BIOSTRATIGRAPHY AND PALEOECOLOGY OF THE PLEISTOCENE INVERTEBRATES FROM THE LEISEY SHELL PITS, HILLSBOROUGH COUNTY, FLORIDA

Roger W. Portell[1], Kevin S. Schindler[2], and David Nicol[3]

ABSTRACT

A Pleistocene macro-invertebrate assemblage from two Leisey Shell Corporation pits, located 1 km inland from Tampa Bay along the Gulf Coast of Florida, is examined. The assemblage is dominated by marine mollusks and consists of 98 species of bivalves, 113 species of gastropods, 3 polyplacophorans, and 3 scaphopods. Other invertebrates identified include 1 poriferan, 3 cnidarians, 16 bryozoans, 1 annelid, 9 arthropods, and 1 echinoderm. The fossil material was collected at Leisey Shell Pit 1 and Leisey Shell Pit 3 from three superposed marine shell beds (and spoil) in each pit. The strata containing the molluscan faunas of the two lowermost shell horizons (lower shell bed and bone bed) are placed in the Bermont Formation and contain approximately 3% extinct marine species each. The uppermost unit (upper shell bed) is most similar to the late Pleistocene Fort Thompson Formation and contains approximately 1% extinct species of marine mollusks.

At both Leisey pits the base of the lower shell bed contains dark, organic lenses or layers with freshwater and estuarine mollusks and freshwater and terrestrial vertebrates. The remainder of the lower shell bed appears to have been deposited under normal marine conditions in relatively quiet waters from 3 to 6 m in depth. The bone bed at each pit (Leisey 1A and 3A) consists of a thin lens containing an extremely rich concentration of terrestrial, freshwater, and nearshore marine vertebrate fossils, in addition to the rich, shallow-marine invertebrate fauna with abundant freshwater gastropods and some terrestrial gastropods. The molluscan assemblage indicates deposition in a shallow (intertidal to -2 m), protected marine bay or lagoon, containing abundant marine grass beds and having a large river flowing into it. The upper shell bed at the Leisey Pits has the least diverse molluscan assemblage, having also been deposited in shallow water (intertidal to -2 m) under relatively high energy conditions, possibly in a tidal channel.

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[1] The senior author is Senior Biological Scientist in Invertebrate Paleontology, Department of Natural Sciences, Florida Museum of Natural History, University of Florida, P. O. Box 117800, Gainesville FL 32611-7800.

[2] Kevin Schindler, 7207 Barcliff Drive, Charlotte NC 28212, U.S.A. (formerly a Biologist in Invertebrate Paleontology, Department of Natural Sciences, Florida Museum of Natural History, University of Florida, P. O. Box 117800, Gainesville FL 32611-7800.

[3] David Nicol is Professor Emeritus, Department of Geology, University of Florida; current address: Box 14376, University Station, Gainesville FL 32604.

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RESUMEN

Se examina un ensamblaje Pleistocénico de macroinvertebrados provenientes de dos depósitos de Conchuelas de Leisey localizados 1 km tierra adentro de la Bahía de Tampa en la Costa del Golfo en Florida. El ensamblaje es dominado por moluscos marinos, consistiendo de 98 especies de bivalvos, 113 especies de gastrópodos, 3 poliplacóforos y 3 scafôpodos. Otros invertebrados identificados incluyen 1 porífero, 3 cnidarios, 16 bryozoos, 1 anélido, 9 artrópodos y 1 equinodermo. El material fósil fue colectado desde tres camas marinas superimpuestas (y estropeadas) del depósito de Conchuelas de Leisey 1 y del depósito de Conchuelas de Leisey 3. En la Formación Bermont se ubican los estratos de faunas de moluscos de los dos horizontes de conchuelas más inferiores (la cama de conchuelas más baja y la cama de huesos), conteniendo cada una aproximadamente 3% de especies marinas extinguidas. La unidad más superior (cama de conchuelas superior) contiene aproximadamente 1% de especies de moluscos marinos extinguidos, siendo la más similar a la formación Fort Thompson del Pleistoceno Tardío.

En ámbos depósitos de Leisey, la base de la cama de conchuelas más baja, inmediatamente por sobre el contacto con los sedimentos del Mioceno de la Formación Arcadia, contiene capas o lentes orgánicos oscuros con moluscos de agua dulce y de estuario, además de vertebrados terrestres y de agua dulce. El resto de las capas de conchuelas más bajas parecen haber sido depositadas bajo condiciones marinas normales con aguas relativamente tranquilas de 3 a 6 m de profundidad. La cama de huesos en Leisey 1A y 3A consiste de lentes delgados que contiene una concentración extremadamente rica de vertebrados fôsiles terrestres, de agua dulce, costeros y marinos; además de la rica fauna de invertebrados marinos de poca profundidad con abundantes gastrópodos de agua dulce y algunos gastrópodos terrestres. El ensamblaje de moluscos indica que éste fue depositado en una bahía marina ó laguna de poca profundidad (intermareal a -2 m), que contenía abundantes praderas marinas y un gran río que desembocaba en ella. La cama superior de conchuelas en los depósitos de Leisey contiene el emsamblaje de moluscos menos diverso, la cual también fue depositada en aguas de poca profundidad (intermareal a -2 m), bajo condiciones de relativa alta energía, posiblemente en un canal de mareas.

INTRODUCTION

This study summarizes the species composition, biostratigraphy and paleoecology of the Pleistocene invertebrate fauna from three superposed marine shell beds at two Leisey Shell Corporation pits (Leisey Shell Pit 1 and Leisey Shell Pit 3) located about 7 km southwest of Ruskin in southwestern Hillsborough County, Florida (Sec.15, T32S, R18E, Ruskin Quadrangle, USGS 7.5 minute series; Fig. 1). Both pits are well known for their extremely rich concentrations of early Pleistocene (Irvingtonian) vertebrate fossils which were collected by the Vertebrate Paleontology Division staff of the Florida Museum of Natural History (FLMNH), Frank A. Garcia, and many volunteers from the Tampa Bay Mineral and Science Club (now Tampa Bay Fossil Club). Their excavations of the main Leisey Shell Pit 1 and Leisey Shell Pit 3 fossil vertebrate sites were conducted between July 1983 and September 1984, and between November 1986 and February 1987, respectively. The vertebrate fossils were collected from thin lenses within the thick sequences of marine shells at both pits. Because of the potential for biostratigraphic correlation, based on marine mollusks and terrestrial mammals, the leaders of the FLMNH excavation crew (G.S. Morgan and R.C. Hulbert, Jr.) collected large samples of invertebrate fossils and bulk matrix from

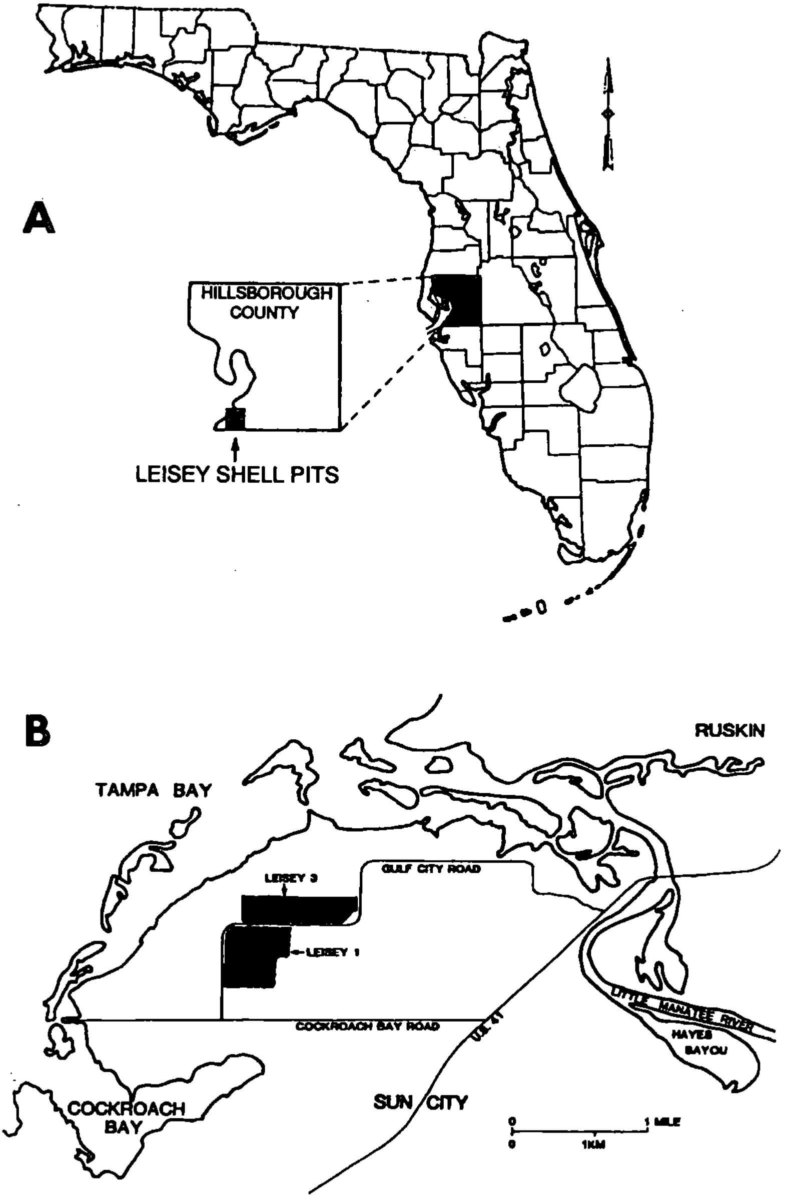

Figure 1. (A) General location map of the Leisey Shell Pits, Hillsborough County, Florida. (B) Specific location map of Leisey Shell Pit 1 and Leisey Shell Pit 3.

not only the thin bone-producing horizons (bone bed) but also the massive shell beds above (upper shell bed) and below (lower shell bed). This paper is based primarily on their invertebrate fossil collections and stratigraphic data. Additional

Leisey Shell Pit 3 material was later collected by a field crew from the Invertebrate Paleontology Division of the FLMNH between February 1989 and May 1990. Both Leisey Shell Pit 1 and Leisey Shell Pit 3 excavations are now water-filled and no longer accessible for additional collecting.

Previous studies of Leisey Shell Pit 1 by Hulbert and Morgan (1989) and Webb et al. (1989), based on preliminary invertebrate identifications, referred the lower shell bed and bone bed to the Bermont Formation, while the upper shell bed was referred to the Fort Thompson Formation. Portell et al. (1992), after compiling a more comprehensive list of fossil mollusks from the three shell units at Leisey Shell Pit 1, concurred with Hulbert and Morgan (1989) and Webb et al. (1989) in their placement of these beds within those formations. However, Portell et al. pointed out that preliminary estimates of extinct species (10% and 12%), given by Hulbert and Morgan (1989) and Webb et al. (1989), respectively, were too high and that two Bermont "index" taxa, *Miltha carmenae* Vokes 1969 and *Fasciolaria okeechobensis* Tucker and Wilson 1932, originally reported were not substantiated. A single specimen of *Strombus mayacensis* Tucker and Wilson 1933, the only other Bermont "index" taxon reported by Hulbert and Morgan (1989) and Webb et al. (1989) is now known to have been collected from spoil (materials out of stratigraphic context) at Leisey Shell Pit 3. Portell et al. (1992) concurred with the placement of the lower shell bed and bone bed within the Bermont Formation because their detailed study of Leisey Shell Pit 1 mollusks revealed the presence of other species, e.g. *Semele perlamellosa* Heilprin 1886 and *Conradostrea sculpturata* (Conrad 1840), which make their last appearance in the Bermont Formation elsewhere in Florida, but have never been recorded from the younger Fort Thompson Formation.

This work represents one of only a few to examine a Bermont invertebrate assemblage stratigraphically; therefore, it may be useful to help interpret the complex Plio-Pleistocene stratigraphy of Florida and correlate this unit with equivalent units outside of Florida. Information contained in this study and derived from the recently completed Leisey Shell Pit 3 invertebrate faunal list and the newly updated Leisey Shell Pit 1 invertebrate faunal list (Appendix 1) confirm most of the previous findings of Hulbert and Morgan (1989), Webb et al. (1989), and Portell et al. (1992). In addition, the new taxonomic data provided in these lists will be useful for ongoing fossil mollusk biodiversity compilations (e.g. Allmon et al. 1993; in press).

ACKNOWLEDGEMENTS

Gary S. Morgan, New Mexico Museum of Natural History (formerly of FLMNH), and Richard C. Hulbert, Jr., Georgia Southern University, were instrumental to this study by providing stratigraphically collected bulk matrix and by measuring the stratigraphic sections from Leisey Shell Pit 1 and Leisey Shell Pit 3. Steven D. Emslie, FLMNH, and the late R. Jerry Britt, Jr. assisted in the collection of additional macro-invertebrate fossils. Fred G. Thompson, Kurt Auffenberg, and Kim T. Massey helped with the identification of certain molluscan taxa and allowed access to the Malacology collections at the FLMNH. William G. Lyons, Florida Department of Natural Resources, St. Petersburg, Florida, and the late Victor A. Zullo, University of North Carolina at Wilmington, kindly identified the polyplacophorans and barnacles, respectively. Frank J. Maturo, University of Florida, Alan Cheetham, National Museum of Natural History, and John and Dorothy Soule, University of Southern California, provided identifications for several bryozoans. Photographs of all invertebrate species were taken by Craig W. Oyen. Douglas S. Jones, FLMNH, and William G. Lyons kindly reviewed an earlier draft of this manuscript. Curation of the Leisey invertebrate fossils into the Division of Invertebrate Paleontology of the FLMNH was supported by National Science Foundation Grants BSR 8711802 and BSR 9002689. This is University of Florida Contribution to Paleobiology 386.

METHODS AND MATERIALS

The fossiliferous portions of the exposed stratigraphic sections at Leisey Shell Pit 1 and Leisey Shell Pit 3 were informally divided into three superposed units: lower shell bed, bone bed, and upper shell bed. The combined thickness of the three beds at Leisey Shell Pit 1 and Leisey Shell Pit 3 totaled 8.0 m and 6.0 m respectively (Fig. 2). In order to obtain adequate samples for microvertebrate analysis, the FLMNH Vertebrate Paleontology crew collected over a metric ton of matrix, directly from the bone bed of each pit . From this, over a 100 kg sample of matrix from Leisey Shell Pit 1 and Leisey Shell Pit 3 was washed and all invertebrate fossils larger than 5.0 mm were removed and identified. A much smaller sample (about 5 kg) of fine matrix from the bone bed at each pit was sorted to obtain a representative sample of the micro-mollusks. In addition, bulk samples of matrix from 5 to 7 kg were collected from the lower and upper shell beds at 1.0 m intervals from three separate stratigraphic sections within each pit. Three samples from both the lower and upper shell beds were washed through a 1.0 mm screen, sorted, and identified. Specimens of macro-mollusks were collected in place from the three main beds in each pit to provide a more accurate picture of the overall molluscan fauna. We acknowledge that because of the much larger sample size taken from each bone bed our estimates of the total number of species of the other units (lower shell bed and upper shell bed) may be comparatively low.

Based on the close proximity of Leisey Shell Pit 1 and Leisey Shell Pit 3 (Fig. 1) and striking similarities in their lithology, faunal preservation, and invertebrate fauna (especially extinct taxa), the authors consider each specific bed at the two Leisey pits to be stratigraphic equivalents (i.e. lower shell bed of Leisey Shell Pit 1 = lower shell bed of Leisey Shell Pit 3, etc.). However, we realize that differences in shell bed thicknesses between the two pits and the occurrence of an unconformity (above dolomitic "hard layer", Fig. 2) at Leisey Shell Pit 1, and not Leisey Shell Pit 3, indicate some differences in the accumulation history between the two pits and, therefore, they may not represent *exact* time equivalents. In addition, although the main bone bed from Leisey Shell Pit 1 (Leisey 1A) and Leisey Shell Pit 3 (Leisey 3A) are herein considered stratigraphic equivalents, both

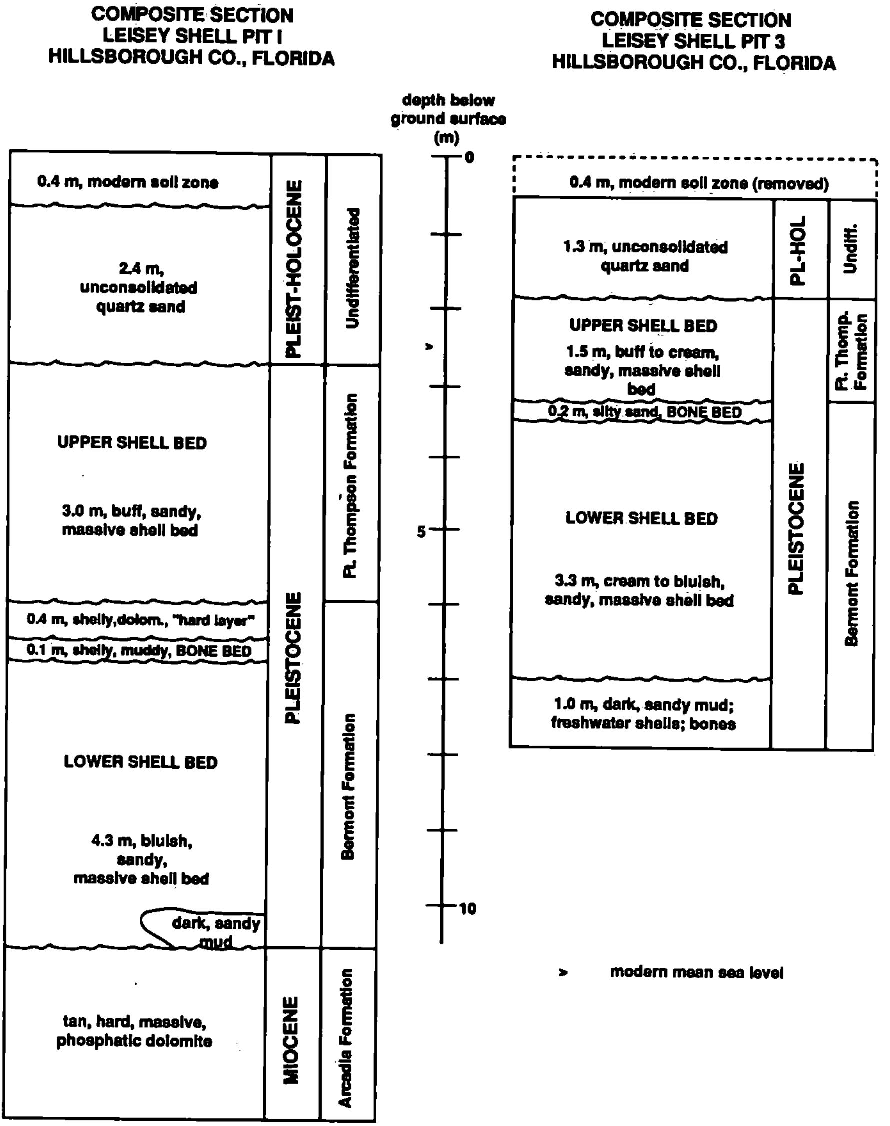

Figure 2. Composite geologic sections of Leisey Shell Pits 1 and 3, modified slightly from Hulbert and Morgan (1989).

were lenses with well defined lateral boundaries and clearly differ with respect to their taphonomic histories.

Identifications were made by comparisons with identified specimens in the Invertebrate Paleontology and Malacology Collections at the Florida Museum of Natural History, and by using the descriptions and figures in Abbott (1974) and

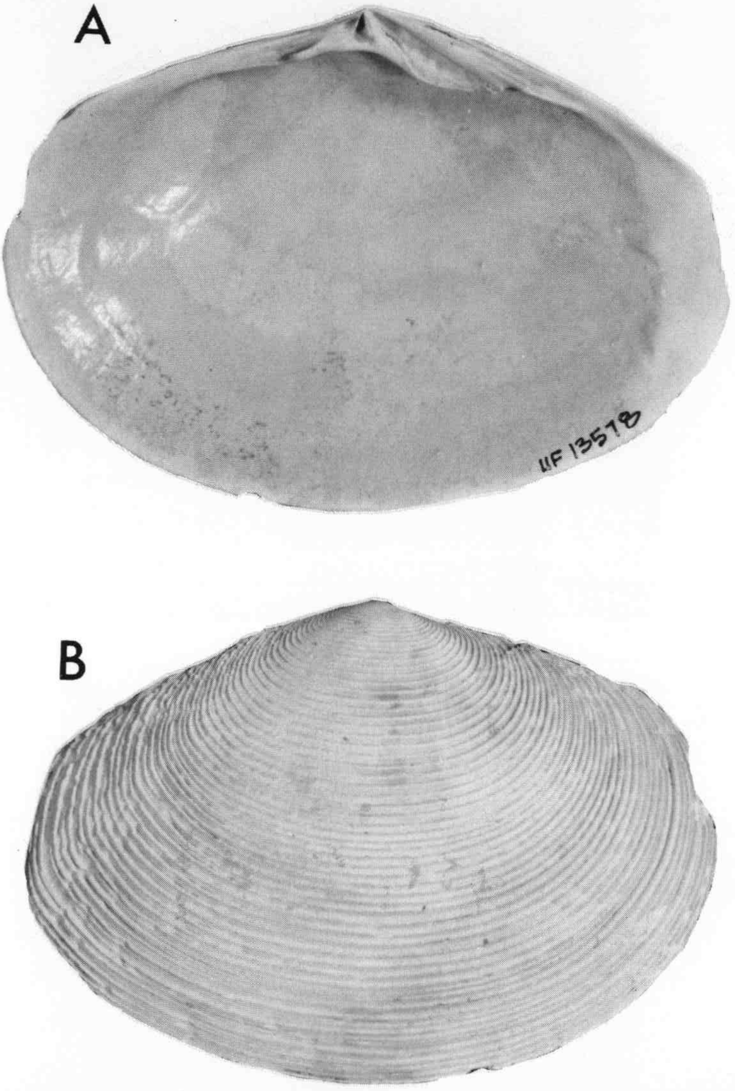

Figure 3. (A, B) *Semele perlamellosa* Heilprin 1886 from Lower Shell Bed of Leisey Shell Pit 1; UF 13578. Interior and exterior view of right valve (x 1.0).

Olsson and Harbison (1953), among others. Specific names separated by a slash (/) represent taxonomically ambiguous species that are either indistinguishable to the authors or represent transitional forms. Typically these taxa, e.g. *Anadara lienosa* (Say 1832)/*floridana* (Conrad 1867), consist of extinct and extant equivalents. Basic ecological data of extant species were obtained primarily from Abbott (1974) and Stanley (1970).

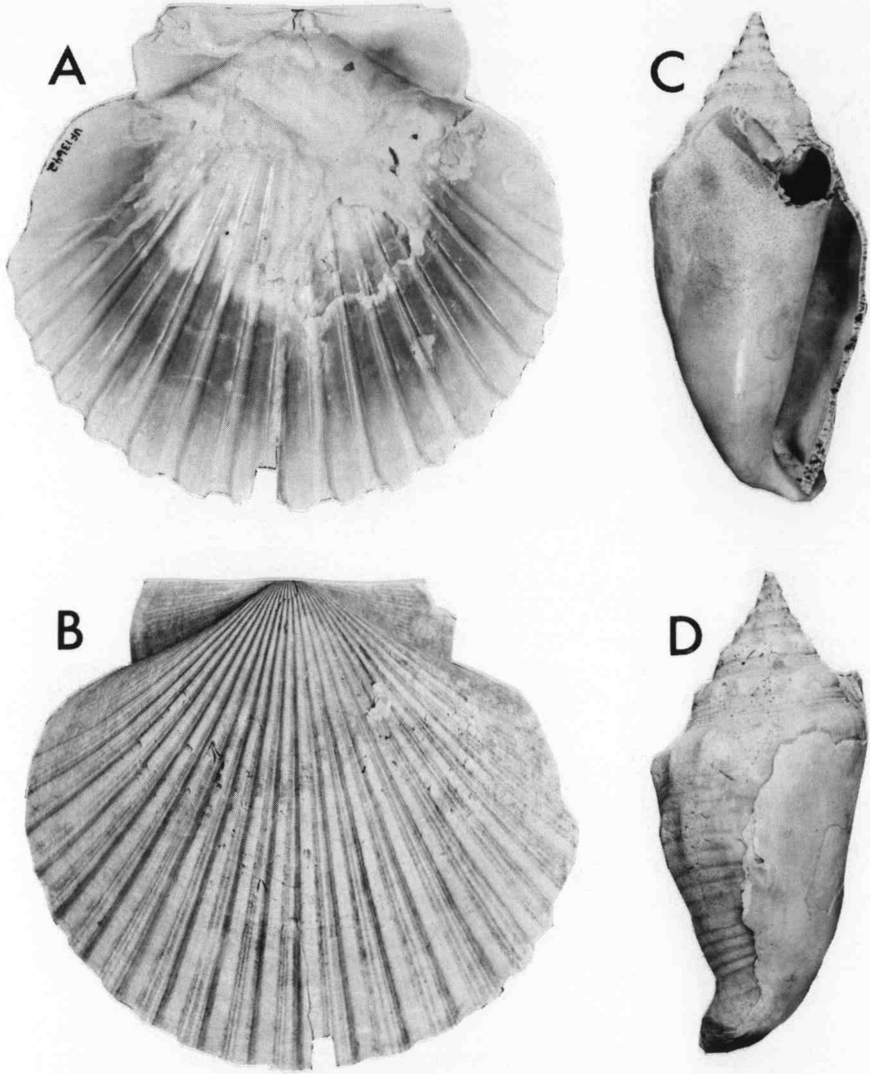

Figure 4. (A, B) *Carolinapecten eboreus solarioides* (Heilprin 1886) from the lower shell bed of Leisey Shell Pit 1; UF 13642. Interior and exterior view of left valve (x 0.5). (C, D) *Strombus mayacensis* Tucker and Wilson 1933 from spoil materials of Leisey Shell Pit 3; UF 37952. Apertural and lateral view of incomplete specimen (x 0.5).

The percentages of extinct taxa, used to help establish placement of the molluscan assemblages of the lower shell bed, bone bed, and upper shell bed into the Bermont and Fort Thompson formations, were calculated by excluding all nonmarine species. Also, the aforementioned taxonomically ambiguous species were judged on the basis of their companion species and therefore considered extant.

Percentages of extinct mollusks were based solely on materials stratigraphically collected; spoil materials were not included. All invertebrate fossils discussed in this paper are housed in the Invertebrate Paleontology Division of the FLMNH.

We follow Harland et al. (1990) in subdividing the Pleistocene into the early Pleistocene (1.64 to 0.79 Ma), middle Pleistocene (0.79 Ma to 0.13 Ma) and late Pleistocene (0.13 Ma to 0.01 Ma).

STRATIGRAPHY AND CORRELATION

Miocene strata of the Arcadia Formation underlie the entire Pleistocene marine shell sequence in the Leisey Shell Pits. The Arcadia sediments consist of a well-indurated tan to light gray, clayey, phosphatic dolomite containing no identifiable invertebrate fossils. A major erosional unconformity separates the Arcadia Formation from the massive, unconsolidated, sandy shell beds that compose most of the stratigraphic section at Leisey.

Below is a brief stratigraphic description and faunal accounting of the shell beds (lower shell bed, bone bed, and upper shell bed) along with a short summary of the more unusual taxa found from spoil. A discussion of the placement of these beds into their appropriate formations and age of these deposits follows.

Lower Shell Bed.— The lower shell bed at Leisey Shell Pit 1 and Leisey Shell Pit 3 is composed primarily of marine mollusk shells in a matrix of fine, quartz sand. Near the base of the lower shell bed at Leisey Shell Pit 1 are irregular lenses of dark, fine-grained organic sediments containing estuarine, freshwater, and terrestrial invertebrates, vertebrates, and plants. Similar sediments are found at the base of the lower shell bed at Leisey Shell Pit 3, not as lenses, but rather as a distinct layer (up to 1 m thick) containing mainly freshwater and terrestrial invertebrates and vertebrates.

The combined fauna of the lower shell bed of Leisey Shell Pit 1 and Leisey Shell Pit 3 consists of the following species distribution: 1 poriferan, 2 cnidarians, 14 bryozoans, 160 mollusks, 1 annelid, 3 arthropods, and 1 echinoderm. This predominately molluscan assemblage contains 84 species of bivalves (79 marine and 5 freshwater), 74 species of gastropods (64 marine and 10 nonmarine), and 2 scaphopods. Of the 145 marine mollusk species recorded, only 5 (3%) are extinct. These are the bivalves: *Semele perlamellosa* (Fig. 3A-B), *Carolinapecten eboreus solarioides* (Heilprin 1886) (Fig. 4A-B), *Conradostrea sculpturata* (Fig. 5A-B), and *Noetia platyura* (Dall 1898) (Fig. 6A-B), and the gastropod *Vermicularia weberi* Olsson and Harbison 1953. *V. weberi* and *S. perlamellosa* were represented at Leisey Shell Pit 1 as single specimens while the remaining three extinct species were common at both pits. The only non-molluscan species recognized from this

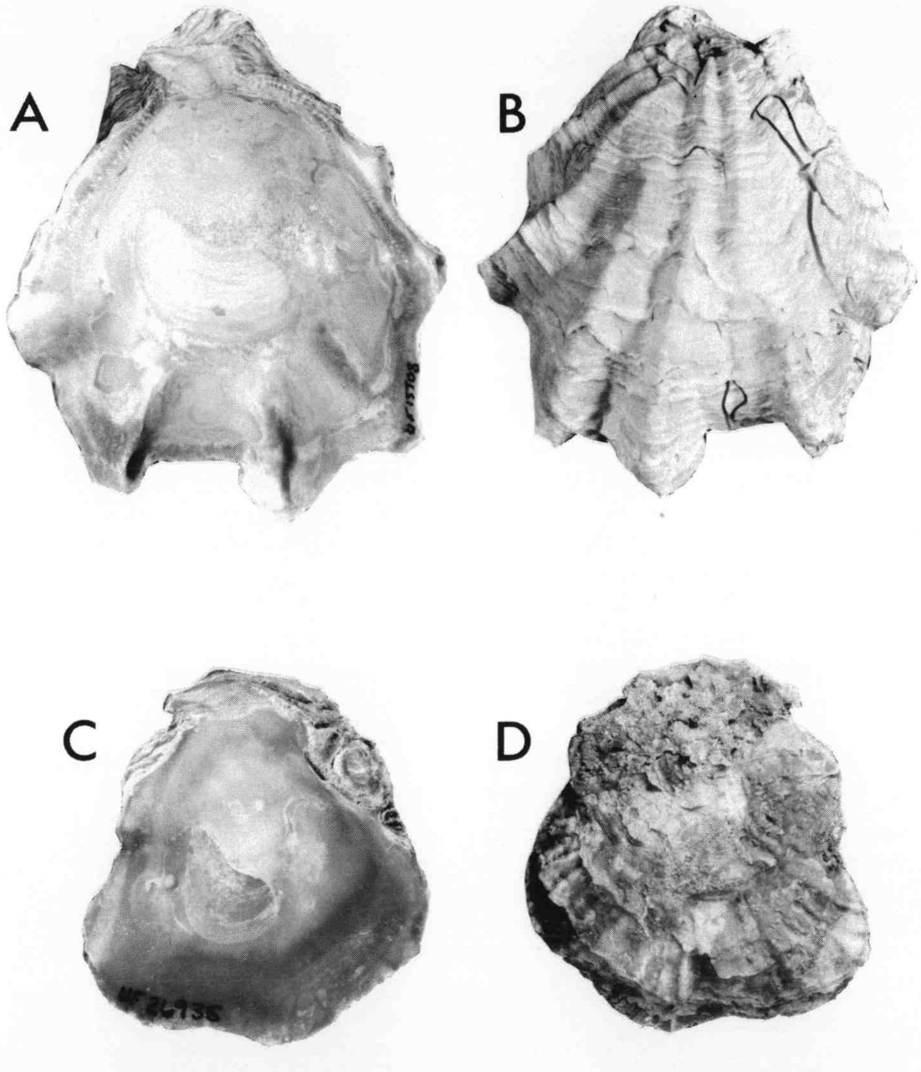

Figure 5. (A, B) *Conradostrea sculpturata* (Conrad 1840) from the lower shell bed of Leisey Shell Pit 1; UF 13708. Interior and exterior view of left valve (x 1.0). (C, D) *Ostreola equestris* (Say 1834) from the bone bed of Leisey Shell Pit 3; UF 26935. Interior and exterior view of left valve (x 1.0).

unit as being extinct are the small, scleractinian corals *Archohelia limonensis* Vaughan 1919 (Fig. 6E) and *Astrangia floridana* (Gane 1895).

Bone Bed.-- Lying above the lower shell bed is the bone bed, an unconsolidated, poorly-sorted mixture of marine and freshwater mollusk shells, bones, fine-grained sand, silt, and dark brown mud. This bed is a well-defined 5-

30 cm thick layer containing most of the rich vertebrate fauna discussed elsewhere in this volume. At Leisey Shell Pit 1, there was a 30-50 cm thick layer of indurated calcareous marl above the bone bed. This "hard layer" contained abundant freshwater gastropods, especially *Planorbella scalaris* (Jay 1839), some fragmented and apparently reworked marine mollusks, fine-grained sand, and occasional bones of freshwater vertebrates.

The combined fauna of the bone bed at Leisey Shell Pit 1 and Leisey Shell Pit 3 consists of the following species distribution: 1 poriferan, 2 cnidarians, 8 bryozoans, 166 mollusks, 1 annelid, 3 arthropods, and 1 echinoderm. Unlike the lower shell bed, this unit is dominated by gastropod rather than bivalve species. All 68 bivalves are marine and of the 93 gastropods, 83 are marine and 10 nonmarine. Two scaphopod and 3 polyplacophoran species are also recorded. Of the 156 marine mollusks recognized, only 4 (3%) are extinct. These include the bivalves: *Noetia platyura*, *Conradostrea sculpturata*, and *Carolinapecten eboreus solarioides*, and the gastropod *Turritella perattenuata* Heilprin 1886 (Fig. 6D). Other extinct taxa recorded from the bone bed include the freshwater gastropod *Stenophysa meigsii* (Dall 1890) (Fig. 6C) from Leisey Shell Pit 3 and the coral *Archohelia limonensis* from both Leisey pits. Only one of the extinct marine mollusk taxa (*C. sculpturata*) occurs in the bone bed at both Leisey pits, while the remainder are found in either Leisey Shell Pit 1 or Leisey Shell Pit 3, but not both (see Appendix 1). Another interesting note involves the occurrence of the oysters. The extinct *C. sculpturata* (Fig. 5A-B) is found in the lower shell bed and bone bed at both Leisey Shell Pits. The extant *Ostreola equestris* (Say 1834) (Fig. 5C-D) is found at Leisey Shell Pit 3 in both the bone bed and upper shell bed. The co-occurrence of these two taxa, as far as the authors know, has never been documented and may represent a replacement of the older *C. sculpturata* by the younger *O. equestris*. The reported occurrence of the extinct bivalve *Juliacorbula scutata* (Gardner 1943) from the bone bed at Leisey Shell Pit 1 by Portell et al. (1992) was in error.

Upper Shell Bed.— Like the lower shell bed and bone bed, the upper shell bed lacks distinct bedding and is composed predominantly of marine mollusks. However, in contrast to the bone bed, the upper shell bed has much fewer freshwater gastropods, is nearly devoid of bones, and has a higher percentage of fine-grained sand and a lower percentage of mud.

The combined fauna of the upper shell bed consists of the following species distribution: 1 poriferan, 1 cnidarian, 6 bryozoans, 106 mollusks, 5 arthropods, and 1 echinoderm. The mollusks are represented by 51 marine bivalves, 53 gastropods (48 marine and 5 nonmarine), and 2 scaphopods. Of the 101 marine mollusks, only 1 (1%) may be extinct. This is the bivalve *Noetia* sp. cf. *N. platyura*, which is represented by a single fragment and as indicated its identification is tentative. Like the lower shell bed and bone bed, the extinct coral *Archohelia limonensis* is found in the upper shell bed at both pits.

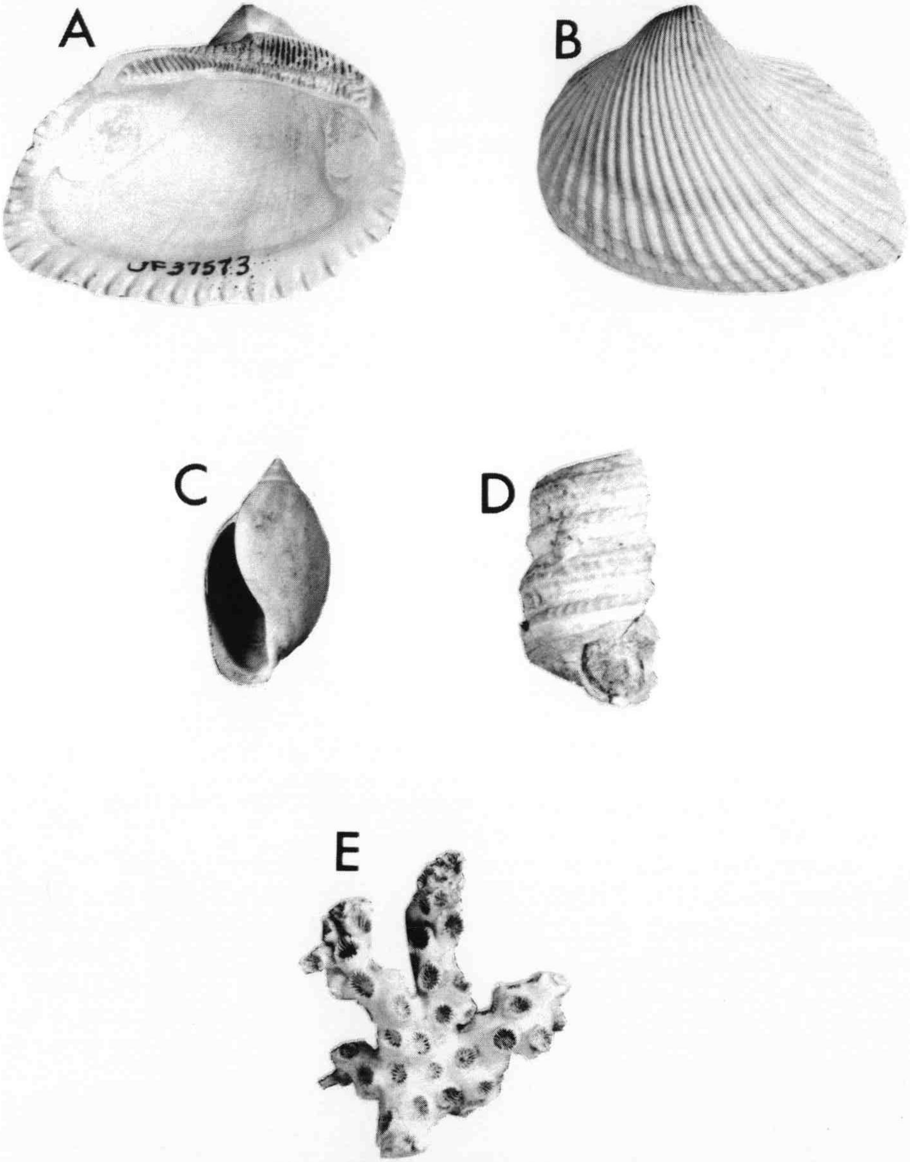

Figure 6. (A, B) *Noetia platyura* (Dall 1898) from the lower shell bed of Leisey Shell Pit 3; UF 37573. Interior and exterior view of left valve (x 1.0). (C) *Stenophysa meigsii* (Dall 1890) from the bone bed of Leisey Shell Pit 3; UF 45869. Apertural view (x 1.0). (D) *Turritella perattenuata* Heilprin 1886 from the bone bed of Leisey Shell Pit 1; UF 10128. Apertural view of incomplete specimen (x 2.0). (E) *Archohelia limonensis* Vaughan 1919 from the lower shell bed of Leisey Shell Pit 1; UF 10574. Corallum (x 1.0).

Spoil.– At Leisey, several taxa worth noting were not collected in stratigraphic context and are known strictly from spoil. These include two bivalve specimens from Leisey Shell Pit 1 donated to the FLMNH by John Waldrop. The first, *Chione procancellata* Mansfield 1932, is known only from the Pliocene Pinecrest Beds and its equivalents. The second, *Anadara scalarina* (Heilprin 1886), is known to occur in both the Pliocene Pinecrest Beds and the Plio-Pleistocene Caloosahatchee Formation and their equivalents . Neither species has been reported from units younger than the Caloosahatchee. These specimens were probably derived from a relict pocket of Pinecrest and are not included in the species counts because they were not part of the study materials collected by FLMNH field crew. As noted earlier, a partial specimen of the gastropod *Strombus mayacensis* (Fig. 4C-D) was collected at Leisey Shell Pit 3.

AGE

All strata in the Leisey Shell Pits bounded by the Arcadia Formation below and the top of the bone bed are referred to the Bermont Formation on the basis of extinct molluscan taxa. DuBar (1974) proposed the name Bermont Formation as an informal stratigraphic unit for the uppermost fossiliferous marine sands exposed along Shell Creek in the Bermont Quadrangle, Charlotte County, Florida. DuBar's (1974) description of the Bermont included scattered excavations and natural exposures along the Gulf Coast from the type area in Charlotte County northward to Levy County, along the Caloosahatchee River in Glades and Hendry counties, in the Lake Okeechobee region, and on the Atlantic coast from Palm Beach County north to Seminole, Volusia, and Putnam counties.

Earlier names applied to strata DuBar (1974) referred to the Bermont Formation include: Unit F (DuBar 1962), Unit A (Olsson 1964), and Glades Unit (Vokes 1963). Hunter (1978) later proposed the informal name Belle Glade Member (of the Fort Thompson Formation) to include strata from the Belle Glade Rock Pit in Palm Beach County and surrounding areas south of Lake Okeechobee that had previously been referred to the Bermont Formation by DuBar (1974). Hunter considered her Belle Glade Member to be a correlative of the Okaloakoochee Member of the Fort Thompson Formation of DuBar (1958).

The Bermont Formation occupies a stratigraphic position between the older Caloosahatchee Formation and the younger Fort Thompson Formation. At most localities where the Bermont is exposed, DuBar (1974) found that all or part of the underlying Caloosahatchee had been removed indicating a period of erosion between these two formations, presumably corresponding to a marine regression(s) during a glacial interval(s). The Caloosahatchee Formation was not observed at the Leisey Shell Pits where the Bermont Formation rests directly upon the unevenly eroded surface of the Miocene Arcadia Formation. The initiation of

Bermont deposition at Leisey is marked by a transgression as the base of the lower shell bed consists of considerable amounts of dark, organic sediments containing freshwater and estuarine mollusks as well as freshwater and terrestrial vertebrates.

Most southern Florida formations currently recognized by geologists/paleontologists are defined by faunal differences based on either Lyellian percentages (percentage of extinct taxa within a particular unit) or the recognition of certain "index" taxa. Lithologic distinctions have played a relatively minor role and this has led to considerable debate and confusion in the literature (see Scott 1992, p. 21-25). Furthermore faunal comparisons between units have often ignored taphonomy, facies changes, and paleogeographic differences, factors which complicate the emerging biozonation schemes for the region.

DuBar (1974) recognized that the Caloosahatchee and Bermont formations were distinct faunally, that many of the mollusks typical of the Caloosahatchee were lacking in the Bermont, and that the Bermont contained many unique taxa. Species listed by DuBar (1962), Vokes (1963), and McGinty (1970) that are restricted to the Bermont Formation include the bivalves *Anadara aequalitas* (Tucker and Wilson 1932) and *Miltha carmenae;* and the gastropods *Fasciolaria okeechobensis, Fusinus watermani* (M. Smith 1936), *Haustellum anniae* (M. Smith 1940), *Latirus jucundus* (McGinty 1940), *L. maxwelli* Pilsbry 1939, *Melongena bispinosa* (Phillipi 1844), *Murexiella graceae* (McGinty 1940), *Strombus mayacensis* Tucker & Wilson 1933, *Turbinella hoerlei* Vokes 1966, and *Vasum floridanum* McGinty 1940. Recently Petuch (1988, 1989) added *Lindoliva griffini* Petuch 1988, *L. spengleri* Petuch 1988, and *Malea petiti* Petuch 1989, and Lyons (1991) added *Latirus carinifer* (Lamarck 1816) to the list of useful biostratigraphic indicators for the Bermont Formation. Additional studies by Petuch (1991) indicate that a considerable number of new "index" taxa will be added to the list of restricted Bermont species.

At the Leisey Shell Pits, none of these unique taxa were collected from in-place Bermont sediments (lower shell bed and bone bed). However, a single broken specimen of *Strombus mayacensis*, one of the "index" taxa listed above, was collected from spoil at Leisey Shell Pit 3. DuBar (1974) noted that individuals of Bermont "index" species are rare and some have never been collected from in-place deposits. In addition, DuBar (1974; written comm. 1993) stated none of these "index" taxa were found in the type Bermont deposits at Shell Creek. The lack of "index" taxa and the absence of more tropical species from both Leisey and the type locality indicate that these two deposits are more closely allied than either is to the better known, "classic" Bermont deposits surrounding Lake Okeechobee which contain many more tropical species and all of the "index" taxa mentioned above.

Previous estimates of extinct molluscan taxa for the Bermont Formation typically ranged from 10% to 30%. Olsson (1969) estimated Unit A (= Bermont Formation) to contain about 600 species, of which 20% to 30% are extinct. Hoerle (1970) recognized that approximately 15% of the 434 species collected in the Belle Glade Rock Pit, Palm Beach County were extinct. However, Lyons (1991) noted that all of the materials collected from Belle Glade Rock Pit were excavated spoil and therefore it is not known how many of Hoerle's (1970) species may have been derived from other stratigraphic units. DuBar (written comm. 1993) stated that when the Bermont molluscan fauna is considered as a whole about 10% of the species may be extinct. The molluscan assemblage in the lower shell bed and the bone bed of the Leisey Shell Pits each contains approximately 3% extinct taxa. If formational assignment was based strictly upon percentages, the entire shell sequence at Leisey should probably be placed in the Fort Thompson Formation, which typically contains fewer than 5% extinct taxa (*fide* Webb et al. 1989). However, even though the lower shell bed and bone bed at Leisey lack Bermont "index" taxa and the percentages of extinct species appear low, placement of these units in the Bermont Formation is justified based on the occurrence of numerous extinct mollusks that elsewhere in Florida make their last appearance in this unit. These taxa are the bivalves: *Noetia platyura*, *Conradostrea sculpturata*, *Carolinapecten eboreus solarioides*, and *Semele perlamellosa*, and the gastropods: *Turritella perattenuata*, *Vermicularia weberi*, and *Stenophysa meigsii*.

As mentioned earlier, the Leisey lower shell bed and bone bed lack many of the more tropical species of mollusks present in the "classic" Bermont faunas (e.g. Belle Glade Rock Pit). Hulbert and Morgan (1989) believed this may reflect the deposition of the Leisey fauna some 100 km farther north in waters that were presumably slightly cooler. It is also possible that the Leisey mollusks (and the type deposits at Shell Creek) may be somewhat younger than those of the more diverse Bermont faunas in southern Florida and that the assemblages of the lower shell bed and bone bed at Leisey may represent a temporal intermediate between the Bermont and Fort Thompson formations.

The upper shell bed is referred to the Fort Thompson Formation because the fauna contains at least 99% extant taxa and all molluscan species that make their last appearance in the Bermont Formation are absent. Originally named by Sellards (1919), the "Fort Thompson beds" were described as a series of alternating marine shell beds and indurated freshwater marls lying unconformably above the Caloosahatchee Formation between LaBelle and Fort Thompson along the Caloosahatchee River, Hendry County, Florida. DuBar (1958) described the marine units of the Fort Thompson in the type area as poorly consolidated tan to cream-colored sandy shell marls, with the most abundant fossil being the bivalve, *Chione cancellata* (Linnaeus 1767). The lithology and faunal composition of the upper shell bed at the Leisey Shell Pits is very similar to the description of the type Fort Thompson Formation (except for the lack of indurated freshwater marls). Outside the type area, the Fort Thompson Formation has been recognized in numerous localities in southern Florida (DuBar 1958, 1962; Brooks 1968).

The common occurrence of the extinct branching-coral, *Archohelia limonensis*, in the upper shell bed from both Leisey Shell Pits may represent its first reported occurrence outside the previously known stratigraphic range.

Weisbord (1974) reported this species from only Caloosahatchee and Unit A (= Bermont Formation) strata.

As pointed out by Lyons (1991) and Allmon et al. (in press), age determination of the Plio-Pleistocene units in southern Florida is poorly understood as are their correlations with deposits outside of the area. Most of these Florida units are inadequately documented, both lithologically and faunally, and are in need of much more study.

A dichotomy of opinion exists about the age of the Bermont Formation. Many early workers, including Vokes (1963), Taylor (1966), Waller (1969), and Hoerle (1970), considered the Bermont to be early Pleistocene or late Pliocene or both. Others workers such as DuBar (1974), DuBar et al. (1991), Petuch (1991), and Muhs et al. (1992) have placed the Bermont in the middle to late Pleistocene.

DuBar (1974) proposed a minimum age of 0.4 Ma for the Caloosahatchee Formation and 0.14 to 0.12 Ma for the Fort Thompson Formation. Although DuBar did not specify an age for the Bermont Formation, it must fall between 0.4 and 0.14 Ma according to his proposed stratigraphic sequence. DuBar et al. (1974) correlated the Bermont with the Canepatch Formation of South Carolina and the Flanner Beach Formation of North Carolina based on their similar stratigraphic positions and molluscan faunas. They stated that all three units are correlative because each lies directly on apparently correlative early Pleistocene units and is overlain by seemingly correlative late Pleistocene units.

Blackwelder (1981) placed the age of the Canepatch and Bermont Formations between 0.5 and 0.4 Ma. Blackwelder assigned the Canepatch Formation to his Mollusk Zone M2 (Myrtlean Substage) corresponding to the beginning of the Longian Stage, a time interval proposed to denote the first appearance in the Atlantic Coastal Plain sequence of essentially modern molluscan assemblages containing 94-96% living species. As discussed above, typical Bermont faunas may contain from 70% to 90% extant species, and thus would appear to be older than Zone M2. Blackwelder's next oldest biozone, Mollusk Zone M3 (Windyan Substage of the Colerainian Stage), includes molluscan assemblages with only 35% living species. He placed the James City and Waccamaw Formations of the Atlantic Coastal Plain and the Caloosahatchee Formation of Florida in Zone M3, and considered these faunas to be early Pleistocene in age (1.8 to 1.1 Ma), based in part on helium-uranium dates of 1.9 to 1.7 Ma of corals from the Caloosahatchee Formation (Bender 1973). Muhs et al. (1992) suggested that these dates are tentative because of evidence of uranium loss in most of Bender's samples. Lyons (1991) argued that the Bermont is probably correlative with the Waccamaw Formation of the Carolinas based on dates provided by Hulbert and Morgan (1989) and Webb et al. (1989). More recently, Zullo and Harris (1992) correlated the Bermont with the early Pleistocene James City Formation of the middle Atlantic Coastal Plain based on sequence stratigraphy.

The Canepatch and equivalent formations of Zone M2 were deposited following a long depositional hiatus in the middle Atlantic Coastal Plain sequence between 1.1 and 0.5 Ma, termed the Windyan hiatus (Blackwelder 1981). The Bermont molluscan faunas could occur in the time period between 1.1 and 0.5 Ma, corresponding to Blackwelder's Windyan hiatus. Climatic and latitudinal differences may also have had a significant effect on the timing of extinctions. It is possible that some extinct species of mollusks survived longer in the more tropical waters of southern Florida.

Szabo (1985) obtained a uranium-series date of 460 ± 100 ka on unaltered aragonite from corals of the Canepatch Formation but DuBar et al. (1991, p. 602) stated these corals were probably from the early Pleistocene Waccamaw Formation. If the Szabo date is correct, then the early Pleistocene age is incorrect; 460 ± 100 ka falls within the middle Pleistocene of Harland et al. (1990). Mitterer (1975) reported an age of 236 ka for the Bermont Formation based on amino acid racemization of shells of the bivalve *Mercenaria*. Recalculation of Mitterer's data by Wehmiller and Belknap (1978) placed an age of 0.6 to 0.4 Ma on the Bermont Formation. Recently, Muhs et al. (1992) obtained uranium-series dates from the coral, *Solenastrea* from several Bermont deposits collected near the town of Okeechobee and from deposits near the southern end of Lake Okeechobee. These dates range in age from 230-360 ka. They also attempted dating a sample of *Solenastrea* sp. cf. *S. hyades* (Dana 1846), found in the bone bed at Leisey Shell Pit 1; but the much too young date was ascribed to added, secondary uranium.

In summary, the few published dates for the Bermont Formation, along with the invertebrate biochronology, fail to resolve the age of this unit beyond suggesting a broad range of ages of between 1.8 and 0.13 Ma (late Pliocene to late Pleistocene). However, new lines of evidence, such as the mammalian biochronology (Hulbert and Morgan 1989, Webb et al. 1989, and other papers, this volume), strontium isotope stratigraphy (Webb et al. 1989, Jones et al., this volume), and paleomagnetic stratigraphy (Webb et al. 1989, MacFadden, this volume) suggest an early Pleistocene age (1.6 to 1.0 Ma) for the strata referred to the Bermont Formation exposed at the Leisey Shell Pits. For a more thorough review for the geochronology of the Bermont Formation see Lyons (1991) and Morgan and Hulbert (this volume).

PALEOECOLOGY

The dominant phylum represented by the fossil assemblages of the Leisey Shell Pits, both in terms of abundance and species diversity, is the Mollusca (Appendix 1). Of the 248 species of invertebrates identified, 217 (88%) are mollusks. Consequently, much of the data presented here deal with this group. General comparisons of species richness, relative abundance, and environment of deposition between the lower shell bed, bone bed, and upper shell bed are discussed below.

The majority of mollusks from the Leisey Shell Pits (97%) are extant species. Therefore, knowledge of the preferred habitats of modern forms is very useful in reconstructing the depositional environments. The salinity indicated by the majority of the mollusks is that of normal sea water, however, freshwater gastropods (9 species) are extremely abundant in the bone bed and in the indurated calcareous marl overlying the bone bed at Leisey Shell Pit 1. The freshwater species *Planorbella scalaris* is especially common in this unit. Most of these nine gastropod species are also found in the lower and upper shell beds but are considerably less abundant, although several freshwater lenses at the base of the lower shell bed contain tremendous numbers of *Viviparus georgianus* (Lea 1834) and *Planorbella duryi* (Wetherby 1879). The freshwater gastropod shells from the indurated calcareous marl and base of the lower shell bed probably accumulated in a freshwater spring, river, or pond habitat. The remainder of the freshwater gastropods were probably transported by a river into the shallow marine environments.

No permanent hard bottom was present in any of the Leisey units. Consequently, infaunal species were generally better preserved and represented by more specimens than epifaunal species. The percentage of infaunal bivalves, for instance, is 77% of all marine bivalves found at Leisey, a higher-than-average infaunal element (Nicol 1968). Some epifaunal genera, such as *Arca*, were absent while others, such as *Chama*, *Arcinella*, *Plicatula*, and *Argopecten* were often poorly preserved. These epifaunal representatives, lacking a hard bottom, probably attached themselves to dead shells and bones.

The counter-sunk borings of naticid gastropods were commonly seen in bivalve shells from both Leisey pits. These carnivorous gastropods preyed preferentially on the small-sized and/or thin-shelled species or the young of larger species. The mortality in some vulnerable species was great. In a sample of 88 specimens (less than 30.0 mm in length) of *Macrocallista nimbosa* (Lightfoot 1786) from the bone bed, 29 (33%) were bored by naticids. Specimens of *Pleuromeris tridentata* (Say 1826) and *Parvilucina multilineata* (Tuomey and Holmes 1856) were also commonly bored by naticids.

Among other groups of invertebrates, small barnacles (*Balanus* spp.) and a small species of branching scleractinian coral (*Archohelia limonensis*) were most common. The barnacles (*Balanus improvisus* Darwin 1854 and *B. venustus* Darwin 1854) were more abundant in the lower shell bed and bone bed, while the corals were more common in the bone bed and upper shell bed. The barnacles were often found attached to mollusk shells in the lower shell bed and bone bed, and were occasionally found on bones in the bone bed. Today, *Balanus improvisus* (an estuarine barnacle typically found in lower salinities) and *B. venustus* (a subtidal barnacle preferring normal marine salinities) are wide-ranging Atlantic Basin species (Zullo 1992). Several specimens of massive colonial coral (*Solenastrea* sp. cf. *S. hyades*) were found in the bone bed, one of which was extensively bored by the bivalves *Gastrochaena hians* (Gmelin 1791) and

Lithophaga sp. Bryozoans were also commonly found in the Leisey deposits, usually attached to mollusk shells. Sixteen species, all cheilostomes, were recovered, including 14 encrusting and 2 free-living forms. A complete analysis of the bryozoans is currently underway (Maturo and Schindler, in preparation).

Lower Shell Bed.– The lower shell bed has more species of bivalves (84) than gastropods (74), in contrast to the bone bed, which has more species of gastropods, and the upper shell bed, in which both groups are almost equally represented. A diagnostic feature of the lower shell bed, which relates to the energy of the depositional environment, is the number of different species and individuals of bivalves preserved as articulated valves. Twenty-eight species are represented in this bed by one or more specimens with paired valves. In the bone bed this is reduced to 12 species; and in the upper shell bed there are only 6 species. Large bivalves such as *Mercenaria campechiensis* (Gmelin 1791), *Dinocardium robustum* (Lightfoot 1786), *Macrocallista nimbosa*, and the thin-shelled *Raeta plicatella* (Lamarck 1818), were less apt to be broken in the lower shell bed sample and were often preserved as articulated valves.

A bed about 20 to 30 cm thick consisting of large numbers of *Rangia cuneata* (Sowerby 1831) was found near the base of the lower shell bed in a limited area at the north end of Leisey Shell Pit 1. A lens of freshwater unionid bivalves occurred below the bed of *Rangia*, immediately above the contact with the underlying Arcadia Formation and also occurred at the base of the lower shell bed at Leisey Shell Pit 3 (see Bogan and Portell, this volume). Freshwater gastropods, particularly *Viviparus georgianus*, and *Planorbella duryi*, were extremely abundant in several lenses of dark, organic, freshwater sediments at the base of the lower shell bed. Well preserved articulated specimens of the brackish water oyster, *Crassostrea virginica* (Gmelin 1791), were also present in this basal unit. Neither these gastropods nor the *Crassostrea*, however, were found in direct stratigraphic superposition with each other or with the unionids or *Rangia*.

The majority of the lower shell bed appears to have been deposited in relatively quiet water with an estimated depth ranging from 3 to 6 m. The most likely depositional environment would have been in the deeper regions of a protected marine embayment similar to present day Tampa Bay (Webb et al. 1989). The absence of freshwater and estuarine mollusks and freshwater and terrestrial vertebrates in all but the basal portion of the lower shell bed suggests deposition farther offshore and in deeper water than the two upper units. It is worth noting that species more typical of an open continental shelf environment, e.g. *Glycymeris americana* (DeFrance 1826) and *Eucrassatella speciosa* (A. Adams 1852), were represented in the lower shell bed and bone bed by a few disarticulated valves which were possibly cast up by storms.

Bone Bed.– Although gastropod diversity (93 species) exceeds that of bivalves (68 species) in the bone bed, most of the gastropods are uncommon and small in size. The bivalves overwhelmingly dominate in both numbers and average size of individuals. The medium-sized bivalves (length from 10 to 40 mm), *Chione cancellata* and *Carditamera floridana* (Conrad 1838), are the two most abundant marine mollusks in the bone bed, the former species comprising more than one-half the volume of mollusk shells in this unit.

Hulbert and Morgan (1989) reported that at Leisey 1A (main bone-producing site), fossils were derived from one of two taphonomically distinct events. The terrestrial and freshwater elements, including invertebrates, vertebrates, and plants represent a transported taphocoenose, while a nearshore marine biocoenose is represented by marine invertebrates and vertebrates. These two taphonomic groups can be identified not only at Leisey 1A, but in the whole, generalized bone bed, as used in this paper.

One of the most characteristic aspects of the bone bed molluscan fauna, and the invertebrate representative of the transported taphocoenose, is the great abundance of freshwater gastropods. The freshwater snail *Planorbella scalaris* (Jay 1839) is the most abundant gastropod in the bone bed. This species and other common freshwater snails in the bone bed, *Tryonia aequicostata* (Pilsbry 1889), *Planorbella duryi*, and *Physella* sp., inhabit freshwater streams, springs, marshes and lakes. These freshwater gastropods were probably transported from inland areas into a nearshore, shallow marine environment by a large river, probably in the same way as the terrestrial and freshwater vertebrates reached the site.

Most of the marine invertebrates in the bone bed represent the nearshore marine biocoenose. An analysis of the 25 most common species of marine mollusks in the bone bed suggests they were deposited in a nearshore marine environment with water depths ranging from intertidal to no more than 2 m. Some of the shells were undoubtedly transported by storms, tides, and currents, as evidenced by some shell breakage and erosion, the presence of a few specimens of species that inhabit somewhat deeper water, and the abundance of freshwater gastropods. The overall well preserved condition of the shells, the common occurrence of articulated bivalves (though as pointed out earlier, not as common as in the lower shell bed), and the comparatively high percentage of silt and clay in the sediment, indicate relatively quiet water conditions and minimal transport. The majority of the species live today in water approximately 1 m in depth. Over 20% of the gastropods in the bone bed, including more than half of the most common species, occur in association with marine grass beds. The most abundant marine grass-dwelling gastropods in the bone bed are *Rissoina catesbyana* Orbigny 1842, *Caecum pulchellum* Stimpson 1851, *Conus jaspideus* Gmelin 1791, *Longchaeus crenulatus* (Holmes 1859), *Bulla striata* Bruguiere 1792, and *Mitrella lunata* (Say 1826). Two of the most abundant bivalves, *Chione cancellata* and *Carditamera floridana* also occur commonly in marine grass beds. Most of the remaining gastropods favor a sandy mud bottom or mud flats, as does another common species of bivalve *Anadara transversa* (Say 1822). Sand-dwelling species are present among both the gastropods and bivalves, but are considerably less common, which is in accordance with the relatively small fraction of fine-grained quartz sand in the bone bed sediment.

The absence of rocks or a permanent hard bottom in the bone bed suggests that certain species were probably attached to dead shells and bones. Bryozoans and oysters (*Conradostrea sculpturata*) were found attached to some of the bones.

The depositional environment suggested by the marine mollusks of the bone bed is a shallow (1 to 2 m depth) marine embayment with near normal salinity, having extensive grass beds, with sediments composed primarily of sand and mud. A large, slow-moving river probably emptied into the bay, accounting for the periodic influx, perhaps during floods, of the abundant freshwater gastropods.

Upper Shell Bed.– The upper shell bed has a reduced diversity of both gastropod (53) and bivalve (51) species when compared to the lower shell and bone beds. Marine gastropods are comparatively rare in the upper shell bed and most are either small species or immature specimens of larger species. This unit also contains the same species of freshwater gastropods found in the bone bed, but they are much less abundant. At Leisey Shell Pit 1, some of these freshwater gastropods have been reworked from the underlying freshwater unit, as they have pieces of indurated marl still attached to them.

Besides shells, the sediment in the upper shell bed consists primarily of fine-grained quartz sand, with only a very small percentage of silt or clay-sized particles. The near absence of silt and clay and the high percentage of abraded shells and shell fragments suggest that the upper shell bed was deposited under higher energy conditions than the other two beds at Leisey. The number of bivalves in the upper unit preserved as articulated valves is greatly reduced. The upper shell bed also seems to have been deposited in the shallowest water depth of the three units. Shallow-water mollusks that prefer depths ranging from intertidal to no more than 2 m dominate the upper shell bed. Like the bone bed, but unlike the lower shell bed, the upper unit contains a number of gastropods that inhabit marine grass beds in shallow protected bays. Attached epifaunal mollusks, bryozoans, and barnacles are less common in the upper shell bed, probably reflecting both the higher energy conditions and the rarity or absence of larger shells and bones as sites for attachment. The most likely depositional environment for the upper shell bed was a shallow, nearshore bay or lagoon or perhaps a tidal channel or inlet leading into a bay.

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APPENDIX 1

List of fossil invertebrates collected from Leisey Shell Pits 1 and 3. Occurrence of each species within the three stratigraphic units (lower shell bed, bone bed, and upper shell bed) and from spoil piles is noted by an "x" in the appropriate column. Extinct species are preceded by an asterisk (*). Specific names separated by a slash (/) represent taxonomically ambiguous species that are either indistinguishable to the authors or represent transitional forms.

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
PORIFERA								
CLIONIDAE								
cf. *Cliona* sp.	x	x	x		x		x	
CNIDARIA								
OCULINIDAE								
**Archohelia limonensis* Vaughan 1919	x	x	x			x	x	x
RHIZANGIIDAE								
**Astrangia floridana* (Gane 1895)	x				x			
FAVIIDAE								
Solenastrea sp. cf. *S. hyades* (Dana 1846)		x						
BRYOZOA								
MEMBRANIPORIDAE								
Membranipora tenuis Desor 1848	x	x			x		x	x

CALLOPORIDAE									
Antropora leucocypha (Marcus 1937)	x	x				x		x	
CUPULADRIIDAE									
Cupuladria biporosa Canu & Bassler 1923		x						x	
Discoporella umbellata depressa (Conrad 1841)		x				x	x	x	
HIPPOPORINIDAE									
Hippoporina verrilli Maturo & Schopf 1968	x	x				x			
SMITTINIDAE									
Hemismittoidea maleposita (Canu & Bassler 1923)	x								x
Parasmittina sp.	x					x	x		
Parasmittina nitida morphotype B Maturo & Schopf 1968								x	
SCHIZOPORELLIDAE									
Schizoporella cornuta (Gabb & Horn 1862)	x								
Schizoporella errata (Waters 1878)	x					x			
Stylopoma minuta Canu & Bassler 1923	x					x			
Stylopoma spongites (Pallas 1766)	x					x			
CLEIDOCHASMATIDAE									
Aimulosia uvulifera (Osburn 1914)	x	x				x			
Cleidochasma contractum (Waters 1899)	x	x				x	x	x	x
HIPPOTHOIDAE									
Celleporella sp.	x								
CELLEPORARIIDAE									
Celleporaria sp.	x								
MOLLUSCA (POLYPLACOPHORA)									
ACANTHOCHITONIDAE									
Acanthochitona pygmaea (Pilsbry 1893)		x							
ISCHNOCHITONIDAE									
Chaetopleura apiculata (Say 1834)		x							
Ischnochiton sp.		x							

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
MOLLUSCA (MARINE GASTROPODA)								
FISSURELLIDAE								
Diodora cayenensis (Lamarck 1822)	x	x	x		x		x	
Diodora meta (von Ihering 1927)		x						
Diodora sayi (Dall 1889)		x						
Lucapinella limatula (Reeve 1851)		x						
TROCHIDAE								
Calliostoma sp.	x	x	x		x	x	x	x
TURBINIDAE								
Turbo castanea Gmelin 1791	x	x						
RISSOIDAE								
Rissoina catesbyana Orbigny 1842		x	x					
CAECIDAE								
Caecum floridanum Stimpson 1851		x						
Caecum imbricatum Carpenter 1858		x						
Caecum pulchellum Stimpson 1851		x						
Caecum vestitum Folin 1870		x						
VITRINELLIDAE								
Cyclostremiscus pentagonus (Gabb 1873)	x	x						
Episcynia inornata (Orbigny 1842)	x	x	x					
Teinostoma biscaynense Pilsbry & McGinty 1945		x						
Vitrinella sp.	x	x						

MODULIDAE									
Modulus modulus (Linnaeus 1758)		x							
CERITHIIDAE									
Bittiolum varium (Pfeiffer 1840)			x						
Cerithium sp.		x	x					x	x
Cerithium muscarum Say 1832		x					x		
CERITHIOPSIDAE									
Cerithiopsis sp. aff. *C. emersoni* (C.B. Adams 1838)		x							
Seila adamsii (H.C. Lea 1845)	x	x	x				x	x	
TURRITELLIDAE									
**Turritella perattenuata* Heilprin 1886		x							
**Turritella subannulata* Heilprin 1886/ *acropora* Dall 1889	x	x				x	x		
Vermicularia fargoi Olsson 1951		x							
**Vermicularia weberi* Olsson & Harbison 1953	x								
TRIPHORIDAE									
Triphora melanura (C.B. Adams 1850)	x	x							
EPITONIIDAE									
Epitonium sp.	x	x	x					x	
STROMBIDAE									
Strombus alatus Gmelin 1791	x	x	x	x		x	x	x	x
**Strombus mayacensis* Tucker & Wilson 1933									x
MELANELLIDAE									
Melanella sp. A	x	x	x						
Melanella sp. B	x								
CALYPTRAEIDAE									
Calyptraea centralis (Conrad 1841)		x							
Crepidula aculeata (Gmelin 1791)	x	x	x			x	x	x	

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
Crepidula fornicata (Linnaeus 1758)	x	x	x		x	x		
Crepidula maculosa Conrad 1846	x	x	x	x	x	x	x	
Crepidula plana Say 1822	x	x	x		x		x	x
Crucibulum striatum Say 1824	x	x	x		x			
ERATOIDAE								
Erato maugeriae Gray 1832	x							
Trivia pediculus (Linnaeus 1758)	x	x						
Trivia quadripunctata (Gray 1827)	x	x						
NATICIDAE								
Natica canrena (Linnaeus 1758)						x		
Polinices duplicatus (Say 1822)	x	x	x	x	x	x	x	x
Sinum perspectivum (Say 1831)	x	x			x			
Tectonatica pusilla (Say 1822)	x	x	x				x	
FICIDAE								
Ficus communis Roding 1798	x							
MURICIDAE								
Calotrophon ostrearum (Conrad 1846)		x				x		
Chicoreus dilectus (A. Adams 1855)	x							
Eupleura sulcidentata Dall 1890	x	x	x		x	x		
Favartia cellulosa (Conrad 1846)		x				x		
Hexaplex fulvescens (Sowerby 1834)	x	x		x	x	x	x	x
Murexiella macgintyi (M. Smith 1938)		x						

Phyllonotus pomium (Gmelin 1791)	x	x	x	x		x			x
Urosalpinx perrugata (Conrad 1846)	x	x	x			x	x		
BUCCINIDAE									
Bailya sp. cf. *B. parva* (C.B. Adams 1850)	x								
Cantharus cancellarius (Conrad 1846)		x	x			x	x	x	
Cantharus multangulus (Philippi 1848)		x					x		
Pisania tincta (Conrad 1846)								x	
COLUMBELLIDAE									
Anachis sp.	x	x					x		
Anachis obesa (C.B. Adams 1845)	x		x						
Mitrella lunata (Say 1826)	x	x	x						
NASSARIIDAE									
Nassarius acutus (Say 1822)		x	x						
Nassarius albus (Say 1826)	x	x					x		
Nassarius vibex (Say 1822)	x	x	x			x	x	x	
MELONGENIDAE									
Busycon contrarium (Conrad 1840)	x	x	x	x		x	x	x	x
Busycon spiratum pyruloides (Say 1822)	x	x		x		x	x	x	x
Melongena corona (Gmelin 1791)	x	x		x			x	x	x
FASCIOLARIIDAE									
Fasciolaria lilium hunteria (G. Perry 1811)	x	x		x		x	x		x
Fasciolaria lilium lilium G. Fischer 1807	x	x		x		x			x
Fasciolaria tulipa (Linnaeus 1758)									x
Pleuroploca gigantea (Kiener 1840)	x	x		x		x			x
OLIVIDAE									
Oliva sayana Ravenel 1834	x	x	x	x		x	x	x	x
Olivella dealbata (Reeve 1850)		x					x		
Olivella floralia (Duclos 1853)	x								
Olivella mutica (Say 1822)	x	x	x						
Olivella pusilla (Marrat 1871)	x	x	x						
MARGINELLIDAE									
Dentimargo eburneolus (Conrad 1834)	x	x	x						

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
Hyalina avenacea (Deshayes 1844)	x							
Marginella sp.	x	x	x		x	x		
Marginella hartleyanum Schwengel 1941	x							
Volvarina albolineata (Orbigny 1842)	x	x						
CANCELLARIIDAE								
Trigonostoma tenerum (Philippi 1848)	x							
CONIDAE								
Conus jaspideus Gmelin 1791	x	x	x		x		x	
TURRIDAE								
Crassispira sp.		x				x		
Crassispira tampaensis Bartsch & Rehder 1939	x		x					
Cymatosyrinx sp.		x						
Drillia acurugata Dall 1890	x							
Pyrgocythara plicosa (C.B. Adams 1850)		x	x					
TEREBRIDAE								
Terebra sp.	x		x					
Terebra concava (Say 1826)		x						
Terebra dislocata (Say 1822)		x	x			x	x	
Terebra protexta (Conrad 1846)		x			x	x		
PYRAMIDELLIDAE								
Boonea seminuda (C.B. Adams 1839)	x	x	x				x	
Longchaeus crenulata (Holmes 1859)		x	x			x	x	

Odostomia sp.		x							
Odostomia laevigata (Orbigny 1842)		x	x						
Odomstomia seminuda (C.B. Adams 1837)	x	x	x					x	
Pyramidella crenulata (Holmes 1859)		x	x				x	x	
Turbonilla sp.	x	x	x				x	x	
ACTEOCINIDAE									
Acteocina candei (Orbigny 1842)	x	x	x				x	x	
CYLICHNIDAE									
Cylichnella bidentata (Orbigny 1841)		x							
BULLIDAE									
Bulla striata Bruguiere 1792	x	x	x				x	x	x
MOLLUSCA (NON-MARINE GASTROPODA)									
VIVIPARIDAE									
Viviparus georgianus (Lea 1834)	x	x	x			x	x		x
AMPULLARIIDAE									
Pomacea sp.						x			
HYDROBIIDAE									
Tryonia aequicostata (Pilsbry 1889)		x	x			x	x		
hydrobiid gen. and sp. undet.		x							
PHYSIDAE									
Physella sp.		x	x			x	x		
**Stenophysa meigsii* (Dall 1890)							x		
PLANORBIDAE									
Micromenetus dilatatus avus (Pilsbry 1905)		x				x	x		
Planorbella duryi (Wetherby 1879)	x	x	x			x	x		x
Planorbella scalaris (Jay 1839)	x	x	x			x	x	x	
SPIRAXIDAE									
Euglandina rosea (Ferussac 1821)	x					x	x		x
POLYGYRIDAE									
Polygyra sp.						x	x		
Polygyra cereolus (Muhlfeld 1816)		x							
Polygyra avara Say 1818						x			

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
MOLLUSCA (MARINE BIVALVIA)								
NUCULIDAE								
Nucula proxima Say 1822	x	x					x	
NUCULANIDAE								
Nuculana acuta (Conrad 1832)	x	x	x			x	x	
ARCIDAE								
**Anadara lienosa* (Say 1832)/ *floridana* (Conrad 1869)	x	x	x	x	x		x	x
**Anadara scalarina* (Heilprin 1886)				x				
Anadara transversa (Say 1822)	x	x	x		x	x	x	x
Arcopsis adamsi (Dall 1886)	x	x	x		x	x		
Barbatia tenera (C.B. Adams 1845)	x	x			x			
**Noetia* sp. cf. *N. platyura* (Dall 1898)							x	
**Noetia platyura* (Dall 1898)	x			x	x	x		x
Noetia ponderosa (Say 1822)	x	x	x	x		x	x	
GLYCYMERIDIDAE								
Glycymeris americana (DeFrance 1826)	x					x		
Glycymeris pectinata (Gmelin 1791)		x	x		x	x	x	x
MYTILIDAE								
Brachidontes exustus (Linnaeus 1758)	x	x	x		x	x	x	x
Lithophaga sp.		x						
Modiolus sp.	x				x			

PTERIIDAE									
Pteria colymbus (Roding 1798)			x						
PINNIDAE									
Atrina sp.	x	x						x	x
LIMIDAE									
Lima sp.	x	x				x			
Limea bronniana Dall 1886		x							
OSTREIDAE									
**Conradostrea sculpturata* (Conrad 1840)	x	x		x		x	x		x
Crassostrea virginica (Gmelin 1791)	x						x		x
Ostreola equestris (Say 1834)			x				x	x	
PLICATULIDAE									
Plicatula sp. cf. *P. gibbosa* Lamarck 1801	x	x	x	x		x		x	x
PECTINIDAE									
Aequipecten sp.		x					x		
Argopecten irradians (Lamarck 1819)	x	x		x		x	x	x	x
**Carolinapecten eboreus solarioides* (Heilprin 1886)	x			x		x	x		x
ANOMIIDAE									
Anomia simplex Orbigny 1845	x	x	x			x	x	x	x
CHAMIDAE									
Arcinella cornuta Conrad 1866	x	x	x	x			x	x	x
Chama congregata Conrad 1833	x	x				x			
Chama macerophylla (Gmelin 1791)	x					x			
LUCINIDAE									
Anodontia sp. cf. *A. philippiana* (Reeve 1850)	x								
Anodontia alba Link 1807	x		x	x		x		x	x
Codakia orbicularis (Linnaeus 1758)	x					x			x
Divaricella quadrisulcata (Orbigny 1842)		x				x			
Linga pensylvanica (Linnaeus 1758)			x			x		x	x
**Linga waccamawensis* Dall 1903/ *amiantus* Dall 1901	x	x	x			x	x	x	
Lucina nassula (Conrad 1846)	x	x	x			x	x	x	x

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
Lucina keenae (Chavan 1971)		x				x	x	x
Parvilucina blanda (Dall & Simpson 1901)	x	x						
Parvilucina multilineata (Tuomey & Holmes 1856)	x	x	x		x	x	x	
Pseudomiltha floridana (Conrad 1833)	x					x	x	
UNGULINIDAE								
Diplodonta sp.	x		x		x	x	x	x
LEPTONIDAE								
Mysella planulata (Stimpson 1857)		x	x				x	
Neaeromya floridana (Dall 1899)	x	x	x		x	x		
LASAEIDAE								
Aligena sp.					x			
Parabornia squillina Boss 1965	x							
CARDITIDAE								
Carditamera floridana Conrad 1838	x	x	x	x	x	x	x	
Pleuromeris tridentata (Say 1826)	x	x	x		x	x		
Pteromeris perplana (Conrad 1841)	x				x			
CRASSATELLIDAE								
Crassinella lunulata (Conrad 1834)	x	x	x		x	x	x	
Eucrassatella speciosa (A. Adams 1852)	x				x	x		
CARDIIDAE								
Dinocardium robustum (Lightfoot 1786)	x	x	x		x		x	x

Laevicardium laevigatum (Linnaeus 1758)	x	x				x	x		x
Trachycardium egmontianum (Shuttleworth 1856)	x	x	x	x		x	x	x	x
Trachycardium muricatum (Linnaeus 1758)						x			
MACTRIDAE									
Mactra fragilis Gmelin 1791	x					x			
Mulinia lateralis (Say 1822)	x	x	x			x	x	x	
Raeta plicatella (Lamarck 1818)	x	x	x			x			x
Rangia cuneata (Sowerby 1831)	x	x	x			x	x		x
SOLENIDAE									
Ensis minor megistus Pilsbry & McGinty 1943	x					x			x
TELLINIDAE									
Psammotreta intastriata (Say 1826)	x	x							
Strigilla mirabilis (Philippi 1841)		x							
Tellidora cristata (Recluz 1842)	x	x	x			x		x	
Tellina sp.	x	x	x			x	x		x
Tellina aequistriata Say 1824		x						x	
Tellina alternata Say 1822	x					x	x	x	x
Tellina magna Spengler 1798	x								
Tellina nitens C.B. Adams 1845	x								
SOLECURTIDAE									
Solecurtus cumingianus (Dunker 1861)	x								
Tagelus divisus (Spengler 1794)	x	x	x			x	x	x	x
SEMELIDAE									
Abra aequalis (Say 1822)	x					x	x		
Cumingia sp.		x							
Semele bellastriata (Conrad 1837)	x	x				x	x		
**Semele perlamellosa* Heilprin 1886	x								
Semele proficua (Pulteney 1799)	x							x	
Semele purpurascens (Gmelin 1791)						x			

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
VENERIDAE								
Anomalocardia auberiana (Orbigny 1842)	x	x	x		x	x	x	
Chione cancellata (Linnaeus 1767)	x	x	x		x	x	x	x
Chione grus (Holmes 1858)	x	x	x		x	x	x	
Chione intapurpurea (Conrad 1849)					x			
Chione latilirata (Conrad 1841)					x			
**Chione procancellata* Mansfield 1932				x				
Dosinia elegans Conrad 1846	x	x	x	x	x	x	x	x
Gouldia cerina (C.B. Adams 1845)		x			x			
Macrocallista maculata (Linnaeus 1758)	x				x			
Macrocallista nimbosa (Lightfoot 1786)	x	x	x	x	x	x	x	x
Mercenaria campechiensis (Gmelin 1791)	x	x	x	x	x	x	x	x
Parastarte triquetra (Conrad 1845)		x	x		x	x	x	
Pitar sp.	x							
Pitar simpsoni (Dall 1889)	x	x	x		x	x	x	
Transennella conradina Dall 1883		x			x	x	x	
MYIDAE								
Sphenia sp.		x				x		
CORBULIDAE								
Corbula contracta Say 1822	x	x	x			x	x	
GASTROCHAENIDAE								
Gastrochaena hians (Gmelin 1791)		x				x		x

HIATELLIDAE									
Panopea bitruncata (Conrad 1872)	x		x						x
MOLLUSCA (NON-MARINE BIVALVIA)									
UNIONIDAE									
Elliptoideus sloatianus (Lea 1840)	x								
Megalonaias bokiniana (Lea1840)	x			x		x			x
cf. *Utterbackia* sp.						x			
Utterbackia sp. cf. *U. imbecillis* (Say 1829)						x			
Villosa sp.						x			
MOLLUSCA (SCAPHOPODA)									
DENTALIIDAE									
Dentalium sp.	x	x	x				x		
Dentalium antillarum Orbigny 1842		x							
Dentalium laqueatum Verrill 1885	x		x					x	
ANNELIDA									
polychaete worm tubes	x	x				x			
ARTHROPODA									
BALANIDAE									
Balanus sp.	x								
Balanus improvisus Darwin 1854	x					x			
Balanus venustus Darwin 1854	x	x	x			x	x	x	
Paraconcavus sp.						x			
PYRGOMATIDAE									
Ceratoconcha sp.									x
CALLIANASSIDAE									
Callianassa sp.			x				x		x
LEUCOSIIDAE									
Persephona sp.								x	
PORTUNIDAE									

Appendix 1 Continued

	Leisey 1				Leisey 3			
	Lower shell bed	Bone bed	Upper shell bed	Spoil	Lower shell bed	Bone bed	Upper shell bed	Spoil
gen. and sp. undetermined			x					
XANTHIDAE								
gen. and sp. undetermined		x	x			x		
ECHINODERMATA								
echinoid spines		x			x		x	