropical to temperate and yield little information on specific water temperatures at the time of deposition of the Ocala.

The wide depth range of extant genera in the Ocala Limestone (Beu, Hendersen,

and Nelson, 1972) gives no clues as to the precise water depth at the time of deposition. The distribution of echinoids is more dependent on substrate conditions than water depth. In part, this is due to their intimate relationship with the bottom for nutrient supply, waste disposal, and protection. The type of substrate suitable to any species is reflected in the test morphology (Nichols, 1959). Most modern echinoid species can live in a wide range of water depths, but most are restricted to a particular type of substrate. Fossil echinoids serve as excellent tools for determining the grain-size of the substrate on or in which they live. Irregular echinoids are predominantly infaunal organisms, although epifaunal forms are not uncommon.

The distribution of echinoids in the Ocala Limestone is not only useful for biostratigraphic zonation (Text-figs. 2 and 3), but also reflects changes in the environment of deposition of the Ocala Limestone. When one ties the sediment preferences of the echinoids to their stratigraphic distribution, the presence of three distinct communities can be recognized. These are here referred to as Community I (*Periarchus floridanus* - *Eupatagus antillarum* Community), Community II (*Agassizia clevei* Community), and Community III (*Wythella eldridgei* - *Paraster armiger* Community). These three communities will be defined later, but basically the species comprising these three communities differ in substrate affinity, specimen size, and abundance.

The inferred substrate type for the Ocala Limestone varies from clay- to sand-sized particles of carbonate composition. Sand-dwelling species are described as small or large (this report only), depending upon the most common test size. Those spatangoid and clypeasteroid species commonly

Table 1
Range in specimen size of *Oligopygus phelani*,
O. haldemani, and *O. wetherbyi*

	Test length (mm)	Test width (mm)	Test height (mm)
<i>Oligopygus phelani</i>	6-17	4-15	3-7
<i>Oligopygus haldemani</i>	9-35	7-30	4-15
<i>Oligopygus wetherbyi</i>	25-55	20-55	10-25

having a test length less than approximately 40 mm are considered small. Those commonly having a test length greater than approximately 60 mm are considered large. The cassiduloids, represented in the Ocala almost entirely by *Cassidulus*, are all sand-dwellers, and regardless of test size are restricted to Communities I and III. Communities I and III, as will be shown later, are composed almost totally of sand-dwelling echinoids. However, in order to follow the general size scheme of large and small echinoid species, an arbitrary value of 35 mm length has been selected to divide the cassiduloids into small and large species. Individual specimen size may vary beyond these arbitrary limits.

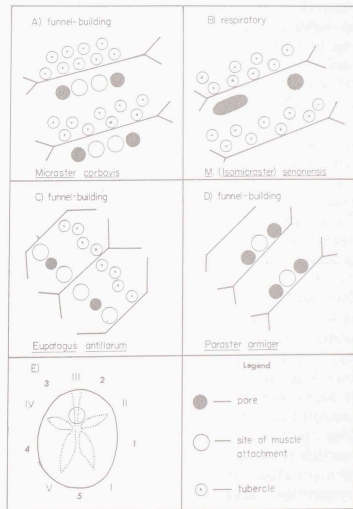
Echinoid test morphology normally reflects the type of substrate preferred by the organism and many of the Ocala echinoids exhibit morphological features indicating the original texture of the sediments. The most useful morphological features among the spatangoids are fascioles, ornamentation and pore size of the dorsal ambulacrum (III in Lovens system of numbering the ambulacral and interambulacral plates), and test shape. Comparisons with modern forms are also helpful. Estimates of the grain size of the substrate inhabited by the clypeasteroid species are based on functional morphology and analogues with modern forms. Determination of the type of substrate inhabited by the cassiduloids is based on comparison with modern forms.

Functional Morphology

The general test shape of *Eupatagus antillarum* is similar to that of many modern burrowing echinoids. The test is relatively high at the posterior end and low at the anterior end (Text-fig. 5B). Nichols (1959) interpreted the relatively higher posterior end as a trend towards deeper burrowing. Nichols also pointed out that many modern burrowing spatangoids, depending upon sediment grain-size, must maintain an open funnel to the sediment surface in order to obtain a supply of fresh oxygenated water to pass over the petaloid region, the location of the respiratory tube feet. The funnel is built and maintained by larger, specially adapted tube feet located in ambulacrum III (Text-fig. 6). Ridges or

bumps located around the pore for each of these tube feet mark the site of muscle attachments used in the operation of these larger tube feet (Text-fig. 6A). The smaller tube feet used for respiration have no need for the ridges or bumps flanking the pores from which they protrude (Text-fig. 6B).

Fossil echinoids that, when alive, built a funnel to the sediment surface can be recognized by the presence of such ridges or bumps in ambulacrum III. However, Smith (1980) reports that funnel-building tube feet are not necessarily muscular, and do not always have associated ridges or bumps. *Eupatagus antillarum* has such ridges in ambulacrum III (Text-fig. 6C) and, presumably, had a series of large tube feet, used to build and maintain the respiratory funnel.



Text figure 6. a-d) Morphology of ambulacrum III with respect to burrowing affinity (a and b from Nichols, 1959). e) Location of ambulacral plates in a-d, and Lovens system of numbering the ambulacral and interambulacral plates. I-V: ambulacras plates; I-5: interambulacral plates.

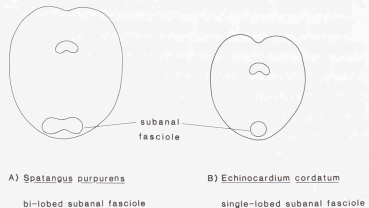
The fasciole is a narrow band of small densely ciliated spines; these cilia beating to create currents that augment normal body ciliatory currents used for respiration, nutrient gathering, and waste disposal. There are six basic types of fascioles – anal, subanal, internal, marginal, lateral, and peripetalous. Each fasciole, or combination of fascioles, reflects various modes of burrowing. *Eupatagus antillarum* has a lateral and subanal fasciole. The lateral fasciole would have aided normal body ciliation in drawing water down through the funnel over the petaloid ambulacra, indicating a burrowing habitat.

Eupatagus antillarum has a series of large tubercles on its aboral surface. By analogy with modern echinoids (Nichols, 1959) these spines maintained contact with the sediment surface during initial stages of burrowing, when a funnel would be most difficult to maintain, and may remain in contact with the sediment surface during burrowing. Echinoids that build a funnel to the sediment surface live in either a sandy or muddy substrate, not a shelly gravel (Nichols, 1959). The large interstices in a shelly gravel negate the need for a respiratory funnel, as water can easily be drawn through them.

In addition to a lateral fasciole *E. antillarum* has a single-lobed subanal fasciole. This indicates that *E. antillarum* was a sand-dweller, not a mud or shelly gravel-dweller. The subanal fasciole is used to build a small tunnel to the rear of the test for sanitary waste disposal. The size and shape of the tunnel is a function of the cohesiveness of the substrate. For stability, the tunnel is lined with mucus, secreted by the echinoid. A tunnel built in mud or shelly gravel requires less mucus per unit area to maintain than one in sand, due to the physical interlocking of large particles in the shelly gravel and flocculation in the mud (Nichols, 1959). Consequently, echinoids living in a shelly gravel or mud build and maintain two sanitary tunnels and exhibit a bi-lobed subanal fasciole (Text-fig. 7). Echinoids living in sand require more mucus per unit area to line the tunnel than in mud or shelly gravel; they build and maintain only one sanitary tube and exhibit a single-lobed subanal fasciole (Text-fig. 7B).

The test shape, the ornamentation of the fascioles together indicate that *E. antillarum* burrowed into a sandy substrate. The relationship of the posterior and anterior test height is an indication of burrowing depth. The higher the posterior end with respect to the anterior end, the deeper the echinoid burrows. *Paraster floridiensis* Kier and Grant, morphologically similar to *P. armiger*, burrows to a depth of approximately 25 cm (Chesher, 1966). *Plagiobrisus grandis* (Gmelin), morphologically similar to *P. dixie* (Cooke) (Text-fig. 5A), burrows to a depth of only several cm (Kier and Grant, 1965). *E. antillarum* is morphologically intermediate between *P. armiger* and *P. dixie* (Text-fig. 5B), it is estimated to have burrowed to a depth of approximately 5-10 cm.

Similar arguments can be made for *Paraster armiger* and *P. dixie* to show that they were sand-dwellers. *Paraster armiger* has a peripetalous, a lateral, and an anal fasciole. The presence of lateral and peripetalous fascioles, as well as a markedly higher posterior end than occurs in *E. antillarum* (Text-fig. 5C), indicates that *Paraster armiger* burrowed deeper than *E. antillarum*. Peripetalous and lateral fascioles together would produce stronger currents than a lateral fasciole alone. Consequently, water could be drawn down a longer funnel, allowing *Paraster armiger* to burrow deeper. The anal fasciole of *P. armiger* was used to build a single waste dis-



Text figure 7. Sketches of a) *Echinocardium cordatum* showing bi-lobed subanal fasciole, and b) *Spatangus purpureus* single-lobed subanal fasciole. (Taken from Nichols, 1959, Fig. 1.)

positional tunnel, much like the one built by *E. antillarum*. *Paraster floridiensis*, a modern species living in the Bahamas and Florida Keys, burrows in calcareous sand to depths of approximately 25 cm (Chesher, 1966). *Paraster armiger* probably burrowed to an equivalent depth. However, Kier (1975) reports *P. floridiensis* and *P. doederleini* living in mud, offshore Carrie Bow Cay, Belize.

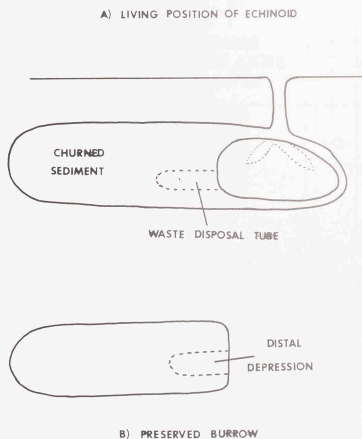
Plagiobrissus has a peripetalous and a single-lobed subanal fasciole. It differs from *Paraster armiger* and *E. antillarum* in that the anterior and posterior test ends are approximately equal in height (Text-fig. 5C). This morphology indicates that *Plagiobrissus dixie* was a shallow sand-burrower. *Plagiobrissus dixie* has a series of large tubercles located on its aboral surface similar to those found on the aboral surface of *E. antillarum*, suggesting a tuft of large spines used during initial stages of burrowing. However, these spines may have been for defense. The poor state of preservation of most specimens prohibits any conclusions based on

analysis of ambulacrum III. Kier (1965) found *Plagiobrissus grandis*, larger but morphologically similar to *P. dixie*, burrowing in shallow, relatively grassless sand. Functional morphology and the modern analogue indicate that *P. dixie* was a shallow burrower (several cm) in a sandy substrate.

Agassizia has a small, high globular test. Living species of *Agassizia* have been observed burrowing in mud (Clark, 1910) and sand (Mortensen, 1951). Substrate affinity and burrowing habitat are generally related to test morphology on a generic level; hence, most species of a particular genus have similar substrate and burrowing preferences. *Agassizia clevei* Cotteau was probably capable of burrowing into a sandy or muddy substrate. The mechanics governing the functional morphology is uncertain, but the affinity of *Agassizia* for both sandy and muddy substrates is possibly a function of its small test size. *Schizaster ocalanus* Cooke has a small, high, globular test similar to *Agassizia clevei*; therefore, it seems reasonable that *S. ocalanus* was also capable of burrowing into sandy or muddy substrates.

Brissopsis steinhatchee Cooke has a bilobed subanal fasciole and a peripetalous fasciole, indicating that it burrowed into a muddy substrate. *Brissopsis luzonica* (Gray) (Mortensen, 1951), *B. elongata* Mortensen (Kier, 1975), and *B. lyrifera* (Forbes) (Mortensen, 1977) are reported burrowing into muddy sediments.

If, in fact, the heart urchins (spatangoids) of the Ocala Limestone were burrowers, then it would seem logical to find preserved echinoid burrows. There are many organisms that burrow into the substrate in nearshore marine environments, and it is often quite difficult, if not impossible, to assign a fossil burrow to a specific organism. Vernon (1951) reported the occurrence of elongated tubular structures in the Ocala Limestone. These structures have been described as sponges, holothurians, concretions, and burrows. The tubes range in size from approximately 30 mm long and 10 mm in diameter to over 230 mm in length and 100 mm in diameter. Almost every tube has a small, elongated, circular, distal depression about 10-30 mm deep, which lies parallel to the long axis of the tube. The diameter of this depression



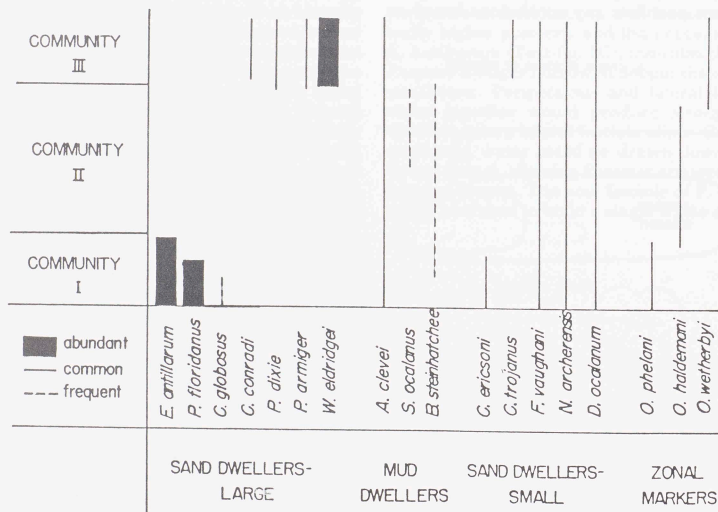
Text figure 8. Relationship between an echinoid burrow (a) and the tubes found in the Ocala Limestone interpreted as preserved echinoid burrows (b).

is typically one-half that of the tube diameter. These tubes may be preserved spatangoid burrows. The small depression in the end might be the remnants of the waste disposal tube (Text-fig. 8). The tubes are similar in appearance to those burrows described by Smith and Crimes (1983) as echinoid burrows (Subphyllochorda); however, the Ocala specimens lack the detail necessary to make a more positive identification.

Large and small tubes are commonly found in the rocks containing Communities I and III, which are typified by sand-dwellers of large and small size. Small tubes only are found in the rocks containing Community II, which are characterized by small echinoid species (see definition of Communities below). If these tubes are preserved echinoid burrows, then their stratigraphic distribution with respect to size and abundance correlates well with the stratigraphic distribution of the spatangoids.

These tubes lack whole or broken echinoid tests, but Ernst *et al.* (1973) stated that many modern spatangoids leave their burrows before dying. One specimen of *Eupatagus antillarum* was found attached to the end of a tube, but it is not certain if the echinoid was in a life position, although the tube was horizontally oriented, as most are, an indication that the echinoid was in a life position. This observation, the shape and structure of the tubes, and their stratigraphic distribution certainly imply that these tubes may be preserved echinoid burrows.

The substrate affinity of the clypeasteroids is based on functional morphology and modern analogues. They lack fascioles, which profoundly affect their burrowing habits. *Periarchus floridanus* (Clypeasteroidea) is a large, flat, circular sand dollar, commonly 70-115 mm in diameter. *Wythella eldridgei* Twitchell (Clypeasteroidea) is a smaller, elongated sand dollar ranging in test length from 10 to



Text figure 9. Stratigraphic range and abundance of 15 Ocala Limestone echinoid species with respect to their burrowing affinities and Communities I, II, and III. The zonation of Zachos and Shaak is also shown.

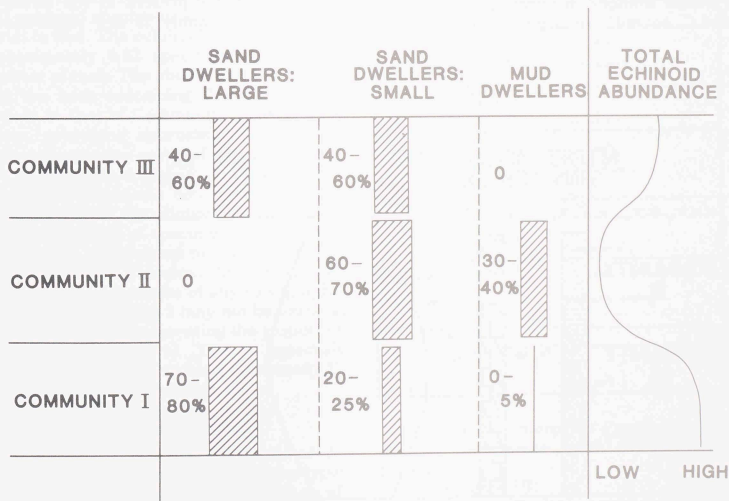
85 mm. Modern sand dollars, such as *Leodia*, *Mellita*, and *Encope*, which are morphologically similar to *P. floridanus* and *W. eldridgei*, burrow about 5 mm deep into the sand (Clark, 1910; Goodbody, 1960; Kier, 1965; Kenk, 1944; Hyman, 1958; Pearse, Hum, and Wharton, 1942). Burrowing sand dollars generally do not live in muddy substrates as the flow of water through fine-grained muddy sediments is restricted by the low permeability of the mud. Without the flow of fresh oxygenated water over the petaloid area the echinoid would die from lack of oxygen. It is probable *P. floridanus* and *W. eldridgei* burrowed into sand, just beneath the sediment surface, much like their modern counterparts.

The neolaganids (Clypeasteroidea) of the Ocala Limestone are represented by *Durhamella*, *Neolaganum*, *Weisbordella*, and *Wythella*. The external morphology of the neolaganids is similar to that of the laganids (Clypeasteroidea), with the primary difference lying in the plate arrangement of the coronal system (Durham,

1954). The laganids live in sandy substrate (Hyman, 1955), and it seems reasonable that the neolaganids lived in a similar manner. These small sand dollars probably burrowed several mm below the sediment surface.

Modern cassiduloids live on a sandy substrate (Kier, 1962; Durham *et al.*, 1966). In feeding cassiduloids and holoctypoids carry sediment particles to the peristomal depression using suckered tube feet. They do not possess tube feet with prehensile grips capable of secreting mucus as do the spatangoids. Disc diameter of the tube feet restricts the cassiduloids to sand and gravel substrates (Smith, 1980). Kier (1975) and Mortensen (1948) reported *Cassidulus* living on a sandy substrate; it is assumed that all species of *Cassidulus* found in the Ocala also lived on a sandy substrate.

The conditions preferred by *Oligopygus* and *Fibularia* are uncertain. *Echinoneus*, a modern genus morphologically similar to *Oligopygus*, has been observed living under rocks and in areas of coarse sand (Kier, 1965). *Fibularids* (Clypeasteroidea)



Text figure 10. Percentage of mud dwellers, and sand dwellers, large and small in Communities I, II, and III. Total echinoid abundance for each community is shown.

have been reported living in coarse sand (Mortensen, 1948). Most holocypoids are restricted to sandy substrates for reasons mentioned above.

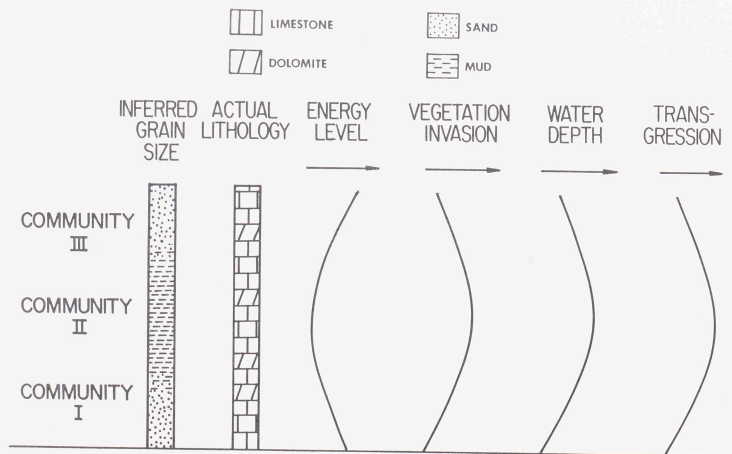
Definition of Communities

Text-fig. 9 lists some of the more common echinoid species of the Ocala Limestone with respect to their substrate affinity. Their stratigraphic distribution is also shown. *Eupatagus antillarum*, *Periarchus floridanus*, *Cassidulus globosus* Fischer, and *C. ericsoni* Fischer are restricted to the lower third of the Ocala (*Oligopygus phelani* biozone). Three of these species, *E. antillarum*, *P. floridanus*, and *C. globosus* are sand-dwellers of large size; *C. ericsoni* is a sand-dweller of small size. These four species define and dominate Community I. The total echinoid abundance of Community I is high (Text-fig. 10).

Five species, *Paraster armiger*, *Wythella eldridgei*, *Plagiobrissus dixie*, *Cassidulus conradi* (Conrad), and *C. trojanus* Cooke are restricted to the upper part of the Ocala (*Oligopygus wetherbyi* biozone). *Paraster armiger*, *W. eldridgei*, *P. dixie*, and *C. conradi* are large echinoid species

with an affinity for a sandy substrate; *C. trojanus* is a sand-dweller of small size. Although there appears to be a discrepancy in the substrate affinity of *P. armiger*, the abundance of *W. eldridgei*, *C. conradi*, and *C. trojanus* clearly indicate a sandy substrate. *Paraster armiger* is not nearly abundant as the known sand-dwelling echinoids in this interval of rock, suggesting perhaps they were mud-dwellers. These five species define and dominate Community III, which is characterized by an abundant echinoid fauna, but not quite as abundant as Community I (Text-fig. 10).

Community II is less rigorously defined than Communities I and III. There are no abundant echinoid species found in Community II, as the total echinoid abundance of Community II is considerably less than that of either Communities I and III (Text-fig. 10). Community II is comprised of echinoids that can tolerate a muddy substrate as well as sand-dwellers of small size (Text-fig. 10). There are no large echinoids with an affinity for a sandy substrate present in the rocks containing Community II. The mud-dwellers present in the strata containing Community II are *Agassizia*



Text figure 11. Inferred grain size of the rocks containing Communities I, II, and III, and the interpretation of those grain sizes (see text).

clevei, *Schizaster ocalanus*, and *Brissopsis steinhatchee*. *Agassizia clevei* also occurs in the rocks containing Communities I and III, but the remaining two mud-dwelling species are restricted to the strata containing Community II. In summary, Community II is defined as that fauna composed of the three mud-dwelling echinoid species, the sand dwellers of small size, and lacking the large echinoid species with a preference for sandy substrate.

Text-fig. 10 also shows a total echinoid abundance curve for the three communities recognized in the Ocala Limestone. The difference in the peak abundance of the echinoids in either Communities I or III, compared to Community II, is overwhelming.

The beds containing Community I display the highest total echinoid abundance of any community. The average number of echinoid specimens per square meter in the rocks containing Community I varies from several to as many as 25. The beds containing Community II display the lowest total echinoid abundance of any community. In the beds containing Community II echinoid specimens are often quite difficult to find. The echinoid abundance is approximately 0.03 specimens per square meter of rock. The abundance of echinoids in the beds containing Community III is close to that of Community I, but slightly less, averaging approximately 1-5 specimens per square meter of rock.

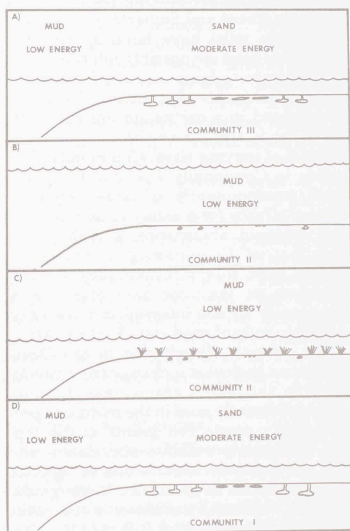
It is essential to note that in benthic communities organisms commonly display a patchy spatial distribution. Consequently, the abundance of specimens for any community as given above may vary considerably between outcrops. As a result, all species representative of any stratigraphic interval in Text-fig. 2 may not be found at every outcrop representing the respective stratigraphic interval. This is especially true of the rocks containing Community II, where echinoid abundance is low.

Interpretation of Communities

The three echinoid communities of the Ocala Limestone contain three major types of echinoids; 1) large echinoids with an affinity for a sandy substrate, 2) small echinoids with an affinity for a sandy substrate, and 3) echinoids with an affinity for

a muddy substrate. Based on the stratigraphic distribution of these three echinoid groups it is possible to draw inferences about sediment grain-size at the time of deposition of the Ocala Limestone.

The Ocala was deposited in a relatively pure carbonate environment, and an understanding of substrate compositions in such environments is essential when analyzing grain-size distribution. In modern carbonate environments there is *in situ* accumulation of clay- to sand-sized particles of biogenic origin. Therefore, the sediment grain-size is not totally a function of water energy conditions, but also partially a function of the type and size of a biogenic material being produced *in situ*. Low water energy environments are characterized by clay, silt, sand, and even



Text figure 12. Interpretive model of the Floridan carbonate bank during Late Eocene.

- Community III.
- Community II, deeper water model.
- Community II, vegetation model
- Community I.

larger sized particles. Increasing water energy conditions result in a winnowing of the fine-grained material first, leaving behind the larger grains. Beyond a critical water energy level relatively pure, sand-sized carbonate substrates can be formed.

Community I is dominated by sand-dwelling echinoids of large size (Text-fig. 10), indicating that the substrate was originally composed of sand-sized grains (Text-fig. 11). Community II is characterized by low echinoid abundance, the absence of large echinoids with an affinity for a sandy substrate, and a high percentage of mud-dwelling echinoids (Text-fig. 10), implying that the sediments contained a large percentage of mud (Text-fig. 11). Fine suspended mud tends to clog the water vascular system of the echinoids and few echinoid species are adapted for such environments (Ernst and Siebertz, 1977). However, there must have been appreciable amounts of sand (or possibly silt) present in the substrate to have sustained the sand-dwelling echinoids of small size. This is to be expected in a carbonate environment, due to the *in situ* accumulation of biogenic material of varying sizes. Community III is similar to Community I in that it is composed predominantly of large echinoids with an affinity for a sandy substrate. The total echinoid abundance is slightly less than that of Community I, but much greater than that of Community II. The sediments at the time of occurrence of Community III are inferred to have been predominantly of sand-size (Text-fig. 11).

The echinoid distribution in the Ocala Limestone indicates a change from predominantly sand-sized grains near the base to predominantly mud in the middle to predominantly sand-sized grains at the top. The changes in relative abundance and size of the individual echinoid species imply the shift in grain-size were gradational. The faunal transition in the rocks containing Communities I, II, and III is not sharp, but gradational. The sand-dwellers of larger size in Community I gradually decreases in abundance upsection until they disappear. The sand-dwellers of large size in Community III decrease in abundance downsection until they eventually disappear. The precise boundaries between Communities I and II, and II and III are

the last and first occurrence, respectively, of the sand-dwellers of large size.

In a general sense, the test size of the sand-dwellers of Community I decreased upsection. Likewise, the test size of the sand-dwellers of Community III decreases downsection. This is to be expected, as the presence of mud in the substrate restricts the growth of the sand-dwellers and the greater the proportion of mud in the substrate, the smaller the test of sand-dwelling echinoids (Nichols, 1959).

The changes in grain-size between substrates of the three communities of the Ocala Limestone can be attributed to changes in the water energy level at the time of deposition (Text-fig. 11). Communities I and III represent higher water energy conditions than Community II. This change in water energy conditions may be attributed to either a change in water depth at the time of deposition, or to an invasion of some type of vegetation, such as turtle grass (Text-fig. 11).

The presence of vegetation would slow water currents (decrease water energy level) at the sediment-water interface, and in effect, trap fine-grained material being carried in suspension. This is assuming high enough water energy conditions were initially present to carry material in suspension. If vegetation were to have reached its peak abundance during the occurrence of Community II, then the substrate would be expected to be composed of a large percentage of mud (Text-fig. 11). A subsequent decline in vegetation abundance would have allowed the formation of a sandy substrate, assuming that high enough water energy conditions were present.

An alternate hypothesis to explain the change in water energy level is a change in water depth. In general, the deeper the water, the lower the water energy level. Therefore, water depth would have been deeper during the occurrence of Community II than that of Communities I and III (Text-fig. 11).

Toulmin (1977) considers the Moodys Branch Formation in the eastern Gulf Coast to be a transgressive unit. The Moodys Branch Formation correlates with the lower Ocala Limestone (Croft, 1980). The fluctuations in the cheilostome bryo-

zoan fauna reflect deepening water during Early and Middle Jacksonian deposition and shoaling in Late Jackson deposition (Cheetham, 1963). Consequently, it is probable that the distribution of echinoids in the Ocala is also a function of changing water depth during deposition. It seems likely that a transgressive-regressive sea was responsible for the changing water depths during deposition of the Ocala Limestone.

The distribution of molluscs in the Ocala Limestone support the conclusions based on the analysis of the echinoid fauna. The molluscs (gastropods and pelecypods) reach their highest abundance in the rocks containing Communities I and III, with oysters being common. This observation implies a nearshore, shallow water, marine environment. The rocks containing Community II are characterized by relatively lower molluscan abundance, suggesting deeper water.

Depositional textures including grainstones, packstones, and wackestones can be recognized in the Ocala Limestone. The rocks containing Communities I and III are generally classified as grainstones and packstones, which grade into wackestones in the beds containing Community II. There are no definitive boundaries between these rock types, as all contacts are gradational. In addition, diagenesis and solution have caused local alteration. The present rock types infer changing water energy conditions at the time of the deposition; that is, lower water energy levels in the middle of the Ocala. This observation is consistent with conclusions reached from paleontological observations.

Oligopygus seems to have no preference for the different substrate types that occurred during deposition of the Ocala Limestone. Although each species of *Oligopygus* in the Ocala is generally restricted to a single Community, there are no significant morphological changes between species that would give preference to a different type of substrate. The specific changes within the genus are probably due to phylogeny rather than ecology; therefore, *O. phelani*, *O. haldemani*, and *O. wetherbyi* represent a time-evolutionary lineage.

V. PALEO GEOGRAPHY

There are few regular echinoids preserved in the Ocala Limestone, during this study less than ten specimens were found. Spines from regular echinoids are often found, but are not abundant. In modern environments, regular echinoids live in the higher water energy nearshore area, whereas heart urchins (spatangoids) and sand dollars (clypeasteroids) commonly live further offshore where the water energy level is relatively low. The absence of abundant regular echinoids in the Ocala implies the absence of a high water energy environment in the littoral zone, suitable to habitation by the regular echinoids and it may be inferred that the slope of the local continental shelf was quite gentle. This is compatible with a carbonate bank environment as suggested by Cheetham (1963). Text-fig. 12 schematically depicts a hypothetical profile across the northern margin of the bank at the time of deposition (Late Eocene). The water depth is uncertain, but probably never exceeded more than 50 meters (Cheetham, 1963).

The total geographic extent of the carbonate bank during the Late Eocene is uncertain. The entire outcrop area of the Ocala Limestone was certainly a part of the bank, as evidenced by the abundant assemblages of echinoids, bryozoans, and molluscs, typical of the bank. The lateral extent of these faunas into the subsurface is unknown. The northern edge of the bank was truncated by the Suwannee Straits (Cheetham, 1963); the southern, eastern, and western extent of the bank during Late Eocene are unknown.

Modern Faunal Analogue

Kier and Grant (1965) reported the occurrence of an echinoid fauna from the Key Largo Reef Preserve similar to that found in Communities I and III. *Encope michelini* Agassiz, *Leodia scabiesperforata* (Leske), *Meoma ventricosa* (Lamarck), and *Plagiobrissus grandis* live in the upper layer of clean, grassless sand comprising the inter-reef deep channel, located behind the main reef-crest. They are frequently found living together in the channel. It should be emphasized that there are

no biohermal structures preserved in the Ocala Limestone; however, the Ocala echinoid fauna and the Key Largo echinoid fauna are quite similar with respect to substrate affinity, as well as general test morphology. Water depth in the Recent channel is shallow (less than 15 meters) and it is probable that environmental conditions (i.e., substrate, salinity, water energy level) were similar during deposition of the Ocala Limestone.

VI. ACKNOWLEDGMENTS

Acknowledgment is made to the donors of the Petroleum Research Fund administered by the American Chemical Society for support of this research. We thank Louis Zachos for sharing his expertise on Cenozoic echinoids. We thank Ramil Wright for his insight. We also acknowledge the Department of Geology, Florida State University, Tallahassee and the Florida State Museum, University of Florida, Gainesville for financial and moral support. Lastly, we thank Porter Kier and Norris Williams for reviewing an earlier draft of this manuscript.

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REVIEWS

SUBURBAN GEOLOGY: An Introduction to the Common Rocks and Minerals of Your Back Yard and Local Park, by Richard Headstrom. Published by Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1985, xvii + 136 pp., illus., paperback, \$8.95

This is the third volume in a suburban trilogy, the first two being *Suburban Wildlife* and *Suburban Wildflowers*; all designed for the amateur naturalist. This small book is clearly designed for the museum sales counter and is fairly well suited for that market, especially for the younger visitor who has only a casual interest in the subject. A clue to the reason for generating this series can be perceived in the author's position as a museum curator and as a consultant for the nature programs of the Boy Scouts and Girl Scouts. The book cannot be of interest to the experienced geologist or rock collector, and this reviewer finds it somewhat overpriced for its slender size and the very sketchy treatment of rocks and minerals.

EXPLORING THE OCEANS: An Introduction for the Traveler and Amateur Naturalist, by Henry S. Parker. Published by Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 1985, xiv + 354 pp., illus., index, paperback, \$15.95

This book is from the pen of an experienced biologist/university faculty member/former U.S. Navy diver. As such, it is much more scholarly and authoritative than the previous reviewed volume (see above). Also designed for the amateur naturalist and traveler, this book is reasonably comprehensive and informative about such topics as marine biology and geology, plate tectonics, ocean chemistry, ocean climate and circulation, and life in the seas. The metric table and conversion factors and the outlined taxonomic classification of marine organisms in the appendix are most useful. An index is included. This volume is recommended; it is reasonably comprehensive and authoritative without being tedious or too involved for the amateur reader.

—H.C.S.