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LOCATION OF CONTINENTS AND OCEANS AND THE DISTRIBUTION OF LIVING OYSTERS (GRYPHAEIDAE AND OSTREIDAE)

DAVID NICOL

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MENIPPE MERCENARIA (DECAPODA: XANTHIDAE) FROM THE PLEISTOCENE OF FLORIDA

ROGER W. PORTELL and KEVIN S. SCHINDLER

Invertebrate Paleontology Division
Florida Museum of Natural History
University of Florida
Gainesville, Florida 32611

ABSTRACT

Over one hundred fossil decapod crustaceans were collected from a shallow excavation site in the late Pleistocene Coffee Mill Hammock Formation at Oldsmar, Pinellas County, Florida. The well-preserved crab fauna is composed primarily of *Menippe mercenaria* (Say) and represents its first reported fossil occurrence from Florida. These specimens occur in a cream to tan, unconsolidated sand-shell matrix with numerous mollusks which are indicative of intertidal to subtidal habitats similar to present Tampa Bay. Dates obtained by amino acid analysis of mollusks from the site indicate an age of between 0.10 to 0.21 Ma.

INTRODUCTION

In contrast to many other large groups of organisms (e.g., mollusks, coelenterates or echinoderms), the fossil record of marine arthropods is comparatively poor. With a relatively thin exoskeleton, decapod crustaceans (crabs, lobsters and especially shrimps) are easily destroyed by biologic or geologic factors. Also, their dominantly epifaunal existence makes them vulnerable to predation, decomposition and scavenging. Chelae and fingers tend to be the thickest, most heavily mineralized; hence, the most persistent parts of their external skeleton and therefore preserve more readily. These are typically the only fossilized remains found in Florida.

In February 1984 Brian Ridgway, while looking for fossil vertebrate remains at a shallow excavation site, made an important discovery. He located an in-place marine shell unit containing numerous whole and partial fossil decapods. This find is particularly exciting because it not only appears to be the first documented Florida Pleistocene decapod-rich locality but also represents the first fossil occurrence of the xanthid crab *Menippe mercenaria* (Say) from Florida. In this paper we will discuss the fossil decapod fauna along with a paleoecologic interpretation and age determination based on the molluscan fauna.

MATERIALS AND METHODS

Between February 1984 and November 1985, B. Ridgway and the senior author collected decapod specimens from the base of the 2.0 meter thick shell bed. Oldsmar 2, the name designated for the pit, is located at the SE corner of State Roads 590 and 584 in Oldsmar, Pinellas County (SW1/4, SW1/4, Sec.14, T28S, R16E, Oldsmar Quadrangle, USGS 7.5 minute series; Figure 1). Sediment overlying the shell bed was composed of 1.0-1.5 meters of surface soil and unfossiliferous sands while the underlying unit consisted of a green clayey sand probably from the Miocene Hawthorne Group. In addition to the crabs, samples of the molluscan fauna were collected and analyzed to provide information relevant to the paleoecology and age of the shell deposit.

The decapod-rich fossil assemblage at Oldsmar 2 contained numerous whole and partial specimens of *Menippe mercenaria* (Say). Other decapod taxa included *Persephona* sp., *Callianassa* sp. and an unidentifiable member of the family Diogenidae. These specimens were not as well preserved as *Menippe* and therefore species determination was not possible. Of the over 100 decapods collected, most were retrieved from a weathered face along the SW corner of the pit. Overburden of sand and shell was carefully removed until the specimens were exposed. After digging around the fragile material and wrapping each in heavy-duty aluminum foil, the crabs were transported to the museum. The decapod specimens were sometimes covered by a hardened, thin veneer of sand and shell and were prepared using a pneumatic air scribe to remove hardened matrix. Afterwards, a thin coat of Butvar 76 dissolved in acetone was applied. The preservation of the decapod exoskeletons was exceptional. Most of the specimens exhibit cracks that are probably due to post-depositional compaction. Walking legs were commonly preserved but usually crushed.

Most of the fossils discussed in this paper are housed in the Invertebrate Paleontology Division at the Florida Museum of Natural History. Some of the fossil crab material was retained by B. Ridgway for his private collection.

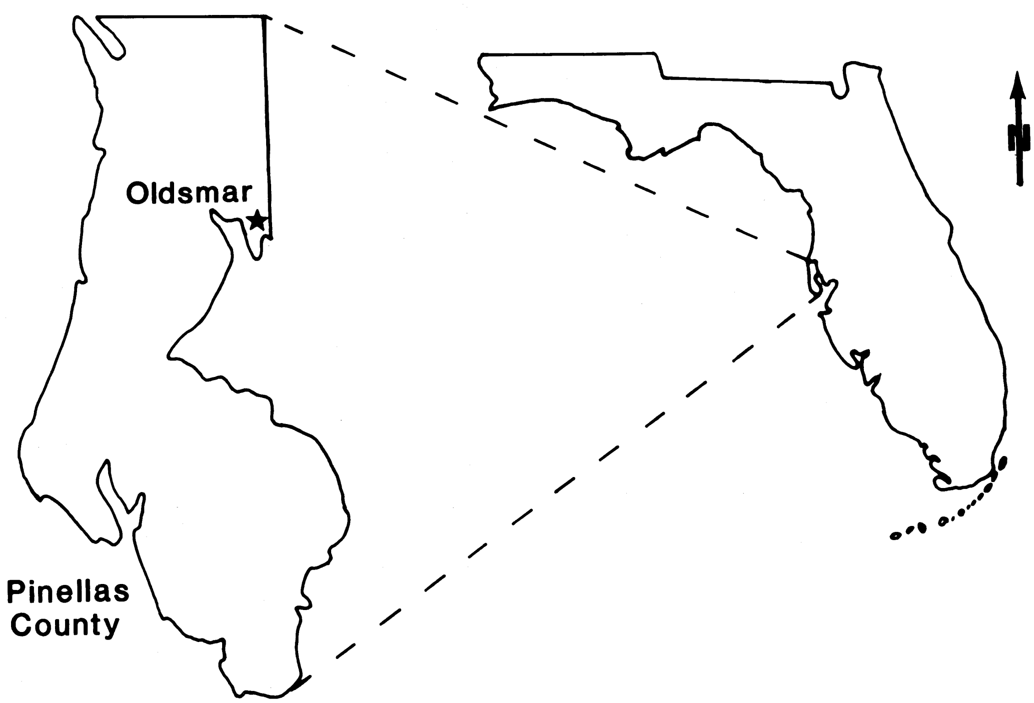

Figure 1. Location of Oldsmar 2, Pinellas County, Florida (SW1/4, SW1/4, sec.14, T28S, R16E, Oldsmar Quadrangle, USGS 7.5 minute series).

DISCUSSION

Modern *Menippe mercenaria*, commonly called a stone or mud crab, ranges from Cape Lookout, North Carolina, around peninsular Florida, through the Bahamas and Greater Antilles, to the Yucatan Peninsula, Mexico, and Belize (Williams, 1984; Williams and Felder, 1986). Prior to this report, *M. mercenaria* had not been recognized from any fossil deposits in Florida. Elsewhere, its fossil record is limited to a single report from the Sandy Beds in Colleton County, South Carolina (Holmes, 1858). The specimens of *M. mercenaria* (Figure 2) from Oldsmar 2 also represent the first addition to the known Pleistocene crab fauna of Florida since Rathbun (1935). In her monograph Rathbun lists *Cancer irroratus* Say and *Ocypode quadrata* (Fabricius) (= *O. albicans* Bosc) as the only known Pleistocene fossil species from Florida. Worldwide, the genus *Menippe* ranges from the middle Eocene to the Recent (Glaessner, 1969; Via Boada, 1969). In Florida the genus is represented in the fossil record by only two other species, *M. nodifrons* Stimpson from the Miocene-Pliocene and *M. floridana* Rathbun from the Miocene (Rathbun, 1935).

Paleoecology and Taphonomy

Besides *Menippe mercenaria* and the other arthropods, fossil specimens of two additional phyla (Mollusca and Bryozoa) are represented at Oldsmar 2 (Table 1). For paleoecologic interpretation and age determination, the most useful of these are the mollusks. All of the 86 mollusks identified to specific level are extant species. Assuming taxonomic uniformitarianism, the paleoenvironment of the site may be reconstructed by studying the modern ecological preferences of these species. A number of paleoenvironomental inferences are possible by applying data compiled by Stanley (1970) and Abbott (1974).

The majority of the marine molluscan taxa recovered are indicative of shallow water, intertidal to subtidal habitats similar to those presently found in nearby Tampa Bay. *Chione cancellata* (Linnaeus) dominated the fauna while other principal molluscan components included *Tagelus divisus* (Spengler) and *Transennella conradina* Dall. The presence of species such as *Cyclinella tenuis* (Recluz), *Rissoina catesbyana* Orbigny, and *Laevicardium mortoni* (Conrad) indicates a restricted bay to lagoonal setting. The substrate conditions varied from mud to muddy sand to clean sand. Patches of seagrass were present, if not dominant, as evidenced by the presence of seagrass-associated species (e.g. *Caecum pulchellum* Stimpson, *Carditamera floridana* Conrad, and *R. catesbyana*). The occurrence of numerous freshwater gastropods (e.g. *Planorbella duryi* (Wetherby), *Tryonia aequicostatus* (Pilsbry), and *Physella* sp.) indicates that a freshwater influence, most likely a river, was present. This interpretation is supported by the presence of the brackish to freshwater bivalve *Mytilopsis leucophaeata* (Conrad), which in modern environments is usually found in close proximity to rivers (Abbott, 1974, p.517). The above molluscan-based interpretation of Oldsmar 2 fits well with the known environments occupied by modern *M. mercenaria*. As adults these crabs usually construct deep burrows in sandy mud flats just below the low-tide line while juveniles dwell under rocks, dead shells or seagrass clumps.

The *Menippe mercenaria* from Oldsmar 2 were probably buried by rapidly accumulating sediment during or after a storm and were most likely dead at the time of burial. This is evidenced by the fact that many of the crabs were found in a relaxed, normal position. Typically, when crabs are buried alive they are preserved with their walking legs and claws raised and open (Escape Position of Bishop, 1986). The completeness of many specimens of *M. mercenaria* indicates they were not transported any great distance. This fact, coupled with the occurrence of numerous non-oriented, articulated bivalves, substantiates a storm-related rapid burial hypothesis.

Correlation and Age

The shell deposit in which these crabs occur appears to represent the late Pleistocene Coffee Mill Hammock Formation (also known as the Coffee Mill Hammock Marl and the Coffee Mill Hammock Member of the Fort Thompson Formation). Some authors disagree as to whether the Coffee Mill Hammock should be considered a formation. Sellards (1919) assigned the name Coffee Mill Hammock Marl to outcrops along the Caloosahatchee River. He considered this unit a separate formation as did Brooks (1968, 1974) and Conklin

Table 1. List of invertebrate fossils recovered from Oldsmar 2.

BRYOZOA
Membranipora tenuis Desor
Schizoporella pungens (Canu & Bassler)

MOLLUSCA
GASTROPODA
Acteon punctostriatus (C.B. Adams)
Acteocina candei (Orbigny)
Anticlimax pilsbryi McGinty
Bulla striata Bruguière
Busycon contrarium (Conrad)
Busycon spiratum pyruloides (Say)
Caecum nitidum (Stimpson)
Caecum pulchellum Stimpson
Caecum strigosum de Folin
Calotrophon ostrearum (Conrad)
Cantharus multangulus (Philippi)
Cerithiidae, gen. and sp. A
Cerithiidae, gen. and sp. B
Cerithiopsis greeni (C.B. Adams)
Conus jaspideus Gmelin
Crepidula maculosa Conrad
Crepidula plana Say
Cyclostremiscus pentagonus (Gabb)
Diodora cayenensis (Lamarck)
Epitonium lamellosum Lamarck
Eupleura sulcidentata Dall
Fasciolaria lilium hunteria (G. Perry)
Fasciolaria tulipa (Linnaeus)
Granulina ovuliformis (Orbigny)
Hydrobiidae, gen. and sp. A
Hydrobiidae, gen. and sp. B
Kurtziella sp.
Marginella sp. A
Marginella sp. B
Melanella sp.
Melongena corona (Gmelin)
Mitrella lunata (Say)
Nassarius vibex (Say)
Odostomia acutidens Dall
Odostomia seminuda (C.B. Adams)
Oliva sayana Ravenel
Olivella sp. A
Olivella sp. B
Olivella mutica (Say)
Physella sp.
Planorbella duryi (Wetherby)
Planorbella scalaris (Jay)
Pleuroploca gigantea (Kiener)
Polinices duplicatus (Say)
Polygyra septemvolva Say
Pyramidella crenulata (Holmes)
Pyrgocythara plicosa (C.B. Adams)
Rissoina catesbyana Orbigny
Seila adamsi (H.C. Lea)
Solariorbis infracarinata Gabb
Strombus alatus Gmelin
Teinostoma sp.
Terebra dislocata (Say)
Tryonia aequicostatus (Pilsbry)
Turbonilla sp. A
Turbonilla sp. B
Urosalpinx perrugata (Conrad)
Vitrinella floridana Pilsbry & McGinty

SCAPHOPODA
Dentalium sp. cf. *D. laqueatum* Verrill

BIVALVIA
Aligena sp.
Anadara floridana (Conrad)
Anadara transversa (Say)
Anodontia alba Link
Anomalocardia auberiana (Orbigny)
Anomia simplex Orbigny
Argopecten irradians (Lamarck)
Brachidontes exustus (Linnaeus)
Carditamera floridana Conrad
Chione cancellata (Linnaeus)
Chione grus (Holmes)
Corbula sp.
Crassinella lunulata (Conrad)
Cyclinella tenuis (Récluz)
Cyrtopleura costata (Linnaeus)
Dinocardium robustum vanhyningi Clench & Smith

Diplodonta semiaspera (Philippi)
Dosinia discus (Reeve)
Dosinia elegans Conrad
Gastrochaena hians (Gmelin)
Laevicardium mortoni (Conrad)
Linga amiantus (Dall)
Lucina nassula (Conrad)
Macrocallista nimbosa (Lightfoot)
Mercenaria campechiensis (Gmelin)
Mulinia lateralis (Say)
Musculus lateralis (Say)
Mysella sp.
Mysella planulata (Stimpson)
Mytilopsis leucophaeata (Conrad)
Nucula proxima Say
Nuculana acuta (Conrad)
Ostrea sp.
Parastarte triquetra (Conrad)
Parvilucina multilineata (Tuomey & Holmes)
Pitar simpsoni (Dall)
Plicatula gibbosa Lamarck
Pseudomiltha floridana (Conrad)
Raeta plicatella (Lamarck)
Sphenia tumida Lewis
Tagelus divisus (Spengler)
Tellidora cristata (Récluz)
Tellina sp. A
Tellina sp. B
Tellina alternata Say
Tellina aequistriata Say
Trachycardium egmontianum (Shuttleworth)
Transennella sp.
Transennella conradina Dall

ARTHROPODA

CIRRIPEDIA
Balanus eburneus Gould

DECAPODA
Callianassa sp.
Diogenidae
Menippe mercenaria (Say)
Persephona sp.

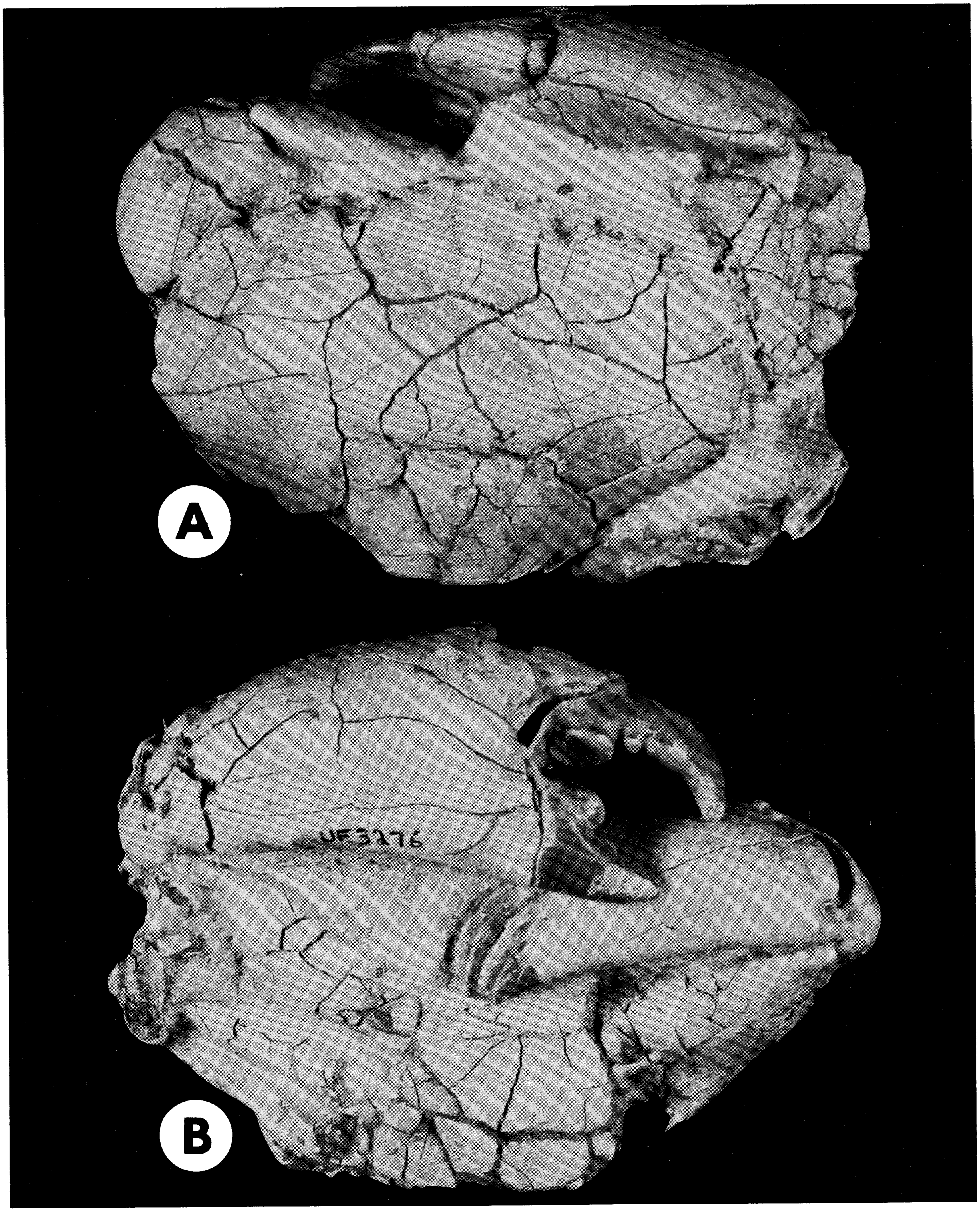

Figure 2. *Menippe mercenaria* (Say) from Oldsmar 2, adult female, UF3276. (A) dorsal view. (B) ventral view. x1.

(1968) while other workers, such as Cooke and Mossom (1929) and DuBar (1958, 1974) have placed it within the Fort Thompson Formation.

Pleistocene formations in Florida have typically been defined by their molluscan composition. This does not agree with the North American Commission on Stratigraphic Nomenclature (1983), which suggests that the lithologic makeup be the dominant criteria for establishing a formation. The faunas of Florida's Pleistocene shell beds are so variable, both temporally and laterally, and the lithology so similar, that it is sometimes difficult to assign a particular deposit to an established formation.

Based solely on molluscan faunas, the distinction between the Fort Thompson Formation and the Coffee Mill Hammock Formation is marginal. The former contains several extinct taxa (e.g. *Pyrazisinus scalatus* (Heilprin) and *Turritella subannulata* Heilprin) whereas the latter contains 100% extant species. The bivalves *Chione cancellata* and *Transennella conradina* and the gastropod *Olivella mutica* (Say) are the most typical species recognized from the Coffee Mill Hammock and they occur in greater abundance than in the Fort Thompson (DuBar, 1958).

Puri and Vanstrum (1969) obtained Th^{234}/U^{238} dates of 0.12 to 0.14 Ma from three mollusks collected at the type Coffee Mill Hammock near Ortona Lock. Belknap (per. comm., 01/26/1990) performed amino acid analyses on the bivalves *Mercenaria campechiensis* (Gmelin) and *Chione cancellata* from the upper part of the Oldsmar 2 shell bed (above the crab horizon) which provided dates of 0.12 to 0.21 Ma and 0.10 to 0.20 Ma, respectively. These dates closely approximate those of Puri and Vanstrum (1969).

On the basis of Belknap's dates, the apparent lack of extinct species, the extreme abundance of *Chione cancellata* and comments by Lyons (1991) in the most recent review of southern Florida marine biostratigraphy, we chose to place the deposits containing *Menippe mercenaria* in the Coffee Mill Hammock Formation. However, the authors recognize that placement of this deposit within the Fort Thompson Formation is not without merit.

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TETHYAN MOLLUSCS OF THE MIDDLE AND LATE EOCENE OF PENINSULAR FLORIDA

DAVID NICOL

Box 14376, University Station, Gainesville, Florida 32604

ABSTRACT

At least 15 of the 19 verified Eocene genera of Tethyan molluscs recorded from peninsular Florida occur in the Inglis Formation, but a few appear for the first time in the Crystal River Formation. However, almost all Tethyan molluscs disappear before the uppermost zone of the Crystal River Formation, the *Rotularia vernoni* zone. Of the 13 extinct genera of Tethyan molluscs, seven became extinct during the Eocene, four during the Oligocene, but only two during the Miocene.

During the middle and late Eocene, the Tethyan seaway extended from Central America and the Caribbean, to the Paris Basin and the Mediterranean, and eastward through Pakistan, India, and Indonesia (Adams and Ager, 1967). This seaway occupied a region that was primarily north of the present equator. The molluscan faunas in the Tethyan region were dominated by shallow and warm-water species that indicate normal salinity. With the large number of Tethyan molluscs already verified from the Avon Park Limestone and the Ocala Group, there is no doubt that the middle and upper Eocene of peninsular Florida was in the Tethyan Province.

In a recent article, Givens (1989) briefly discussed and listed 21 Tethyan molluscan genera in middle and upper Eocene strata in peninsular Florida. The first report of Tethyan genera of molluscs in the Avon Park Limestone and Ocala Group in peninsular Florida is that of Richards and Palmer (1953). Further discussion of the Tethyan genera has been given by Palmer (1957, 1967). The latest Tethyan molluscs to be reported are clavagellids (Jones and Nicol, 1989). Because the molluscan faunas of the Avon Park Limestone and the Ocala Group are imcompletely known, further study will no doubt reveal more Tethyan molluscs in middle and upper Eocene strata in peninsular Florida.

In Table 1 I have given what I think are 19 presently verified Tethyan molluscan genera, with their geologic ranges, in peninsular Florida. Seven of these are pictured in Figure 1. The genera I have presented do not wholly coincide with the 21 listed by Givens (1989). This clearly indicates that more descriptive taxonomic work is badly needed on the middle and late Eocene molluscan faunas in peninsular Florida.

Fifteen, or possibly 16, genera listed in Table 1 occur in the Inglis Formation. Meeder (1976) stated that Ms. Muriel Hunter and Drs. Emily and Harold Vokes had collected specimens of *Gisortia* from the Inglis Formation, but I have not seen specimens of this genus from the Inglis. Therefore, I have placed a question mark before the Inglis occurrence of *Gisortia*. Further collecting may increase the geologic ranges of these Tethyan molluscs.

The large number of Tethyan molluscs in the Inglis Formation may be misleading. The molluscs from the Inglis Formation are better preserved and better known than they are in the Avon Park Limestone and the Williston and Crystal River formations. A few Tethyan genera appear for the first time in the Crystal River Formation, but all Tethyan groups, except *Clavagella*, disappear before the uppermost zone of the Crystal River Formation in peninsular Florida, which is Puri's *Asterocyclina-Spirulaea vernoni* zone (1957). This zone is now known as the *Rotularia vernoni* zone (Nicol, Jones, and Hoganson, 1989).

Table 1. Tethyan molluscan genera with their stratigraphic ranges in the Eocene of peninsular Florida. Avon Park Limestone (A), Inglis Formation (I), Williston Formation (W), and Crystal River Formation (C).

Genera	A	I	W	C
Bellatara	X	X		
Fimbria	X	X		
Pseudomiltha	X	X		
Ampullinopsis		X		
Seraphs		X		
Caricella		X		
Batillaria		X		
Pseudoaluca		X		
Lapparia		X		
Eovasum		X		
Athleta		X		
Voluticella		X		
Lyria		X		
Velates		X	X	
Exputens		X	X	X
Gisortia		?		X
Lithophaga				X
Clavagella				X
Meiocardia				X

Figure 1 (opposite page). Illustrations of seven of the Tethyan molluscan genera occurring in the Avon Park Limestone or the Ocala Group in peninsular Florida. All specimens are housed in the Invertebrate Paleontology Collection at the Florida Museum of Natural History (acronym UF). A. *Gisortia harrisi* Palmer, 1957, UF 30580. Internal mold, apertural view, width of whorl 135.0 mm. Crystal River Formation, locality unknown; B. *Eovasum vernoni* Palmer, 1953, UF 19123. Height of spire, 68.2 mm. Inglis Formation, Gulf Hammock, Levy County, Florida, SW¼ sec. 34, T14S, R16E, Lebanon Station Quadrangle; C. *Caricella obsoleta* Palmer, 1953. UF 19129, height of spire, 42.1 mm. Inglis Formation, Gulf Hammock, Levy County, Florida, SW¼ sec. 34, T14S, R16E, Lebanon Station Quadrangle; D. *Velates floridanus* Richards, 1946, UF 22131. Internal mold, width of outer whorl, 69.2 mm. Inglis Formation, spoil bank on N side of Cross-Florida Barge Canal, 2.0 mi. W. of U. S. 19 bridge, Citrus County, Florida (Hunter loc. 6007); E. *Clavagella* sp., UF 20125. Internal mold, length of mold, 30.2 mm. Crystal River Formation, 8.0 mi. W. of Gainesville on SR 26, Alachua County, Florida; F. *Pseudomiltha megameris* (Dall, 1901), UF 24603. Internal mold, left valve, height 140.0 mm. Inglis Formation, Dolime Quarry (Loc. CI009), Citrus County, Florida, SE¼ sec. 11, T17S, R16E, Yankeetown Quadrangle; G. *Exputens ocalensis* (MacNeil, 1934), UF 15876. Left valve, length 38.4 mm. Crystal River Formation, Bed 2, Newberry Corporation Pit (Loc. AL017), Alachua County, Florida, SW¼, SE¼ sec. 13, T9S, R17E, Newberry Quadrangle.

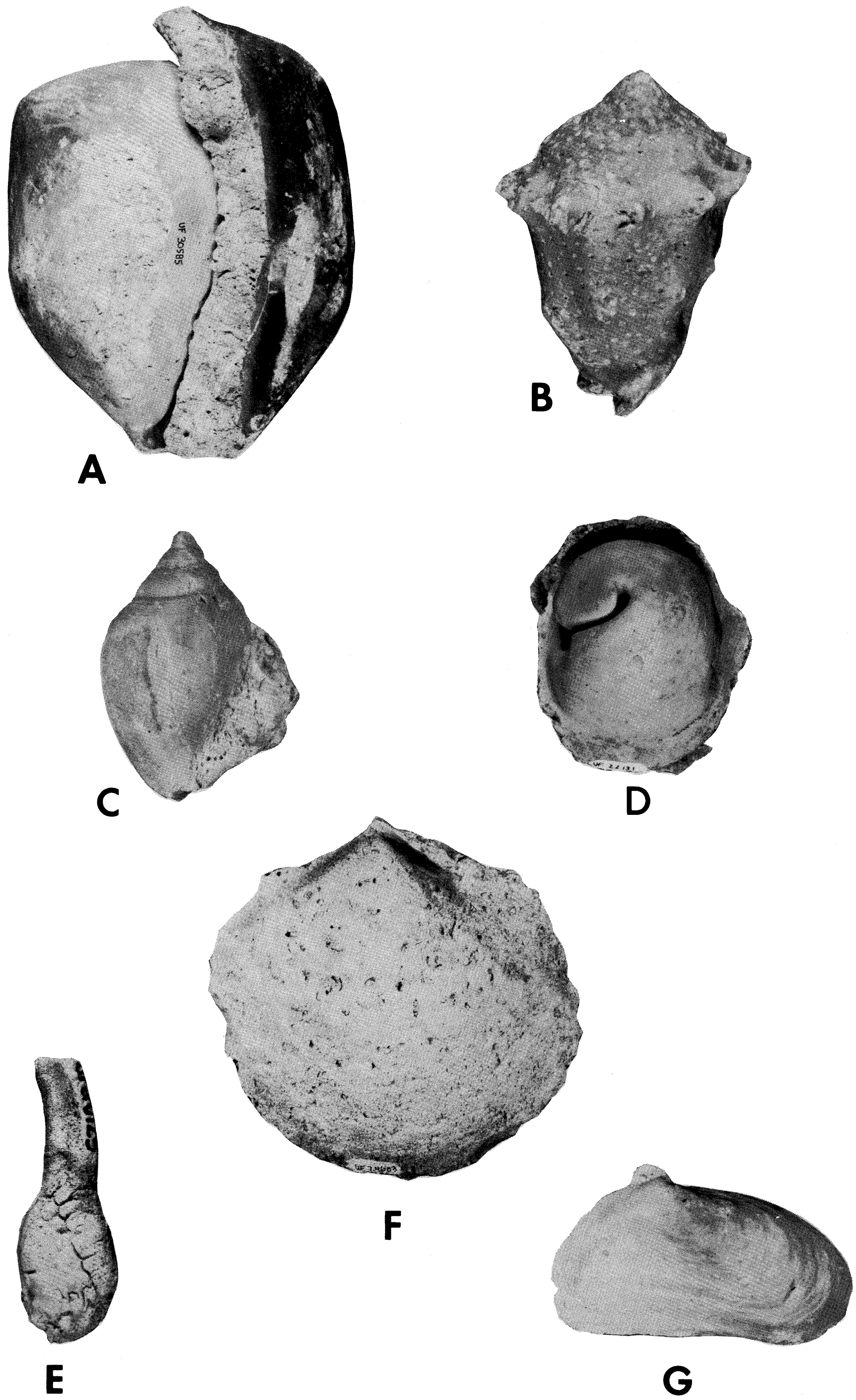
A
B
C
D
E
F
G

Table 2. Tethyan molluscan genera occurring in the Avon Park Limestone and the Inglis, Williston, and Crystal River formations in peninsular Florida that are extinct and their time of extinction.

Genera	Time of extinction
1. *Gisortia*	Eocene
2. *Velates*	Eocene
3. *Eovasum*	Eocene
4. *Pseudoaluca*	Eocene
5. *Lapparia*	Eocene
6. *Voluticella*	Eocene
7. *Exputens*	Eocene
8. *Caricella*	Oligocene
9. *Bellatara*	Oligocene
10. *Seraphs*	Oligocene
11. *Pseudomiltha*	Oligocene
12. *Ampullinopsis*	Miocene
13. *Athleta*	Miocene

Six of the 19 genera of Tethyan molluscs presented in Table 1 are pelecypods, the remaining 13 are gastropods. The six pelecypod genera are: *Pseudomiltha*, *Fimbria*, *Exputens*, *Lithophaga*, *Meiocardia*, and *Clavagella*. With few exceptions, the Tethyan molluscs found in the Eocene of peninsular Florida are either extinct or are now almost all confined to the western Pacific and Indian oceans. One species of living clavagellid also occurs in the Mediterranean, and *Meiocardia* also lives in the Caribbean as well as the western Pacific.

Of the 19 genera listed in Table 1, 13 are extinct. I have listed the time of extinction of these 13 genera in Table 2. Seven of the genera became extinct before or at the end of the Eocene; four became extinct in the Oligocene; and only two became extinct in the Miocene. Some of the genera that became extinct during the Oligocene or Miocene may have disappeared earlier from the Gulf of Mexico and the Caribbean. All of these extinctions occurred, apparently, before the formation of the Isthmus of Panama and the onset of the the Plio-Pleistocene glaciations. Of the living genera, *Fimbria* (Nicol, 1988) and the clavagellids appear to have departed from the Western Hemisphere at the end of the Eocene.

Ivany et al. (1990) noted that two common seagrass genera, *Thalassodendron* and *Cymodocea*, in the Avon Park Limestone are now found primarily in the western Pacific and Indian Oceans. They hypothesize that these genera may have lived in the western Atlantic until the beginning of the Plio-Pleistocene glaciations and the formation of the Isthmus of Panama. The past and present distribution of the Tethyan molluscs does not confirm this hypothesis, and the fossil record of molluscs is far better than that of seagrasses. It is more likely that *Thalassodendron* and *Cymodocea* disappeared from the western Atlantic and Caribbean regions as early as the Eocene and most likely no later than the Miocene.

Some of the Tethyan molluscs are rare whereas others are common. *Velates* and *Exputens* are probably the most common. *Exputens* is so common in the lower and middle parts of the Crystal River Formation that Williams et al. (1977) used it as a zone fossil in mapping the western part of Alachua County. On the other hand, *Meiocardia*, *Gisortia*, and *Clavagella* are rare.

The Tethyan province in peninsular Florida is separated from the Eocene of the Gulf Coast by a channel of deeper water known as the Suwannee Strait. A few Tethyan species do occur northward in the Ocala Group in southwestern Georgia and in the Castle Hayne Formation of North Carolina (Kellum, 1926; Nicol and Shaak, 1973). It is unfortunate that these two areas have not been more intensively studied. Some Tethyan molluscs have been reported in Eocene strata from Jamaica, Dominican Republic, Baja California, Panama, Colombia, Peru, and southern California (Palmer, 1967).

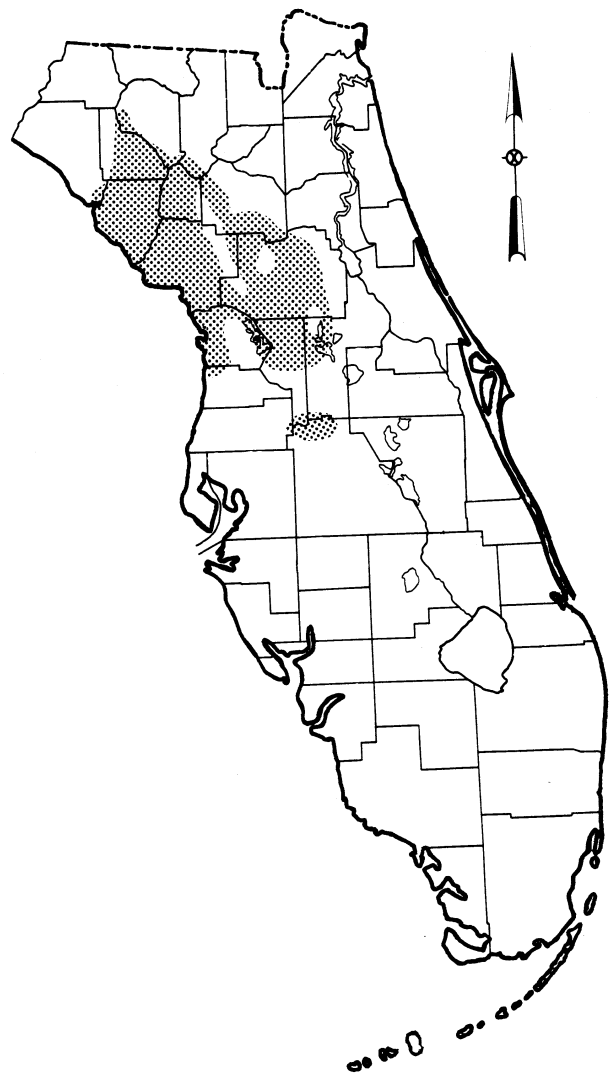

Figure 2. Map of peninsular Florida showing the general distribution of Eocene rocks at or near the surface.

The most common outcrops of Eocene carbonates are in quarries that are primarily in Alachua, Citrus, Dixie, Lafayette, Levy, Marion, Sumter, and Suwannee counties. These counties comprise the axis of the Ocala Uplift. A map of the outcrop area of the Avon Park Limestone and Ocala Group in peninsular Florida is presented in Figure 2.

Other Eocene marine invertebrates probably exhibit Tethyan affinities. For example, it would be worthwhile to examine the large echinoid fauna of the Ocala Group for these affinities.

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LOCATION OF CONTINENTS AND OCEANS AND THE DISTRIBUTION OF LIVING OYSTERS (GRYPHAEIDAE AND OSTREIDAE)

DAVID NICOL

Box 14376, University Station, Gainesville, Florida, 32604

ABSTRACT

Owing to the greater amount of land surface in the Northern Hemisphere, the area of shallow water surrounding it is much greater. This gives the species of shallow-water marine pelecypods a much larger area in which to live and, thus, increases their diversity. It is an example of vicarious geographic distribution.

It is well known that the land area in the Northern Hemisphere is more than twice that of the Southern Hemisphere. Because of the greater amount of land surface in the Northern Hemisphere, the area of shallow water surrounding it is, of course, much greater. This gives the species of shallow-water marine molluscs a much larger area in which to live and increases their diversity.

The distribution of the living species of oysters seems certainly related to the present location of continents and oceans. In a splendid paper written by Harry (1986), he pointed out that all but one of the 36 species of living oysters occurs in depths less than 200 m. It should be noted that the Ostreacea are all sessile and epifaunal. The Gryphaeidae and Ostreidae are among the best fossils to indicate depth, salinity, and temperature of the seas. They are also well preserved and abundant in the fossil record. The information that is of significance to the biogeographer is found in Harry's Table 2, p. 161, which shows the geographic distribution of the living species of oysters.

Harry divided the seas into four longitudinal provinces: Indo-Western Pacific, Eastern Pacific, Western Atlantic, and Eastern Atlantic. At least 18 species occur in the Indo-Western Pacific region, or half of the living species of oysters. The Eastern Pacific has ten species, the Western Atlantic eight, and the Eastern Atlantic nine. It should be noted here that some of the species are found in more than one longitudinal province. The fact that the Indo-Western Pacific region has the largest number of species should be expected because it has the largest area of warm and shallow water. Harry (1985) has divided the living oysters into ten tribes. The Indo-Western Pacific has nine of these tribes, the Eastern Pacific has seven and there are six each in the Western Atlantic and Eastern Atlantic. Four of the tribes occur in all of the longitudinal provinces.

The latitudinal distribution of living species of oysters is of far greater significance. Shell-cemented pelecypods, like oysters, do not live in seas where the water temperature does not reach 10°C in the warmest month of the year (Nicol, 1978). Harry has divided the latitudinal zones into North Cool Temperate, North Warm Temperate, Tropical, South Warm Temperate, and South Cool Temperate. In Table 1 I have listed the ten tribes of oysters with the distribution of their species in each of the latitudinal zones, and have eliminated the questionable occurrences cited by Harry. The longitudinal provinces have been ignored for the data in Table 1. For each species I have listed only one occurrence in each latitudinal zone, although a species may occur in the same latitudinal zone in more than one longitudinal province. Of the 36 living species of oysters, 18 occur in only one zone, 12 occur in two zones, and six occur in three zones, for a total of 60 records. In other words, Table 1 shows the species diversity in each of the five latitudinal zones. The Ostreini is the only tribe that lives in all of the latitudinal zones. Only the Ostreini and Crassostreini have species that live in temperate water, and the Crassostreini have species that live only in the Northern Hempisphere or in the tropics. Thus, oysters are most diverse in warm water.

Table 1. Number of species in each of the ten tribes of oysters (families Gryphaeidae and Ostreidae) arranged by latitudinal zones: NC (North Cool Temperate); NW (North Warm Temperate); TR (Tropical); SW (South Warm Temperate); SC (South Cool Temperate).

	Number of Species in Latitudinal Zones				
Tribes	NC	NW	TR	SW	SC
Hyotissini	0	2	5	0	0
Neopycnodontini	0	1	1	1	0
Lophini	0	5	4	0	0
Myrakeenini	0	1	1	0	0
Ostreini	3	3	5	1	1
Cryptostreini	0	2	2	0	0
Pustulostreini	0	0	1	0	0
Undulostreini	0	0	1	0	0
Striostreini	0	3	5	2	0
Crassostreini	2	4	4	0	0
Totals	5	21	29	4	1 = 60

Table 1 shows that the North Cool Temperate Zone has five living species of oysters, but there is rapid increase in the number of species in the North Warm Temperate Zone to 21. This increase in diversity continues into the Tropical Zone, which has 29 species. The progression of increasing diversity toward the tropics in a group of epifaunal animals is like that shown by Thorson (1957). However, Thorson examined the progression only from the Arctic region to the tropical areas and did not consider the Southern Hemisphere. The diversity of oysters declines abruptly in the South Warm Temperate Zone, which has only four species, and only one species is found in the South Cool Temperate Zone. There are 21 more species found in the two northernmost zones than in the two southernmost zones. In other words, if one eliminates the tropics, 84% of the remaining oysters live north of the tropical zone as compared to only 16% that live south of the tropics.

The pattern of diversity in the geographic distribution of the ten tribes is like that of the species. All ten tribes live in the Tropical Zone and eight occur in the North Warm Temperate Zone. However, only three tribes live in the South Warm Temperate Zone, two in the North Cool Temperate Zone, and one in the South Cool Temperate Zone.

The 36 living species of Ostracea are grouped into two families, the Ostreidae and Gryphaeidae. As I pointed out (Nicol, 1988), the Gryphaeidae is a relict family and is represented by only six living species which are allocated to the Pycnodonteinae. These six species comprise 17% of the living species of Ostracea. None of the six species of the Pycnodonteinae lives in cool temperate water, and the occurrences of the fossil Pycnodonteinae indicate warm water of normal salinity. This is true of the pycnodont species *Hyotissa podagrina* (Dall, 1989) found abundantly in the upper part of the Crystal River Formation in peninsular Florida.

There are some basic differences in the present geographic distribution of the Ostreidae and Gryphaeidae. There is a higher percentage of endemic species amongst the Ostreidae (14 or 47%) as compared to the Gryphaeidae (two or only 33%). Endemic species are defined as those that are confined to a single latitudinal or longitudinal region. Furthermore, of the species that are confined to a single longitudinal province, although some of these species may occur in more that on latitudinal region, 27 species of 90% of the Ostreidae occur in only one longitudinal region, but only three or 50% of the Gryphaeidae are so restricted. The Ostreidae have six living species that live in cool temperate water, but no Gryphaeidae lives in cool temperate water.

Seven species of living oysters have been reported from the warm water surrounding Florida. This limited geographic region has more species of oysters than the South Warm Temperate Zone and the South Cool Temperate Zone. Six tribes are represented in Floridian waters, but only four occur in the South Warm Temperate and South Cool Temperate regions. This is a good example of the much greater diversity of species of oysters in the Northern Hemisphere as compared to the Southern Hemisphere.

Because Florida has been surrounded by warm shallow water throughout the Cenozoic, oysters are common fossils in these strata. However, they have received little study. Three examples of oyster diversity in the Tertiary of Florida are given herein. There are at least five species of oysters in the Eocene Ocala Group in peninsular Florida (Palmer and Brann, 1965). One, or possibly two, species of *Hyotissa* are the most common oysters in the two uppermost zones of the Crystal River Formation. Four species of oysters are found in the early Miocene Tampa Limestone (Mansfield, 1937). Six species of oysters, five species of *Ostrea* and one species of *Hyotissa*, have been reported from the Pliocene Pinecrest Beds of southern Florida (Stanley, 1986).

The present distribution of continents and oceans appears to have affected the distribution and diversity of shallow-water marine pelecypods. This is an example of vicarious geographic distribution. The location of continents and oceans in the past must also have affected the distribution and diversity of shallow-water benthic animals.

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