FLORIDA FOSSIL INVERTEBRATES

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LARGER FORAMINIFERA

Introduction, Biology, Ecology, Taxonomic and Stratigraphic Listings

Comments on Florida Fossil Assemblages

JONATHAN R. BRYAN

Earth Sciences
Okaloosa-Walton College
100 College Blvd.
Niceville, FL 32578-1295
e-mail: bryanj@owc.edu

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Florida Fossil Invertebrates is a publication of the Florida Paleontological Society, Inc., and is intended as a guide for identification of the many common invertebrate fossils found within the state. Two parts per year will be completed and each part will deal with a specific taxonomic group and contain a brief discussion of that group's life history along with the pertinent geological setting. This series deals solely with published taxa; no new species descriptions are included. Previously, five parts have been published [Part 1 (June 2001) Eocene echinoids, Part 2 (January 2002) Oligocene and Miocene echinoids, Part 3 (June 2002) Pliocene and Pleistocene echinoids, Part 4 (February 2004) Pliocene and Pleistocene decapod crustaceans, and Part 5 (September 2004) Eocene, Oligocene, and Miocene fossil decapod crustaceans. Part 6 (this issue) and Part 7 (December 2004) discuss larger Foraminifera. Each issue will be image-rich and, whenever possible, specimen images will be at natural size (1x). Some of the specimens figured in this series are on display at Powell Hall, the museum's Exhibit and Education Center. **This publication is made possible through the generous financial support of James and Lori Toomey.**

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Florida Paleontological Society
Florida Museum of Natural History
P. O. Box 117800
University of Florida
Gainesville, FL 32611-7800

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Jonathan R. Bryan

Earth Sciences, Okaloosa-Walton College, 100 College Blvd., Niceville, FL 32578-1295
e-mail: bryanj@owc.edu

INTRODUCTION

WHAT ARE LARGER FORAMINIFERA?

Foraminifera are a group of marine protists that are closely related to the familiar freshwater protozoan, *Amoeba*. But foraminifera (or, "forams") are housed in a small shell called a *test* that is normally made of calcium carbonate (calcite—$CaCO_3$), but may also be constructed of organic material or a mosaic of tiny sediment particles that are cemented together. Extending through one or more openings in the foram test are long, thread-like extensions of protoplasm called *pseudopods* that gather food and assist in many other vital functions. Foraminifera may be *planktic* (floaters) or *benthic* (bottom dwellers) in habit. There are an estimated 10,000 species of extant (living) foraminifera.

Because of their great abundance in sedimentary rocks, foraminifera are one of the most useful of all fossil organisms to the geologist and paleontologist. They first appear in strata of the Cambrian Period and are found in abundance up to the present time. Forams can be used to identify specific geological time intervals, to reconstruct past environments, to decipher ancient climate changes, and to document evolutionary patterns. Their small size, usually less than 1-2 millimeters (mm), ensures that fossil foraminifera can be preserved in rock cores, so they have been used extensively in the search for petroleum and in other subsurface geologic investigations. The study of fossil foraminifera and other skeletal protists generally falls under the branch of paleontology called *micropaleontology*.

Larger foraminifera are a subset of the foraminifera that are characterized by their relatively large tests (usually more than 3 cubic mm in test volume) and complex internal shell morphologies (Figures 1, 2) (Hottinger 1978, 1986). Some large forams, in fact, hardly seem to qualify as "microfossils." In the Permian Period, for example, some large forams called fusulinids (genus *Parafusulina*) reached 10 centimeters (cm) in length (Dunbar, 1963). Extinct *Lepidocyclina elephantine* reached 14 cm in length (Grell, 1973), and there are reports of *Nummulites* from the Eocene reaching 16 cm in diameter (Purton & Brasier, 1999), and perhaps even larger (specimens have been found reaching 19 cm or more according to Pavlovec, 1987). Modern *Cycloclypeus* from the Pacific can reach over 12 cm (Koba, 1978). In Florida, some fragments of *Lepidocyclina* found in Eocene and Oligocene strata approach 7 cm or more in diameter (Figure 3). Considering that these creatures are single-celled protozoa, these are extraordinary sizes. Most fossil species routinely found in Florida's Tertiary strata are between about 3-5 mm, with larger forms averaging up to 1-3 cm in size. Because they are sea bottom dwellers, larger foraminifera are frequently referred to as *larger benthic foraminifera*, or LBF for short.

BIOLOGY AND ECOLOGY OF LARGER FORAMINIFERA

With few exceptions, the relatively large and complex tests of extant species of larger foraminifera are related to algal symbiosis. The highly compartmentalized test contains multiple "greenhouses" for the shelter of single-celled algae. These symbiont-algae provide photosynthetic nutriment to the foram, and probably facilitate calcification of the foram test. In return, the foram provides shelter and some biochemical nutritive assistance to the algae (Hallock, 2002; Lee and Hallock, 1987; Leutenegger, 1984; Cowen, 1983). Algal symbionts in larger foraminifera include chlorophytes (green

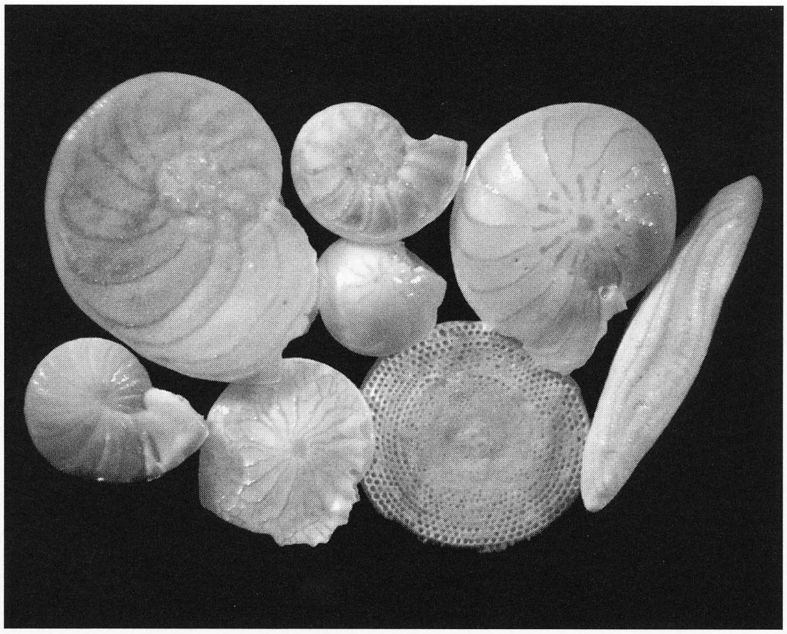


Figure 1. A variety of larger benthic foraminifera from the Philippines (magnification 14x).

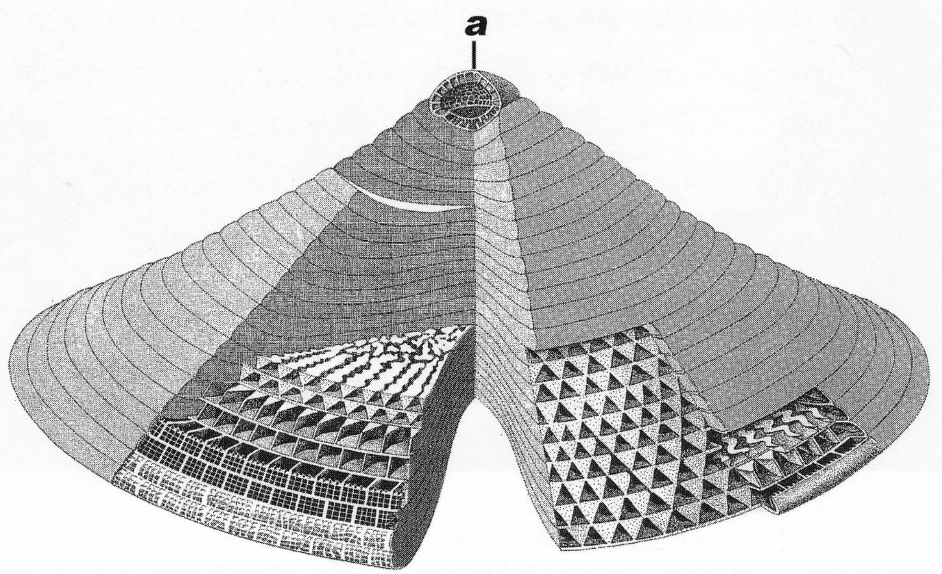


Figure 2. The Cretaceous larger foraminferan, *Orbitolina*, with several planes cut away to show the internal complexity of the test. Shown are the megalospheric embryon (*a*), and a variety of chambers, partitions, and chamberlets (from Douglass, 1960).

Figure 3. A very large microspheric specimen of *Lepidocyclina* from the Eocene Ocala Limestone, collected at Marianna, Florida (magnification 1.4x).

algae), rhodophytes (red algae), diatoms (golden-brown algae), and dinoflagellates (yellow-green algae) (Leutenegger, 1984; Lee and Anderson, 1991).

Larger foraminifera have highly variable life cycles (Lee and Capriulo, 1990) that can extend up to one year or more (e.g., Ross, 1977; Lutze and Wefer, 1980). Most large forams are characterized by an alternation of generations in which a haploid *gamont* (gamete-producing) form (also called the A-generation) alternates with a diploid *agamont* (asexual) form (also called a *schizont*, or B-generation). The gamont normally has a smaller test than the agamont but a much larger *embryon* (the first two chambers of the test, also called *embryonic chambers*). The embryon of the gamont normally consists of two rather large chambers (*protoconch* and *deuteroconch*; or *proloculus* and *deuteroloculus* if they are part of a spire of chambers), and is designated *megalospheric* (Figure 4). These two, initial chambers housed the juvenile foraminifer when first released from the parent test during asexual reproduction. The larger, agamont has many nuclei (*multinucleate*) which control various vital functions of the cell. The agamont, formed by the fusion of gametes, has an extremely small initial chamber (*proloculus*), and is designated *microspheric* (Loeblich and Tappan, 1964; Lipps, 1982).

In living and fossil assemblages, megalospheric tests are always far more numerous than microspheric tests. This observation has led to the hypothesis of biologic *trimorphism*, in which it is thought that microspheric schizonts produce megalospheric schizonts, which produce megalospheric gamonts, which produce microspheric schizonts (Leutenegger, 1977). Several generations, in fact, of megalospheric schizonts are thought to precede gametogenesis in some cases. This life cycle has been observed in living *Heterostegina depressa* (Rottger et al., 1986, 1990).

Larger forams were particularly abundant during certain intervals of geologic history, particularly the Pennsylvanian, Permian, Cretaceous, and Tertiary Periods. During these times, LBF are usually associated with various types of reefs and other shallow water, tropical marine environments. It is the ecological strategy of hosting algal photosymbionts that has proven to be so advantageous for the larger foraminifera in these settings. Surprisingly, tropical, photic zone reefs normally grow in nutrient-poor

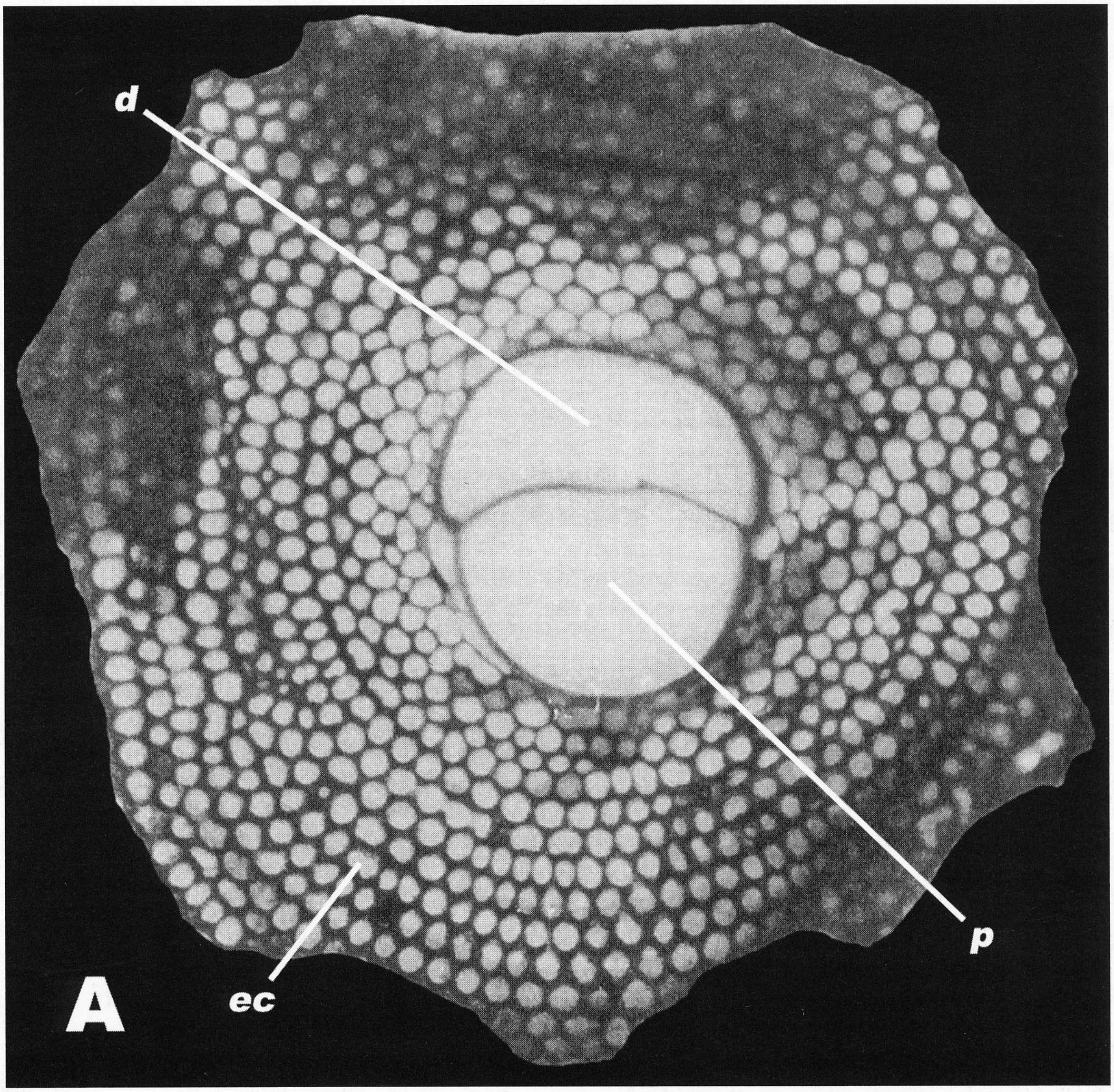
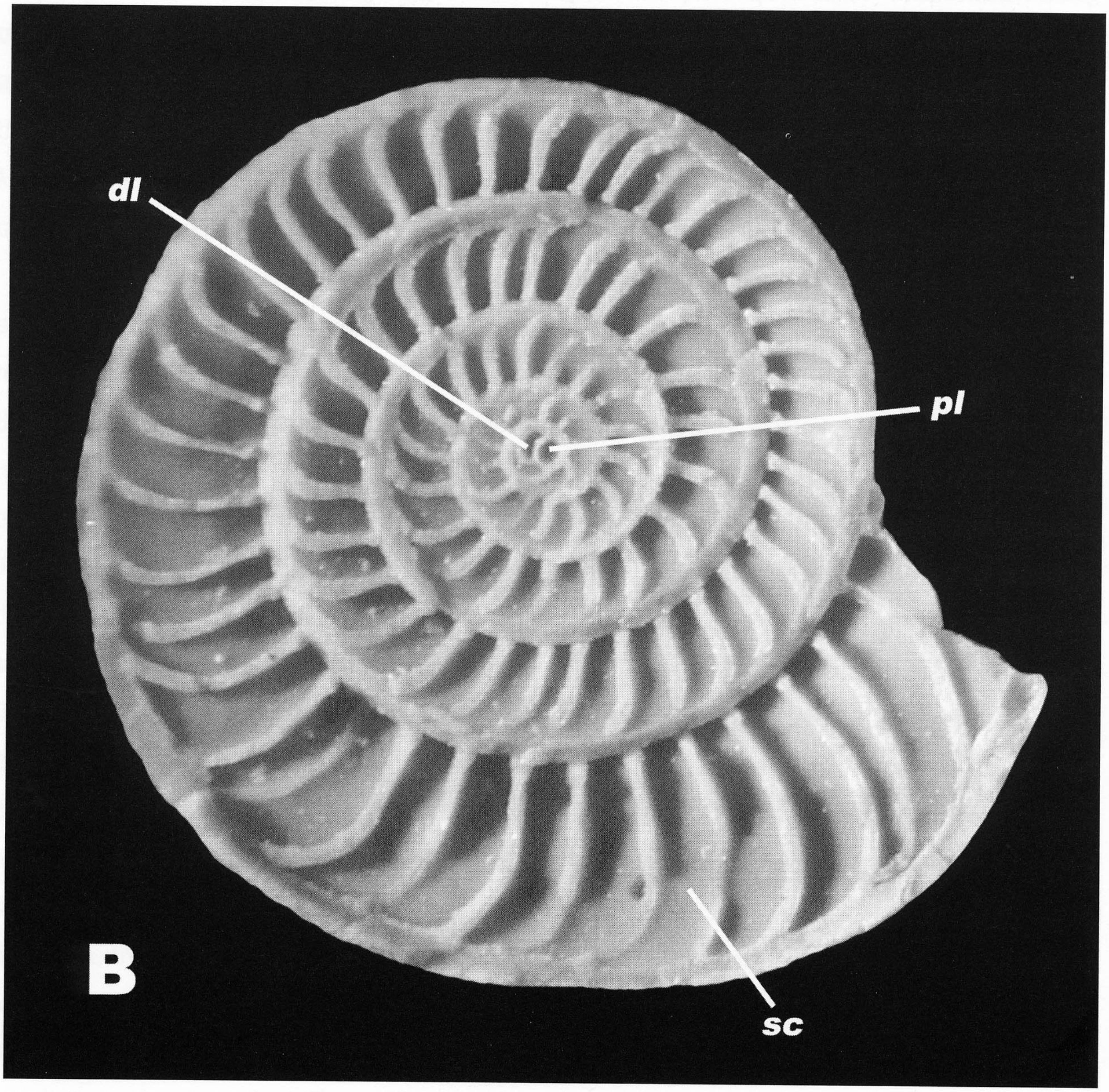


Figure 4. Equatorial (or, medial) views of two megalospheric gamonts, or A forms. *A. Lepidocyclina* (*Nephrolepidina*) *chaperi*, from the Upper Eocene/Early Oligocene Bumpnose Limestone, Chipola River, Marianna, Florida (x32; image from Cole, 1952). *B. Nummulites willcoxi*, from the Upper Eocene Ocala Limestone, Dixie County, Florida (x35). *p*, protoconch; *d*, deuteroconch; *pl*, proloculus; *dl*, deuteroloculus; *ec*, equatorial chambers; *sc*, spiral chambers.


dl
pl
B
sc

(*oligotrophic*) waters. In such marine environments, algal symbiosis is especially advantageous because the algae provide for much of the nutritional needs of the foram. Most modern LBF and reef corals also have algal symbionts (this gives corals their typical, golden-yellow color), and even some molluscs host algal symbionts (e.g., the giant reef clam, *Tridacna*). Reef ecosystems are, in fact, largely constructed by creatures that can take advantage of algal symbiosis and thereby thrive in what are otherwise nutrient-poor waters. Because extinct larger foraminifera are almost always associated with ancient tropical or subtropical marine environments, most are inferred to have had algal symbionts (Hallock, 1982; Hottinger, 1982).

Like many invertebrate organisms, LBF have *indeterminate growth*, which means they will continue to grow throughout their life, which normally ends at reproduction. During asexual reproduction, the parent distributes all of its protoplasm to its progeny by multiple fission. Under favorable conditions, LBF will mature and reproduce normally. However, if the population is stressed by low light (necessary for algal symbionts), low temperature, or other suboptimal conditions, the forams may delay reproduction and simply continue to grow. This occurs, for example, when LBF are washed into deeper water. Paradoxically, if a population contains many exceptionally large individuals, conditions for growth and reproduction may have been marginal (Hallock, 1985; Hallock and Glenn, 1986; Hallock et al., 1986).

Larger foraminifera are often so abundant that their tests comprise a substantial volume of calcium carbonate sediment, rivaling corals and calcareous algae in their volumetric contribution (Hallock and Glenn, 1986; Hallock, 1981; Ross, 1977). Thus larger forams, corals, and algae are some of the primary limestone-producing organisms found in tropical, shallow marine environments. Many fossiliferous limestones are composed of nearly 100% larger foraminifera. Such limestone may be called a *coquina*. LBF-rich limestones and coquinas are common in the Ocala Limestone and other Florida formations (Figure 5). The Middle Eocene Giza Limestone of Egypt, for example, is rich in LBF called *Nummulites*. This limestone comprises much of the building stone for the great pyramids (Figure 6). Egyptian nummulites were recognized as curiosities as early as the fifth century B.C., and were considered to be

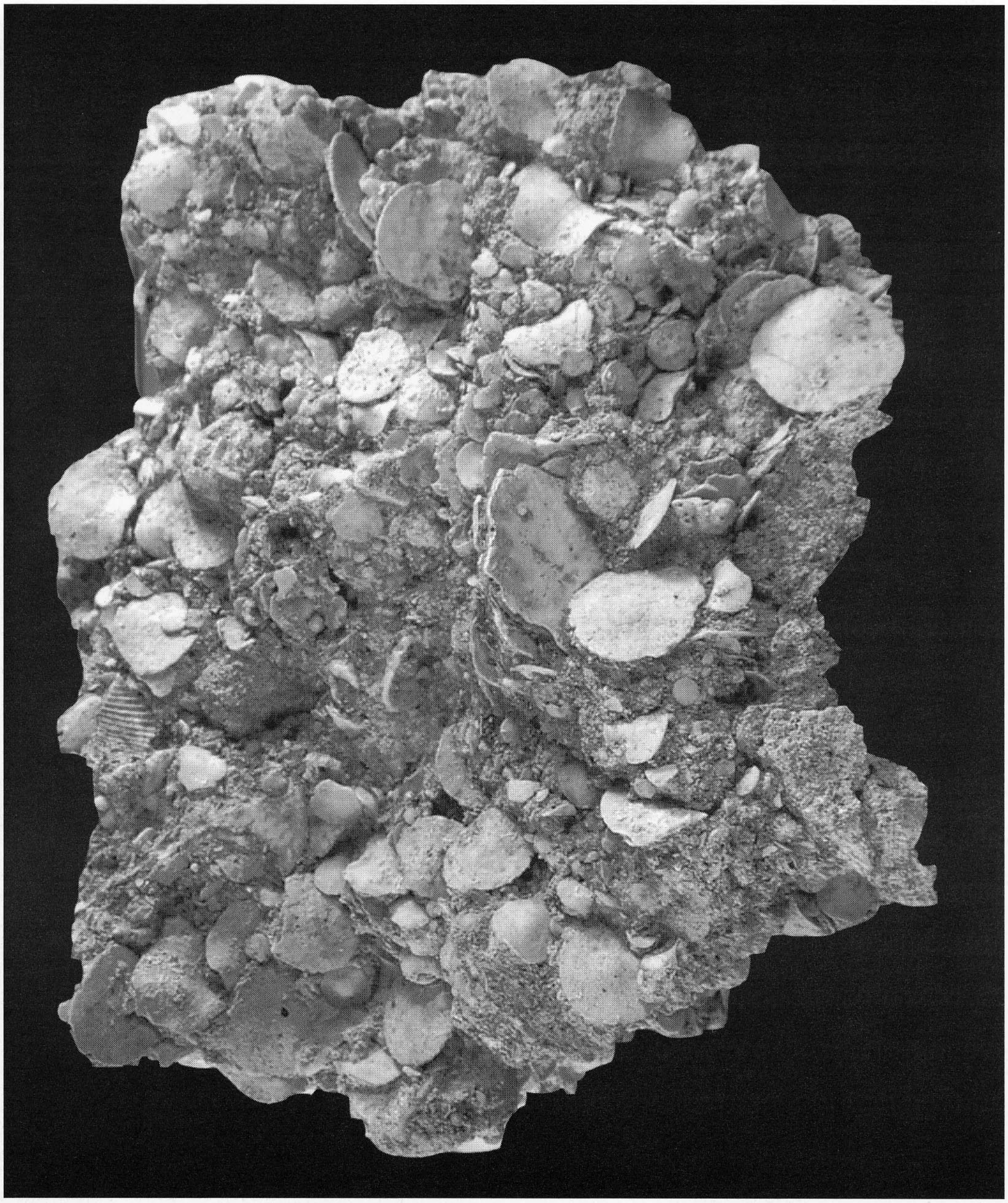


Figure 5. Larger foraminiferal limestone/coquina, containing *Nummulites* and *Lepidocyclina*. Upper Eocene Ocala Limestone, Haile Quarries, near Gainesville, Florida (magnification 1.7x).

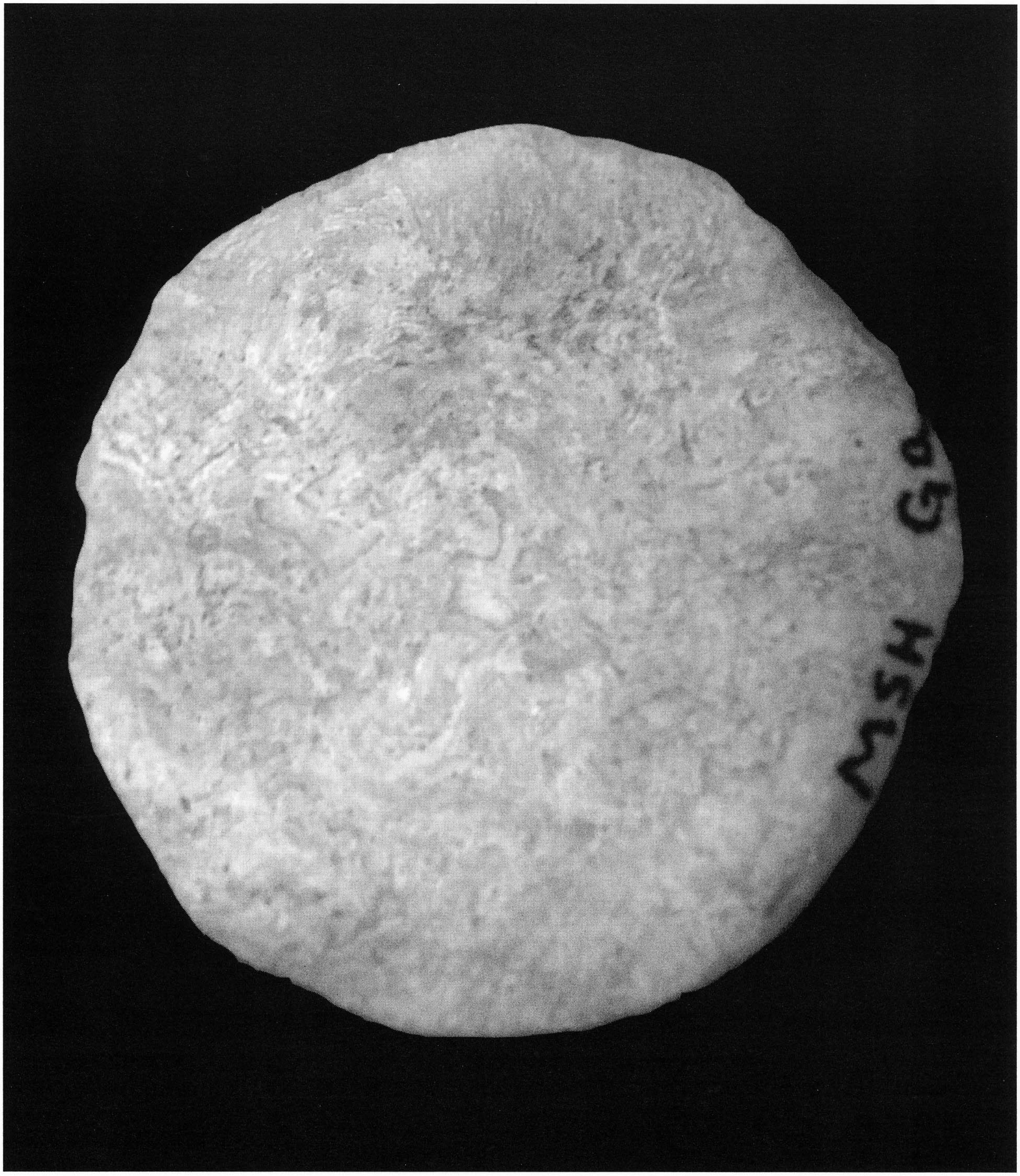


Figure 6. *Nummulites gizenesis,* from the Middle Eocene Giza Limestone of Egypt (magnification 3.5x).

the remains of petrified lentils left over from the rations given to the slaves who build the Great Pyramids. Fossil nummulitids have also been nicknamed “mermaid’s pennies.”

Larger foraminifera in general have distinctive environmental tolerances, and individual species may be restricted to particular habitats. This habitat-specific association is largely a function of the light tolerances of algal symbionts. LBF that host chlorphyte (green) algal symbionts for example, such as the modern Floridan species *Laevipeneroplis proteus* and *Archaias angulatus*, require very shallow waters and are typically found in backreef and seagrass habitats. Other LBF, such as Indo-Pacific nummulitids *Nummulites venosus* and *Heterostegina operculinoides*, host algae that can carry out photosynthesis in deeper photic zone waters with restricted light penetration. But modern algal-symbiont-hosting LBF rarely live in waters exceeding 100 meters (m) depth.

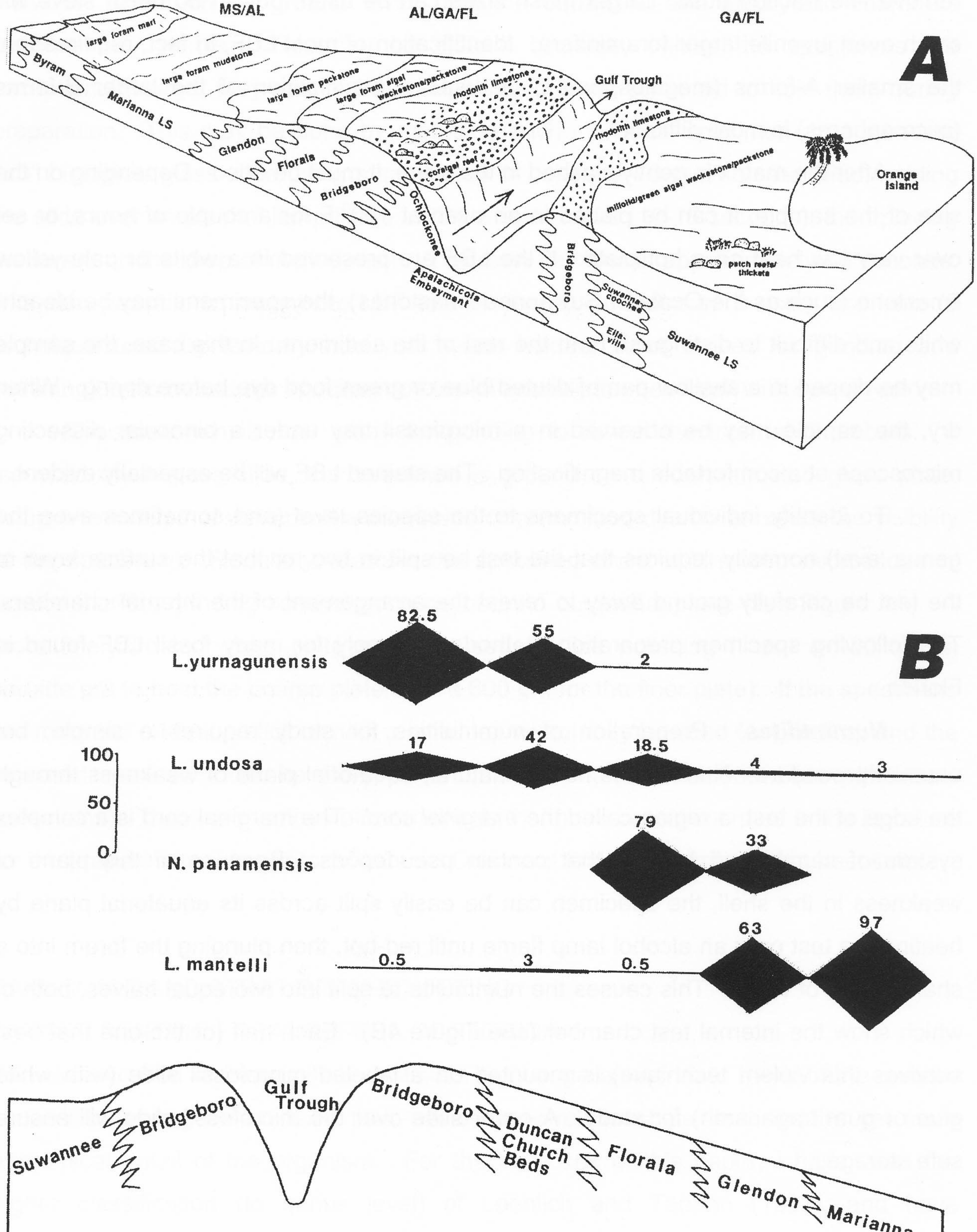
Similar habitat associations can be reasonably inferred for fossil LBF, making them extremely valuable in the reconstruction of past marine environments. Many studies have documented the paleoenvironmental (*biofacies*) distributions of LBF (Drooger, 1983; Hottinger, 1977, 1983, 1997). It is common, for example to map the ecologic zonation of LBF along a shallow-to-deep transect within reef-associated limestones (Figure 7).

PREPARATION OF FOSSIL LARGER FORAMINIFERA

The study of larger foraminifera requires a variety of special preparation techniques. If the forams are preserved in hard, well-cemented limestones, then individual specimens can be nearly impossible to remove. In such cases, polished thin-sections of the rock must be made to observe the forams through transmitted light with a petrographic microscope. A variety of special saws and other equipment is generally needed to prepare petrographic thin sections. Fortunately, most fossil LBF in Florida are preserved in soft limestones or other loosely consolidated sediments, so simpler and more cost-effective methods can be employed to prepare specimens.

The first step in preparing LBF is to isolate a sufficient number of quality specimens for study from the rest of the rock or sediment. Most LBF-rich limestones can be carefully broken several times with a rock hammer until sufficient loosened

Figure 7. Larger foraminiferal zonation across an Early Oligocene reef tract and associated environments. *A.* block diagram reconstruction of shallow marine environments extending from Mississippi, southeastward to Florida (rock formations are shown in side panel). The Bridgboro Limestone is a reef deposit rich in coralline algae. The Gulf Trough was a current-swept channel that extended from the eastern Florida panhandle through southern Georgia. The Florida peninsula is represented by the Suwannee Limestone. *B.* Distribution (percent) of four species of Shelf Assemblage larger foraminifera from the reef to deeper shelf. Not shown are abundant *Fallotella cookei* and *Fallotella floridana*, representing the Bank Assemblage of the Suwannee Limestone (from Bryan, 1995).


MS/AL
AL/GA/FL
GA/FL
A
large foram marl
Byram
large foram mudstone
Marianna LS
large foram packstone
large foram algal wackestone/packstone
rhodolith limestone
Gulf Trough
rhodolith limestone
Glendon
Florala
Bridgeboro
coralgal reef
Ochlockonee
miliolid/green algal wackestone/packstone
Orange Island
Apalachicola Embayment
Bridgeboro
patch reefs/thickets
Suwannee Coochee
Ellaville
Suwannee LS
82.5
55
L.yurnagunensis
2
B
17
42
18.5
100
L. undosa
4
3
50
0
79
33
N. panamensis
63
97
L. mantelli
0.5
3
0.5
Gulf Trough
Bridgeboro
Bridgeboro
Suwannee
Duncan Church Beds
Florala
Glendon
Marianna