FLORIDA MUSEUM

BULLETIN
of the Florida Museum of Natural History

NEOGENE ECHINOIDS OF FLORIDA

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Vol. 57, No. 3, pp. 237–469
ISSN 2373-9991

July 10, 2020

UNIVERSITY OF FLORIDA

GAINESVILLE

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ISSN: 2373-9991

Publication Date: July 10, 2020. This number concludes volume 57.
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Send communications about this publication to:

Editor of the Bulletin; Florida Museum of Natural History; University of Florida; P.O. Box 117800;
Gainesville, FL 32611-7800 USA

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Cover image. Aboral view of *Abertella dengleri* (UF 116702), Peace River Formation (upper Miocene), Hardee County, Florida (FM locality HR005). See p. 384.

NEOGENE ECHINOIDS OF FLORIDA

ADAM S. OSBORN[1], ROGER W. PORTELL[2], and RICH MOOI[3]

ABSTRACT

Forty-three species, and five indeterminate taxa of Florida Neogene echinoids are discussed and their geographic and stratigraphic distributions provided. These include 16 species documented from the Pleistocene, 20 from the Pliocene, and 12 from the Miocene. Eight new species are described: *Rhyncholampas meansi* n. sp. from the Pleistocene; *Fernandezaster whisleri* n. sp., *Genocidaris oyeni* n. sp., and *Lovenia kerneri* n. sp. from the Pliocene; and *Clypeaster petersonorum* n. sp., *Gagaria hunterae* n. sp., *Brissopsis hoffmani* n. sp., and *Abertella carlsoni* n. sp. from the Miocene. Additionally, we herein recognize *Abertella floridana*, from the Sopchoppy Limestone, as a species distinct from *Abertella aberti*, and provide the first documentation of *Echinolampas lycopersicus, Rhyncholampas sabistonensis*, and *Arbia aldrichi* from the fossil record of Florida. We update the taxonomy for all referred species and their known distributions. This document is intended to be a compilation of the entire Neogene echinoid record from Florida, which is now understood to have the most speciose and diverse assemblage of Neogene echinoids in the eastern United States.

Key words: Echinoids, Echinoidea, Florida, Neogene, Miocene, Pliocene, Pleistocene, new species.

TABLE OF CONTENTS

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Osborn, A. S., R. W. Portell, and R. Mooi. 2020. Neogene echinoids of Florida. Bulletin of the Florida Museum of Natural History 57(3):237–469.

INTRODUCTION

In 1825, Thomas Say documented the first fossil echinoid from North America when he read his description of *Scutella 5-faria* (=*Periarchus quinquefaria*), from the upper Eocene strata of Georgia, to the Philadelphia Academy of Natural Science (Say, 1827). Although many species now recognized from the Cenozoic strata of Florida were documented in the next few decades from regional strata outside the state, such as *Clypeaster rogersi* (Morton, 1834), *Encope macrophora* (Ravenel, 1842), *Mellita caroliniana* (Ravenel, 1842), *Oligopygus haldemani* (Conrad, 1850), and many others, it would be more than 50 years before de Loriol (1887) described *Oligopygus wetherbyi* and *Agassizia floridana*, the first officially named fossil echinoids from Florida. The following 130 years have seen significant urban development within the state and resulting excavations have in turn launched a corresponding increase of species documented from Florida strata (Fig. 1), though the documentation of Neogene echinoids would lag tremendously behind the more prolific echinoid faunas of the Paleogene of the state.

One of the earliest reports of fossil echinoids from Florida was by McCrady (1859) when he erected the genus *Ravenelia* for specimens now recognized as *Rhyncholampas gouldii* (Bouvé, 1846) (originally described from Georgia) from a tributary of the Suwannee River.

Dall and Harris (1892:106) noted the occurrence of an "Echinus" in the Chipola Limestone (now Chipola Formation), though to which species he was referring is indeterminable. However, it is potentially the herein described new species, *Clypeaster petersonorum*. Dall and Harris (1892:147) also noted the presence of a "flat Echinidae" in Alligator Creek, most likely referring to what is now recognized as *Encope tamiamiensis* Mansfield, 1932, which occurs in profusion along the banks of Alligator Creek.

Vaughan (1909) documented the occurrence of a *Cassidulus* in chert beds of the Hawthorn Group near White Springs, Florida; however, this is now determined to be *Rhyncholampas gouldii* (Bouvé, 1846), in strata referable to lower Oligocene Suwannee Limestone, and not Neogene in age. Vaughan (1909) also documented the presence of an echinoid bed in the Chattahoochee Formation of northern Florida, undoubtedly what is now referable to *Lovenia clarki* (Lambert in Lambert and Thiéry, 1924), as well as the presence of *Scutella* sp. in the Sopchoppy Limestone, which is likely *Abertella floridana* (Cooke, 1942), which is abundant in certain horizons within the unit. Vaughan (1910) subsequently documented the occurrence of *Mellita sexforis* (Lamarck, 1816) (=*Leodia sexiesperforata* [Leske, 1778]) from the Miami Oolite (now Miami Limestone) at Buena Vista, near Miami.

Clark and Twitchell (1915) completed the first monograph of North American echinoids, encompassing all previously documented species, as well as a plethora of new species from the region. They documented 17 species within the Cenozoic strata of Florida, a great leap forward in our understanding of the Paleogene echinoid faunas of northern Florida. However, only three echinoid species (as currently recognized) within their monograph were attributed to the Neogene strata of the state: *Encope macrophora* (Ravenel, 1842), *Echinocardium depressum* Clark in Clark and Twitchell, 1915 [=*Lovenia clarki* (Lambert in Lambert and Thiéry, 1924)], *Diplothecanthus dalli* Twitchell in Clark and Twitchell, 1915 (=*Clypeaster rosaceus* Linnaeus, 1758), and *C. rosaceus.*

Cooke and Mossom (1929), in their seminal work on the geology of Florida, documented the distribution of Eocene echinoids within the state, but added no new Neogene occurrences beyond those discussed by Clark and Twitchell (1915). Therefore, after more than 100 years of intensive study of the region's fossil echinoid faunas, which began with the work of Say (1827), just three species had been documented from the Neogene of Florida.

Mansfield (1932) described *Encope tamiamiensis* (as a subspecies, *Encope macrophora tamiamiensis*, see below) and *Rhyncholampas evergladensis* from the upper Pliocene portion of the Tamiami Formation of southern Florida. Cooke (1941) added three new species of regular echinoids to the Paleogene fauna of Florida: *Gagaria*

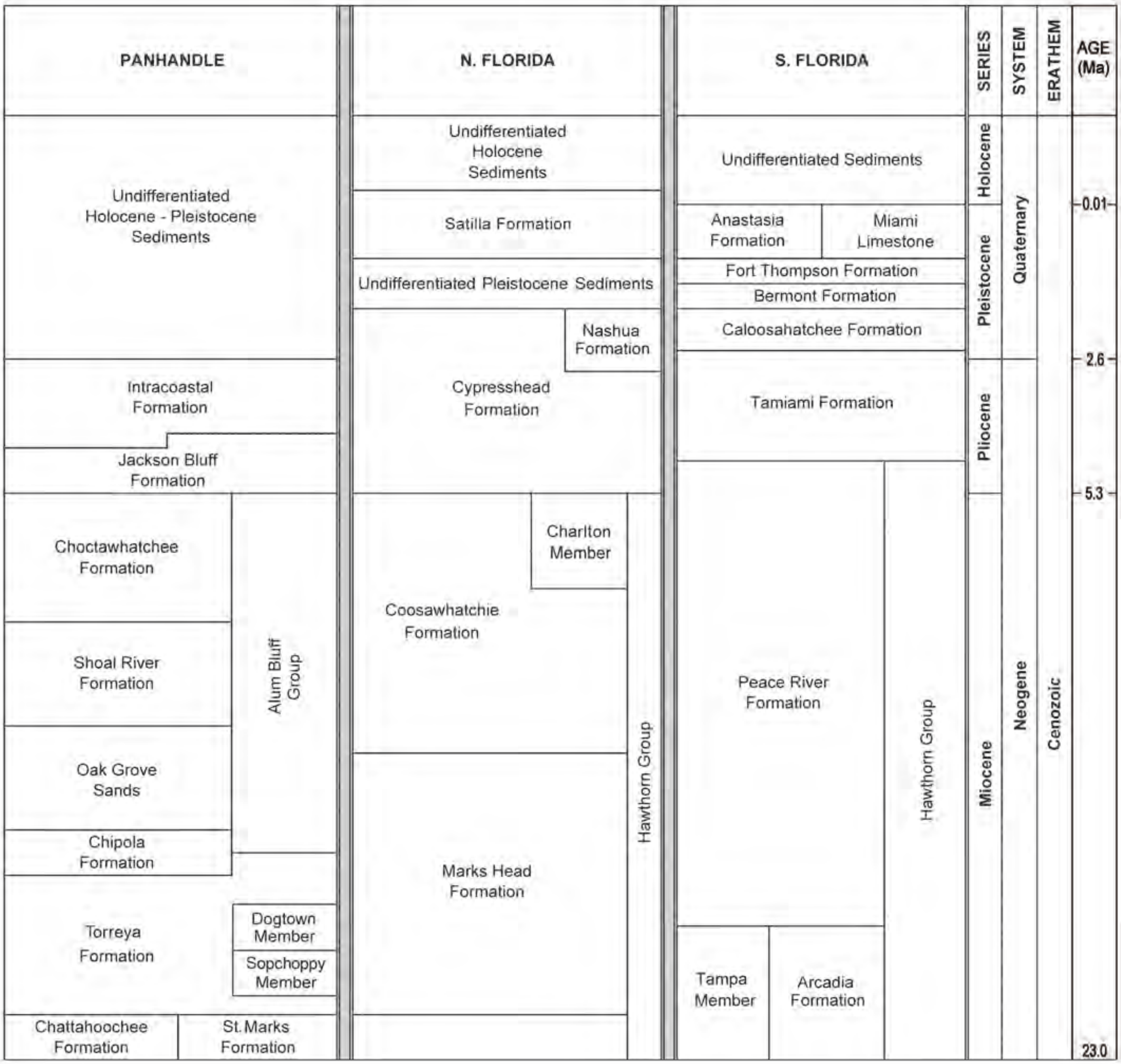


Figure 1. Diagram of Florida stratigraphic units referenced herein. Modified from Scott et al. (2001).

mossomi (Cooke, 1941), *Phymosoma dixie* (Cooke, 1941) (=*Acanthechinus dixie*), and *Phymotaxis mansfieldi* Cooke, 1941. Cooke (1942) subsequently discussed the occurrence of nine species of echinoid from the Florida Neogene: *Clypeaster gatuni* Jackson, 1917 (herein referred to *C. petersonorum* n. sp.), *Scutella floridana* Cooke, 1942 (=*A. floridana*), *Echinocyamus chipolanus* Cooke, 1942, and *L. clarki* from the Miocene; *E. tamiamiensis* and *R. evergladensis* from the Pliocene, and *Encope michelini* L. Agassiz, 1841, *L. sexiesperforata,* and *C. rosaceus* from the Pleistocene.

Since written more than 65 years ago, Cooke's 1959 opus, *Cenozoic Echinoids of Eastern United States*, has been considered the authoritative guide to the Cenozoic echinoid faunas of the region. This work did not describe any new species from the Florida Neogene; however, it did discuss new echinoid occurrences. Cooke (1959) added *Echinocardium orthonotum* (Conrad 1843) from the late Pliocene at Jackson Bluff; *Encope aberrans* Martens, 1867 (as *E. michelini*); and mistakenly added *Encope emarginata* (Leske, 1778) (as discussed herein, Cooke was actually referring to *E. michelini*) to the Neogene strata of the state. In addition to the occurrences reiterated from Cooke (1941, 1942), Cooke (1959) also listed *Abertella aberti* (Conrad, 1842) as occurring in the Florida Miocene, though this record is herein referred to *A. floridana*. Furthermore, Cooke (1959) included *Rhyncholampas sabistonensis* Kellum, 1931, from the Florida stratigraphic record; however, this reference is due to Cooke's consideration that *R. evergladensis* was a subjective junior synonym of *R. sabistonensis*, an assertion that Kier (1963) did not recognize. However, herein we recognize the occurrence of *R. sabistonensis* within the upper Pliocene-lower Pleistocene Nashua Formation of northeastern Florida.

Leutze (1956) reported the occurrence of *E. michelini* in the Florida Pleistocene. DuBar (1958, 1962) discussed the paleontology of Florida's fossiliferous Neogene strata and the echinoids within it, but he did not add new records to the echinoid distribution of the Florida Neogene.

Kier's (1963), treatment of the late Pliocene to Pleistocene echinoids of the southern Florida added tremendously to our knowledge of Florida faunas. He documented the occurrence of seven species in the lower Pleistocene Caloosahatchee Formation: *Lytechinus variegatus plurituberculatus* Kier, 1963 (herein referred to *Lytechinus variegatus* Leske, 1778); *Echinometra lucunter* Linnaeus, 1758; *Encope michelini imperforata* (referred to *E. aberrans* by Phelan, 1972); *Clypeaster subdepressus* Gray, 1825; *Clypeaster rosaceus dalli* (Twitchell in Clark and Twitchell, 1915), herein referred to *C. rosaceus*; *Rhyncholampas ayersi* Kier, 1963; and *Agassizia porifera* Ravenel, 1848. Kier (1963) further documented the occurrence of nine species in the upper Pliocene Tamiami Formation: *Arbacia crenulata* Kier, 1963 (=*A. improcera* herein); *L. variegatus*; *Clypeaster crassus* Kier, 1963, which Kier (1964) subsequently renamed *Clypeaster romani*; *Clypeaster sunnilandensis* Kier, 1963; *E. tamiamiensis; E. michelini; Mellita aclinensis* Kier, 1963; *R. evergladensis*; and *Echinocardium gothicum* Ravenel, 1848, which Kier (1972) considered a subjective junior synonym of *E. orthonotum*, an assertion with which we concur.

The last half of the 20th century saw a dramatic rise of works concerning Florida fossil echinoids: (Fischer, 1951; Zachos 1968; Zachos and Shaak, 1978; McKinney and Jones, 1983; McKinney, 1984; Croft and Shaak, 1985; McKinney and Zachos, 1986; Carter and Beisel, 1987; Carter, 1987, 1990; Carter and Hammack, 1989; Carter et al., 1989, 2008; Carter and McKinney, 1992; McKinney et al., 1992; Rice, 1997), but these works focused on the Paleogene, especially the Eocene faunas. Papers concerning the Neogene echinoids of the state were much less prevalent. Cutress (1976) described *Prionocidaris cookei* from the lower Miocene Chipola Formation and Oyen and Portell (1996) described *Rhyncholampas chipolanus* from that unit as well. Additionally, McKinney (1985) discussed the occurrence of *Abertella* in the Florida Miocene and Portell and Oyen (1997) documented the presence of *Eucidaris tribuloides* (Lamarck, 1816) in the Tamiami Formation of southern Florida.

Up to this point, 23 species of echinoid that are still recognized as valid today, were documented from Florida's Neogene strata. Oyen et al. (2000) subsequently documented occurrence of moldic echinoids in offshore Plio-Pleistocene deposits in the Gulf of Mexico; referred to *Pericosmus* sp. and Brissidae gen. et sp. indet.

In 2001, Craig Oyen completed his University of Florida doctoral thesis on the Cenozoic echinoderms of Florida, and in the process conducted a thorough review of the Invertebrate Paleontology collections of the Florida Museum of Natural History. His efforts enabled him to recognize many previously undocumented taxa from the Neogene strata of the state, including *Arbia* sp. (herein referred to *Arbia aldrichi* [Clark in Clark and Twitchell, 1915]), *Gagaria* sp. (herein described as *Gagaria hunterae* n. sp.), *Echinarachnius* sp. (herein considered as juvenile *Abertella* sp. from the Chipola

Formation), and an unspecified *Agassizia* sp. (also discussed herein as *Agassizia* sp.) from the state's Miocene strata. Oyen (2001) also documented new occurrences of *Mellita caroliniana* (Ravenel, 1842) and *Plagiobrissus grandis* (Gmelin, 1791), herein referred to as *Plagiobrissus sarae* (Ciampaglio et al., 2009), from the Florida Pliocene, as well as *Moira atropos* (Lamarck, 1816) and *Mellita quinquiesperforata* (Leske, 1778), herein referred to *Mellita isometra* Harold and Telford, 1990, in the Pleistocene strata of the state. This work was formalized in Oyen and Portell (2001).

The efforts of Oyen constituted a leap forward in our understanding of the Florida Neogene echinoid fauna, which had historically received much less attention than the more echinoid-rich Paleogene strata of the state. Oyen was able to demonstrate that the diversity of the Florida Neogene included 29 species, as well as many other taxa documented by Oyen (2001) and Oyen and Portell (2001) that remained unidentified to species level.

Osborn and Ciampaglio (2010a) subsequently documented and described *Abertella dengleri* from the upper Miocene Peace River Formation of Hardee County, provided new stratigraphic records for *R. chipolanus* and *P. cookei* in the Peace River Formation, and reported the occurrence of *Brissopsis* sp. in the unit (herein described as *Brissopsis hoffmani* n. sp.). Ciampaglio and Osborn (2011) reported *Schizaster kieri* Osborn, 2011 from the upper Pliocene Intracoastal Formation of Liberty County, and provided the first documentation of two species within the state: *Brissus glenni* Cooke, 1959, within the Tamiami Formation, and *Plagiobrissus sarae* Ciampaglio et al., 2009, from both the Tamiami and Intracoastal Formations. They also documented the occurrence of a species of *Genocidaris* in the Intracoastal Formation that we herein describe as *Genocidaris oyeni* n. sp., and provided numerous new records for Intracoastal Formation echinoids.

This work is the first to focus entirely on the echinoid fauna of the Florida Neogene. We document the occurrence of 43 species and five additional taxa left as open nomenclature below the genus level. We recognize 16 species of echinoids from the Pleistocene, 20 from the Pliocene, and 12 from the Miocene. Eight new species are described: *Rhyncholampas meansi* n. sp. from the Pleistocene; *Fernandezaster whisleri* n. sp., *Genocidaris oyeni* n. sp., and *Lovenia kerneri* n. sp. from the Pliocene; and *Clypeaster petersonorum* n. sp., *Gagaria hunterae* n. sp., *Brissopsis hoffmani* n. sp., and *Abertella carlsoni* n. sp. from the Miocene strata of the state. Additionally, we recognize *Abertella floridana* (Cooke, 1942), from the Sopchoppy Limestone as a species distinct from *Abertella aberti* (Conrad, 1842), and provide the first documentation of *Echinolampas lycopersicus* Guppy, 1866, *Rhyncholampas sabistonensis* Kellum, 1931, and *Arbia aldrichi* (Clark in Clark and Twitchell, 1915) in the fossil record of Florida.

We also provide updated taxonomy for all species and document their known distributions, which includes an extensive expansion of occurrences for many. The importance of echinoids in modern ecosystems underscores the need to understand how their diversity has changed in the past as well. These paleontological benchmarks are crucial if we are to comprehend how echinoids, and indeed entire biomes in which they live, might respond to the global changes we are observing today. Therefore, this work attempts to provide the most accurate picture to date of the diversity of the Neogene echinoid fauna of Florida. In the process, it demonstrates that the state has the most speciose and diverse assemblage of Neogene echinoids in the eastern United States.

METHODS AND MATERIALS

The Florida Museum of Natural History, Invertebrate Paleontology (FM-IP) collections at the University of Florida were examined in detail, revealing new species and new stratigraphic records of Florida Echinoidea. Material cataloged into these collections is indicated by "UF", followed by a catalog number, and Florida Museum localities are indicated by "FM". In some instances, we examined or figured Recent material from the Florida Museum's Invertebrate Zoology (FM-IZ) collections. Other institutions to whose localities or material we refer include the United States Geological Survey (USGS). We also examined specimens from the Smithsonian Institution's National Museum of Natural History (USNM) and from the California Academy of Sciences' Geology collections (CASG). Perhaps most importantly, material borrowed from numerous avocational collectors (see Acknowledgments) was examined and specimens necessary for the completion of this work were donated to the FM-IP collections. Unless otherwise indicated, all type and figured specimens are deposited at the FM-IP at the University of Florida in Gainesville.

Standard measurements taken include test length (TL: greatest length on a longitudinal axis), test width (TW: greatest width on a latitudinal axis), test height (TH: greatest height), and test diameter (TD: for regular echinoids with symmetrical tests). Measurements taken with a digital caliper with a ± variance of 0.2 mm.

Liquid archival Room Temperature Vulcanizing (abbreviated as RTV) silicone rubber (product designation GI 1120), produced by Silicones Inc., was used to make casts of several specimens (i.e., Figs. 11 and 27). The external molds first were gently cleaned using tap water and a very soft, fine, paintbrush to remove any loose, adhering, sediment and then allowed to air dry. Once dried, sulfur-free clay was used to construct dams around the outside of the external molds and then the RTV rubber was poured onto the external molds and de-aerated under vacuum for three minutes to remove excess air bubbles. After curing for approximately 12 hours, the RTV rubber casts were carefully lifted from the external mold surface. For more information regarding this technique, see Chaney (1989).

Digital images of specimens were taken using a Sony DSC-R1 camera. Plates with scales constructed in Photoshop 21.02. Lateral views of Irregularia are from left side unless otherwise noted.

THE MIOCENE

The Miocene was a time of significant change in the depositional history of Florida. Carbonate deposition, which dominated during the Paleogene, continued over much of the state during the early portion of the epoch, but by the end of the early Miocene, the deposition of carbonate sediments was occurring only in southern peninsular Florida. Siliclastic deposition dominated statewide by the middle Miocene, a trend that would continue into the late Miocene (Scott, 1992a).

The echinoid fauna of the Florida Miocene was inadequately documented previously, most likely due to poor specimen preservation and collector bias. Oyen and Portell (1993, 1999, 2001) conducted a thorough review of the curated and uncurated FM-IP collections, and by focusing on fragmentary and poorly preserved material, which many collectors tended to disregard, they were able to increase the known diversity substantially, adding seven taxa and 14 new stratigraphic records to the echinoid fauna of the Florida Miocene. Prior to those studies, Florida echinoid distribution showed a distinct drop in species from the Oligocene into the Miocene (Oyen and Portell, 1993, 1999). However, this trend was anomalous when compared with the global pattern that showed an increase in diversity from the Oligocene to the Miocene (Kier, 1977; McKinney et al., 1992).

Subsequent to the Oyen and Portell studies, Osborn and Ciampaglio (2010a) described *Abertella dengleri* from the upper Miocene Peace River Formation, in the bed of the Peace River above Zolfo Springs, Hardee County, Florida. They also documented the occurrence of *Prionocidaris cookei* Cutress, 1976, *Rhyncholampas chipolanus* Oyen and Portell, 1996, and the herein described *Brissopsis hoffmani* n. sp., as co-occurring with *A. dengleri* in the lower Peace River Formation.

The current study expands previous work and increases the Miocene echinoid fauna by four new species: *Gagaria hunterae* n. sp., *Clypeaster petersonorum* n. sp., *Abertella carlsoni* n. sp., and *Brissopsis hoffmani* n. sp. Furthermore, we document the occurrence of *Echinolampas lycopersicus* Guppy, 1866 in the Chipola Formation, and recognize *Abertella floridana* (Cooke, 1942) as a species distinct from *Abertella aberti* (Conrad, 1842). Together, this provides a more complete picture of the Florida Miocene echinoid fauna, and shows it to be far more diverse than previously suspected, with 12 species, as well as four additional taxa recognizable only to genus, and two recognizable as distinct but not identifiable to the genus.

Within Florida, 12 Miocene formations contain echinoids (Fig. 2). The echinoid-bearing Miocene units are generally distributed from the central peninsula northward to the Florida-Georgia border and westward into the panhandle of the state. Although the Florida Miocene was dominated by siliclastics, as opposed to the carbonate-rich Paleogene strata in the state, the carbonate and shelly beds provide the greatest abundance of echinoids.

The Florida Miocene has three species that are found in more than one stratigraphic unit (Fig. 2). These are: *P. cookei*, which occurs in the Chipola, Torreya, and Peace River Formations; *Arbia aldrichi* (Clark in Clark and Twitchell, 1915), which occurs in the St. Marks and Chattahoochee Formations; and *R. chipolanus*, which occurs in the upper Arcadia, Chipola, Torreya, and Peace River Formations (Fig. 2). Only three of these taxa are documented outside the state: *Arbia aldrichi* also occurs in the uppermost Oligocene Chickasawhay Limestone of southwestern Alabama and southeastern Mississippi, and the River Bend Formation in North Carolina. Cutress (1980) documented *P. cookei* from the Miocene of Cuba and *Echinolampas lycopersicus* Guppy, 1866 has a widespread distribution in the Miocene of the West Indies.

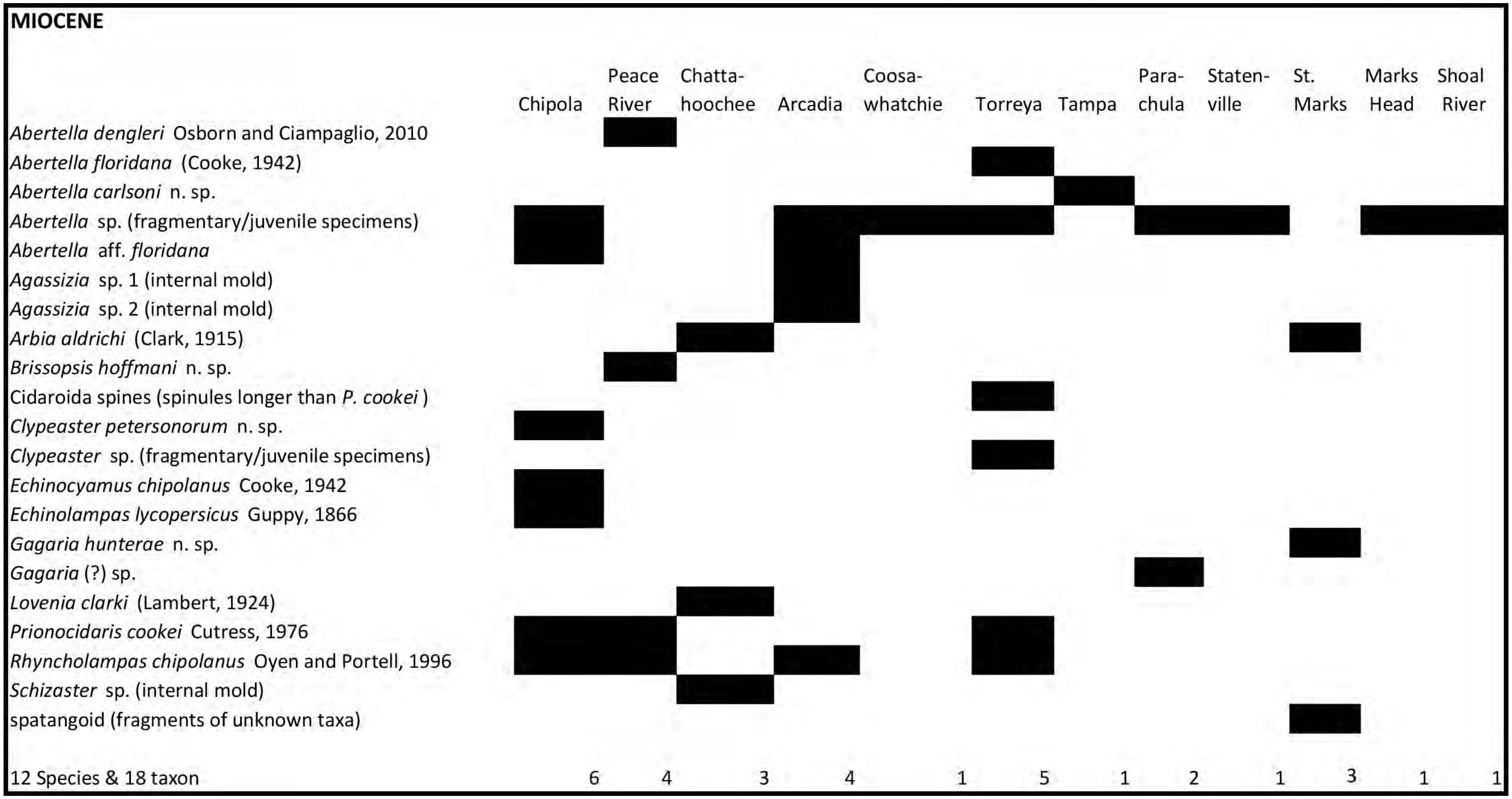
Abertella is the most widely represented echinoid genus in the Florida Miocene, being known by three species: the herein described *A. carlsoni* n. sp., as well as *A. dengleri* and *A. floridana*. Cooke (1942) described *Scutella floridana* from the Chipola Formation near Sopchoppy, Wakulla County (strata now referred to the Sopchoppy Member of the Torreya Formation). Durham (1953b) suggested that *Scutella floridana* be placed in the genus *Abertella*; and subsequently, Cooke (1959) synonymized his own *A. floridana* with *A. aberti*. However, additional material from the type locality in Wakulla County (FM locality WA013) allowed us to assess the variability of *A. floridana*, and as discussed in the remarks for the species herein, we confidently recognize the species as distinct from *A. aberti*.

The genus *Abertella* occurs in 10 of the 12 echinoid-bearing Miocene formations within the state; however, many of these occurrences consist of fragmentary material not identifiable to species (Fig. 2). Specimens referable only to genus, lacking material complete enough for species determination, are represented in the FM-IP collections from no fewer than eight Miocene units: the Arcadia (upper portion), Chipola, Coosawhatchie, Marks Head, Parachula, Statenville, Shoal River, and Torreya Formations.

Historically these fragments have been attributable to *A. aberti*, lacking a suitable alternative. However, with recognition of *A. floridana* as a distinct species, designation of *A. dengleri* for the wide-bodied upper Miocene Peace River Formation specimens from Hardee County, Florida, and recognition of *A. carlsoni* n. sp. from the lower Miocene portion of the Tampa Member of the Arcadia Formation, fragmentary material can no longer be attributed by default to *A. aberti*. Furthermore, we are unaware of Florida specimens that can be identified reliably as *A. aberti*. As discussed within the remarks for *Abertella* sp. herein, the population of *Abertella* in the upper portion of the Arcadia Formation is perhaps the only one that is morphologically closest to *A. aberti*.

Specimens of *Abertella* from the late Miocene strata of the Peace River area of southern peninsular Florida have been discussed in the literature as *A. aberti* (McKinney, 1985; Oyen, 2001), but closer examination reveals that specimens from the Peace River Formation belong to a distinct species, with a wide test, shallow or absent indentations opposite the anterior ambulacra, and a pronounced and narrow posterior notch that distinguishes specimens of *A. dengleri* from the subcircular test of *A. aberti*. An updated key to the species of *Abertella* is provided in Kroh et al. (2013). However, this key does not include *A. carlsoni* n. sp. or *A. floridana* as neither were recognized at that time.

Most echinoid species within the Florida Miocene are rare, though notable concentrations do occur. One such concentration is an abundance of moldic specimens of *Lovenia clarki* (Lambert in Lambert and Thiéry, 1924) in the dolomitic limestones of the Chattahoochee Formation below Lake



MIOCENE	Chipola	Peace River	Chatta-hoochee	Arcadia	Coosa-whatchie	Torreya	Tampa	Para-chula	Staten-ville	St. Marks	Marks Head	Shoal River
Abertella dengleri Osborn and Ciampaglio, 2010		■										
Abertella floridana (Cooke, 1942)						■						
Abertella carlsoni n. sp.							■					
Abertella sp. (fragmentary/juvenile specimens)	■			■	■	■		■	■		■	■
Abertella aff. *floridana*	■			■								
Agassizia sp. 1 (internal mold)				■								
Agassizia sp. 2 (internal mold)				■								
Arbia aldrichi (Clark, 1915)			■							■		
Brissopsis hoffmani n. sp.		■										
Cidaroida spines (spinules longer than *P. cookei*)						■						
Clypeaster petersonorum n. sp.	■											
Clypeaster sp. (fragmentary/juvenile specimens)						■						
Echinocyamus chipolanus Cooke, 1942	■											
Echinolampas lycopersicus Guppy, 1866	■											
Gagaria hunterae n. sp.										■		
Gagaria (?) sp.								■				
Lovenia clarki (Lambert, 1924)			■									
Prionocidaris cookei Cutress, 1976	■	■				■						
Rhyncholampas chipolanus Oyen and Portell, 1996	■	■		■		■						
Schizaster sp. (internal mold)			■									
spatangoid (fragments of unknown taxa)										■		
12 Species & 18 taxon	6	4	3	4	1	5	1	2	1	3	1	1

Figure 2. Distribution of Miocene echinoids documented from Florida. Fragmentary remains of *Abertella* that are unidentifiable to species are not included in the taxon total for units already containing recognizable species of the genus. Taxon total does not include specimens that are indistinguishable as distinct taxa.

Seminole in Jackson County. The lower Miocene Chipola Formation in the panhandle of the state contains concentrations of echinoids both below Alum Bluff, and in the stratotype area along the Chipola River in Calhoun County. Another notable concentration occurs in the lower portion of the Peace River Formation, above Zolfo Springs, Hardee County (FM locality HR013), where abundant fragments and rare complete tests of *A. dengleri* occur in a horizon of sandy, siliclastic dolostone less than 20 cm thick. These echinoid concentrations are further discussed below.

Although the Miocene echinoid fauna of Florida spans 12 formations, echinoid occurrences are concentrated within the Peace River, Chipola, Torreya, St. Marks, and Chattahoochee Formations, as well as Tampa Member (upper portion) of the Arcadia Formation. Echinoid remains in other Miocene units are rare and consist mostly of fragmentary material. We focus our efforts on the fauna of the six above-mentioned units, though all Miocene echinoid occurrences are documented in Figure 2.

Peace River Formation

The Peace River Formation is part of the Hawthorn Group. In the central southern Florida peninsula, the Hawthorn Group generally consists of a basal carbonate unit, the Arcadia Formation, and an upper siliclastic unit, the Peace River Formation (Scott, 2001). The Hawthorn Group has been problematic since being named by Dall and Harris (1892). It is a complex unit of interbedded and intermixed carbonate and siliclastic sediments containing varying concentrations of phosphate (Scott, 1990). Scott (1988) upgraded the Hawthorn to group status in Florida and defined its component formations.

The Peace River Formation is exposed beneath a thin layer of overburden, on the southern part of the Ocala Platform, extending into the Okeechobee Basin in south Florida (Scott, 2001). The unit reaches a maximum known thickness of 198 m in the Okeechobee basin (Scott, 1990), and is unconformably underlain by the Oligocene to lower Miocene Arcadia Formation, which is largely a subsurface unit over its entire extent (Brewster-Wingard et al., 1997). The Peace River Formation is typically overlain by the Pliocene Tamiami Formation (Missimer, 2002). Missimer (2002) divided the Peace River Formation into distinct lower and upper stratigraphic units. The lower unit is late Miocene (Tortonian) and consists of relatively flat-bedded, predominantly siliclastic, nearshore ramp, beach and carbonaceous lagoonal deposits, and is capped by a distinct disconformity. The upper unit is a mixed siliclastic/carbonate unit containing deltaic characteristics, such as graded beds and angular bedding, of early Pliocene (Zanclean) age (Missimer, 2002).

The siliclastics of the Peace River Formation are typically dolomitic, phosphatic, clayey quartz sands. Carbonate beds are common and are generally sandy, phosphatic, clayey dolostones (Scott, 1990); however, the siliclastic component predominates and is the distinguishing lithologic feature of the unit. The siliclastics typically comprise two-thirds or more of the Peace River Formation (Scott, 1988). Strontium-isotope analysis enabled Missimer (2002) to provide an age range of 11 to 8.5 Ma for the lower Peace River Formation, and 5.23 to 4.29 Ma for the upper portion.

Lithologic units of the phosphate-rich Hawthorn Group are characterized as being deposited in inner shelf, nearshore environments. During the early Miocene, terrigenous siliclastics derived from the southern Appalachians filled the Gulf Trough, and encroached into the carbonate producing environments of peninsular Florida. These siliclastics represent the first recorded Cenozoic influx of terrigenous sediments onto the carbonate bank of peninsular Florida (Scott, 1990). This change from carbonate to siliclastic deposition was, in part, due to the continued influx of large amounts of siliclastics from the eroding southern Appalachians (Scott, 1988).

Until recently, the echinoid fauna of what is now the Peace River Formation was unknown. Cooke (1959) recognized some Miocene echinoids from the Tamiami Formation. However, that unit is now considered Plio-Pleistocene in age. The prior lack of documentation of echinoids of the Peace River Formation may be attributed to the lack of exposures; however, the most echinoid-rich units of the Peace River Formation consist of natural exposures along the Peace River. The lack of documentation of this fauna therefore seems more likely due to collector bias towards more notable Miocene and Pleistocene age vertebrate faunas of the region and the rarity of complete echinoid tests.

Since Cooke (1959), four species of echinoid have been documented from the upper Miocene Peace River Formation of the central portion of the southern Florida peninsula. These include: *P. cookei*, *A. dengleri*, *R. chipolanus,* and the herein described *Brissopsis hoffmani* n. sp. (Osborn and Ciampaglio, 2010a; Oyen, 2001; Oyen and Portell, 2001). Echinoid-bearing strata of the unit are best exposed along the banks of the Peace River near Arcadia, and upriver from Zolfo Springs. Above Zolfo Springs, abundant fragments and rare complete tests of *A. dengleri* occur in a horizon of sandy, siliclastic dolostone <20 cm thick. The *Abertella* bed is largely devoid of other invertebrates, with the exception of rare specimens of the echinoids *R. chipolanus*, the herein described *Brissopsis hoffmani* n. sp., and spines of *P. cookei*. Specimens are often eroded from the very resistant, silica-rich matrix in the riverbed, typically rendering the surface details of the specimens indistinct or even totally obliterated (Osborn and Ciampaglio, 2010a).

The *Abertella* biozone above Zolfo Springs occurs within the lower Peace River Formation in light gray, weathered brown, siliclastic dolostone that is rich in opaline chert. The strata represent a terrigenous marine facies, where nearshore habitats were subject to significant inputs of coarse clastic material from a prograding Miocene delta (McKinney, 1985). Though mollusks are not uncommon in the horizons above and below the *Abertella* biozone, they are rare within it (Osborn and Ciampaglio, 2010a).

Outside of the above-described occurrences, echinoids are rare in the Peace River Formation.

CHATTAHOOCHEE FORMATION

The Chattahoochee Formation is predominantly a fine-grained, yellowish gray, poorly to moderately indurated, often fossiliferous (moldic), silty to sandy dolostone which is variable to a limestone (Huddleston, 1988; Scott, 2001) of early Miocene age. The unit represents deposition in a shallow and warm transgressive sea over the eroded surface of the Oligocene or older limestones (Puri, 1953) and though it occurs in a limited area of the central panhandle, it is best exposed in Jackson County. The Chattahoochee grades into the basal Hawthorn Group northward into Georgia (Huddleston, 1988) and grades across the Gulf Trough into the St. Marks Formation through a broad transitional area (Scott, 2001). The unit was deposited nearer to shore than the St. Marks Formation (Puri, 1953).

Cooke (1959) documented *L. clarki* from the Chattahoochee Formation; abundant moldic *L. clarki* are present in pale soft, yellow, dolomitic limestone in a road cut along the access road to Jim Woodruff Dam in Jackson County (FM locality JA003), where, *Lovenia* is joined by a variety of molluscan and decapods molds and rare fragmentary molds of regular urchins tentatively referred to the genera *Gagaria* and *Arbia* by Oyen (2001). RTV silicone casts of these molds provide sufficient details to attribute these specimens with confidence to *A. aldrichi*. Furthermore, a very weathered internal mold of a spatangoid echinoid (UF 229789; Fig. 143) was also collected at this locality. Given the sparse echinoid fauna of the Chattahoochee Formation, other than the abundant presence of *L. clarki*, this specimen is significant. The gross morphology of this specimen resembles the genus *Schizaster* but preservation is insufficient to determine the species definitively. Herein, we treat this specimen as *Schizaster* sp., increasing the diversity of the Chattahoochee Formation to three taxa (Fig. 2).

CHIPOLA FORMATION

The lower Miocene Chipola Formation is a richly fossiliferous unit of the Alum Bluff Group of the Florida panhandle. Of all of the formations within the Alum Bluff Group, the Chipola Formation is probably best known because of its spectacular molluscan fauna, which may contain over 1000 species (Vokes, 1989 and references therein). This fauna was documented by Gardner (1926-1950) and more recently by Vokes (1989 and references therein) and others who noted its Burdigalian (early Miocene) affinities (Jones et. al., 1993). Strontium isotope dating of the unit at Alum Bluff provided an age range of 18–19 Ma (Jones et al., 1993).

The name Chipola Formation was first suggested by Burns (Dall and Harris, 1892) for a shell bed exposed on the Chipola River below Bailey's Ferry (near the mouth of Tenmile Creek) and at Alum Bluff on the Apalachicola River. The Chipola Formation is mostly confined in outcrop to Calhoun and Liberty Counties in the central panhandle, where it consists of clays, sands, and shell beds that are all at least somewhat fossiliferous. The formation is often mapped as undifferentiated Alum Bluff Group, as the units within the group are largely indiscernible other than by their molluscan faunas (Scott, 2001). The Chipola Formation is perhaps best known for exposures in the stratotype area along the Chipola River, below the mouth of Tenmile Creek, though it is well exposed elsewhere: notably along the banks of Tenmile Creek below the Highway 73 bridge north of Clarksville and at Alum Bluff, along the Apalachicola River. In addition to the Chipola Formation, the Alum Bluff Group consists of the Oak Grove Sand, Shoal River, Choctawhatchee, and Jackson Bluff Formations (Scott, 2001).

Moving over sediments of the Chattahoochee Formation, the transgressing Alum Bluff Sea deposited the warm-water, inner neritic, distinctly shallow-water Chipola Formation fauna under stable conditions (Puri, 1953). The unit includes biofacies ranging from shoreline beach to lagoonal with oyster reefs to coral patch reefs in an offshore back-reef setting probably no deeper than 30 m (Vokes, 1989). Vokes (1989) suggests that the Chipola Formation reflects the last truly tropical climatic conditions of the Miocene. The succeeding Shoal River Formation represents a cooler, more temperate climate that corresponds to middle Miocene growth of the Antarctic Ice Sheet (Jones, 1997).

Though the molluscan, bryozoan (Di Martino et al. 2017), and coral faunas (Weisbord, 1971) of the Chipola Formation have been documented in part, the echinoid fauna has received little study, likely due to the rarity and often fragmentary nature of its echinoids. Cooke (1959) documented three species from the Chipola Formation: *A. aberti* (=*A. floridana* herein), *Clypeaster concavus* Cotteau, 1875 (=*C. petersonorum* n. sp. herein), and *Echinocyamus chipolanus* Cooke, 1942. As this study demonstrates, with six species, the Chipola Formation contains the most diverse echinoid assemblage in the Florida Miocene (Fig. 2).

Oyen and Portell (1996) documented and described *R. chipolanus* from a single, fairly well-preserved specimen collected in the bed of the Chipola River. This represented the first Miocene occurrence of the genus *Rhyncholampas* in the region. The specimen was collected within 1 m of the top of the Chipola Formation, within the type area of the formation. Subsequent collecting revealed a significant concentration of this species within the lower exposed Chipola Formation at the bottom of the Apalachicola River below Alum Bluff. *Rhyncholampas chipolanus* has subsequently also been documented from the lower Peace River (Osborn and Ciampaglio, 2010a), Arcadia, and Torreya Formations.

Oyen (2001) documented juvenile and incomplete tests of a sand dollar he tentatively referred to cf. *Echinarachnius* sp. from the Chipola Formation in Calhoun County. He ruled out the possibility of *Abertella* for these specimens based on test shape. However, juvenile specimens of *Abertella* typically do not show the anal notch and other characteristics of mature specimens of the genus. We examined these specimens, and though we are unwilling to make a specific determination due to their small size (<1 cm), it is highly probable these are juvenile *Abertella* (likely *A. floridana*). It is doubtful they belong to the genus *Echinarachnius*, which has not been documented from rocks older than Pleistocene in the region. These juvenile *Abertella* were collected during screening of bulk samples from Reef B in the river bed of the Chipola River Formation type area, and were associated with fragments of larger *Abertella* sp., spines of *P. cookei*, and a fragment of a regular urchin which Oyen (2001) tentatively referred to the genus *Psammechinus*.

This fragment is too incomplete to place positively within a genus, and we continue to consider it only tentatively identified until better material is collected. Oyen (2001) also documented fragments of a brissid from the Chipola Formation in Calhoun County. Though this fragment is not identifiable to genus, it does represent the first documentation of a spatangoid echinoid within the formation, which is otherwise dominated by members of the Clypeasteroida and Cassiduloida.

We herein add *Echinolampas lycopersicus* Guppy, 1866 to the echinoid fauna of the Chipola Formation, and reassign specimens previously attributed to *Clypeaster concavus* Cotteau, 1875 (*sensu* Cooke, 1959) to *Clypeaster petersonorum* n. sp. Our study expands the echinoid fauna of the formation to six species: *P. cookei*, *Echinocyamus chipolanus*, *Clypeaster petersonorum* n. sp., *R. chipolanus*, *E. lycopersicus,* and *Abertella* sp. (Fig. 2).

The most diverse echinoid fauna of the Chipola Formation occurs in the stratotype area within the lowest shell bed and indurated horizon immediately overlying it, above the contact with the underlying Chattahoochee Formation, along the Chipola River below the mouth of Tenmile Creek, in Calhoun County. Here, a fine yellow-brown, sand-rich shell bed with intermittent indurated layers contains innumerable well-preserved mollusks, an abundance of the solitary coral *Trachyphyllia bilobata* Duncan, 1863, and rare occurrences of the echinoids *Clypeaster petersonorum* n. sp., *E. lycopersicus*, *R. chipolanus,* and *P. cookei*.

Cooke (1942) described *Echinocyamus chipolanus* from a single specimen collected from the Chipola Formation at Alum Bluff, Liberty County (FM locality LI001). A tremendous amount of collecting at this locality, including extensive serial sieving of bulk sediments, has yet to provide a single additional specimen of this species. The holotype, and only known specimen, has been badly damaged (Cooke, 1959) since being figured by Cooke (1942).

Torreya Formation

The Torreya Formation, a member of the Hawthorn Group, is limited in outcrop to Leon, Gadsden, and Wakulla Counties of the eastern panhandle, and is the only formation of the Hawthorn Group in north Florida and Georgia where limestone is an important and consistent component of the lithology (Scott 1998). The unit is variably indurated, and the white to olive gray carbonate sediments commonly have abundant mollusk molds. The Torreya Formation overlies the Chattahoochee Formation and/or St. Marks Formation through its areal extent (Scott, 2002), and likely interfingers with the Chipola Formation (Bryant et al., 1992). Jones *et al*. (1993) conducted strontium isotope dating of the Torreya Formation in the lowest beds of the Taft Pit, Wakulla County, as 19.6 Ma. They provided a slightly younger age of 17.4 Ma for the Sopchoppy Member, confirming the conclusion of Bryant et al. (1992) that there is considerable chronologic overlap between the Torreya and Chipola Formations.

The Torreya Formation was deposited in a shallow marine environment in and on the southeastern flank of the Gulf Trough (Scott, 2002). It consists of two members: the Sopchoppy Member, a limestone facies that occurs in Wakulla County, and the Dogtown Member, which is a clay-rich member that occurs in Gadsden County (Scott, 2002). The mollusks and echinoids of the Sopchoppy Member indicate that it was deposited in a shallow-water, open marine setting. The Dogtown Member was deposited in a peri-marine environment, as evidenced by the abundant occurrence of palygorskite (Scott, 2002).

Cooke (1942) described *A. floridana* from the Chipola Formation, north of Sopchoppy, Wakulla County, Florida. However, the stratum in which the holotype was collected is now considered the Sopchoppy Member of the Torreya Formation. *Abertella floridana* remained the only species of echinoid documented from the Torreya Formation for over 60 years. An extensive review of the collections of Muriel Hunter and Joe Banks in the FM-IP collections revealed a previously undocumented diversity of echinoids within the Torreya Formation. Collections of largely fragmentary material from the Torreya Formation from the old Taft Quarry, 3 miles south of Crawfordsville, Wakulla County (FM locality WA001), revealed a diverse echinoid fauna, including *R. chipolanus*, fragmentary remains of *Clypeaster* sp. and *Abertella* sp., as well as spines of *P. cookei*. Therefore, the Torreya Formation contains five taxa: *P. cookei*, *A. floridana*, *R. chipolanus*, *Clypeaster* sp. (likely *C. petersonorum* n. sp.) and spines of an indeterminate cidarid.

St. Marks Formation

The St. Marks Formation is a lowermost Miocene, moderately indurated, sandy, fossiliferous (moldic) pale limestone exposed in Wakulla, Leon, and Jefferson Counties on the northwestern flank of the Ocala Platform (Scott, 2001). The St. Marks overlies Oligocene strata, and is in turn overlain by the Chipola and Torreya Formations. The St. Marks Formation can be traced in cores grading into the Chattahoochee Formation (Scott, 1986) north of its outcrop area.

Echinoids have not been documented from the unit previously. However, herein we record the occurrence of *A. aldrichi*, which the unit shares with the correlative Chattahoochee Formation, as well as fragments of an undetermined spatangoid, which occurs with *A. aldrichi* in channel dredgings along the gulf shore west of Shell Point, Oyster Bay, Wakulla County. We also document the occurrence of *Gagaria hunterae* n. sp. in the St. Marks Formation, collected east of Woodville, Wakulla County (FM locality WA011).

The echinoid fauna of the St. Marks Formation therefore contains three taxa: two regular echinoids, *G. hunterae* n. sp., *A. aldrichi*; and one spatangoid of uncertain genus (Fig. 2).

Tampa Member, Arcadia Formation

The Tampa Member of the Arcadia Formation ranges from late Oligocene to early Miocene (Brewster-Wingard et al., 1997) and varies from white to yellowish gray limestone with varying amounts of quartz sand, silt, and clay (Scott, 1988). As discussed in Jones et al. (1993), the age and stratigraphic position of the Tampa Limestone (now Tampa Member of the Arcadia Formation) has been debated for over a century. Some authors considered it to be late Oligocene and others early Miocene (Brewster-Wingard et al., 1997). The unit is currently considered to straddle the Oligocene-Miocene boundary (Green et al., 2012), and is documented in outcrop only in the Tampa region, but is recognized more extensively from core material (Jones et al., 1993).

In the west central Florida peninsula, the Tampa Member overlies the Suwannee Limestone, and the contact appears to be conformable, at least locally (Green et al., 2012). Additionally, in this area, the unit is overlain unconformably by the Peace River Formation. Further east and southward, the Tampa Member grades laterally into the generic Arcadia Formation (Arthur et al., 2008).

The Tampa Member contains sporadic concentrations of fossil coral (Weisbord, 1973; Upchurch et al., 1982) and a diverse molluscan assemblage was well-documented by Dall (1915) and Mansfield (1937). However, echinoids have not previously been documented from this unit. In 2012, discovery by Joseph R. Dumont (of Oldsmar, Florida), of material from the early Miocene portion of the unit, dredged in St. Joseph Sound, west of Dunedin, Pinellas County (FM locality PI025), revealed the abundant, localized presence of a new species of *Abertella*. With a lowermost Miocene age, *A. carlsoni* n. sp. is the earliest documented species of *Abertella* in the region. As discussed in the species remarks below, with a maximum test length of less than 50 mm, it is the smallest *Abertella* species found in North America.

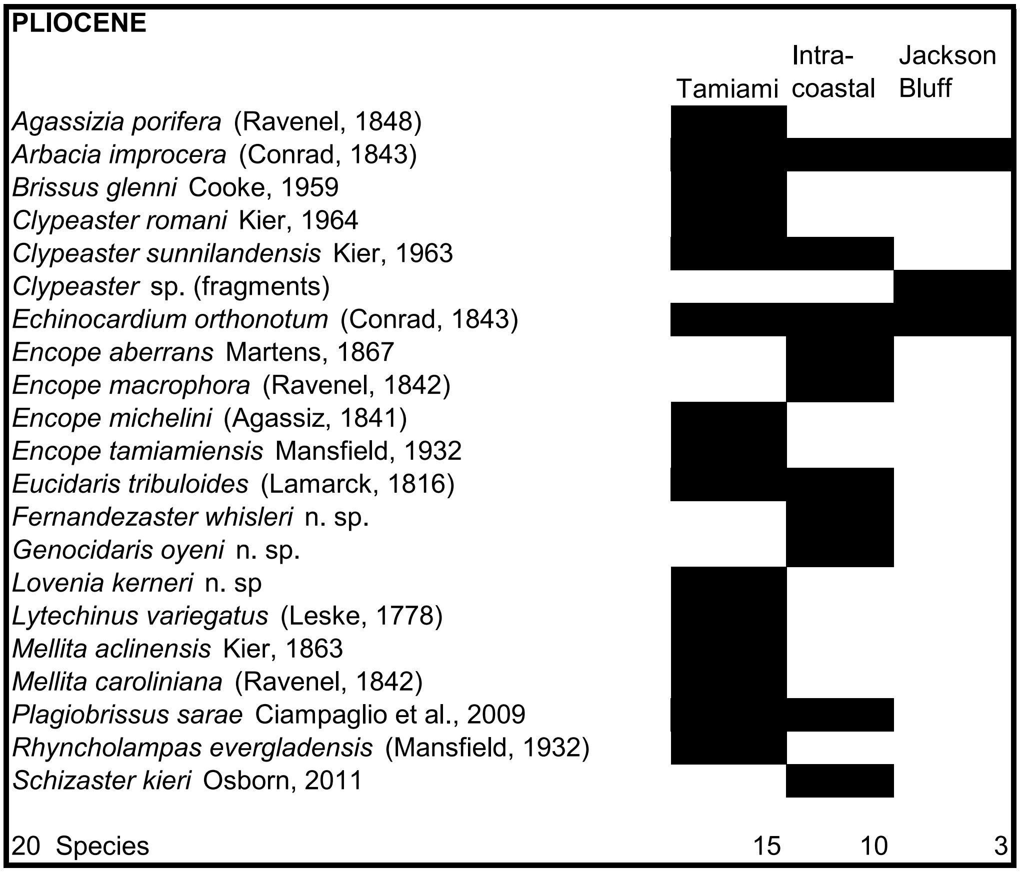
THE PLIOCENE

There was a return of warm tropical climates and biogenic carbonate deposition to southern Florida during the late Pliocene. After a period of sea level regression during the early Pliocene, the late Pliocene saw a significant marine transgression that resulted in the deposition of the Tamiami Formation. Although early Pliocene, Zanclean stage strata do occur in Florida, primarily represented in the upper portion of the Peace River Formation, echinoids have yet to be documented within this stage. Strata of the late Pliocene (Piacenzian Stage) contain the most abundant and diverse echinoid fauna of the Florida Neogene; a fauna exceeded in diversity only by the Eocene echinoid fauna of the state.

Recent revisions to the Neogene timescale (Ogg et al., 2008), coupled with a 2009 ratification of the definition of the base of the Quaternary Period from the International Commission on Stratigraphy, reassigned the base of the Pleistocene downward to include the Gelasion Stage/Age, which previously was considered to reside solely in the latest Pliocene. This redesignation shifted a small portion of the Tamiami Formation, the Upper Pinecrest beds, into the early Pleistocene and completely confines the Caloosahatchee Formation and most of the correlative Nashua Formation to the Pleistocene (Missimer and Wise, 2012; Kittle et al., 2013). Previously, the lower portion of the Caloosahatchee Formation was considered to extend into the Pliocene. The Florida Pliocene echinoid fauna, totaling 20 species, therefore largely extends across three formations: the Tamiami, Intracoastal, and Jackson Bluff Formations. All described Pliocene species occur within two of these units: the Tamiami and Intracoastal Formations. Of these, the Tamiami Formation contains the greatest diversity, with 15 species (Fig. 3).

Cooke (1959) documented three species from the Florida Pliocene: *Encope macrophora* (Ravenel, 1842) from Alligator Creek, Charlotte County (Cooke considered the Alligator Creek beds to belong to the Caloosahatchee Formation, though the *Encope* beds along Alligator Creek have since been firmly placed within the Tamiami Formation [DuBar, 1962]); *Encope tamiamiensis* Mansfield, 1932; and *Rhyncholampas sabistonensis* Kellum, 1931 (Cooke believed this latter species to be synonymous with *Rhyncholampas evergladensis* Mansfield, 1932, although Kier [1963] provided contrary evidence).

The extent of the Florida Pliocene echinoid fauna became more completely known when Kier (1963) documented the echinoids of the Tamiami Formation, identifying the following species: *Arbacia crenulata* Kier, 1963 (which Kier [1972] considered to be synonymous with *Arbacia impro-*



PLIOCENE	Tamiami	Intra-coastal	Jackson Bluff
Agassizia porifera (Ravenel, 1848)	■		
Arbacia improcera (Conrad, 1843)	■	■	■
Brissus glenni Cooke, 1959	■		
Clypeaster romani Kier, 1964	■		
Clypeaster sunnilandensis Kier, 1963	■	■	
Clypeaster sp. (fragments)			■
Echinocardium orthonotum (Conrad, 1843)	■	■	■
Encope aberrans Martens, 1867		■	
Encope macrophora (Ravenel, 1842)		■	
Encope michelini (Agassiz, 1841)	■		
Encope tamiamiensis Mansfield, 1932	■		
Eucidaris tribuloides (Lamarck, 1816)	■	■	
Fernandezaster whisleri n. sp.		■	
Genocidaris oyeni n. sp.		■	
Lovenia kerneri n. sp	■		
Lytechinus variegatus (Leske, 1778)	■		
Mellita aclinensis Kier, 1863	■		
Mellita caroliniana (Ravenel, 1842)	■		
Plagiobrissus sarae Ciampaglio et al., 2009	■	■	
Rhyncholampas evergladensis (Mansfield, 1932)	■		
Schizaster kieri Osborn, 2011		■	
20 Species	15	10	3

Figure 3. Distribution of Pliocene echinoids documented from Florida.

cera Conrad, 1843); *Lytechinus variegatus pluri-tuberculatus* Kier, 1963; *Clypeaster crassus* Kier, 1963 (redesignated as *Clypeaster romani* by Kier [1964] as the name *C. crassus* was preoccupied); *C. sunnilandensis*; *E. tamiamiensis*; *Mellita aclinensis*; *Rhyncholampas evergladensis;* and *Echinocardium gothicum* (Ravenel,1848), which was later placed in synonymy with *Echinocardium orthonotum* (Conrad, 1843) by Kier (1972).

Kier (1963) also described *Encope michelini imperforata* Kier, 1963 from the Tamiami and Caloosahatchee Formations. However, Phelan (1972) re-identified Kier's *E. michelini imperforata* as *E. aberrans* Martens, 1867, and stated the population merely had more variation than expected for a normal population. Furthermore, Phelan abandoned the subspecific designation *imperforata* when he included it in the synonomy of *E. aberrans*. Kier (1992) agreed with Phelan's specific assessment but still considered his subspecific designation of *imperforata* to be valid. Kier (1963) did use a specimen of *E. aberrans* as his holotype of *E. michelini imperforata* (USNM 648167). However, at least one of his paratypes (USNM 648169; Kier, 1963:fig. 25, p. 34) is clearly *E. michelini* Agassiz, 1841.

We have examined numerous specimens of both *E. aberrans* and *E. michelini* with reduced and absent anal lunules collected from populations of otherwise typical representatives of the species from both the Florida Pleistocene and the Pleistocene Waccamaw Formation of South Carolina. Though an absent, or greatly reduced, anal lunule is uncommon in Recent populations of *E. michelini*, as documented by Kier (1963), this occurrence is not rare in Neogene populations of both *E. aberrans* and *E. michelini*. Considering that these specimens occur within populations of otherwise typical members of these species, it is our opinion that this tendency represents variation within these species that is more widespread in at least some parts of the fossil record than among modern populations. Kier (1992) demonstrated that this variation is also present in the Caribbean when he described reduced or absent anal lunules in *E. aberrans* from Neogene strata in the Dominican Republic, and postulated that specimens from the Pliocene of Venezuela are also specimens of *E. aberrans imperforata*. We agree with Phelan (1972) in not recognizing the subspecies *imperforata*.

Additional collecting over the past two decades has expanded the known echinoid fauna of the Florida Pliocene. Portell and Oyen (1997) documented *Eucidaris tribuloides* (Lamarck, 1816) from the Tamiami Formation, and Oyen (2001) provided new stratigraphic records for many species, also recording the occurrence of additional, fragmentary specimens that he could not assign below genus level. Osborn and Ciampaglio (2010b) documented the occurrence of *Plagiobrissus sarae* Ciampaglio et al., 2009 from the Tamiami Formation. Ciampaglio and Osborn (2011) described and documented *Schizaster kieri* Osborn, 2011 from the Intracoastal Formation, and documented new stratigraphic records that added *Brissus glenni* Cooke, 1959 and *Genocidaris* sp. to the Florida Pliocene fauna. Herein, we describe *Genocidaris oyeni* n. sp. and *Fernandezaster whisleri* n. sp. from the upper Pliocene Intracoastal Formation, and *Lovenia kerneri* n. sp. from the upper Pliocene Tamiami Formation.

The documented Florida Pliocene echinoid fauna is now known to contain 20 species (Fig. 3). Of these, six are found in more than one stratigraphic unit: *A. improcera* and *E. orthonotum* are found in the Intracoastal, Jackson Bluff, and Tamiami Formations, *C. sunnilandensis*, *E. tribuloides,* and *P. sarae* are shared by the Intracoastal and Tamiami Formations, and *Mellita caroliniana* (Ravenel, 1842) occurs in the Nashua Formation of St. Johns and Putnam Counties, in strata likely referable to the lower Pleistocene.

This surge in species documented from the Florida Pliocene over the past six decades from three to 20 (Fig. 3) is likely attributable to significant excavation associated with urban development in areas underlain by Pliocene sediments, especially in southern Florida (Oyen, 2001). Though Pliocene strata occur widely in Florida, the sediments are seldom naturally exposed and usually occur in areas of low relief.

As documented by Petuch (2004), the beginning of the late Pliocene saw a return to tropical and subtropical conditions for most of eastern North America. Sea levels rose to their highest point since the Tortonian, once again inundating coastal areas. This warmer marine climate, coupled with greatly expanding seas, created conditions conducive for creating one of the richest invertebrate faunas ever seen in North America (Petuch, 2004). The echinoid faunas of this period are best represented in sediments of the Tamiami and Intracoastal Formations, and are discussed below in detail.

TAMIAMI FORMATION

The Tamiami Formation is the primary late Pliocene unit of southern Florida, consisting of a complex series of carbonate and siliclastic lithologies that are variably horizontally consistent, with distinct disconformities observed between some of the members or facies (Missimer, 1992). The informal name "Tamiami Limestone" was first applied to the unit as observed in a series of sandy limestone outcrops along the Tamiami Trail in Collier County (Mansfield, 1939). This pale, sandy limestone horizon, exposed in ditches along the Tamiami Trail and rich with specimens of the echinoids *Encope tamiamiensis* and *Rhyncholampas evergladensis*, is now redefined as the Ochopee Limestone member of the Tamiami Formation (Missimer, 1992).

Strontium isotope dating has provided an age of 2.79 to 4.70 Ma for the Tamiami Formation (Missimer, 1993). As noted by Missimer and Wise (2012), a portion of the Pinecrest beds, in the uppermost Tamiami Formation near Sarasota, probably resides in the early Pleistocene. If proven correct, this redesignation could impact the echinoid distribution within the Florida Neogene discussed herein, as *E. tamiamiensis* is found within the shell beds of the Pinecrest beds. The remainder of the echinoid faunas documented within the unit reside in older strata, below the unconformity that divides the Pinecrest beds from the sand facies (*sensu* Missimer, 1992), in strata that is firmly in the late Pliocene, Piacenzian stage (Missimer and Wise, 2012).

The upper Pliocene lower Tamiami Formation contains the best-documented Pliocene echinoid faunas (Kier, 1963; Oyen 2001; Ciampaglio and Osborn, 2011). This unit also contains the greatest diversity of all Neogene faunas in the state, with 15 documented species: *Eucidaris tribuloides*, *Lytechinus variegatus*, *Arbacia improcera*, *Clypeaster romani*, *C. sunnilandensis*, *Encope tamiamiensis*, *E. michelini*, *Mellita aclinensis*, *M. caroliniana*, *Rhyncholampas evergladensis*, *Agassizia porifera*, *Echinocardium orthonotum*, *Brissus glenni, Plagiobrissus sarae*, and the herein described *Lovenia kerneri* n. sp. (Fig. 3).

Although Kier (1963) documented *Encope aberrans* Martens, 1867 from the Tamiami Formation, as noted previously in this paper, all identifiable specimens of *E. aberrans* he worked with were from the Caloosahatchee Formation. Additional specimens from the Tamiami Formation are unknown. However, we recognize *E. michelini* from the unit due to its occurrence at the top of the formation in the Quality Materials Quarry, Charlotte County (FM locality CH080).

Missimer (1992) divided the Tamiami Formation into numerous members, two of which contain notable concentrations of echinoids, the Ochopee Limestone member and the sand facies. Though the pale, sandy limestone of the Ochopee Limestone member, well exposed in Collier County, contains an abundance of echinoids, the concentrations are virtually monospecific, often consisting of dense accumulations of *E. tamiamiensis*, with *R. evergladensis* being present, though much less common. Other species are very rare in the Ochopee Limestone, though Kier (1963) documented *Clypeaster romani* and *C. sunnilandensis* in this horizon near Sunniland, Collier County.

The greatest diversity of echinoids within the Tamiami Formation occur in the vicinity of Punta Gorda within the sand facies of Missimer (1992), which consists of a series of poorly bedded and slightly consolidated light to dark gray marls, sands and limestones with no argonitic shell preservation, and an abundance of large barnacles and echinoids (DuBar, 1962; Missimer, 1992). The best exposures of these strata available in the past two decades have been in a series of quarries in Charlotte County, notably a series of small pits along Burnt Store Road south of Punta Gorda, and the Quality Materials Quarry near Placida (FM localities CH046–CH048, CH079, CH080). Twelve echinoid species from the Tamiami Formation have been collected in the Quality Materials Quarry, with notable concentrations of a diversity of echinoids in a weakly indurated series of pale to dark gray sandy calcarenites with intermittent concentrations of large barnacles. This spectacular assemblage often contains echinoids that retain their spines. In fact, representatives of nearly the entire echinoid fauna of the Tamiami Formation have been collected with their spines intact within the Quality Materials Quarry. The following species are recognized from this source: *Eucidaris tribuloides*, *Lytechinus variegatus*, *Arbacia improcera*, *Clypeaster sunnilandensis*, *Encope tamiamiensis*, *E. michelini*, *Mellita aclinensis, Rhyncholampas evergladensis*, *Agassizia porifera*, *Echinocardium orthonotum*, *Brissus glenni,* and *Plagiobrissus sarae*.

Preserved Echinoid Spination in the Tamiami Formation

The high frequency of spine retention, coupled with the diverse fauna within the Quality Materials Quarry, Charlotte County (FM locality CH080), combine to create an unparalleled opportunity to study spination of the entire fauna. While other instances of retained spination (i.e., spine cover) on echinoids in the North American fossil record have been documented, preservation of spination is either rare, or the number of species preserved with articulated spines is low in a given deposit.

We do not endeavor to detail all additional occurrences of echinoids with articulated spines in the North American fossil record. However, a few notable occurrences include a population of *Echinocardium marylandiense* Kier, 1972 in the middle Miocene sandy clay of the basal Choptank Formation, Scientist's Cliffs, Maryland, where the majority of the specimens retain at least some their spines. However, specimens of *Abertella aberti* that co-occur with the *Echinocardium* rarely retain their spines. Another instance occurs in the Pliocene San Joaquin Formation of the Kettleman Hills, California in which a thin, silty, sandstone layer contains a dense, monospecific concentration of the small sand dollar, *Merriamaster perrini* (Weaver, 1908) with their short spines.

Additional, notable fossil assemblages of echinoids retaining their spines in the North American fossil record occur in the Pennsylvanian age Winchell Formation of Texas where a spectacular accumulation of *Archaeocidaris brownwoodensis* Schneider et al., 2005 occurs in a horizon with only very rare occurrences of two additional species of regular echinoid (Schneider et al., 2005). Furthermore, Zullo et al. (1964) documented a concentration of spine-bearing specimens of *Salenia schencki* (Zullo et al., 1964) in the Oligocene Keasey Formation, near Mist, Oregon. Other clypeasteroids are also known for almost complete spine cover, notably members of the genus *Scutellaster* (Durham, 1953a). In Florida, a concentration of dozens of specimens of *Lytechinus variegatus* Leske, 1778 with nearly complete spination (e.g., UF 118114) was exposed in a late Pleistocene sandstone near Cape Coral in Lee County. Spine retention is otherwise rare and exceptional in the North American echinoid faunas, though careful attention paid to specimens, particularly of clypeasteroids with miniaturized spines that appear to invite vigorous but damaging cleaning, will turn up more.

In light of this, the Tamiami Formation echinoid fauna of the Quality Materials Quarry (FM locality CH080) is the most species-rich fauna of echinoids displaying spine retention in North America. Ten species, representing six echinoid orders, have so far been collected with retention of at least some spines. Though describing the morphology of the spination of these species is outside of the scope of this project, it remains a fruitful area for further study, as spine morphology can furnish important phylogenetic characters for some groups. Here, we provide a brief overview of the fauna with spines preserved, and include figures of many of these species.

Of the 12 species of echinoids documented from the Quality Materials Quarry (FM locality CH080), the regular echinoids *Lytechinus variegatus*, *Arbacia improcera,* and *Eucidaris tribuloides* are most commonly found retaining their spines. The next most abundant group of echinoids displaying spine retention is the spatangoids (heart urchins), with all four species found with spines attached, most notably *Echinocardium orthonotum*, and more rarely *Brissus glenni*, *Agassizia porifera*, and *Plagiobrissus sarae*. *Clypeaster sunnilandensis*, *Encope tamiamiensis,* and *Rhyncholampas evergladensis* are much more rarely found with spine retention, though careful examination of dozens of specimens of each of these species provides evidence of rare retention of fine spines most frequently preserved on the oral surface.

Arguably, the most notable occurrence of spine preservation within the Quality Materials Quarry was discovered in 2011 when Robert Carlson (of St. Petersburg, Florida) collected numerous slabs of limestone containing an assemblage of dozens of specimens of *E. tribuloides* in a dense bed of both articulated and disarticulated spines. This assemblage is concentrated in a bed four inches thick, spanning a surface area of roughly 2 m^2, with rare, largely fragmentary remains of *B. glenni*, *R. evergladensis,* and *L. variegatus* occurring along with *Eucidaris*.

The regular echinoids present in the deposit typically inhabit substrates that inhibit burrowing (rock, dense sea grass, coral rubble, etc.) (Kier, 1963; Kier and Grant, 1965), and the irregular taxa of spatangoid and clypeasteroid echinoids often inhabit unconsolidated sand/mud substrates suitable for burrowing. The fact that they occur together in this deposit implies that some of the animals with spination were transported prior to deposition. Though given the often near-complete spine cover displayed by many specimens, this transportation could not have been significant, and burial must have been rapid.

Spine preservation requires special conditions. Though it is usually assumed that burial of the spine-bearing echinoids must have been rapid, the fact that the echinoids are not found in life position, with many haphazardly arranged in the deposit, implies that a significant amount of turbulence was involved in the event that led to their burial. The event causing this burial is unknown, though it is likely the result of a storm, or storm-generated currents carrying large amounts of sediment.

Greenstein (1991) conducted experiments to determine the rates of disarticulation after death in four species of regular echinoids. He reported that specimens of *E. tribuloides* retained a largely intact spine canopy up to three days after death. After five days, significant spine loss had occurred, and spine loss continued through seven days of decay. Using *Eucidaris* as an indicator, Greenstein's results imply that burial may have occurred within three days of death, though it is most likely that death and burial occurred within a very short interval of disturbance and transportation. Nebelsick and Kampfer (1994) conducted a similar study on two clypeasteroid species and demonstrated that spine loss began one day after death and lasted up to four days.

Dense concentrations of *Encope tamiamiensis* occur in numerous horizons within the Tamiami Formation, both in the sand facies and the Ochopee Limestone. In all cases, they occur in the sandier facies. In the Quality Materials Quarry (FM locality CH080), *E. tamiamiensis* are typically size sorted with concentrations of similarly sized specimens preserved in dense accumulations. This is not surprising, as Ebert and Dexter (1975) documented populations of *Encope grandis* Agassiz, 1841, likely the closest modern analog of *E. tamiamiensis*, that consisted primarily of specimens of the same test size (and therefore year groups). They also indicated that size classes were not uniformly distributed by depth. Though they stated that large specimens were more abundant in the lower intertidal zone, concentrations of small individuals were distributed throughout their study area. Therefore, using *Encope* size to ascertain depth of a concentration in the fossil record is problematic.

Some concentrations of *E. tamiamiensis* in the Quality Materials Quarry are largely composed of specimens that were dead and lying on the sea floor prior to accumulation and burial, as evidenced by extensive epibionts (bryozoan encrustations and attachment of barnacles) on many tests. However, rare accumulations occur that indicate rapid entombment, as some of the specimens retain their fine spines, especially on the oral surface. Research by the authors found no other published case of members of the genus *Encope* preserved with their spines intact in the fossil record.

Radwański and Wysocka (2001) described the occurrence of an assemblage of *Echinocardium leopolitanum* Radwański and Wysocka, 2001, in the Ukrainian Miocene, with their spination preserved nearly intact. This preservation appears to be almost identical to that found in *E. orthonotum* in the Quality Materials Quarry. However, the Ukrainian fauna was monospecific with no other echinoid species found with the *Echinocardium*.

Intracoastal Formation

The Intracoastal Formation was first described by Huddleston (1976) and takes its name from the Intracoastal Waterway #1 core, located in Walton County, Florida (Schmidt, 1984). The unit is restricted to the Apalachicola Embayment of the south-central Florida panhandle, and is late Pliocene (Scott, 2001). The formation is extremely fossiliferous and contains a highly diverse micro- and mega-invertebrate fauna within a very sandy, poorly consolidated argillaceous limestone that generally is referred to as a poorly consolidated wackestone or biomicrite (Schmidt, 1984). The Intracoastal Formation thickens and dips to the south-southwest, approaching around 30.5 m in thickness in the southeastern corner of Liberty County (Rupert, 1991). The diverse group of marine organisms, as well as the significant amount of quartz sand, heavy minerals, clays, glauconite, and phosphate leads to the conclusion that the Intracoastal Formation was deposited on a shallow shelf, supplied by fluvial sources (Schmidt, 1984).

The echinoid fauna of the Intracoastal Formation in the south-central Florida panhandle has received little study primarily due to lack of surface exposures of the unit. However, over the past decade, operations in the Langston Quarry (FM locality LI005), Liberty County, Florida, have offered an unprecedented opportunity to examine and collect this unit (Portell et al., 2003; Osborn and Ciampaglio, 2010b).

Oyen (2001) listed *Clypeaster* sp., *Encope aberrans* Martens, 1867, and *Echinocardium orthonotum* in the echinoid fauna of the Intracoastal Formation. This was later formalized by Oyen and Portell (2001), which constituted the first published reference to the echinoid fauna of the Intracoastal Formation.

Ciampaglio and Osborn (2011) described *Schizaster kieri* Osborn, 2011 from the unit, and detailed the diverse echinoid assemblage of the Langston Quarry (FM locality LI005). Here, a highly fossiliferous, 3-m-thick, tan-gray, poorly consolidated, sandy biocalcarenite facies contains a diverse echinoid assemblage of ten species, including: *Arbacia improcera*, *Eucidaris tribuloides*, *Clypeaster sunnilandensis*, *Encope macrophora*, *E. aberrans*, *Echinocardium orthonotum*, *Schizaster kieri, Plagiobrissus sarae*, as well as the herein described *Genocidaris oyeni* n. sp. and *Fernandezaster whisleri* n. sp. This represents the first occurrence of the genus *Fernandezaster* outside of Cuba and Costa Rica. (Sánchez-Roig, 1949; Fischer, 1985).

The echinoid fauna of the Intracoastal Formation is closely allied to the upper Pliocene Tamiami Formation of the southern Florida peninsula. Both units contain the species *E. tribuloides*, *A. improcera*, *C. sunnilandensis*, *E. orthonotum,* and *P. sarae* (Fig. 3).

Jackson Bluff Formation

The Jackson Bluff Formation is a late Pliocene unit named by Vernon and Puri (1964) for a fossiliferous deposit at the top of Jackson Bluff, a short distance southwest of Lake Talquin Dam, on the Ochlockonee River, in Leon County. The formation occurs at or near the surface in a limited area of the panhandle in Leon, Liberty, and Wakulla Counties (Scott, 2001), and is typically represented as a sandy, clay rich shell bed with abundant mollusks, corals, foraminifera, and rare echinoids. The unit is perhaps best exposed at Alum Bluff, Liberty County (Schmidt, 1985) and Jackson Bluff, where echinoids have been documented, though the fossils are rare, containing just three taxa: *Arbacia improcera*, *Echinocardium orthonotum*, and fragments of *Clypeaster* sp. that cannot be identified to species (Oyen, 2001) (Fig. 3).

THE PLEISTOCENE

Oyen and Portell (2001) noted that the contrast between the Pliocene and Pleistocene echinoid faunas of Florida is interestingly characterized by a significant reduction in taxa from the former to the latter. They postulated that this reduction is the result of numerous contributing factors, including the shorter duration of the Pleistocene, collector bias, and preservation potential. These factors likely contribute to a decrease in documented taxa from the Pleistocene, but the decrease from the Pliocene to the Pleistocene documented in this study, from 20 Pliocene to 16 Pleistocene species, is much less dramatic than the decrease to just six species that were known at the time of their study.

Kolbe et al. (2011) considered that mollusk species with greater variation—those found to be "highly variable"—might be better suited to survive the early Pleistocene extinction event. They determined that morphological variation likely played a significant role in governing a species' likelihood of becoming extinct by providing the species a broader range of adaptations that reduced their sensitivity to rapid environmental and ecological changes. Only four species of echinoids survived this event and continued into the Pleistocene in Florida: *L. variegatus*, *E. michelini*, *R. sabistonensis*, and *A. porifera*. None of these four species seems to have a higher degree of variability than other elements of the Pliocene echinoid fauna, so it is likely that other factors contributed in determining which echinoids would survive the event.

Pleistocene sediments occur over much of Florida. In the panhandle, and northern part of the state, these sediments are often non-fossiliferous sands. In contrast, in southern peninsular Florida, Pleistocene age sediments are often exceptionally fossiliferous and famous for their spectacular molluscan assemblages.

The Pleistocene sediments of Florida have been a topic of much debate among regional geologists, as many of the units are discernible solely based on their molluscan faunas (Scott, 1992b). This creates significant lithostratigraphic issues in defining the units. Perkins (1977) described the Pleistocene sequence of southern Florida as characterized by similar lithologies separated by discontinuities. Perkins further stated that without these discontinuities, these sequences would appear to belong to a single formation. Scott (1992b) and Scott and Wingard (1995) discussed the problems associated with the biostratigraphy and lithostratigraphy of the Plio-Pleistocene of southern Florida and asserted them to be biostratigraphic units, and not "formations". Scott (1992b) suggested grouping the Caloosahatchee, Bermont, and Fort Thompson Formations into a single informal lithostratigraphic unit: the Okeechobee Formation. The Okeechobee Formation therefore would consist of variably shelly, siliclastic and carbonate sediments that may reach 30.5 m feet thick in southern Florida. Though this unit was originally defined as straddling the Pliocene-Pleistocene boundary, the Okeechobee Formation would now be considered as completely confined to the Pleistocene. However, current geologic maps of southern Florida most frequently do not use the terms Caloosahatchee, Fort Thompson, Bermont, or Okeechobee Formations. This series of sediments is now most often mapped as undifferentiated Tertiary shell units. Given the common usage and vast body of literature detailing the Caloosahatchee, Bermont, and Fort Thompson Formations, herein, we will continue to use these formational names.

Perhaps because Florida Pleistocene units are extensively collected, primarily for their vertebrate and molluscan faunas, or perhaps because the sediments are younger and therefore less likely to contain extinct taxa, we have just one new echinoid species to describe and add to the fauna, *Rhyncholampas meansi* n. sp. from the Caloosahatchee, Bermont and Anastasia Formations. However, new stratigraphic occurrences are numerous, and include the first documentation of *Rhyncholampas sabistonensis* Kellum, 1931 in the Pleistocene of Florida (Fig. 4).

As noted in the Pliocene discussion above, due to recent revisions to the Neogene timescale and other factors (Ogg et al., 2008), the Caloosahatchee Formation and most of the correlative Nashua Formation now fall within the Pleistocene (Missimer and Wise, 2012). The lower portions of these formations were previously considered to extend into the Pliocene and their echinoid faunas often designated as Pliocene in age (Oyen and Portell, 2001). Therefore, echinoid faunas previously

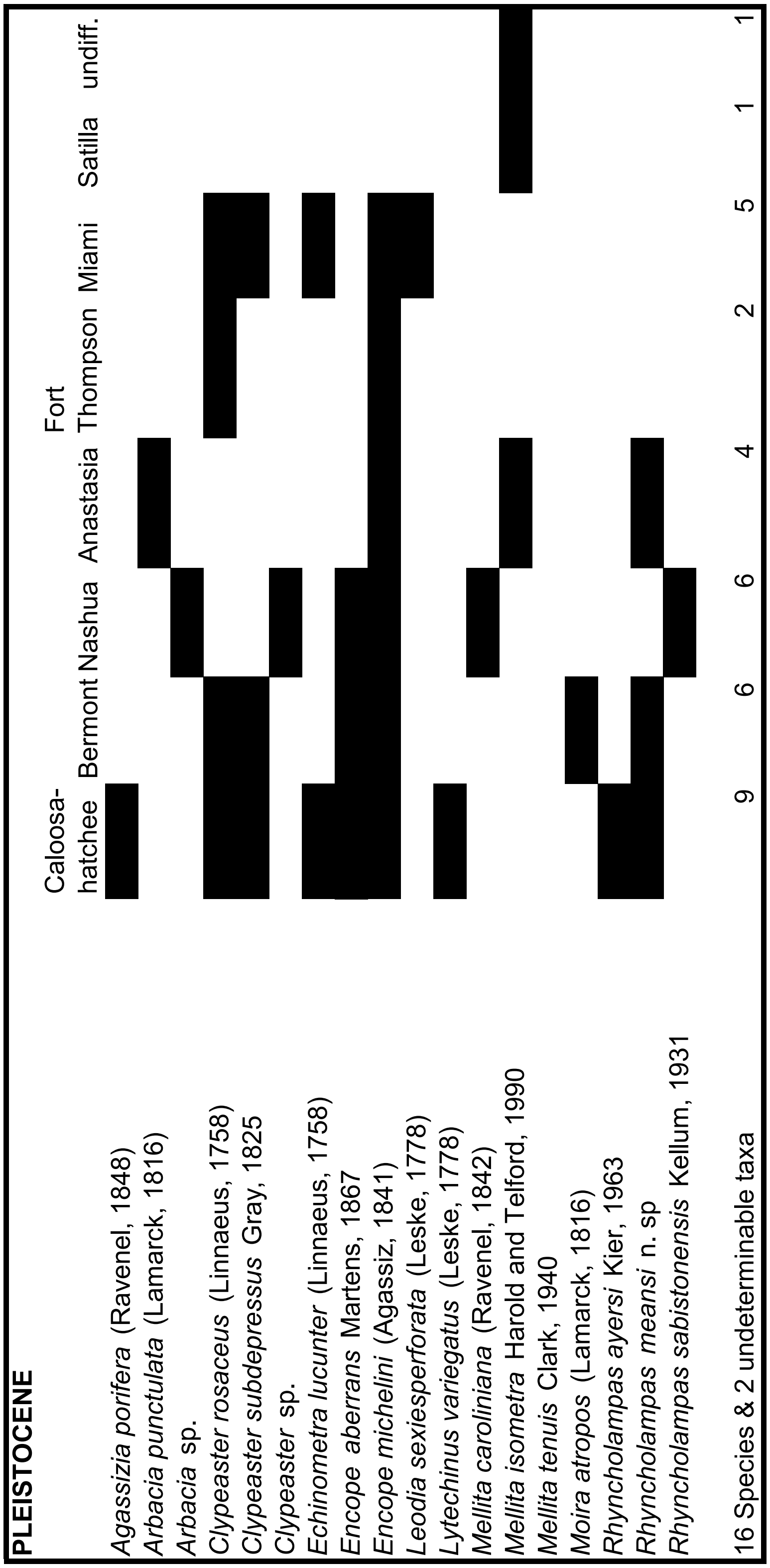


Figure 4. Distribution of Pleistocene echinoids documented from Florida.

documented from the basal beds of these units are considered herein to be Pleistocene, increasing known Florida Pleistocene echinoids from six species (Oyen and Portell, 2001) to 16 species (Fig. 4).

During interglacial intervals in the Pleistocene, low-lying portions of the state, especially in the southern peninsula, were covered by shallow marine waters during a series of marine transgressions. It is within sediments of these shallow seas that the Florida Pleistocene echinoids were entombed.

The Florida Pleistocene echinoid fauna was poorly understood until Kier (1963) documented seven species from the Caloosahatchee Formation. Prior to that work, documentation of the fauna was meager: Clark and Twitchell (1915) described and documented *Clypeaster dalli* Twitchell in Clark and Twitchell, 1915 from the Caloosahatchee Formation, though Cooke (1942) considered this species to by synonymous with *C. rosaceus* Linnaeus, 1758. Kier (1963) resurrected the usage as a subspecies within the Florida Pleistocene: *Clypeaster rosaceus dalli* Twitchell in Clark and Twitchell, 1915; however, we herein do not recognize this subspecific designation.

DuBar (1958:61) documented the abundant occurrence of echinoids within his Bee Branch Member of the Caloosahatchee Formation, stating numerous regular forms and cassiduloids were present in the fauna. However, the only species he mentioned by name is *Clypeaster rosaceus*. Kier (1963) provided a more complete picture of the echinoid fauna of the Florida Pleistocene, documenting the following species, largely from the Caloosahatchee Formation: *Lytechinus variegatus plurituberculatus* Kier, 1963; *Echinometra lucunter* Linnaeus, 1758; *Encope aberrans imperforata* Kier, 1963; *Clypeaster subdepressus* Gray, 1825; *C. rosaceus dalli*, *Rhyncholampas ayersi* Kier, 1963, and *Agassizia porifera*.

Oyen (2001) provided additional new stratigraphic records for Florida Pleistocene strata, adding *Mellita caroliniana* (Nashua Formation), *Encope aberrans*, *E. michelini,* and *Moira atropos* Lamarck, 1816 (all from the Bermont Formation), as well as *Mellita isometra* Harold and Telford, 1990 from the Anastasia and Satilla Formations. *Arbacia punctulata* Lamarck, 1816 was subsequently added to the fauna from a middle to late Pleistocene deposit in St. Lucie County (Herrera et al., 2006). We herein add *Rhyncholampas meansi* n. sp. (Caloosahatchee, Bermont and Anastasia Formations) to the fauna of the Florida Pleistocene, the youngest documented fossil species of *Rhyncholampas* in the eastern United States. We also document the occurrence of *Rhyncholampas sabistonensis* Kellum, 1931 in the Pleistocene portion of the Nashua Formation of St. Johns County, and provide the first definitive record and figures of *Leodia sexiesperforata* from the Pleistocene of the state.

The occurrence of the genus *Rhyncholampas* in the late Pleistocene of Florida is intriguing; though *Rhyncholampas* has a nearly continuous presence in the fossil record of the region since the genus made its first appearance in North America in the late middle Eocene [*Rhyncholampas carolinensis* (Twitchell in Clark and Twitchell, 1915)] in the Castle Hayne Limestone of North Carolina), the genus is not present in the modern fauna of the region. The stratigraphic succession of *Rhyncholampas* in Florida, not to imply any evolutionary succession, is: *Rhyncholampas georgiensis* (Twitchell in Clark and Twitchell, 1915); *Rhyncholampas ericsoni* (Fischer, 1951), and *Rhyncholampas conradi* (Conrad, 1850) from the late Eocene; *Rhyncholampas gouldii* (Bouvé, 1846) from the Oligocene; *R. chipolanus* from the Miocene; *R. evergladensis* from the late Pliocene; *R. ayersi* and *R. sabistonensis* from the early Pleistocene, and now *R. meansi* n. sp. from the latest early to late Pleistocene. Today, the genus is represented by one surviving species, *Rhyncholampas pacificus* A. Agassiz, 1863, which is restricted to the tropical eastern Pacific. Of the extant forms, only *Cassidulus caribaearum* Lamarck, 1801 remains in the shallow-water fauna of the region to represent the cassiduloid echinoids (sensu Kier, 1962, 1975; Serafy, 1979). *Rhyncholampas meansi* n. sp. is therefore the youngest fossil *Rhyncholampas* described from North America, and likely the global fauna, outside of the extant *R. pacificus*.

This more complete picture of Florida Pleistocene echinoids, totaling 16 species (Fig. 4), reveals a decidedly modern assemblage, nine of the species continue to live off the coast of Florida today. The echinoids are distributed in seven formations, with their remains being common in the Caloosahatchee, Nashua, and Bermont Formations, and more rarely represented in the Anastasia, Satilla, and Fort Thompson Formations and the Miami Limestone.

Caloosahatchee Formation

The Caloosahatchee Formation is well exposed in southern and central Florida, and is perhaps the best-known Pleistocene unit in the state, recognized world-wide for its abundant, diverse, and well-preserved molluscan fauna. The unit consists of fossiliferous quartz sand with variable amounts of carbonate matrix interbedded with variably sandy, shelly limestones (Scott, 1992b) that were deposited in subtropical conditions; tropical and subtropical mollusks are abundant (Allmon et al., 1996). Carbonate deposition predominated, with coastal influxes of quartz sand, and a diversity of depositional environments included within the unit, including carbonate-shelf, open-bay, and lagoonal (Missimer, 2001).

The Caloosahatchee Formation disconformably overlies the Tamiami Formation. DuBar (1958) recognized three members in the type area of the formation along the Caloosahatchee River in Hendry County, in ascending order: Ft. Denaud, Bee Branch, and Ayers Landing members. Within the Sarasota area, differentiating the Caloosahatchee Formation from the underlying Pinecrest beds of the Tamiami Formation is difficult, as both units consist of similar lithologies of dense shell beds. Differentiating the units can only be done based on their faunal elements. However, in the type area of the unit, the base of the Caloosahatchee Formation consists of a lower shell bed, where shell material is beautifully preserved, overlying the variably indurated limestones and sands of the Tamiami Formation, within which non-calcareous mollusks are usually preserved as molds and casts, making distinction of the two units comparatively simple (DuBar, 1958). The echinoid-rich facies of the Caloosahatchee Formation are best exposed near the unit's type area, where lithologies are more readily defined, so mixing of faunas between the Tamiami and Caloosahatchee Formations is less likely.

Documentation of the Caloosahatchee Formation echinoids was initially slow: Clark and Twitchell (1915) described and documented *Clypeaster dalli* (Twitchell in Clark and Twitchell, 1915) from the unit, though Cooke (1942) considered this species to by synonymous with *C. rosaceus*. Kier (1963) resurrected the usage as a subspecies within the Florida Pleistocene: *Clypeaster rosaceus dalli* (Twitchell in Clark and Twitchell, 1915). However, as discussed in the remarks for *C. rosaceus* herein, we do not recognize the *dalli* subspecies.

DuBar (1958:61) documented the abundant occurrence of echinoids within the Bee Branch Member of the unit west of LaBelle, stating numerous regular forms and cassiduloids were present in the fauna. However, the only species he mentioned by name is *C. rosaceus*. Cooke (1959), in his substantial monograph of the Cenozoic echinoids of the region added no new taxa to the fauna. Kier (1963) was first to provide a more complete picture of the echinoid diversity of the unit, documenting the following species: *Lytechinus variegatus plurituberculatus*, *Echinometra lucunter*, *Encope michelini imperforata* (recognized herein as *E. aberrans*), *Clypeaster subdepressus*, *C. rosaceus dalli*, *Rhyncholampas ayersi,* and *Agassizia porifera*. *Encope michelini* is herein added to the fauna of the unit, based on specimens figured in Kier (1963: 34, fig. 25) collected from the Bee Branch Member, west of LaBelle, Hendry County.

We also describe *Rhyncholampas meansi* n. sp. from the uppermost beds of the Caloosahatchee Formation east of LaBelle, where it occurs with *Encope michelini* and *Clypeaster subdepressus* just below the overlying Fort Thompson Formation. Therefore, the Caloosahatchee Formation is now known to contain the following nine species: *Lytechinus variegatus*, *Echinometra lucunter*, *Encope aberrans*, *E. michelini*, *Clypeaster subdepressus*, *C. rosaceus*, *Rhyncholampas ayersi, R. meansi* n. sp., and *Agassizia porifera* (Fig. 4).

Nashua Formation

The Nashua Formation, exposed in the northern and central portion of eastern Florida, is a heterogeneous unit containing calcareous quartz sands and sandy shell coquina (Huddlestun, 1988). A biostratigraphic equivalent of the Caloosahatchee Formation, the Nashua Formation contains less limestone and more quartz sand and dark clays than its southern counterpart and represents deposition in a shallow-water nearshore to open-marine neritic continental shelf (Huddleston, 1988). The extent of the Nashua Formation in northern Florida is not well understood (see Kittle et al., 2013). It extends some distance into Georgia and appears to grade laterally into the Cypresshead Formation (Huddleston, 1988).

The echinoids of the Nashua Formation are poorly known, with the first reported occurrence by Oyen (2001). At Cracker Swamp Ranch (FM locality PU004), Putnam County, Oyen (2001) documented: *Arbacia* sp., *Clypeaster* sp., *Encope* cf. *aberrans*, *Leodia sexiesperforata* Leske, 1778*, Mellita* cf. *caroliniana* Ravenel, 1842, and *Echinocardium* cf. *orthonotum*. Much of this material was fragmentary, thus Oyen's tentative specific assignments.

Examination of this material confirms Oyen's (2001) identifications. Oyen's attribution of *E*. cf. *orthonotum* is verified after examining UF 84281, which consist of fragmentary material that is *Echinocardium*, and lacking other alternatives, most likely *E. orthonotum*. Spines and test fragments of an arbaciid (UF 84283) are most likely *Arbacia*, perhaps *A. improcera*. However, the material is insufficient to assign to species, and if the material originated in the Pleistocene portion of the Nashua Formation, *A. punctulata* remains a possibility.

Re-examination of the specimen attributed by Oyen (2001) to *Leodia sexiesperforata* (UF 31969) has undermined his identification. Oyen assigned the specimen to *Leodia* based on the ambulacral lunule arrangement and overall size. However, this specimen is indistinguishable from very large specimens of *Mellita caroliniana* Ravenel, 1842 from the upper Pliocene, upper Goose Creek Limestone in the type area of South Carolina. The authors do not recognize *L. sexiesperforata* within the Nashua Formation.

In the East Coast Aggregates Quarry, St. Johns County (FM locality SJ007), echinoids are abundant within the Nashua Formation, both in a cemented sand horizon and an upper shell bed. The indurated horizon contains *M. caroliniana, Encope michelini,* and *Encope* aff. *macrophora*. The shell bed contains a more distinctly lower Pleistocene fauna with molluscan and echinoid affinities with both the Waccamaw Formation of the Carolinas and the Caloosahatchee Formation of southern Florida. This should come as no surprise, as this is one of the most northerly echinoid-bearing deposit of this age currently documented in Florida. The echinoids include *Rhyncholampas sabistonensis* Kellum, 1931, *Clypeaster* sp. (likely *C. subdepressus*), and *Mellita* sp. This is the first documented occurrence of *R. sabistonensis* in Florida, and coupled with the presence of *M. caroliniana* in the Nashua Formation, gives the echinoid fauna strong affinities with the lower Pleistocene Waccamaw Formation fauna of Carolinas.

A notable occurrence of well-preserved specimens of *Encope* and *Mellita* sp. occurs within shells of *Dinocardium robustum* (Lightfoot, 1786) from the Cracker Swamp Ranch excavations (FM locality PU004). These small specimens would have been fragmented in the shell hash, but were protected within the large, paired bivalves (e.g., UF 104524; Fig. 71).

The echinoid fauna of the Nashua Formation consists of seven taxa: *Arbacia* sp. (likely *A. improcera*), *Clypeaster* sp. (as incomplete tests likely referable to *C. subdepressus*), *E. aberrans*, *M. caroliniana, R. sabistonensis*, and *Echinocardium* cf. *orthonotum* (Fig. 4). However, specimens of *Encope* aff. *macrophora* (a species documented from the middle to late Pliocene of north Florida and the Carolinas) collected in the cemented sand horizon in the basal Nashua Formation of the East Coast Aggregates Quarry, St. Johns County (FM locality SJ007), mentioned above, occur with a molluscan and vertebrate assemblage indicative of the late Pliocene rather than the early Pleistocene. The occurrence of Pliocene elements in the fauna here was noted in Green et al. (2014) who documented that three cores drilled just across the county line from the East Coast Aggregates Quarry, in the Big Horse Aggregates Quarry, Putnam County, revealed that the lithology of these beds was highly variable over short distances. As such, they opted to not distinguish this sequence of likely late Pliocene–Pleistocene shelly sediments as the Nashua Formation and referred to it as undifferentiated Pliocene/Pleistocene shelly sediments.

This creates a need for reevaluation of the age of the lowermost Nashua Formation in western St. Johns and eastern Putnam Counties. We have retained the designation of *Mellita caroliniana* within the unit in the Pleistocene record herein (although it also occurs in the lower horizon of cemented sand). However, we have left *Encope macrophora* out of the Pleistocene record (Fig. 4) as its age is questionable and we are not keen to extend its range upward into the Pleistocene without a more definitive age assignment of the horizon. We simply document its occurrence here and in the discussion for the species herein, however we have opted to leave it off the Pleistocene stratigraphic distribution table (Fig. 4) pending further study of the base of the Nashua Formation. Likewise, without being able to pinpoint the bed from which Oyen's (2001) *Arbacia* sp. and *Echinocardium* cf. *orthonotum* came, we are unable to ascertain if the material originated in the Pliocene or Pleistocene portion of the Nashua Formation. Therefore, these species are not referred to either the Pliocene or Pleistocene in Figures 3 and 4.

Bermont Formation

The Bermont Formation is a middle Pleistocene unit which, as informally defined by DuBar (1974), was separated from the Caloosahatchee Formation even though the two units cannot be distinguished readily by their lithologic characteristics. Rather, the separation of the two units is based on comparative faunal analysis. The majority of the members of the molluscan fauna of this unit can still be found living today along Florida's coast. The type area of the unit is along Shell Creek, Charlotte County, beds that DuBar (1962) initially considered to be the uppermost bed of the Caloosahatchee Formation. The formation is distributed throughout southern peninsular Florida.

DuBar (1962) noted the mixture of ecological types in the molluscan fauna of the Bermont Formation in its type area, and postulated that the fauna lived nearshore on the inner continental shelf where enough current activity was available to cause some mixture of inlet, bay, and shelf species, at a maximum depth of 10–15 fathoms (18–27 m). He further postulated that the lack of tropical Caloosahatchee Formation species implied that the water was cooler than that of any of the underlying Caloosahatchee units, and likely closer to the water temperature of southern Florida today, with a minimum water temperature of 65°F, as *Chione cancellata* Linnaeus, 1767 [now identified as *Chione elevata* (Say, 1822)], an abundant bivalve species within the unit, has been suggested not to survive below that temperature (DuBar, 1962).

Petuch and Roberts (2007) informally divided the formation into three members: Belle Glade, Okeelanta, and Holey Land, and provided their interpretation of the lithology and fauna which implied a fauna of far greater diversity than that interpreted by DuBar (1962).

Kier (1963) was first to document echinoids from strata which would later be referred to the Bermont Formation, documenting *C. rosaceus dalli* and *E. aberrans* (=*E. michelini imperforata* of Kier [1963]) from strata he referred to post-Caloosahatchee and pre-Fort Thompson formations in a pit on the south side of Florida route 80 southwest of Belle Glade, Palm Beach County. Oyen (2001) added: *Clypeaster* sp. (UF 54188) which we attribute to *C. subdepressus*, *Encope michelini,* and *Moira atropos* to the fauna. Petuch and Roberts (2007) documented *C. rosaceus* and *Rhyncholampas* cf. *evergladensis* from Petuch's Holey Land Member of the Bermont Formation in Palm Beach County. As discussed in the Pleistocene overview section, we describe this *Rhyncholampas* as *R. meansi* n. sp.

The Bermont Formation therefore contains six species of echinoid: *C. rosaceus*, *C. subdepressus*, *E. michelini*, *E. aberrans*, *M. atropos,* and *R. meansi* n. sp. Not surprisingly, similar to the molluscan fauna of the unit, this echinoid fauna is decidedly modern, only the described *Rhyncholampas meansi* n. sp. is not represented in the Recent fauna of the region.

ANASTASIA FORMATION

The Anastasia Formation underlies the Atlantic Coastal Ridge from St. Johns County southward to Palm Beach County. The unit generally is recognized near the coast, but extends inland as much as 20 miles in St. Lucie and Martin Counties (Scott, 2001). The Anastasia Formation was named by Sellards (1912) and consists of interbedded sands and coquinoid limestones. The unit is perhaps best recognized in the form it takes near its type locality on Anastasia Island as an orangeish, partially indurated coquina largely composed of whole and fragmented valves of the small clam *Donax variabilis* Say, 1822, with varying levels of integration of other mollusks.

The Anastasia Formation is the youngest mapped stratigraphic unit in Florida. Murphy (1973) provided radiocarbon dates of 8.5–9.0 Ka for samples taken in the type area on Anastasia Island, which implies that at least a portion of the unit extends into the Holocene. No extinct mollusk taxa have been reported from the unit (Johnson, 1993) and it is likely that deposition of the formation continues into the present (Portell et al., 2003).

Echinoids are rarely encountered within the Anastasia Formation. Oyen (2001) was first to recognize echinoids from this unit, reporting *Encope michelini* and *Mellita quinquiesperforata* Leske, 1778. Harold and Telford (1990) attempted to bring some clarity to assumed variability among populations of *M. quinquiesperforata* in the region by recognizing that the genus *Mellita* along the coast of Florida was actually represented by two distinct species: *Mellita tenuis* Clark, 1940, found along the Florida Gulf Coast and *Mellita isometra* along the Atlantic Coast. The specimens derived from the Anastasia Formation are *M. isometra*.

Herrera et al. (2006) documented an abundant echinoid fauna in middle to late Pleistocene deposits in the Dickerson Quarry, St. Lucie County (FM locality SL004). The specimens were collected from Unit 4 in a sandy coquina limestone similar to the Anastasia Formation. The age and lithology lend credibility to attribution of this material to the Anastasia Formation. Herrera et al. (2006) documented *Arbacia punctulata* Lamarck, 1816 (the first documented occurrence of *A. punctulata* in the Florida fossil record), *Encope michelini,* and a new species of *Rhyncholampas* from this horizon. Herein, we describe this new species, which also occurs in the Bermont and upper Caloosahatchee Formation, as *R. meansi* n. sp. The echinoid fauna of the Anastasia Formation therefore consists of four species: *A. punctulata*, *E. michelini*, *M. isometra,* and *R. meansi* n. sp. (Fig. 4).

SATILLA FORMATION

The Satilla Formation was named for sparsely fossiliferous, late Pleistocene coastal terrace deposits along the Satilla River in southeastern Georgia (Veatch and Stephenson, 1911). Huddleston (1988) redefined the Satilla Formation in Georgia, South Carolina, and Florida to include deposits formerly mapped as the Pamilco Formation, as the Satilla Formation designation had precedence. The fossil fauna of the Satilla Formation is sparse and not well documented, but a single species of echinoid has been documented from the unit at Rose's Bluff (FM locality NA002), Nassau County, Florida (Pirkle et al., 2007). Here, *Mellita isometra* is represented by fragmentary tests in a fossil fauna of extant mollusk species. This occurrence of *M. isometra* is notable, because while this sand dollar has a nearly ubiquitous presence along the Recent coasts of Florida, it is not abundantly represented in the late Pleistocene of Florida. It is present only in the Anastasia and Satilla Formations and, when found, never in abundance, which is in stark contrast to the dense populations of *M. isometra* that thrive in clean sands along Florida's modern coast.

FORT THOMPSON FORMATION

The Fort Thompson Formation is a late Pleistocene unit that was first recognized by Sellards (1919) and later raised to formational status by Cooke and Mossom (1929). The unit was initially described as alternating fresh, brackish, and marine marls and limestones along the Caloosahatchee River at Fort Thompson, Hendry County.

Although the unit is perhaps best exposed along the Caloosahatchee River, it extends well beyond the river throughout much of the southern Okeechobee region and Palm Beach and Broward Counties (DuBar, 1958). Substantial exposures were also documented by DuBar (1962) along Shell Creek in Charlotte County. The formation is thin, does not exceed 10 m in thickness, typically overlies the Bermont Formation, and is overlain by surficial sands.

The shell beds of the Fort Thompson Formation are characterized by seemingly countless valves of *Chione elevata*, and echinoids are not common in the unit. Oyen and Portell (2001) documented no echinoids from the formation. However, a search of the FM-IP collections provided two species attributed to this unit: *Clypeaster rosaceus* from Broward County (FM locality BD005) and *Encope michelini* from Miami-Dade County (FM locality DA0012).

Miami Limestone

Sanford (1909) named the late Pleistocene surficial limestone of the southern Atlantic Coastal Ridge the "Miami Oolite". The unit occurs at or near the surface in southeastern peninsular Florida from Palm Beach to Miami-Dade and Monroe Counties (Scott, 2001) and extends westward beneath the Everglades where it is commonly covered by thin organic and freshwater sediments. The unit also extends to the southern Florida Keys, from Big Pine Key to Marquesas Keys. To the north, in Palm Beach County, the Miami Limestone grades laterally northward into the Anastasia Formation.

The Miami Formation consists of two facies: an oolitic facies and a bryozoan facies (Hoffmeister et al., 1967). The oolitic facies consists of white to orange-gray, poorly indurated sandy oolitic limestone with scattered concentrations of fossils. The bryozoan facies underlies and extends west of the western boundary of the oolitic facies, and consists of white to orangeish-gray, poorly to well indurated sandy fossiliferous limestone. Preservation of these mollusks is typically poor, with molds and casts being common (Scott, 2001). The Miami Limestone is the result of deposition of ooids produced on and behind the Key Largo Reef system during Marine Isotope Stage 5 (Petuch and Roberts, 2007).

Echinoids are typically uncommon in the unit. Oyen and Portell (2001) documented no echinoids from the formation. A search of the FM-IP collections provided specimens of *Clypeaster rosaceus* from strata attributed to the unit in Miami-Dade County (e.g., FM locality DA008). A search of the Paleontological Research Institute (June 2017) by RWP also located *Echinometra lucunter*, *C. rosaceus,* and *C. subdepressus* from the formation. Additionally, the National Museum of Natural History at the Smithsonian Institution contains representatives of *Leodia sexiesperforata* and *Encope michelini* from the Miami Limestone in Buena Vista, near Miami. Therefore, the documented echinoid fauna of the Miami Limestone now includes five species (Fig. 4).

SYSTEMATICS

Classification follows Kroh and Smith (2010), with updates from Mongiardino-Koch et al. (2018), Kroh (2020), and the World Echinoidea Database (Kroh and Mooi, 2019). Species within the genera are listed alphabetically. Synonymies are abbreviated, consisting of unique usages of names referring to the taxon in question, as well as major monographs. Descriptions are provided for new species only; readers interested in descriptions of previously named taxa can reference initial descriptions listed in the synonymy for each species. Descriptions and diagnoses utilize the system proposed by Lewis and Donovan (2007); diagnoses contain pertinent characters to define the new taxon to the species level.

Class **ECHINOIDEA** Leske, 1778
Subclass **CIDAROIDEA** Smith, 1984
Order **CIDAROIDA** Claus, 1880
Family **CIDARIDAE** Gray, 1825
Subfamily **CIDARINAE** Mortensen, 1928
Genus ***EUCIDARIS*** Pomel, 1883

EUCIDARIS TRIBULOIDES (Lamarck, 1816)

Figures 5–7

Cidarites tribuloides Lamarck, 1816, p. 56; 2d ed. (1840), v. 3, p. 380.

Cidaris tribuloides (Lamarck). A. Agassiz, 1872, pp. 99, 253, pl. 1d; pl. 2, figs. 1–3; pl. 2c, fig. 13.

Cidaris tribuloides (Lamarck). H. L. Clark, 1907, p. 185.

Eucidaris tribuloides (Lamarck). Mortensen, 1928, p. 400, pl. 41, figs. 9–16; pl. 48, fig. 1; pl. 73, fig. 1; pl. 86, fig. 16. (includes additional synonymy.)
Eucidaris tribuloides (Lamarck). H. L. Clark, 1933, p. 76.
Cidaris tribuloides (Lamarck). Cooke, 1941, p. 5.
Cidaris tribuloides (Lamarck). Cooke, 1959, p. 9, pl. 1, figs.1, 2.
Eucidaris tribuloides (Lamarck). Kier and Grant, 1965, pp. 12, 13, pl. 2, figs. 2, 3, text fig. 7.
Eucidaris tribuloides (Lamarck). Kier, 1966, p. 6.
Eucidaris tribuloides (Lamarck). Maloney, and Macsotay, 1968, p. 276.
Eucidaris tribuloides (Lamarck). McPherson, 1968, pp. 400–443.
Eucidaris tribuloides (Lamarck). Kier, 1975, pp. 16, 17. pls. 11.3–11.5.
Eucidaris tribuloides (Lamarck). Serafy, 1979, pp. 15–19, fig. 3.
Eucidaris tribuloides (Lamarck). Cutress, 1980, pp. 66–70.
Eucidaris tribuloides (Lamarck). Greenstein, 1991, pp. 519–540.
Eucidaris tribuloides (Lamarck). Donovan, 1993, p. 377, figs. 4.1, 4.2, 5.
Eucidaris tribuloides (Lamarck). Donovan et al., 1994, p. 353.
Eucidaris tribuloides (Lamarck). Hendler et al., 1995, pp. 206–208, figs. 110, 134A.
Eucidaris tribuloides (Lamarck). Donovan and Embden, 1996, pp. 486–488.
Eucidaris tribuloides (Lamarck). Portell and Oyen, 1997, pp. 99–104, text fig. 2, pl. 1.
Eucidaris tribuloides (Lamarck). Lessios et al., 1999, pp. 806–817.
Eucidaris tribuloides (Lamarck). Oyen and Portell, 2001, pp. 193–218, pl. II, fig. 3.
Eucidaris tribuloides (Lamarck). Donovan et al., 2001, p. 3.
Eucidaris tribuloides (Lamarck). Pomory, 2003, pp. 28–30, fig. 11.
Eucidaris tribuloides (Lamarck). Donovan and Lewis, 2009, pp. 20–24.
Eucidaris tribuloides (Lamarck). Ciampaglio and Osborn, 2011, fig. 2.
Eucidaris tribuloides (Lamarck). Madeira et al., 2011, pp. 245–248, text figs. 2A–I, 3A–C.

Occurrence.—*Eucidaris tribuloides* occurs very rarely in the upper Pliocene Intracoastal Formation in the Langston Quarry (FM locality LI005), Liberty County (Ciampaglio and Osborn, 2011). The species is more common in the Tamiami Formation in southern Florida, especially in the Quality Materials Quarry (FM locality CH080), Charlotte County (see below remarks). Portell and Oyen (1997) documented it in the Tamiami Formation in a shell pit 1.2 km east of Grove City (FM locality CH026), Charlotte County.

Eucidaris tribuloides also occurs in the lower Pleistocene Waccamaw Formation of the Carolinas, and is widespread in the Neogene deposits of the Caribbean: Cutress (1980), Donovan and Gordon (1993), Donovan (1993), Donovan et al. (1994, 2001), Donovan and Embden (1996), Donovan and Lewis (2009); and in the Azores (Madeira et al., 2011).

Discussion.—*Eucidaris tribuloides* is the common, modern nearshore cidarid of Florida and the Caribbean, occurring from Cape Hatteras, North Carolina, south throughout the Caribbean to Rio de Janeiro Brazil.

The first documentation of *E. tribuloides* in the fossil record of North America was in the upper Pliocene Tamiami Formation of southern Florida (Portell and Oyen, 1997) (specimen UF 72022; Fig. 5). Ciampaglio and Osborn (2011) documented its presence in the upper Pliocene Intracoastal Formation of north Florida and provided additional occurrences in the Tamiami Formation.

A spectacular assemblage of dozens of complete tests of *E. tribuloides*, many adorned with their spines, was unearthed in the Tamiami Formation in the Quality Materials Quarry (FM locality CH080), Charlotte County, Florida. This assemblage occupied roughly 2 m^2 of surface and consisted of a dense accumulation of tests, many with associated spines, surrounded by a decreasingly concentrated bed of spines. The tests were preserved haphazardly, not in life position, and are likely the result of a storm deposit in a depression of the Pliocene sea floor that was rapidly covered with sediment. A specimen of *E. tribuloides* (UF 114517) with associated spines from this locality is figured herein, embedded in matrix with *L. variegatus* and *E. tamiamiensis* (Fig. 6).

Greenstein (1991) documented the rate of disarticulation of modern *E. tribuloides*. In his study, he noted that spines remained intact after one day of burial. After six days, decay was sufficient that spines, lantern, and the apical system had disarticulated from the corona; however, the spines remained adjacent to the specimen. Only coronal material and disarticulated spines remained after 12 days. Greenstein asserted that under normal marine conditions, six to 12 days is sufficient to bleach an intact echinoid carcass of its organic material. Although, he did document that speci-

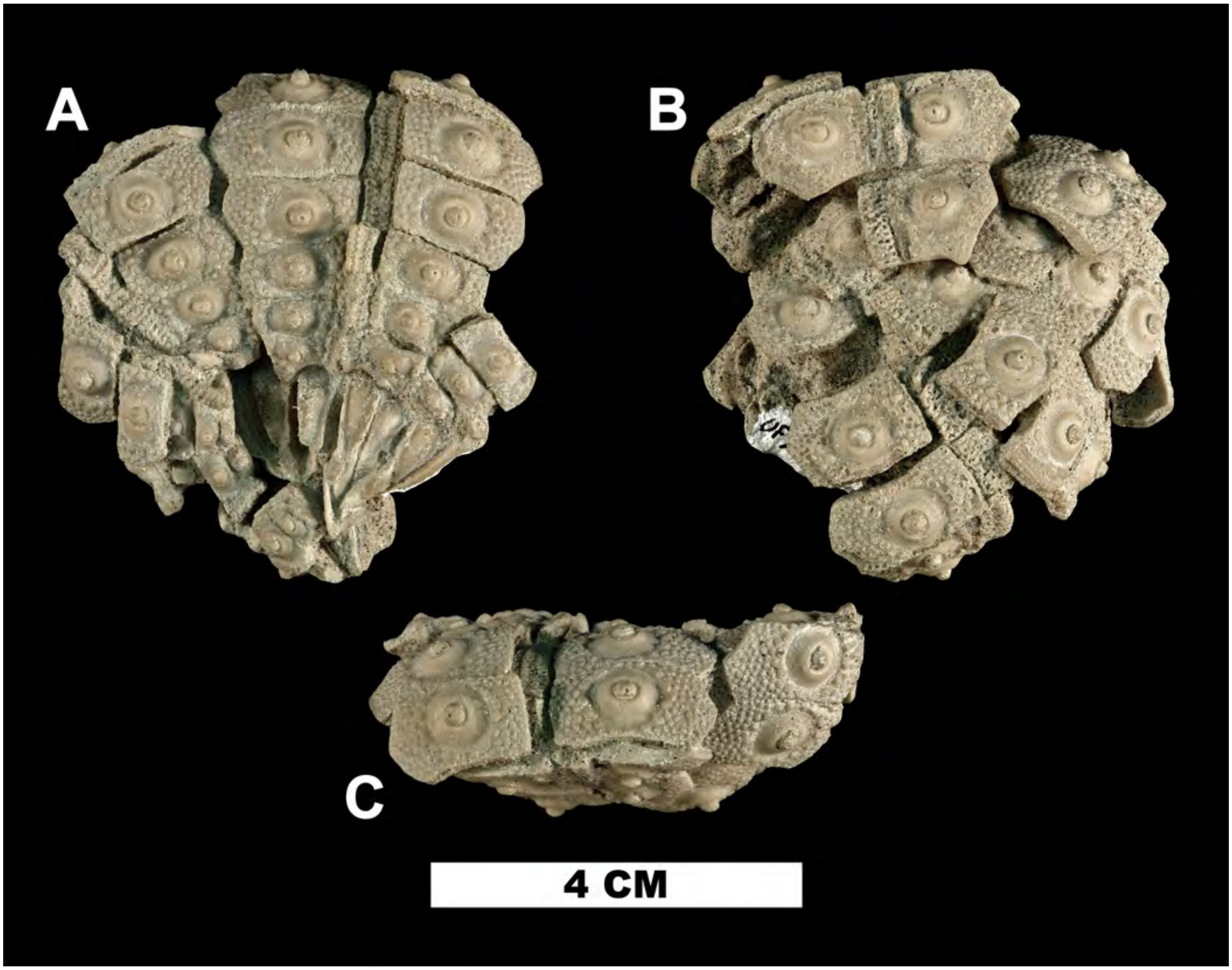


Figure 5. *Eucidaris tribuloides* (UF 72022), Tamiami Formation (FM locality CH026). A. oral surface of compressed test with lantern partially exposed, B. aboral view of compressed test, C. lateral view.

mens of *E. tribuloides* remained articulated longer than specimens of *Diadema antillarum* Philippi, 1845, *Echinometra lucunter* (Linnaeus, 1758), and *Tripneustes ventricosa* Lamarck, 1816, which were also examined as part of the study.

Though the presence of this species in the fossil record of Florida is limited, it is widespread in the Neogene deposits throughout the Caribbean, often represented by isolated spines and test plates. Complete plating can be seen in a modern representative of the species (Fig. 7).

Subfamily **STYLOCIDARINAE** Mortensen, 1903

Genus ***PRIONOCIDARIS*** A. Agassiz, 1863

PRIONOCIDARIS COOKEI Cutress, 1976

Figures 8–11

Prionocidaris cookei Cutress, 1976, pp. 191–198, figs. 1, 2.

Prionocidaris cookei (Cutress). Cutress, 1980, pp. 104–106, pl. 9, figs. 11–12.

Prionocidaris cookei (Cutress). Osborn and Ciampaglio, 2010a, p. 207.

Occurrence.—This species was described from the lower Miocene Chipola Formation along the west bank of the Chipola River, Calhoun County, roughly a mile south of the mouth of Tenmile Creek. Isolated test plates and spines are common in material sifted from this Chipola Formation shell bed. Spines attributable to this species also

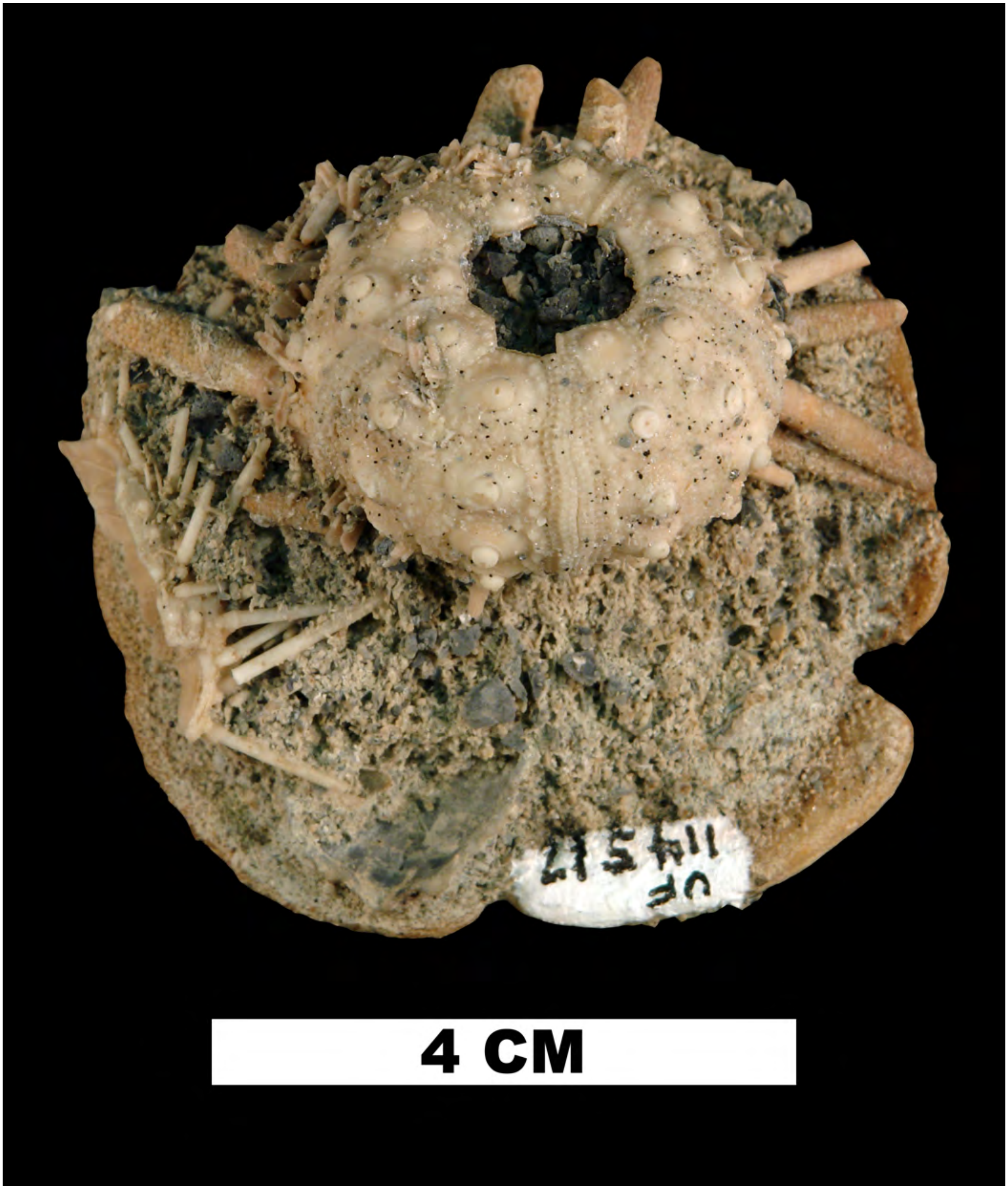


Figure 6. *Eucidaris tribuloides* (UF 114517) with attached spines (Aboral view), *Encope tamiamiensis* (underneath), and attached to left side *Lytechinus variegatus*, Tamiami Formation (FM locality CH046).

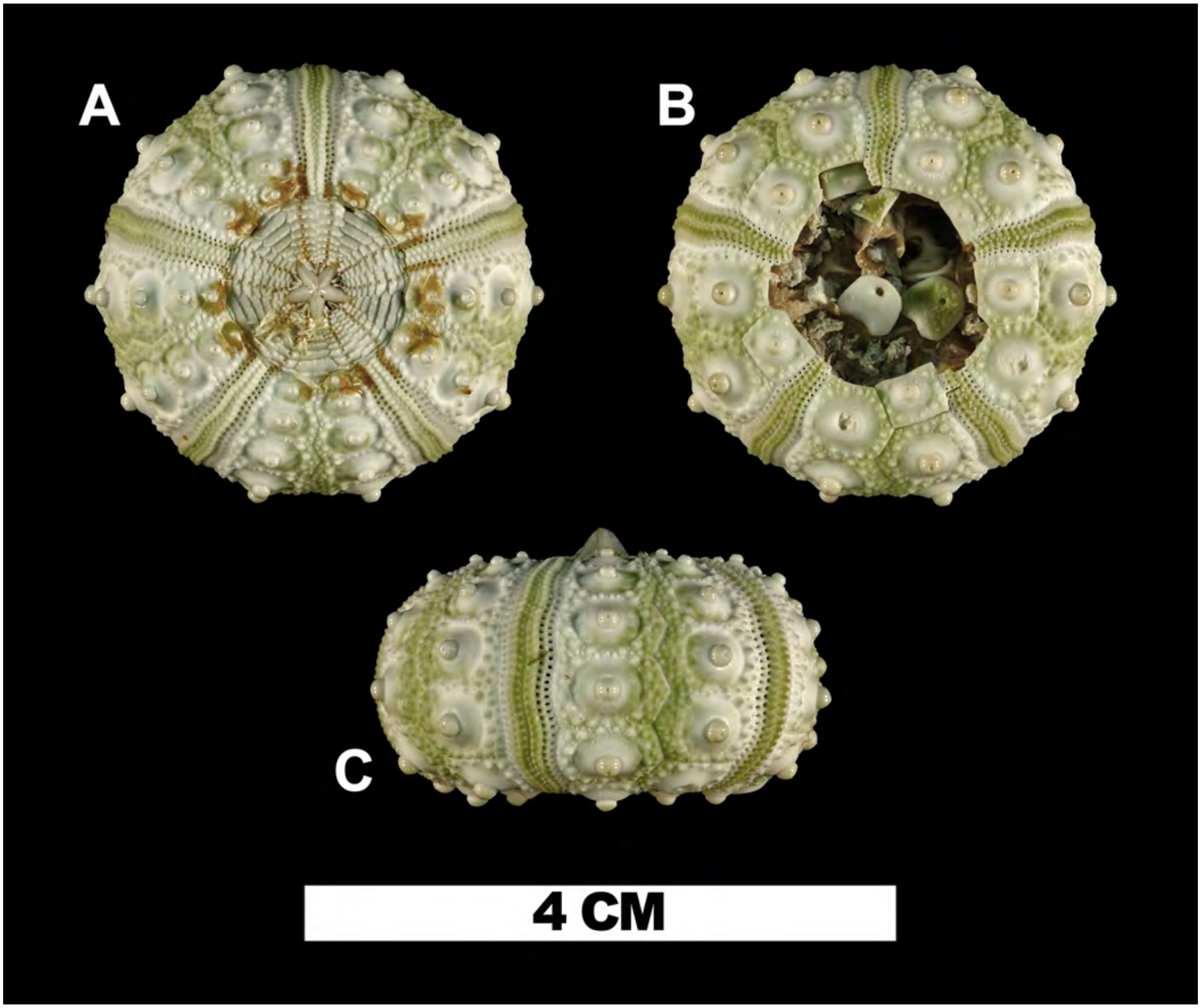


Figure 7. *Eucidaris tribuloides* (UF-IZ 7031), modern specimen for comparison (Gulf of Mexico, 25 miles SW of Pensacola, Florida in 75 m trawl, USA). A. oral view, B. aboral view, C. lateral view.

occur in the upper Miocene Peace River Formation in the bed of the Peace River upstream from Zolfo Springs, Hardee County, Florida (Osborn and Ciampaglio, 2010a), and in the Torreya Formation in the old Taft Pit, near Crawfordsville, Wakulla County (FM locality WA001). *Prionocidaris cookei* is also documented from the Neogene of Cuba (Cutress, 1980).

Discussion.—Cutress (1976) described *P. cookei* from isolated spines and test plates collected from the lower Miocene Chipola Formation of north Florida. Cutress (1980) reviewed this material and expanded the occurrence of the species to the Miocene–Pliocene(?) of Cuba. Cutress (1976) noted that spinules on the shaft project as much as 0.5 mm on the Cuban specimens and not more than 0.4 mm in the Florida specimens. There are no distinct nodules on the collars of the Cuban fragments, but this may be attributed to the small sample of basal fragments from Cuba. Otherwise, the Cuban spines agree well with those from Florida (Cutress, 1980).

Osborn and Ciampaglio (2010a) documented the occurrence of cidarid spines attributable to this

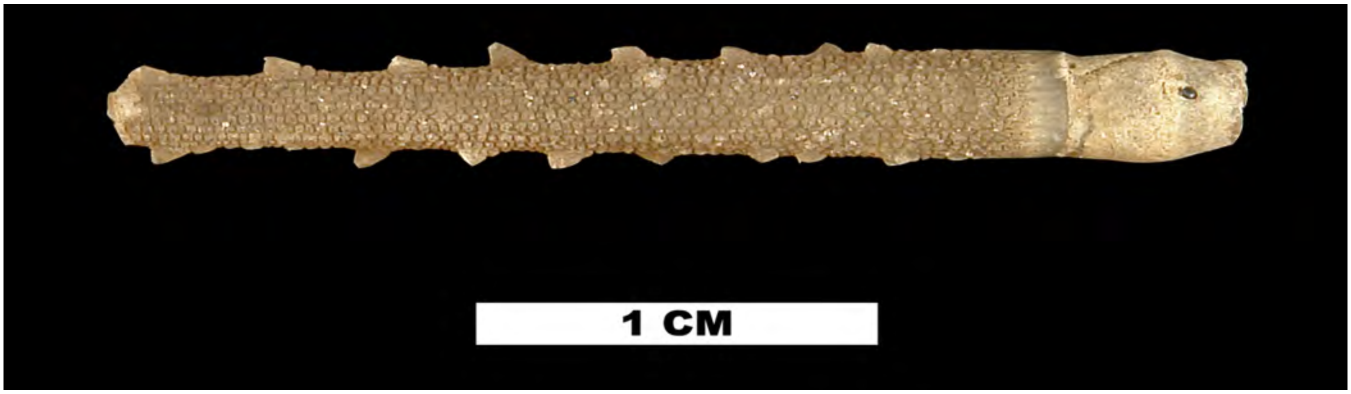


Figure 8. *Prionocidaris cookei* spine (UF 289224), Peace River Formation (FM locality HR005).

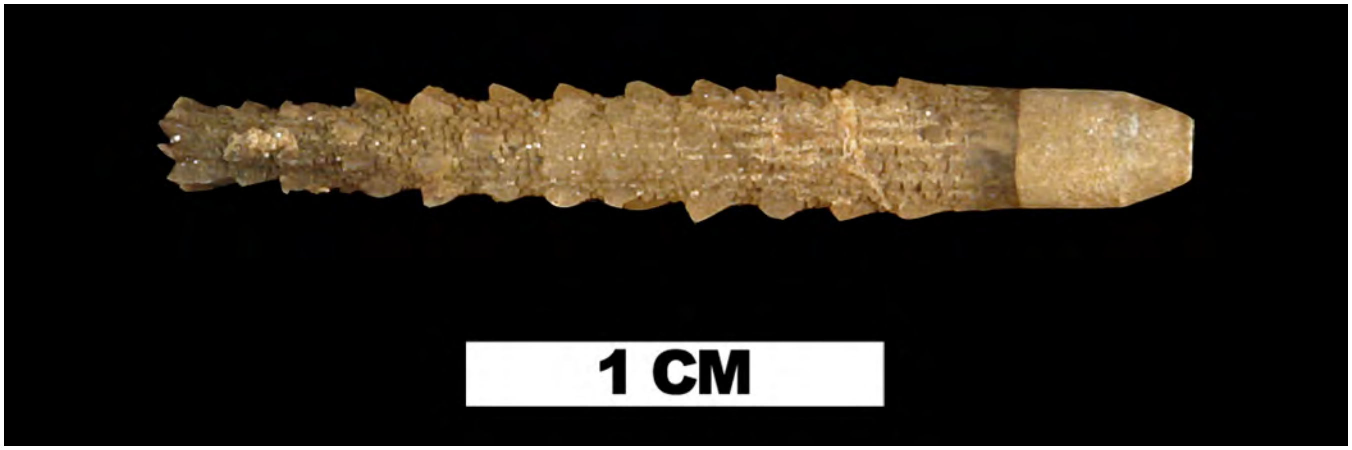


Figure 9. *Prionocidaris cookei* spine (UF 304834), Peace River Formation (FM locality HR013).

species from the upper Miocene Peace River Formation in the bed of the Peace River, upstream from Zolfo Springs, Hardee County, Florida (UF 289224 and UF 304834; Figs. 8–9). These spines are associated with *A. dengleri*, *Brissopsis hoffmani* n. sp., and *R. chipolanus*.

Spines similar to *P. cookei* occur in the Torreya Formation in the Taft Pit, Wakulla County (FM locality WA001), with *R. chipolanus* and fragments of a *Clypeaster* (potentially *C. petersonorum* n. sp).

Subclass **EUCHINOIDEA** Bronn, 1860
Infraclass **CARINACEA** Kroh and Smith, 2010
Order **ARBACIOIDA** Gregory, 1900
Family **ARBACIIDAE** Gray, 1855
Genus ***ARBIA*** Cooke, 1959
ARBIA ALDRICHI (Clark in Clark and Twitchell, 1915)
Figures 12–13

Coelopleurus aldrichi Clark in Clark and Twitchell, 1915, p. 158, pl. 73, figs. 6a, b, 7a–c.
Arbacia aldrichi (Clark). Cooke, 1941, p. 11.
Arbia aldrichi (Clark). Cooke, 1948, p. 606.
Arbia aldrichi (Clark). Mortensen, 1951, p. 558, figs. 280a–c.
Arbia aldrichi (Clark). Cooke, 1959, p. 21, pl. 3, figs. 15–17.
Arbia aldrichi (Clark). Fell and Pawson, 1966, p. 410, fig. 305.3.
Arbia aldrichi (Clark). Kier, 1997, p. 4, fig. 1, pl. 1, figs. 5, 6.
Arbia sp. (Clark). Oyen, 2001, pp. 112, 113, figs. 3–14, f, g.
Arbia aldrichi (Clark). Osborn and Ciampaglio, 2014, p. 142.

Occurrence.—This species occurs in the lower Miocene St. Marks Formation in channel dredgings along the Gulf shore west of Shell Point, Oyster Bay, Wakulla County (FM locality WA014). It has also been collected rarely in the lower Miocene Chattahoochee Formation below Jim Woodruff Dam in Jackson County (FM locality JA003). The holotype of *Arbia aldrichi* (Clark in Clark and Twitchell, 1915) was collected in the upper Oligocene Chickasawhay Limestone at Perdue Hill,

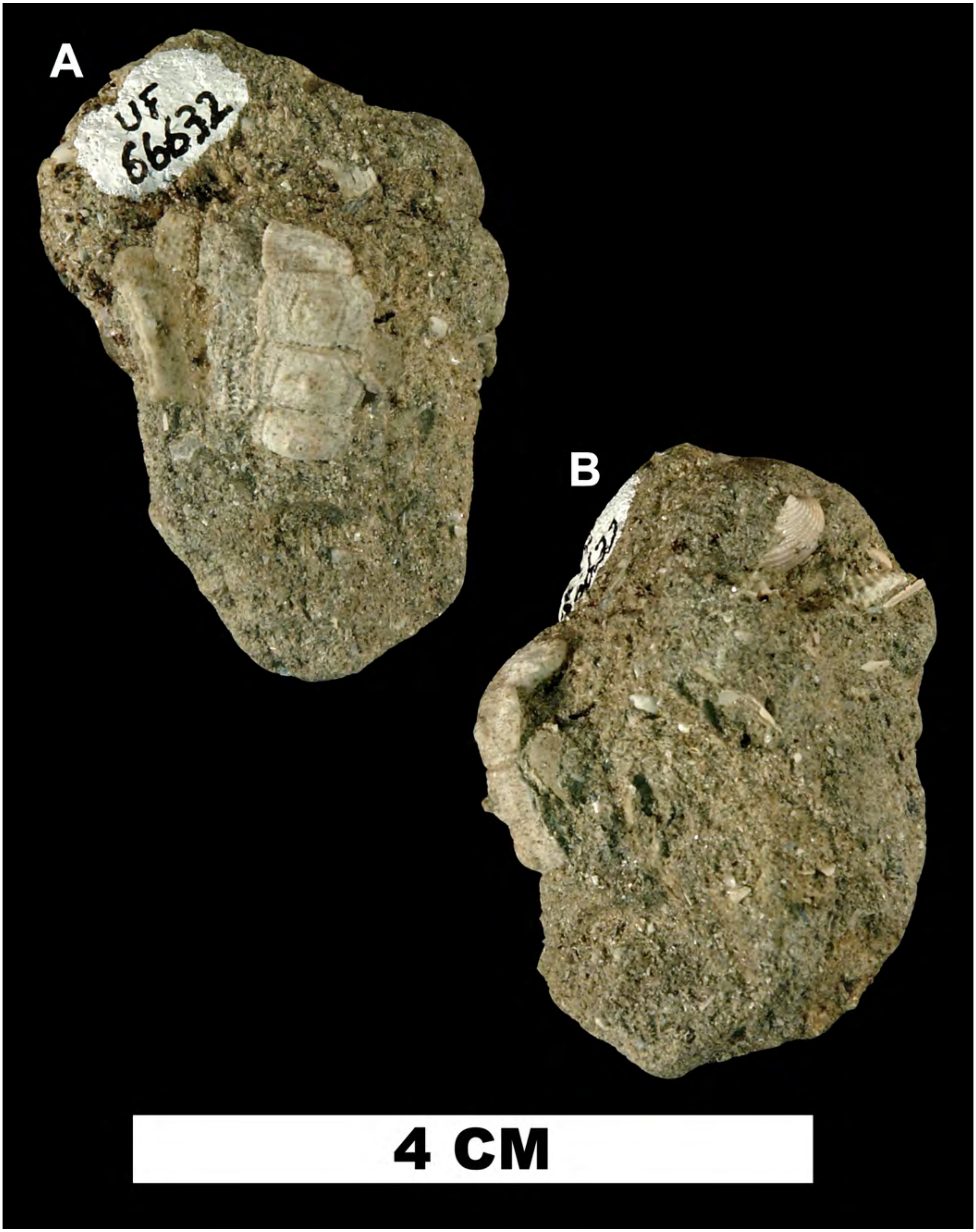


Figure 10. *Prionocidaris cookei* test fragment (UF 66632), Chipola Formation (FM locality CA011).

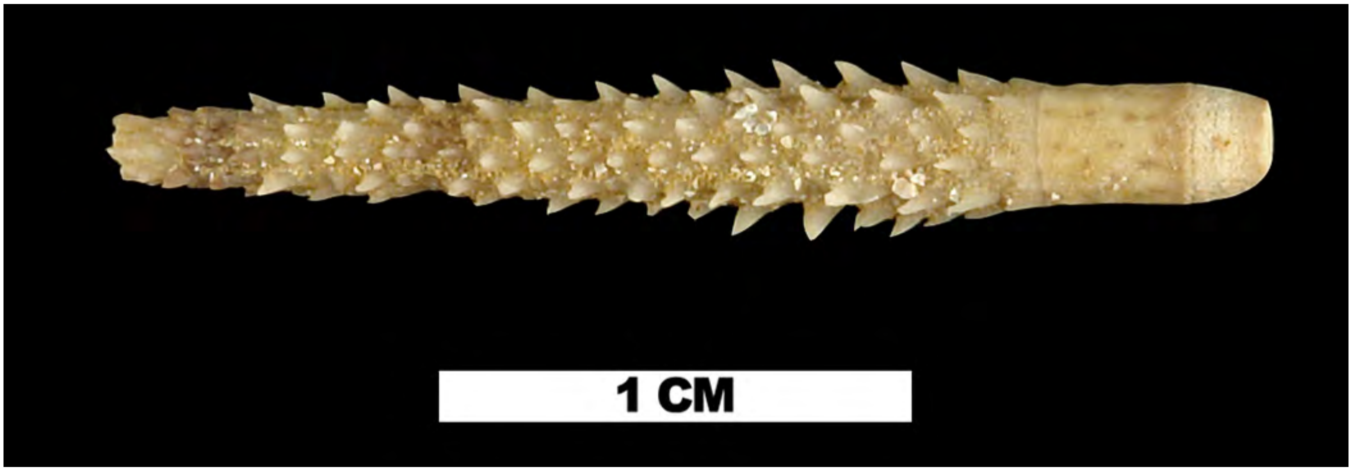


Figure 11. *Prionocidaris cookei* spine (UF 305540), Chipola Formation (FM locality CA020).

Monroe County, Alabama (USNM 559494). This species is also present in the uppermost Oligocene Paynes Hammock Sand in Mississippi and the upper Oligocene River Bend Formation of North Carolina (Kier, 1997).

Discussion.—This is the first documentation of *A. aldrichi* in the fossil record of Florida. Oyen (2001) noted the presence of *Arbia* sp. in the Chattahoochee Formation below the Jim Woodruff Dam, Jackson County, Florida (FM locality JA003), where it rarely occurs with abundant *Lovenia clarki* (Lambert in Lambert and Thiéry, 1924). The material consists of an external mold with RTV cast (UF 102309; Fig. 12) and an internal mold (UF 60668) that are inseparable morphologically from *A. aldrichi*.

Fragmentary material from the St. Marks Formation, which cannot be distinguished from *A. aldrichi* (UF 233541; Fig. 13), was obtained in channel dredgings along the Gulf shore west of Shell Point, Oyster Bay, Wakulla County. The only other echinoid present in this material consists of a collection of test fragments from an unidentifiable spatangoid that is not a member of the Loveniidae. Note that this specimen displays crenulate primary tubercles which are not described for *A. aldrichi* in Clark and Twitchell (1915) or Cooke (1959), but Kier (1997) documented the presence of crenulate tubercles on this species.

These occurrences expand the distribution of this late Oligocene–early Miocene species southwestward from its typical area of abundance in southwestern Alabama and southeastern Mississippi. It is the only species of echinoid in the region to be definitively documented in both the Miocene (St. Marks and Chattahoochee Formations) and Oligocene (Chickasawhay Formation of Alabama and Mississippi, and River Bend Formation of North Carolina).

Genus ***ARBACIA*** Gray, 1835
ARBACIA IMPROCERA (Conrad, 1843)
Figures 14–15

Echinus improcerus Conrad, 1843a, p. 310.
Psammechinus improcerus (Conrad). Stefanini, 1911, p. 705.
Coelopleurus sloani Clark in Clark and Twitchell, 1915, p. 181, pl. 84, figs. 5a, b.
Coelopleurus improcerus (Conrad). Clark and Twitchell, 1915, p. 180, pl. 84, figs. 4a–c.
Arbacia improcera (Conrad). Cooke, 1941, p. 11, pl. 1, figs. 7–9.
Arbacia sloani (Clark). Cooke, 1941, p. 11.
Arbacia improcera (Conrad). Cooke, 1959, p. 20, pl. 4, figs. 1–3.
Arbacia sloani (Clark). Cooke, 1959, p. 21, pl. 4, figs. 12–14.
Arbacia crenulata Kier, 1963, p. 11, pl. 1, figs. 1–15, text figs. 3–7.
Arbacia improcera (Conrad). Kier, 1972, p. 8, pl. 1.
Arbacia improcera (Conrad). Kier, 1983, p. 501, pl. 1, fig. 6.
Arbacia sp. cf. *A. sloani* (Clark and Twitchell) Weaver et al., 2006, p. 75, figs. 3, 4.
Arbacia improcera (Conrad). Ciampaglio et al., 2009, fig. 2.
Arbacia improcera (Conrad). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—The holotype of *A. crenulata* was collected at the stratotype locality for the Buckingham Limestone Member of the Tamiami

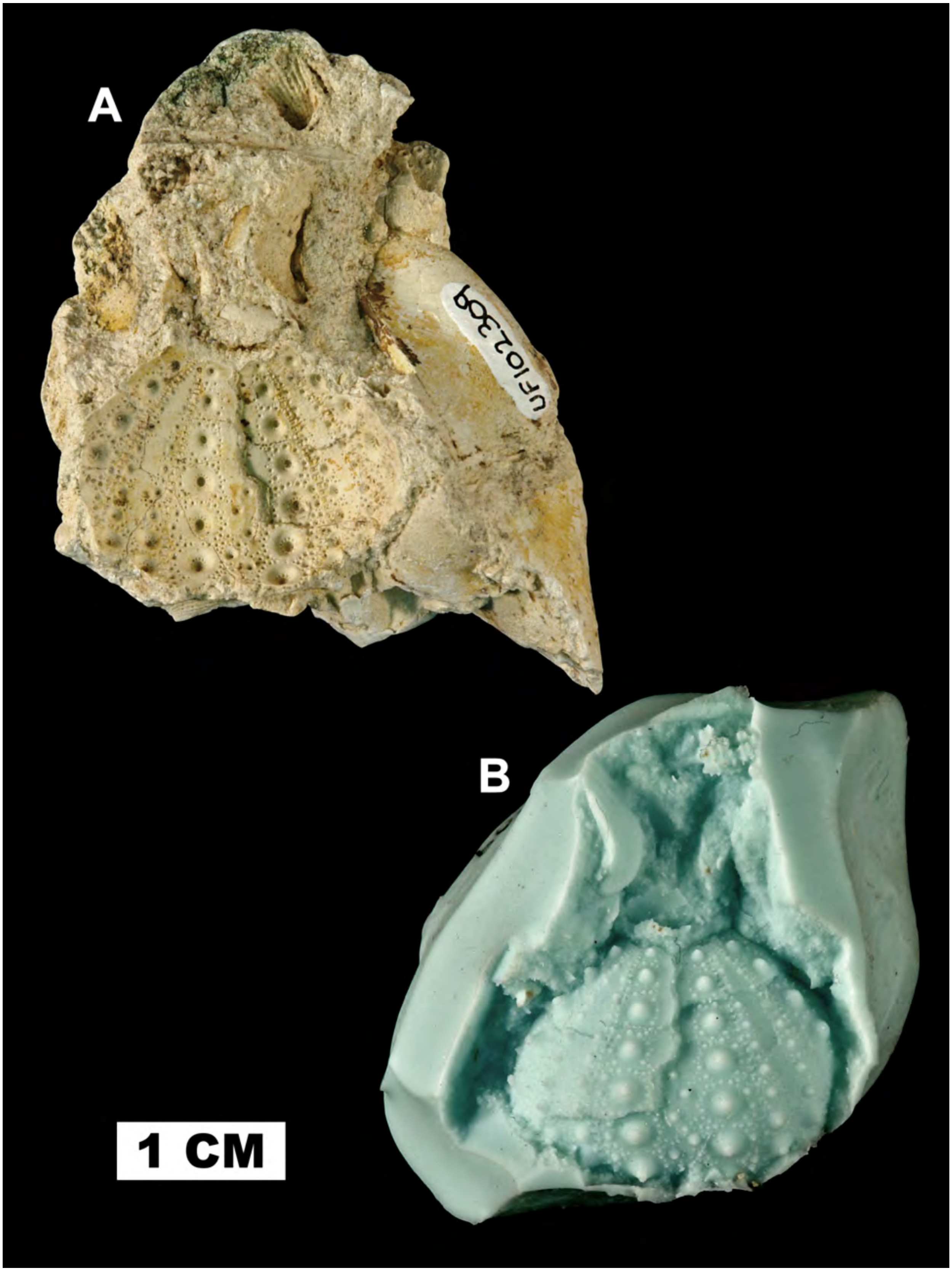


Figure 12. *Arbia aldrichi* (UF 102309), Chattahoochee Formation (FM locality JA003). A. external mold, B. room-temperature vulcanizing (RTV) rubber peel.

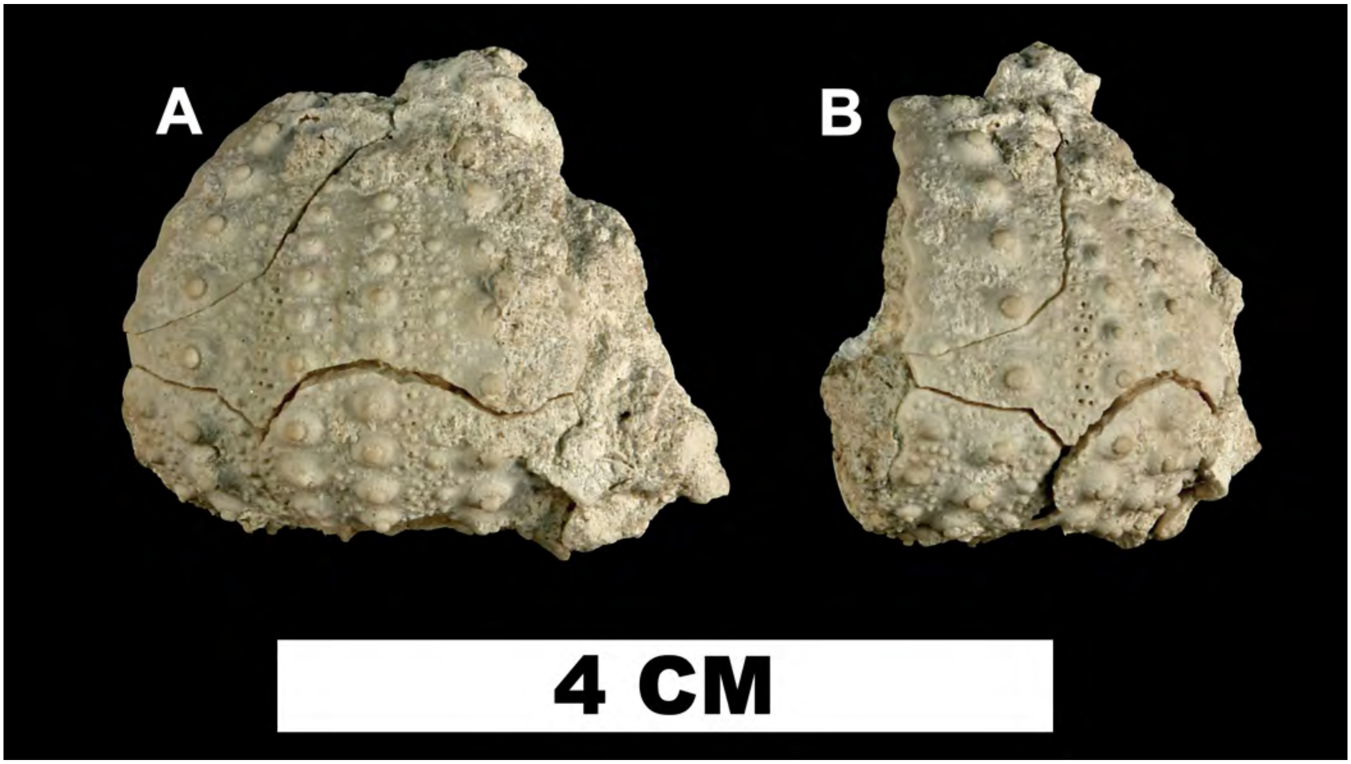


Figure 13. *Arbia aldrichi* (UF 233541), St. Marks Formation (FM locality 5706). A. test fragment in lateral view, B. same.

Formation, Buckingham, Lee County, in SW½ sec 5, T. 44 S, R. 26 E, and Kier (1963) listed additional localities within the Tamiami Formation. *Arbacia improcera* is common in certain horizons of the Tamiami Formation in the Quality Materials Quarry (FM locality CH080), with some of the specimens retaining many of their spines. *Arbacia improcera* also occurs in the Intracoastal Formation in Liberty County (FM locality LI005) (Ciampaglio and Osborn, 2011).

Specimens of spines and test fragments from the Nashua Formation in St. Johns County are potentially referable to this species. However, the material (UF 84283), though definitely an *Arbacia*, is too incomplete to identify to species level.

Arbacia improcera also occurs in the middle Pliocene Yorktown Formation of North Carolina (Kier, 1983); the upper Pliocene Goose Creek Limestone of South Carolina (Campbell and Campbell, 1995; Ciampaglio et al., 2009; Ciampaglio and Osborn, 2011); and the type locality Yorktown Formation of Virginia (Cooke, 1959; Kier, 1972).

Discussion.—Kier (1963) described *A. crenulata* from the upper Pliocene Tamiami Formation in south Florida. However, he later questioned the validity of his own *A. crenulata*, stating it was likely synonymous with *A. improcera* (Conrad, 1843) (Kier, 1972). Kier (1972) also documented the presence of *A. improcera* in the Yorktown Formation at numerous additional localities in southeastern Virginia, including many near Smithfield, the type locality. These specimens prompted Kier (1972) to agree with Cooke (1959) that *A. improcera* was conspecific with *A. sloani* (Clark in Clark and Twitchell, 1915) from the Duplin Marl (also known as the lower Goose Creek Limestone of Campbell and Campbell [1995]) at Bostick Landing, Pee Dee River, South Carolina.

Kier (1972) also stated that *A. improcera* may be conspecific with his own *A. crenulata*, which he described from the upper Pliocene Tamiami Formation of south Florida. When Kier described *A. crenulata*, he had but one specimen of *A. improcera* for comparison. Ornamentation on that specimen is different from that of his *A. crenulata*. In *A. crenulata*, the ornamentation typically consists of fine crenulations, whereas in the single specimen of *A. improcera* that Kier (1963) had available they were granules. However, on the newly acquired specimens of *A. improcera* that Kier (1972) had available for study, these granules are commonly joined together into crenulations that Kier (1972: pl. 1, fig. 5) figured. Thus, Kier (1972) stated that *A. improcera* and *A. crenulata* are most likely synonymous, and *A. crenulata* has not been recognized since by echinoid specialists working in the region (Oyen and Portell, 2001; Ciampaglio and Osborn, 2011).

A large number of *Arbacia* have since been collected from the Tamiami Formation for comparison with the type material of *A. improcera*, and it is clear that the crenulations seen on *A. crenulata* are also present on many specimens of *A. improcera* and that some specimens of *A. improcera* from the Tamiami Formation have less crenulated tests, with more granulated ornamentation. The two species are otherwise indistinguishable, and there can be no doubt that Kier's (1972) suspicions concerning his own *A. crenulata* were correct, and we herein also consider *A. crenulata* a subjective junior synonym of *A. improcera*.

Collecting in the upper Pliocene Tamiami Formation in the Quality Materials Quarry, Charlotte County (FM locality CH080), has provided numerous specimens of *A. improcera* that retain articulated spination. The spines are often broken with only the basal portion remaining. However, some specimens with retention of largely complete spines have been found and these specimens reveal

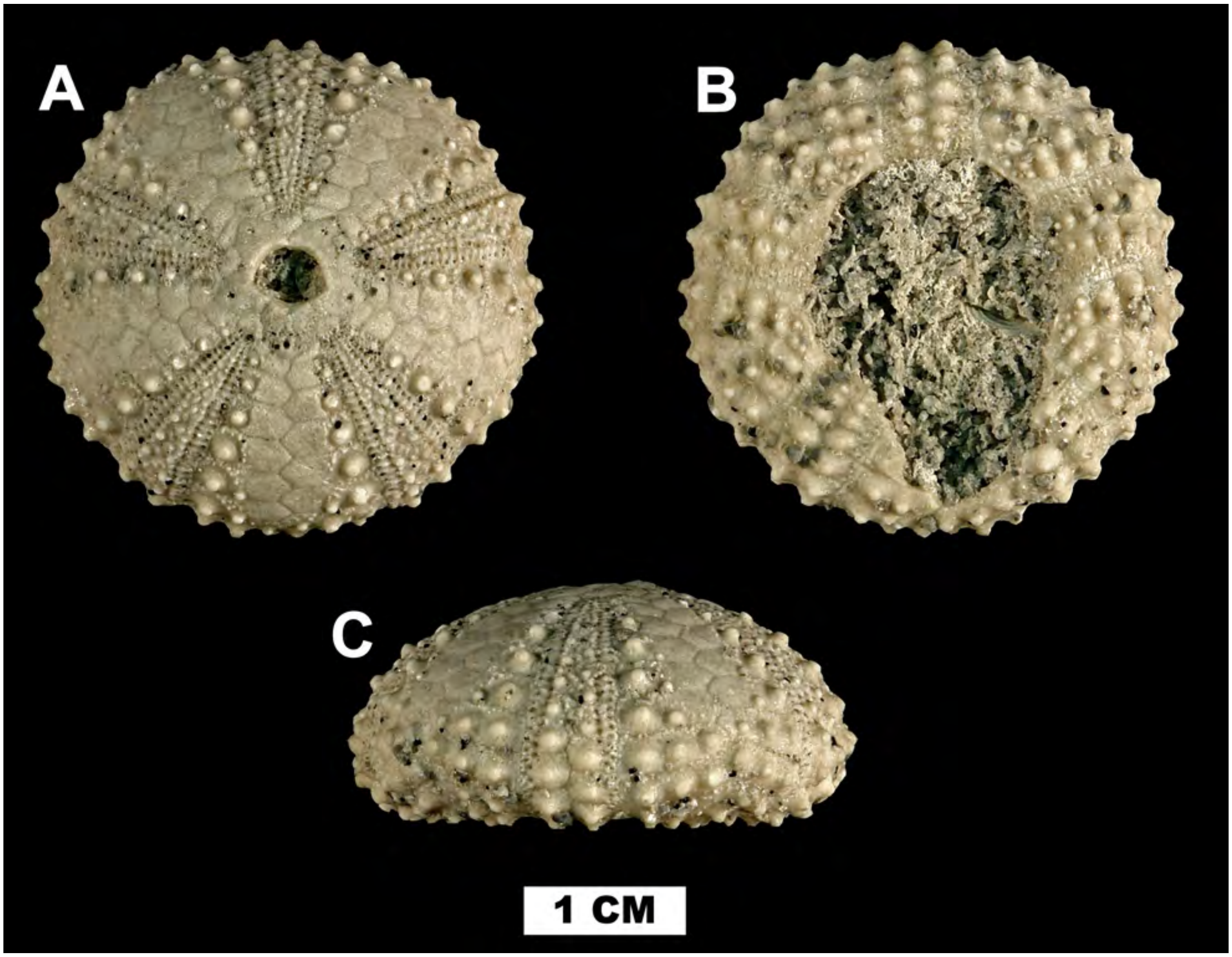


Figure 14. *Arbacia improcera* (UF 289212), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

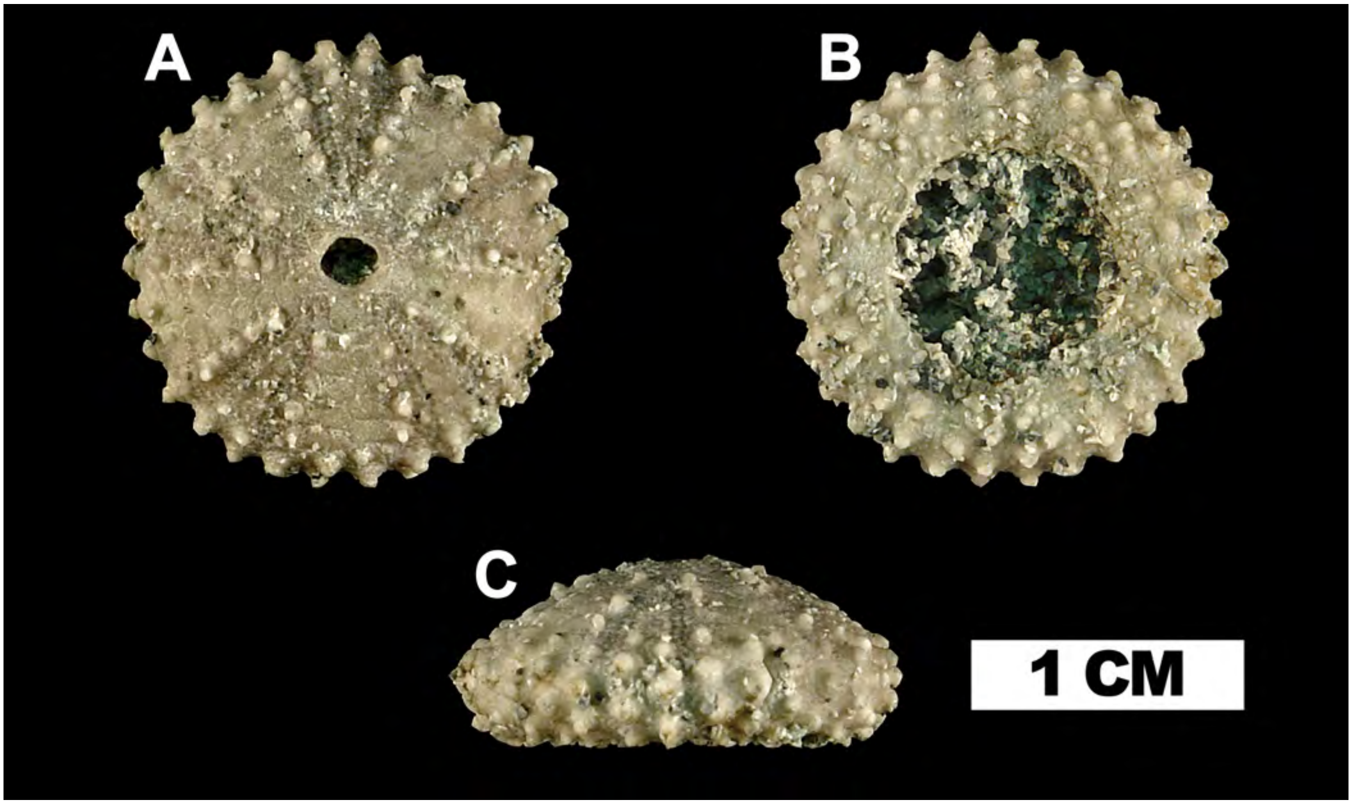


Figure 15. *Arbacia improcera* (UF 289215), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

that the spines of *A. improcera* are similar to those of the modern *A. punctulata*, although spination of *A. punctulata* is highly variable and dependent on habitat (see the discussion for that species herein).

Ciampaglio and Osborn (2011) documented the occurrence of *A. improcera* in the upper Pliocene Intracoastal Formation, in Liberty County, Florida, where the species is often smaller than typical for its more northern or southern poopulations (UF 289215; Fig. 15).

This species displays a high degree of variation in TH and shape, similar to that demonstrated by the modern *A. punctulata*, as documented by Harvey (1956).

ARBACIA PUNCTULATA (Lamarck, 1816)
Figures 16–18

Echinus punctulatus Lamarck, 1816, p. 47; 2d ed., 1840, v. 3, p. 363.
Arbacia punctulata (Lamarck). Gray, 1835, p. 58.
Anapesus carolinus (Troschel). Holmes, 1860, p. 5, pl. 2, fig. 2.
Arbacia punctulata (Lamarck). Jackson, 1927, pp. 437–565.
Arbacia punctulata (Lamarck). Mortensen, 1935, p. 573, pl. 87, figs. 7–10. (includes additional synonymy).
Arbacia punctulata (Lamarck). Cooke, 1941, p. 10.
Arbacia punctulata (Lamarck). Harvey, 1956, 298 p.
Arbacia punctulata (Lamarck). Cooke, 1959, p. 19, pl. 4, figs. 7–9.
Arbacia punctulata (Lamarck). Kier and Grant, 1965, pp. 17, 18. pl. 2, figs. 8, 9. pl. 10, fig. 5, text fig. 4.
Arbacia punctulata (Lamarck). Kier, 1975, p. 17, pl. 11.1.
Arbacia punctulata (Lamarck). Serafy, 1979, pp. 30–39. fig. 9.
Arbacia punctulata (Lamarck). Serafy and Fell, 1985, pp. 13, 21, fig. 23.
Arbacia punctulata (Lamarck). Hendler et al., 1995, pp. 214–215, figs. 113, 134A.
Arbacia punctulata (Lamarck). Pomory, 2003, pp. 17–19, fig. 6.
Arbacia punctulata (Lamarck). Ciampaglio et al., 2009, fig. 2.
Arbacia punctulata (Lamarck). Mihaljevic et al., 2010, pp. 3, 4, fig. 3.

Occurrence.—Herrera et al. (2006) documented the occurrence of *Arbacia punctulata* from a middle to upper Pleistocene deposit in the Dickerson Quarry, St. Lucie County (FM locality SL004), tentatively referred to the Anastasia Formation. This species also occurs in the middle Pleistocene Canepatch Formation in the Carolinas (Ciampaglio et al., 2009).

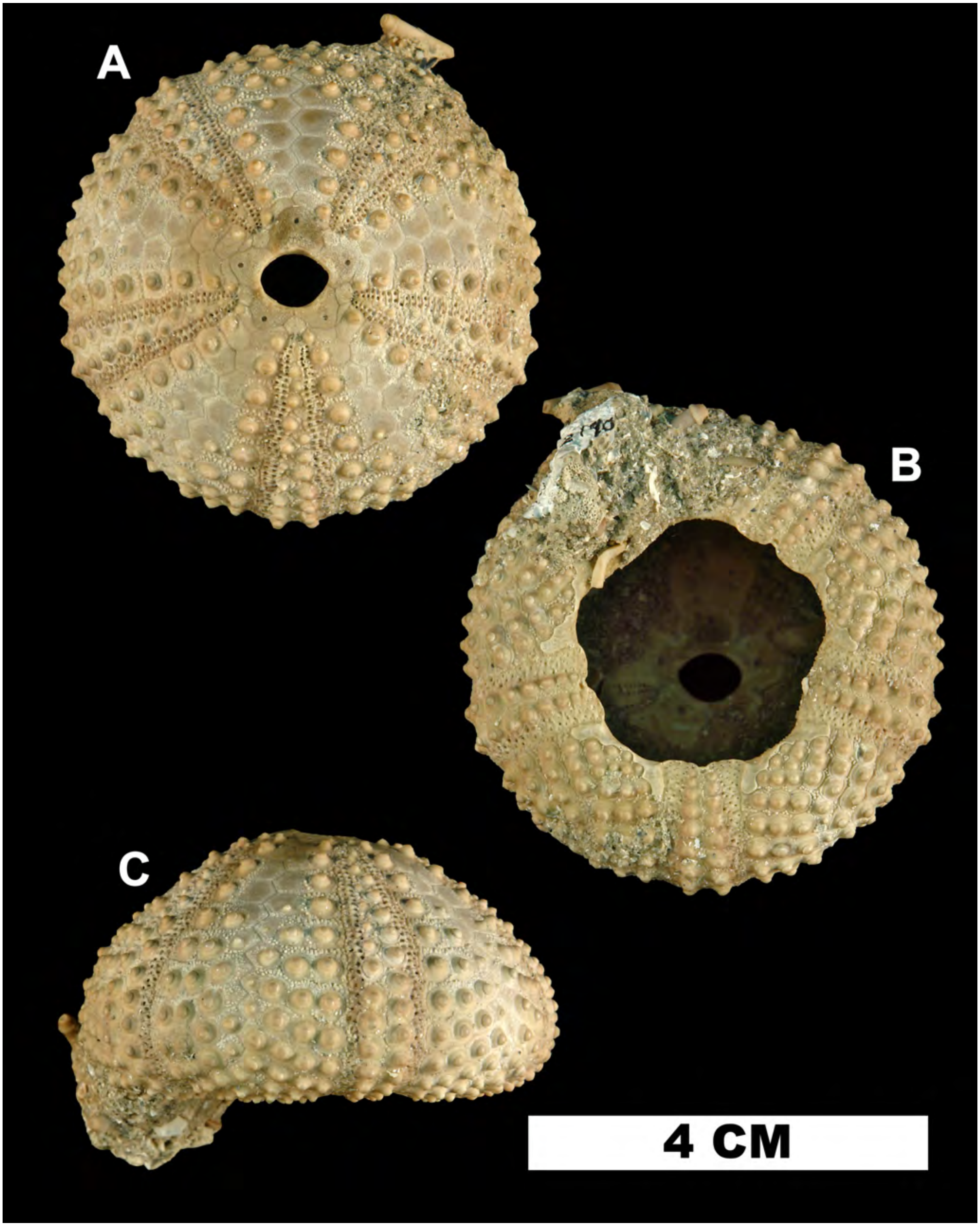


Figure 16. *Arbacia punctulata* (UF 112190), Anastasia Formation (FM locality SL003). A. aboral view, B. oral view, C. lateral view.

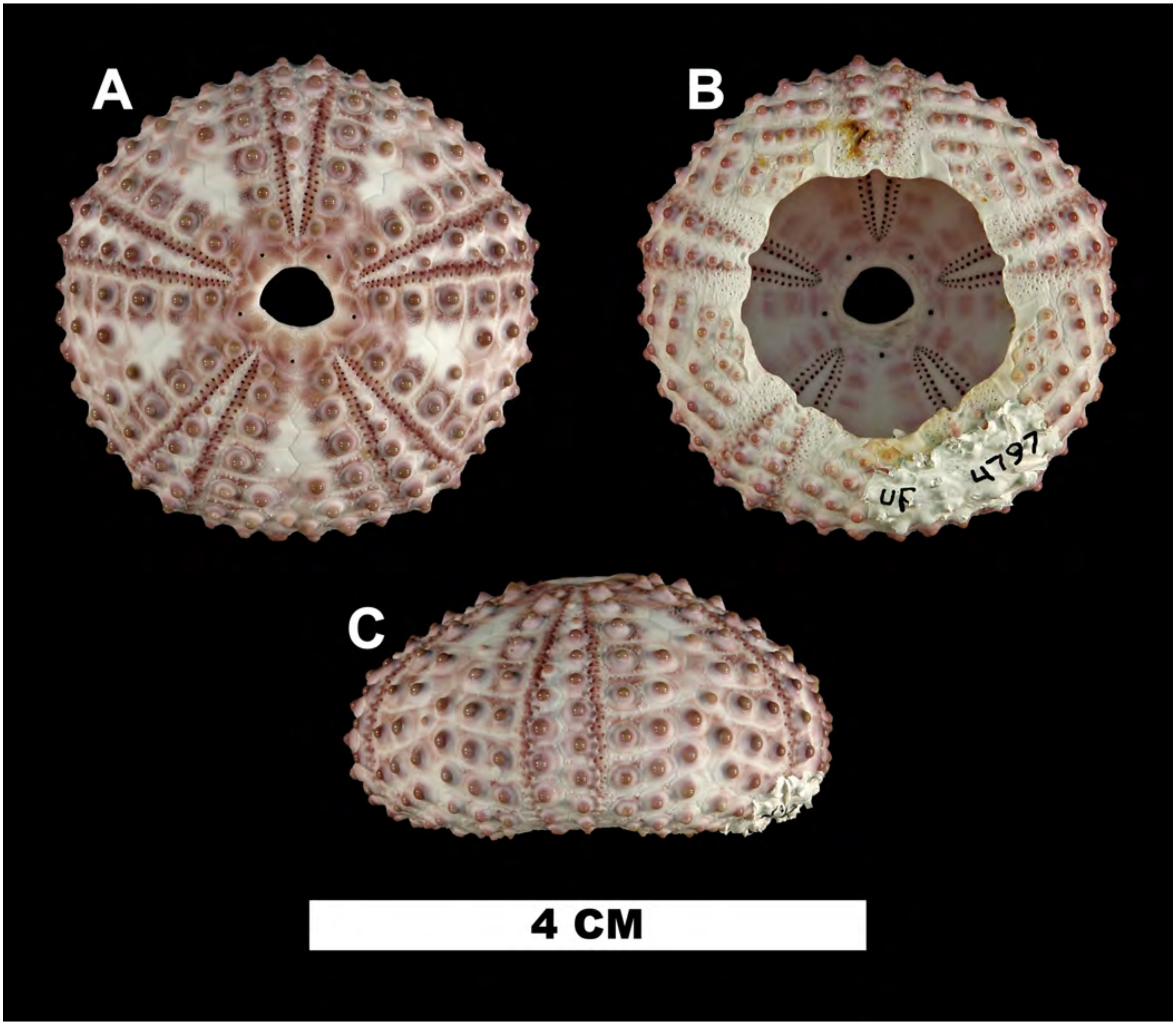


Figure 17. *Arbacia punctulata* (UF-IZ 4797), modern specimen for comparison (Gulf of Mexico, off Tarpon Springs, 36 foot depth, Pinellas County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

Discussion.—This is a common urchin in warmer waters of the east coast of North America today. Serafy and Fell (1985) documented it from the south side of Cape Cod to the Bahamas and northern Cuba and throughout the Gulf of Mexico. A southern population occurs from Panama to Surinam, but it is absent from Hispaniola, Jamaica, the south coast of Cuba, and the Lesser Antilles north of Barbados.

Adults of *A. punctulata* are often greater than 90 mm across including spines, 45 mm TD without spines (Hendler et al., 1995), though Mortensen (1935) stated the largest specimen of which he was aware was 53 mm TD. Specimens from the Anastasia Formation in St. Lucie County (FM locality SL004) are large for the species. We figure UF 112190, a specimen that measures 48 mm TD from this locality (Fig. 16).

Gonopores first appear when the test is 10 mm in diameter (Mortensen, 1935) and the spines vary from short and stout to slender and pointed, depending on the degree of exposure to wave action. This

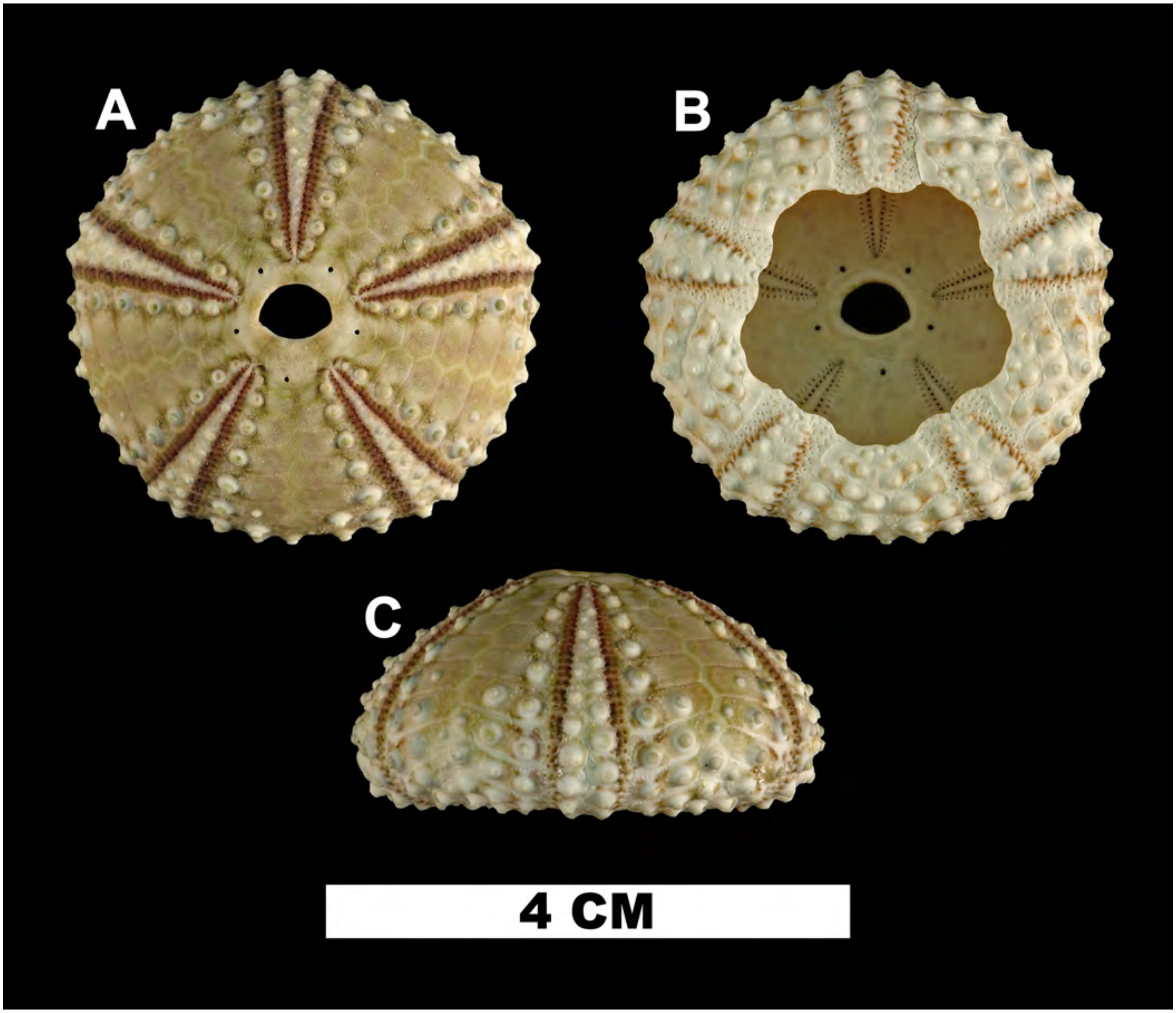


Figure 18. *Arbacia punctulata* (UF-IZ 18897), modern specimen for comparison (Murrels Inlet, 1 m depth, Horry and Georgetown Counties, South Carolina, USA). A. aboral view, B. oral view, C. lateral view.

trait is not limited to this species, as Serafy and Fell (1985) state many species of echinoid from areas subject to wave action have shorter, more robust spines, whereas specimens from calm water have longer, more slender spines. The spines on the oral surface are spatulate distally, likely an adaptation for locomotion. Harvey (1956) noted that there is considerable variation in the shape of the test with some being much more depressed than others.

Herrera et al. (2006) documented the occurrence of *A. punctulata* (UF 112190; Fig. 16) in a middle to upper Pleistocene deposit (likely Anastasia Formation) at FM locality SL004, in St. Lucie County, Florida, where *A. punctulata* occurred with *Encope michelini* and *Rhyncholampas meansi* n. sp. This is the first documented occurrence of *A. punctulata* in the fossil record of Florida, where it should presumably be more common, at least in late Pleistocene deposits, given its abundance in the region's nearshore Recent faunas.

Order **CAMARODONTA** Jackson, 1912
"Triplacidiids" temporary family (Kroh and Mooi, 2019)
Genus ***GAGARIA*** Duncan, 1889
GAGARIA HUNTERAE n. sp.
Figure 19

Diagnosis.—*Gagaria* with low test, TH approximately 50% of TD; ambulacra on average 62% the width of interambulacra at ambitus; lacking vertical line of secondary tubercles in interambulacra between pore-pairs and primary tubercles; narrow naked median area aborally in interambulacra between columns of primary tubercles.

Description.—Description based on only known specimen, holotype (UF 235973). Test subpentagonal, small, maximum diameter 16.1 mm TD; low, height 8 mm TH; TH = 49.6% TD. Apical system missing, opening damaged, presumably pentagonal, maximum diameter 3.8 mm (= 23% TD). Peristome nearly circular, central, moderately notched, maximum width 5.8 mm (= 36% TD). Ambulacra on average 62% width of interambulacra at ambitus; poriferous zones uniserial, nearly straight, three pore pairs per plate; two vertical rows of large, crenulate, imperforate, primary tubercles in each area; compound plates presumably trigeminous. In interambulacra, plates wider than tall, two rows of large, crenulate, imperforate primary tubercles, similar in size to those in ambulacral area; intermediate-sized tubercles in medial area near ambitus, medial area becomes naked aborally; primary tubercles surrounded by ring of smaller tubercles, granules fill interspaces.

Zoobank Nomenclatural Act.—F7427AE6-C314-442B-AC2C-1344EDBE7F0E.

Discussion.—This species is currently known only from the holotype (UF 235973; Fig. 19) collected in the lower Miocene St. Marks Formation near Woodville in Wakulla County (FM locality WA011). Although the holotype is well preserved, plating is largely indiscernible, and we are unwilling to prepare the specimen to reveal additional plating details until additional specimens are available. Additional techniques such as Micro-CT scannings or x-ray techniques were cost prohibitive at the time of preparation of this work, but may prove advantageous to better understand this specimen in the future. The specimen is sufficient to describe the species as new and different from its regional Oligocene congener, *Gagaria mossomi* (Cooke, 1941), which is the only species in the regional fauna with which it could potentially be confused. *Gagaria chickasawhay* (Cooke, 1941), from the upper Oligocene Chickasawhay Limestone of Mississippi, is the only other species of *Gagaria* documented in the region, but is based on test fragments insufficient for comparison.

Gagaria hunterae n. sp. is distinguished from *G. mossomi* by its lower test. One of the two cotypes of *G. mossomi* described by Cooke (1941) (USNM 372885) has a diameter of 15 mm; nearly the same size as the specimen of *G. hunterae* herein described, thereby providing a suitable comparison to the holotype of *G. hunterae*. Cooke (1959:18) stated the 15mm TD cotype of *G. mossomi* has a TH of 14.5 mm—a TH equal to 96.6% TD. However, the specimens Cooke figured do not reflect a species with such a proportionately high test. Thankfully, Cooke (1941) provided a TH of 8.2 mm for the cotype with a 15 mm TD. Cooke's (1959) statement might have been an oversight, as we now know that the specimen has a TH 54.6 % TD, whereas the holotype of *G. hunterae* has a TH of only 49.6% TD. Other measurements provided by Cooke (1941), such as peristome width, are very similar to those of *G. hunterae*.

Cooke (1959:pl. 3, fig. 13) also figured a specimen (USNM 498884a) that he identified as a paratype of *G. mossomi*, that clearly shows a vertical line of secondary tubercles in the interambulacra, between the pore-pairs and primary tubercles. No such tubercle arrangement exists on *G. hunterae*, which also has a narrower naked median area between the rows of primary tubercles in the interambulacra on the aboral surface than *G. mossomi*. This is not only well displayed on the paratypes of Cooke (1959) but also on specimens of *G. mossomi* figured by Kier (1997: pl. 2) from the Oligocene of North Carolina.

Cooke (1941) designated cotypes (USNM 372885) but no holotype for *G. mossomi*. Cooke (1959) listed the same cotypes in his discussion for

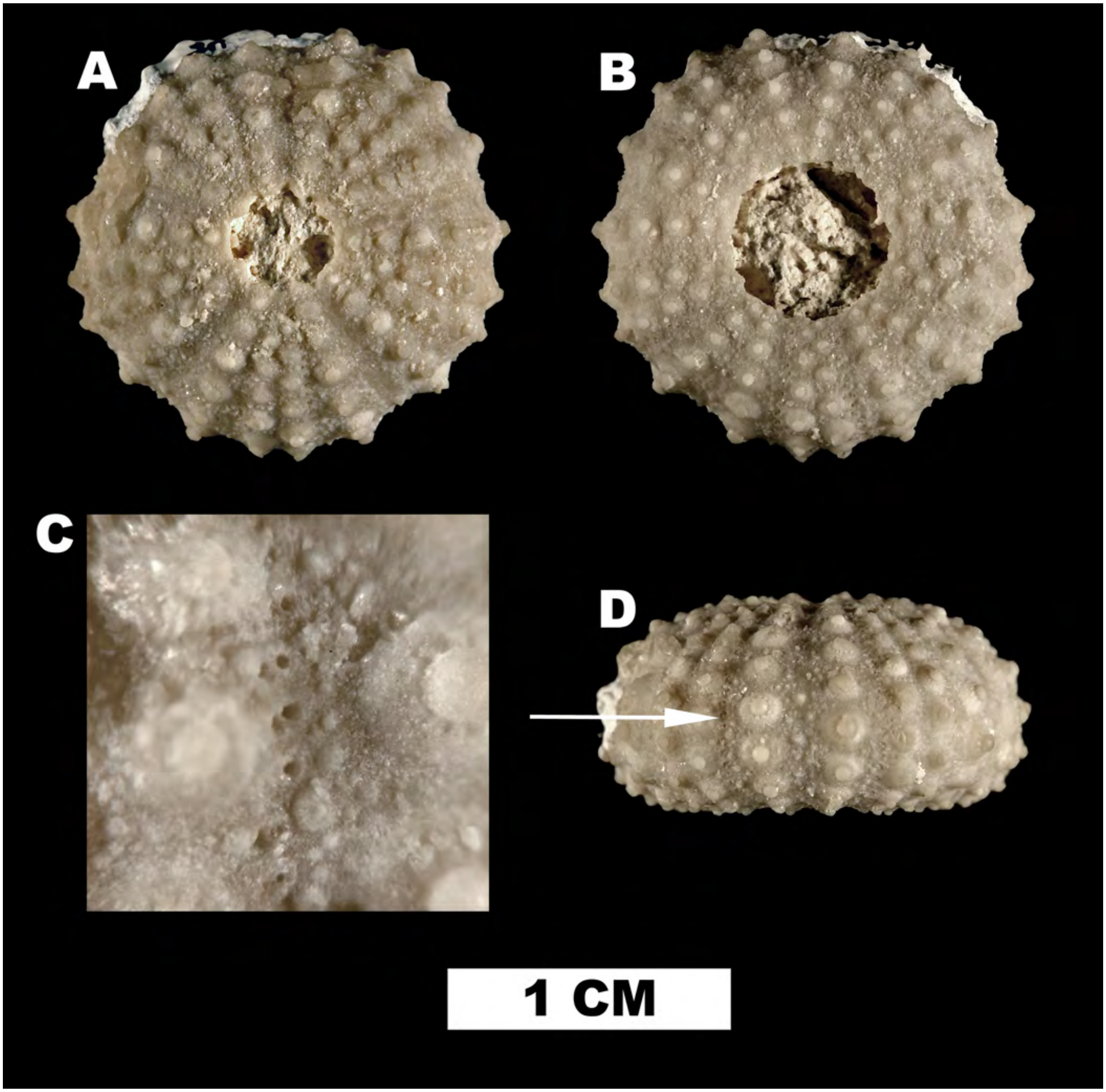


Figure 19. *Gagaria hunterae* n. sp., holotype (UF 235973), St. Marks Formation (FM locality WA011). A. aboral view, B. oral view, C. close-up of poriferous zone; arrow indicates area of test included in close-up view, D. lateral view.

G. mossomi. However, as noted above, he identified three specimens (USNM 498884a–c) as paratypes (Cooke, 1959:pl. 3). Being designated after the original description, these specimens have no status as types of *G. mossomi*. One of the two cotypes will need to be designated as a lectotype, leaving the other specimen as a paralectotype.

Given the dearth of Miocene age regular echinoids in the regional faunas (other than abundant remains of *Prionocidaris cookei* and very rare occurrences of *Arbia aldrichi*), the specimen of *G. hunterae* is significant. It is only the third documented species of regular urchin in the Miocene of the region and the first occurrence of *Gagaria* in the Miocene of North America. It is hoped that additional specimens will come to light to increase understanding of variation within this species.

A single interambulacrum (UF 25339) and associated spines (e.g., UF 25130) from the Parachucla Formation in Hamilton County (FM locality HA001) may belong to the genus *Gagaria* but this material is characterized by a more heavily tuberculated medial area and more strongly crenulated poriferous zones than *G. hunterae* n. sp. We designate this occurrence as *Gagaria*? sp. in Fig. 2.

Hunter's collection from the type locality also contained fragments of a spatangoid echinoid that are too incomplete to be identified to genus. This is the only other echinoid species Hunter collected along with the lone specimen of *G. hunterae* n. sp. at the type locality.

Etymology.—The species is named in honor of Florida biostratigrapher Muriel Hunter, collector of the only known specimen. Without her diligence in the field and meticulous notes, this species would remain undocumented.

Material and Occurrence.—Known from the holotype UF 235973, collected in the St. Marks Formation (FM locality WA011).

Family **TRIGONOCIDARIDAE** Mortensen, 1903

Genus ***GENOCIDARIS*** A. Agassiz, 1869

GENOCIDARIS OYENI n. sp.

Figures 20–23

Genocidaris sp. Ciampaglio and Osborn, 2011, fig. 2.

Diagnosis.— *Genocidaris* of large size, up to 11.3 mm TD, with high test, TH on average 62.4% TW; small apical system on average 29.5% TW, that apparently lacks a large suranal plate, and proportionately small peristome on average 41% TW. Three elongate vertical depressions below primary tubercles in interambulacra.

Description.—Description based on holotype and five paratypes; only holotype (UF 202640) retains apical system. Test small, hemispherical, ambitus slightly below mid-height; holotype = 10.3 mm TW, 6.7 mm TH; dimensions of six specimens: 6.6–11.3 mm TW, 3.9–7.5 mm TH; on average TH = 62.4% TW. Oral surface slightly flattened, slightly sunken towards peristome. Peristome on average 41% TW, decreasing in size relative to TW as specimens increase in size. Apical system dicyclic, ocular plates widely exsert, 2.9 mm greatest diameter on holotype (= 31% TW), maximum diameter of apical opening on missing apical system on average 29.5% maximum TW; five genital plates, surface often uneven, with gonopore and three additional shallow pores (possibly eroded tubercles) situated between gonopore and periproct on each plate, otherwise lacking in ornamentation; gonopores nearly circular; characteristic large suranal plate of *Genocidaris maculata* A. Agassiz, 1869 apparently lacking. Periproct slightly subpentagonal, 10.5% TL at widest point. Ambulacra on average 55% width of interambulacra at ambitus. Pore-pairs uniserial, nearly straight, arranged in slight arc adjacent to each primary tubercle; pore zones narrow, not widened adorally. Single small, non-crenulate, imperforate primary tubercle (largely eroded in holotype, leaving pit-like scar) to each trigeminate ambulacral plate, surrounded by dense population of secondary and miliary tubercles, small pits around tubercles constitute sculpting of test. Primary tubercles of interambulacra about same size as those of ambulacral regions; often inconspicuous among secondary tubercles; three vertically elongate depressions below each primary tubercle in interambulacrum (distinct in uncorroded specimens, especially UF 202640; Fig. 20).

Zoobank Nomenclatural Act.—E2E5A5C6-5B5E-4E09-9364-7F810592A342.

Discussion.—The occurrence of a species of *Genocidaris* in the upper Pliocene Intracoastal Formation of Liberty County, Florida was first documented in Ciampaglio and Osborn (2011). Sufficient specimens have now been collected to differentiate the species with confidence from *G. maculata*, an extant congener that thrives at depths of 12–420 m in regional waters (Serafy, 1979). *Genocidaris oyeni* n. sp. is the first documented occurrence of the genus in the fossil record of the region and has not been documented outside of the upper Pliocene Intracoastal Formation in the Langston Quarry, Liberty County, Florida (FM locality LI005).

Genocidaris oyeni n. sp. (Figs. 20–23) is similar in gross morphology to *G. maculata* (Fig. 24), which is also very small, rarely exceeding 13 mm in diameter (Serafy 1979) but is typically much smaller. Serafy (1979:fig. 17) documented the diameter of 299 specimens of *G. maculata* from a single station in the Gulf of Mexico, at a depth of 73 m, 92 nautical miles due west of Sanibel Island that demonstrate a typical diameter between 2 and 5 mm, with rare specimens up to 6 mm in TD. Mortensen (1943) stated the largest specimen of *G. maculata* is 12.7 mm but the adults are usually 7–9 mm in TD. The specimens of *G. oyeni* n. sp. range from 6.6–11.3 mm in TD. However, this is based only on six specimens. The specimens of *G. oyeni* appear proportionately higher than specimens of *G. maculata* in the FM-IP collections, but due to the small sample size, it remains problematic to rely on overall test dimensions for positive identification.

Although only the holotype (Fig. 20) of *G. oyeni* retains its apical system, this feature reveals one of the most reliable distinguishing features between this species and *G. maculata*. *Genocidaris oyeni* n. sp. apparently lacks a large suranal plate, which Mortensen (1943) described as a

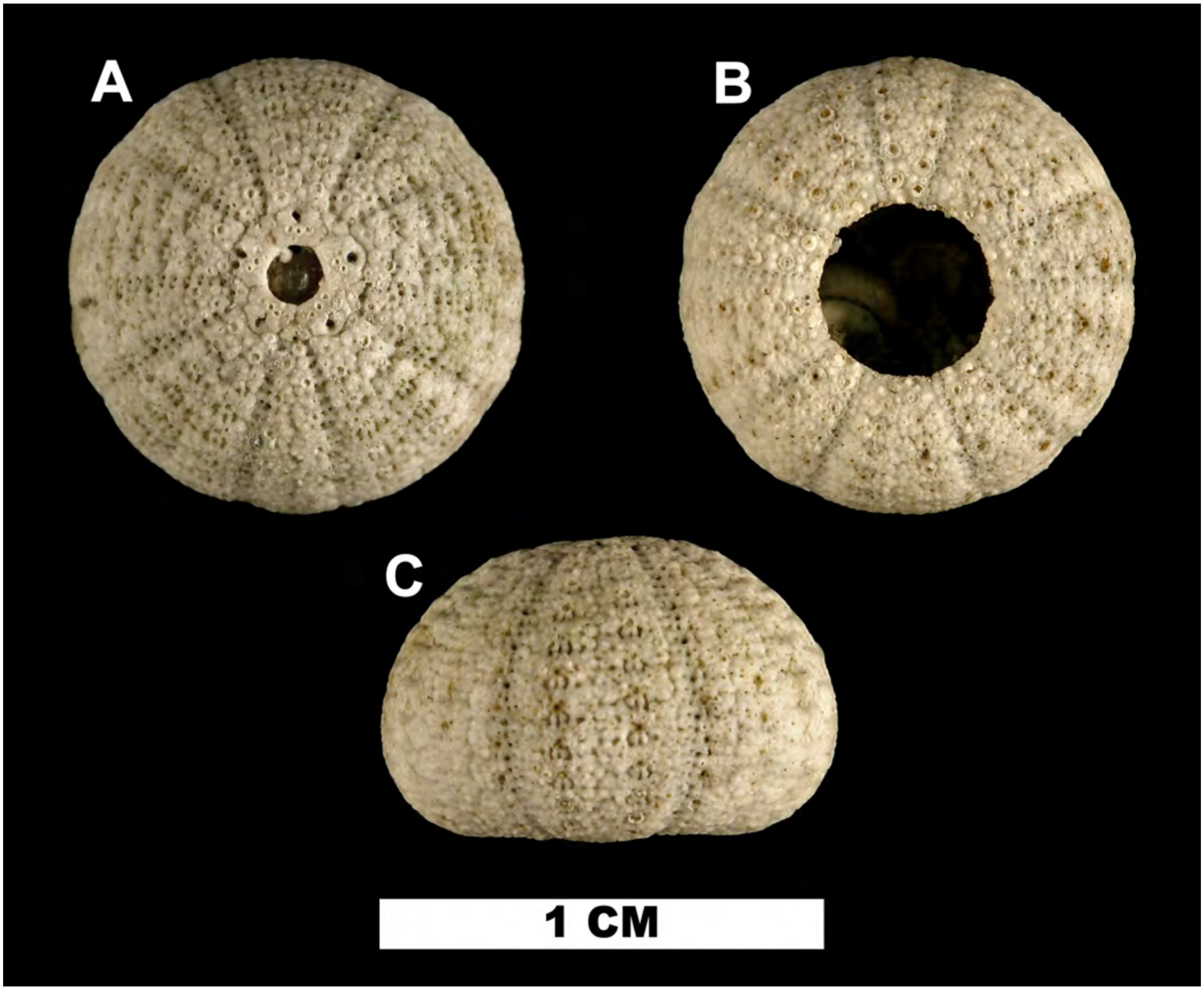


Figure 20. *Genocidaris oyeni* n. sp., holotype (UF 202640), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

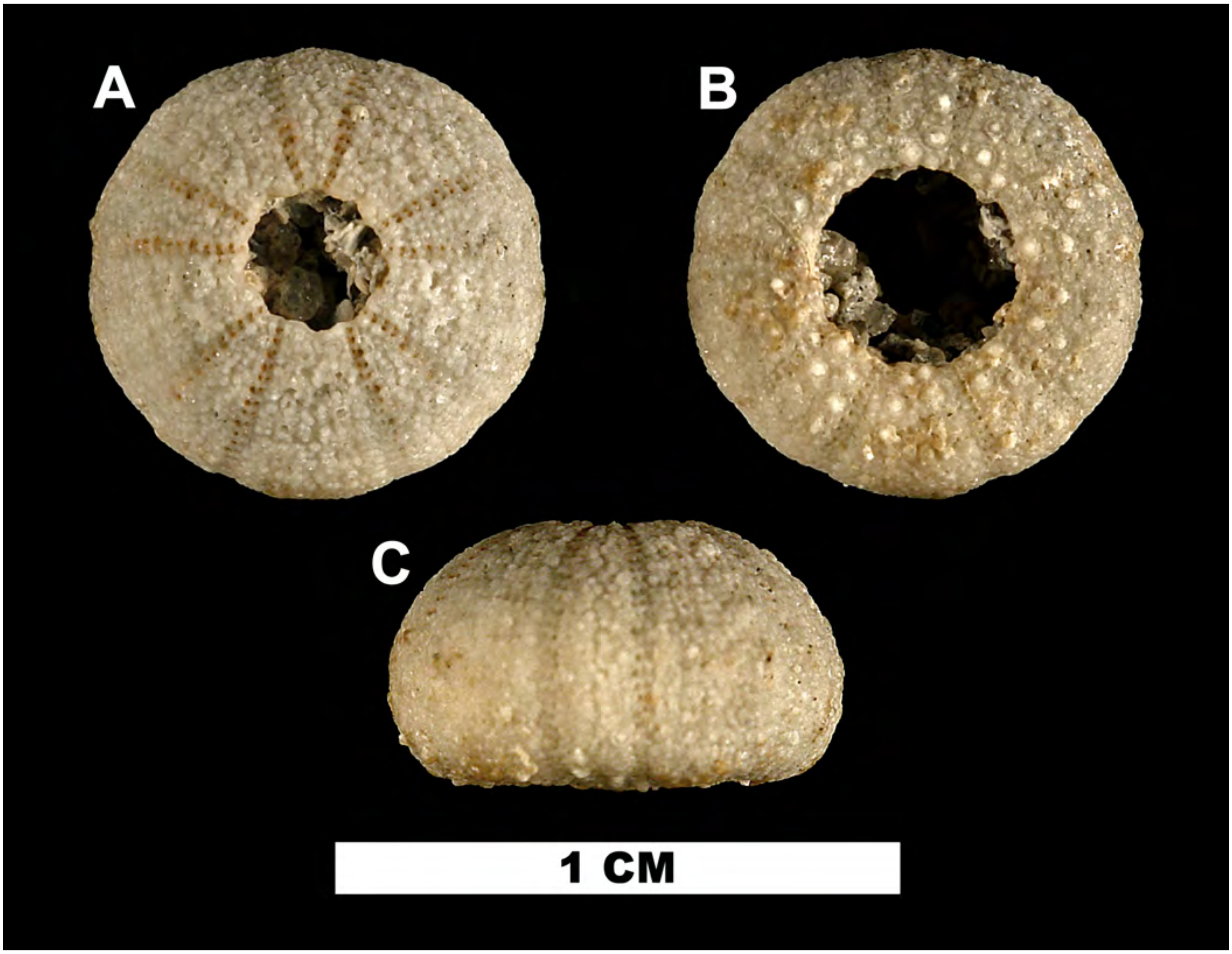


Figure 21. *Genocidaris oyeni* n. sp., paratype (UF 202638), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

"very characteristic, large, shining suranal plate". Such a plate often covers the periproct of *G. maculata*, and is clearly figured by Agassiz (1872: pl. VII, fig. 3). In addition, the peristome of *G. maculata* is demonstrated by Mortensen (1943:360) to be on average 46.2% TW, whereas in *G. oyeni* the peristome is proportionately smaller, with a TW on average of 41%. Furthermore, the apical system of *G. maculata* is on average 42.1% TW, whereas in *G. oyeni* the maximum width of the opening where the apical system should be (apical system is missing in all specimens except the holotype) is on average 29.5% maximum TW. Additionally, in *G. oyeni*, three elongate vertical depressions are present below the primary tubercles in interambulacral areas. These depressions are sharply defined in the well-preserved holotype (Fig. 20) and are not present in *G. maculata*.

The holotype (UF 202640) of *G. oyeni*, and, to a lesser extent, other specimens (such as UF 202638; Fig. 21), have large pits on the test. This is especially visible on the genital plates of the holotype, which display three pits each. We interpreted these features as the remnants of tubercles lost to an undetermined taphonomic or diagenetic process.

The genus *Genocidaris* is very similar to *Arbacina* Pomel, 1869, another small camarodont urchin very common in the Plio-Pleistocene of the Mediterranean region. Mortensen (1943) stated "it can scarcely be doubted that this genus [*Genocid-*

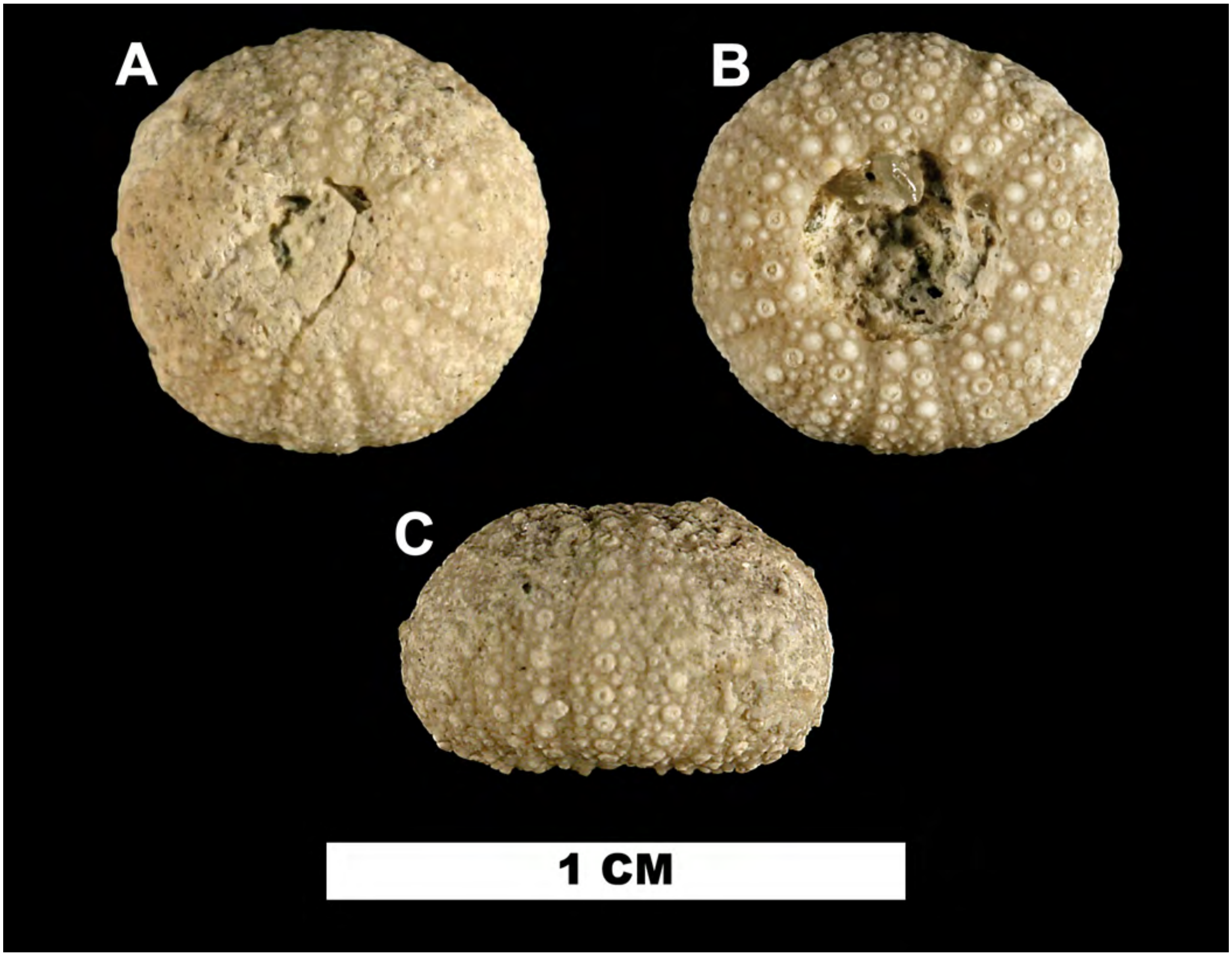


Figure 22. *Genocidaris oyeni* n. sp., paratype (UF 202639), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

aris] is closely related to the fossil genus *Arbacina*, and it is not at all surprising that the Mediterranean specimens of *G. maculata* were designated as a Recent species of *Arbacina* (*A. pallaryi* Gauthier, 1897).” Mortensen (1943) reported that the two genera must be regarded as distinct due to the indentations at the bases of the primary tubercles in *Genocidaris*, and by sutural depressions in *Arbacina*, which are very rare in *Genocidaris*. Kroh (2003:161) followed Mortensen (1943) and also distinguished *Genocidaris* from *Arbacina* by the presence of indentations in the bases of the primary and marginal tubercles and the lack of sutural depressions in the horizontal sutures.

Borghi et al. (2005) discussed the similarities of *Arbacina* and *Genocidaris* and cast doubt on the validity of both genera. They documented indentations around the base of primary tubercles in representatives of *Arbacina romana* (Merian in Desor, 1858) from the lower Pleistocene of Sicily, and other localities. They also documented the frequent lack of sutural depressions on plates of *A. romani*. Thus, the distinguishing traits of these two genera are not constant. However, Borghi et al. (2005) came to no firm conclusions regarding the retention of either, or both, genera. If future authors decide the retention of both genera is untenable, some additional research will be required to decide which genus has precedence, as both date from 1869 (*Arbacina* Pomel, 1869; *Genocidaris* A.

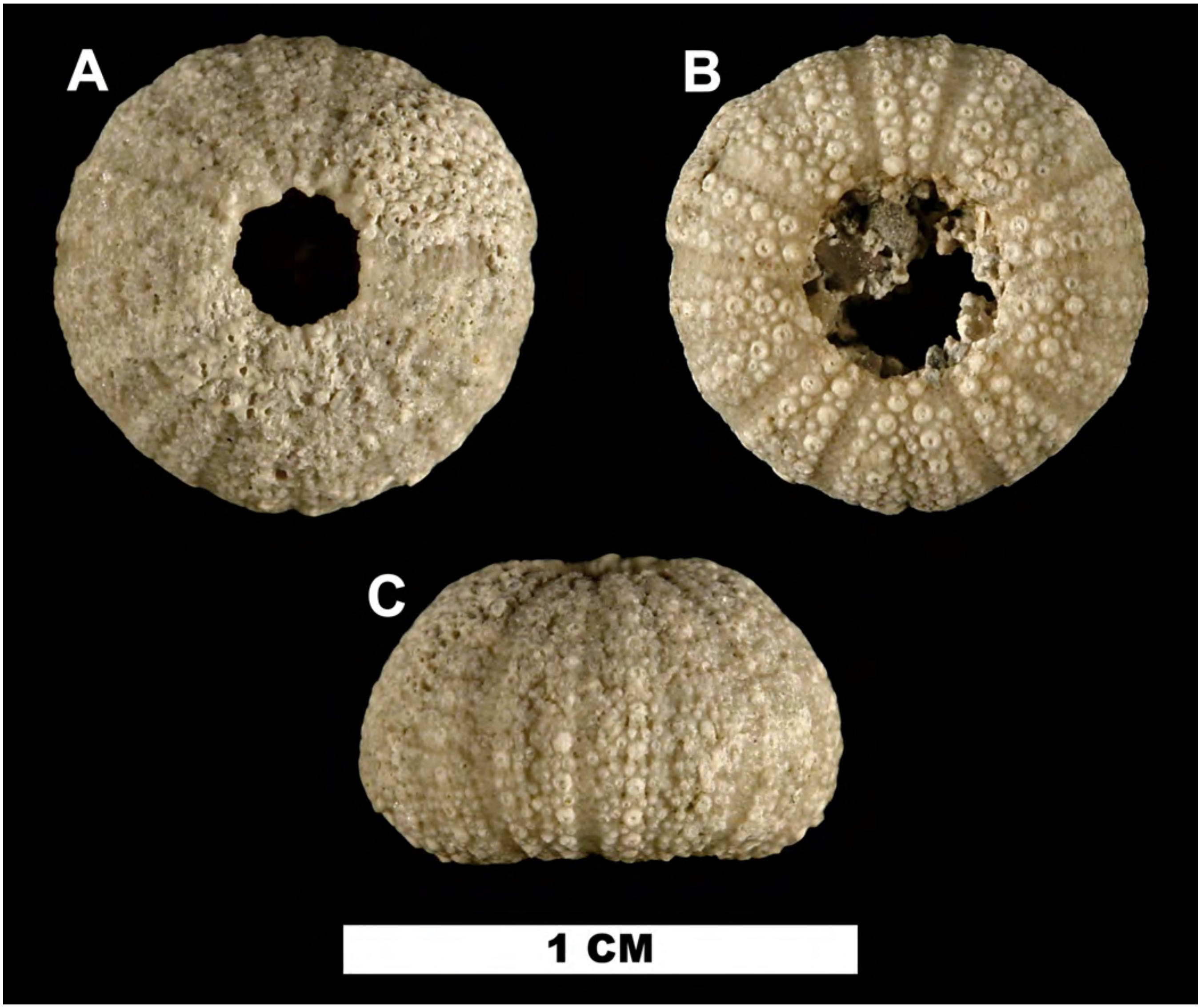


Figure 23. *Genocidaris oyeni* n. sp., paratype (UF 202635), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

Agassiz, 1869).

Genocidaris oyeni n. sp. is associated with *Argyrotheca* sp., a small articulate brachiopod, and a diverse suite of echinoids within the Intracoastal Formation (Ciampaglio and Osborn, 2011).

Etymology.—*Genocidaris oyeni* n. sp. is named in honor of the late Dr. Craig Oyen in recognition of his significant contributions to our knowledge of Florida fossil echinoids.

Material and Occurrence.—Holotype UF 202640 and five paratypes UF 202635, UF 202639, UF 202641, UF 202638, UF 202637, collected from the upper Pliocene Intracoastal Formation in the Langston Quarry (FM locality LI005), Liberty County, Florida. This species has not been documented outside of the type locality.

Family **TOXOPNEUSTIDAE** Troschel, 1872
Genus ***LYTECHINUS*** A. Agassiz, 1863
LYTECHINUS VARIEGATUS (Leske, 1778)
Figures 25–29

Cidaris variegata (part) Leske. 1778, p. 149, pl. 10, figs. B, C.
Echinus variegatus (Lamarck). Holmes, 1860, p. 4, pl. 2, fig. 1.

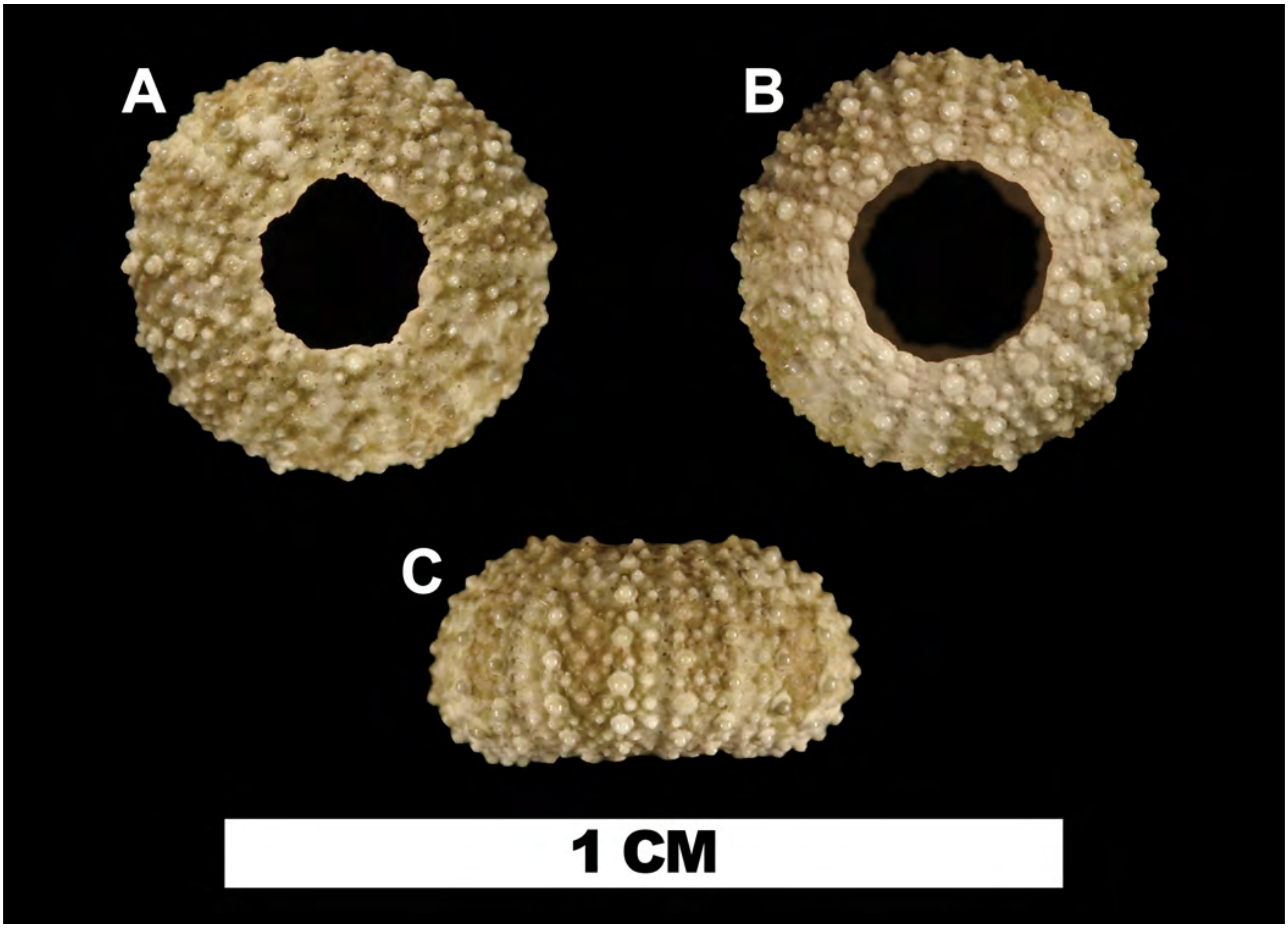


Figure 24. *Genocidaris maculata* (UF-IZ 18917), modern specimen for comparison from (Gulf of Mexico, 140 miles off Cape Ramano, Florida, USA). A. aboral view, B. oral view, C. lateral view.

Toxopneustes variegatus (Lamarck). Clark and Twitchell, 1915, p. 222.

Lytechinus variegatus (Leske). Cooke, 1941, p. 17.

Lytechinus variegatus (Lamarck). Mortensen, 1943, pp. 437–446. (includes additional synonymy)

Lytechinus variegatus (Leske). Cooke, 1959, p. 15, pl. 2, figs. 12, 13.

Lytechinus variegatus (Leske). Cooke, 1961, p. 10, pl. 5, figs. 1, 2.

Lytechinus variegatus plurituberculatus, Kier, 1963, p. 15, pl. 2, figs, 1, 2, pl. 3, fig. 1, pl. 4, fig. 4, text figs. 8–11.

Lytechinus variegatus (Leske). Kier and Grant, 1965, pp. 21, 22, 24, pl. 3, fig.1. text fig. 5.

Lytechinus variegatus variegatus (Leske). Serafy, 1973, pp. 525–533.

Lytechinus variegatus (Leske). Kier, 1975, p. 17, pls. 11.1, 11.2.

Lytechinus variegatus carolinus (A. Agassiz). Serafy, 1979, pp. 49–56, figs. 21–24. tbl. 10. (includes additional synonymy).

Lytechinus variegatus (Leske). Hendler et al., 1995, pp. 216–218, figs.114, 134D.

Lytechinus sp. cf. *L. variegatus* (Leske). Donovan, 2000, pp. 316–317.

Lytechinus variegatus (Leske). Oyen and Portell, 2001, pp. 193–218, pl. II, fig. 1.

Lytechinus variegatus (Leske). Donovan et al., 2001, pp. 6–9, figs. 2, 3.

Lytechinus variegatus (Leske). Pomory, 2003, pp. 30–32, fig. 12.

Lytechinus variegatus (Leske). Zigler and Lessios, 2004, pp. 1225–1241.

Lytechinus variegatus (Leske). Ciampaglio et al., 2009, fig. 2.

Lytechinus variegatus (Leske). Ciampaglio and Osborn, 2011, fig. 2.

Lytechinus variegatus plurituberculatus (Kier). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—This species is a common in the sand facies of the upper Pliocene Tamiami Formation of southern Florida, as well in the lower

Pleistocene Caloosahatchee Formation and undifferentiated upper Pleistocene deposits in the southern portion of the state. The type locality for *L. variegatus plurituberculatus* is the Caloosahatchee Formation in the old Denaud pits, in NW¼ sec. 14, T. 43 S., R 28 E., Sears Quadrangle, Hendry County, near LaBelle (Kier, 1963). This species was also common at the Caloosahatchee Formation in the Cochran Shell Pit, Hendry County (FM locality HN004).

In the Quality Materials Quarry, Charlotte County (FM locality CH080), specimens of *L. variegatus* retaining delicate spination are often found in the Tamiami Formation (UF 204298; Fig. 25). Large specimens of this species (e.g., UF 118114) retaining their spines were also collected in an undifferentiated upper Pleistocene-Holocene deposit in spoil from canal dredging near Cape Coral, Lee County (FM locality LE020) (Fig. 26).

Lytechinus variegatus is noticeably absent in correlative upper Pliocene deposits of north Florida, including the Intracoastal Formation of the panhandle (which incorporates many other elements of the echinoid fauna of the Tamiami Formation) and the lower portion of the Nashua Formation, which includes a late Pliocene fauna in

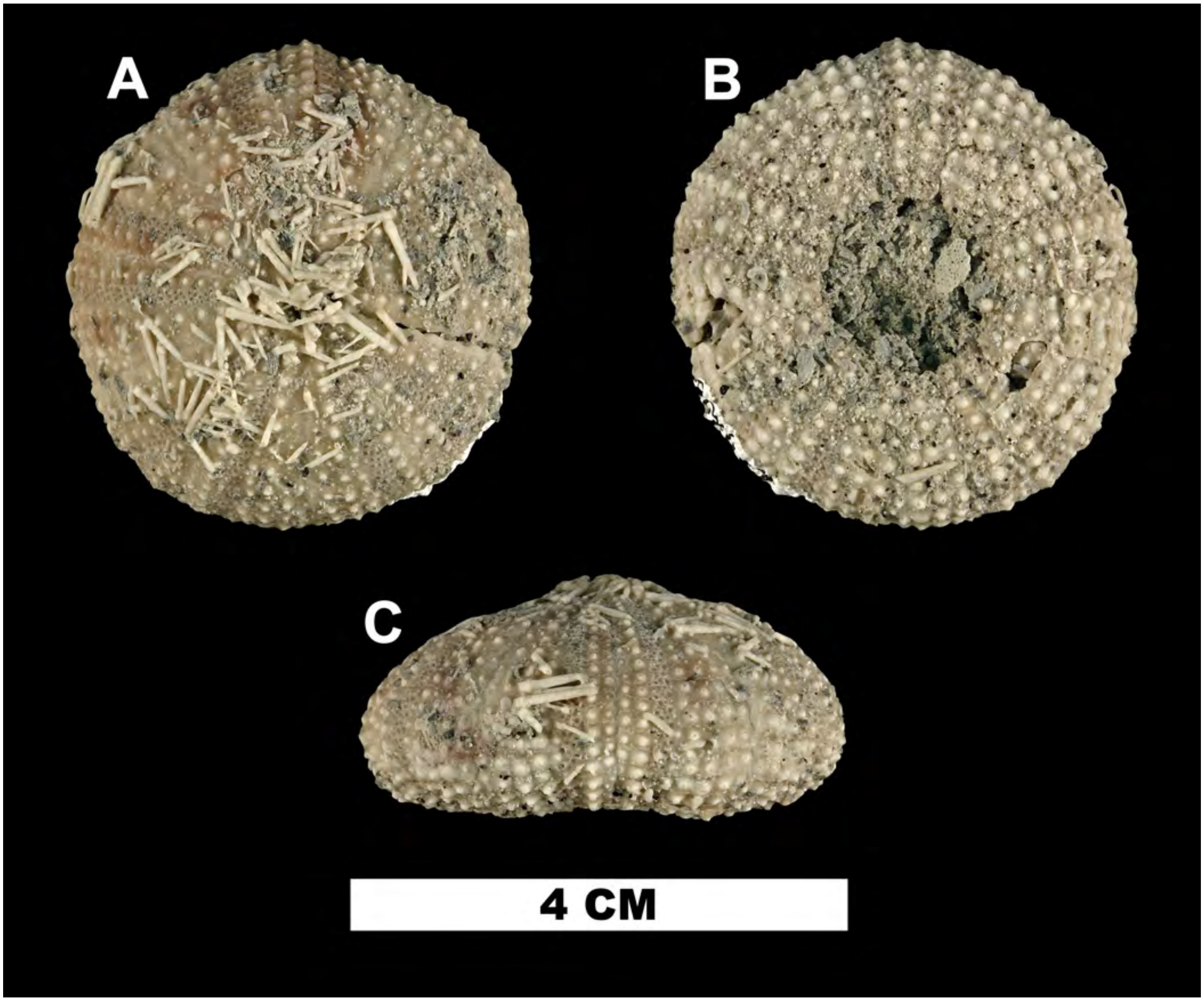


Figure 25. *Lytechinus variegatus* with spines (UF 204298), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

north Central Florida. This absence is not due to a northerly limit of the species in the late Pliocene as the species also occurs in the upper Pliocene–Pleistocene strata of the Carolinas (Ciampaglio et al., 2009; Ciampaglio and Osborn, 2011).

The fossil record of *L. variegatus* in the Caribbean includes occurrences in the Pliocene and Pleistocene of Barbados, Jamaica, Tobago, and Venezuela (Donovan et al., 2001).

Discussion.—*Lytechinus variegatus* is a common nearshore species of the southeastern United States and Caribbean south to Brazil (Hendler et al., 1995). Color of the test and spines is highly variable, from green, red, purple, to nearly white, and this variation has been used as partial basis for separation of the species into subspecies (Serafy, 1973). Mature specimens in the modern faunas can be 110 mm across with spines and 85 mm TD, though it is usually much smaller (Hendler et al., 1995). Specimens in the fossil record

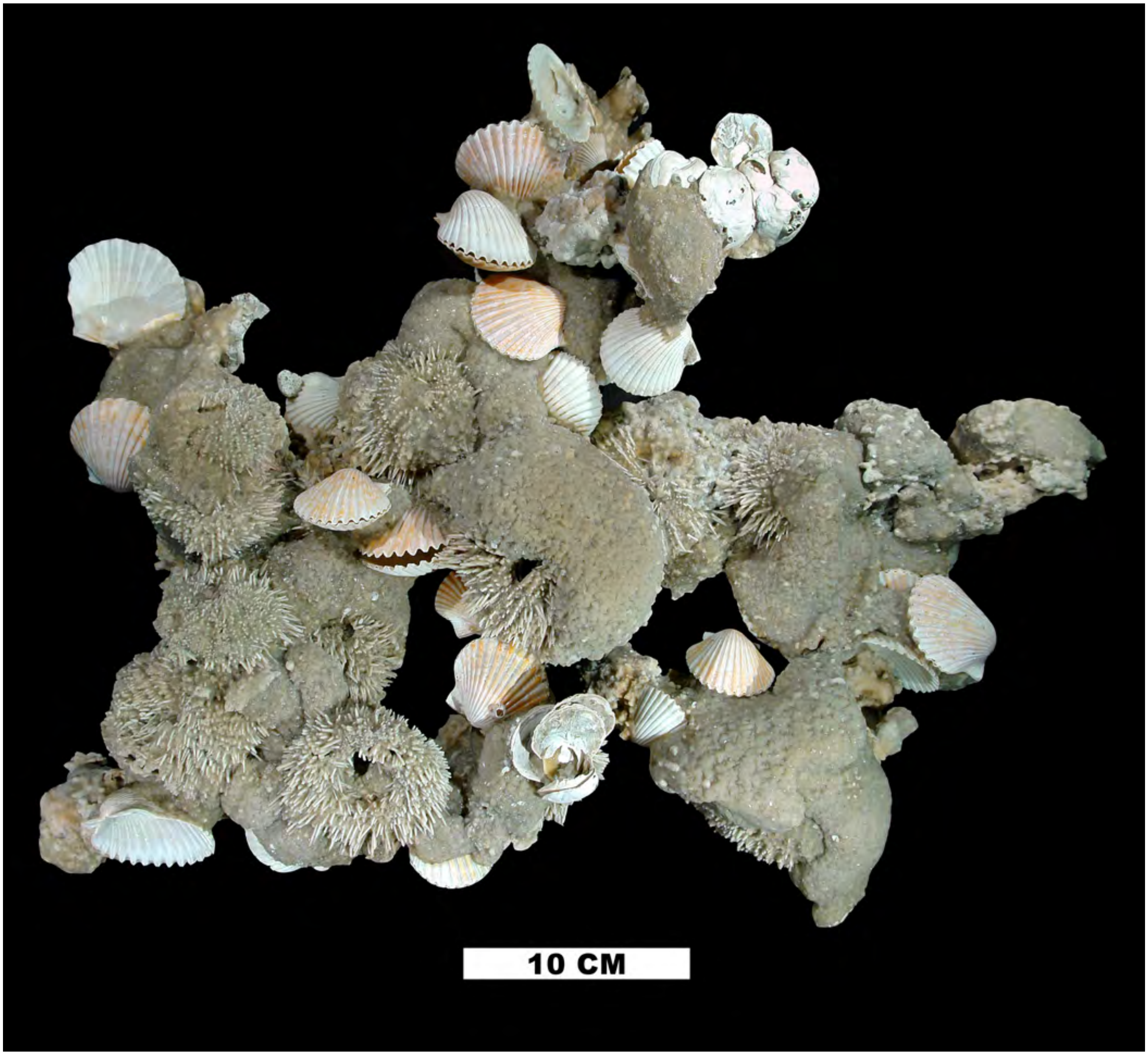


Figure 26. A rare accumulation of *Lytechinus variegatus* (UF 118114) retaining almost complete spination, undifferentiated upper Pleistocene-Holocene deposit (FM locality LE020).

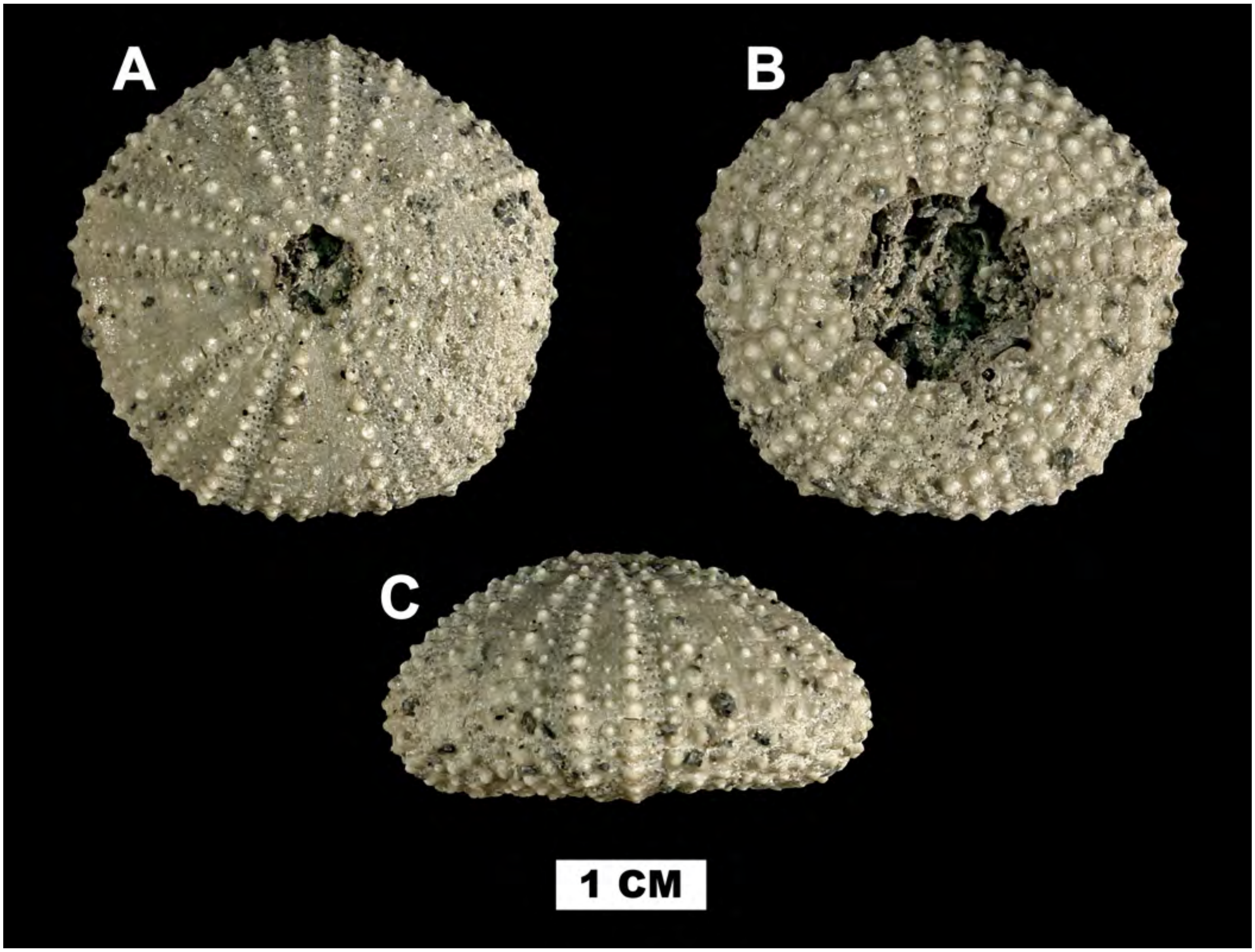


Figure 27. *Lytechinus variegatus* (UF 289216), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

seldom, if ever, attain these maximum sizes.

In contrast to the other common species of Recent regular urchins found throughout the region, such as *Diadema antillarum* (Philippi, 1845)*, Tripneustes ventricosus* (Lamarck, 1816)*, Eucidaris tribuloides,* and *Echinometra lucunter* (Linnaeus, 1758); *L. variegatus* is much better represented in the Neogene fossil record of the region, in spite of the factors inhibiting fossilization of these species (Greenstein, 1991, 1993a, b). The abundant occurrence of a fragile regular urchin such as *Lytechinus* in deposits discussed herein can only be explained by rapid burial. The presence of tests that often retain their spines (especially those in the Tamiami Formation near Placida, Charlotte County, Florida), indicates that deposition occurred with very minimal transport (Greenstein, 1993b).

Notable fossil *L. variegatus* include an exceptional assemblage collected from a calcareous upper Pleistocene-Holocene sandstone deposit during canal dredging near Cape Coral, Lee County (FM locality LE020) (UF 118114). This assemblage is remarkable for both near complete preservation of spination, and the large size of the specimens (Fig. 26).

Lytechinus variegatus is also commonly collected with at least some spines in place in the upper Pliocene Tamiami Formation in the Quality Materials Quarry, Charlotte County (FM locality CH080) (UF 204298; Fig. 25), as well as in addi-

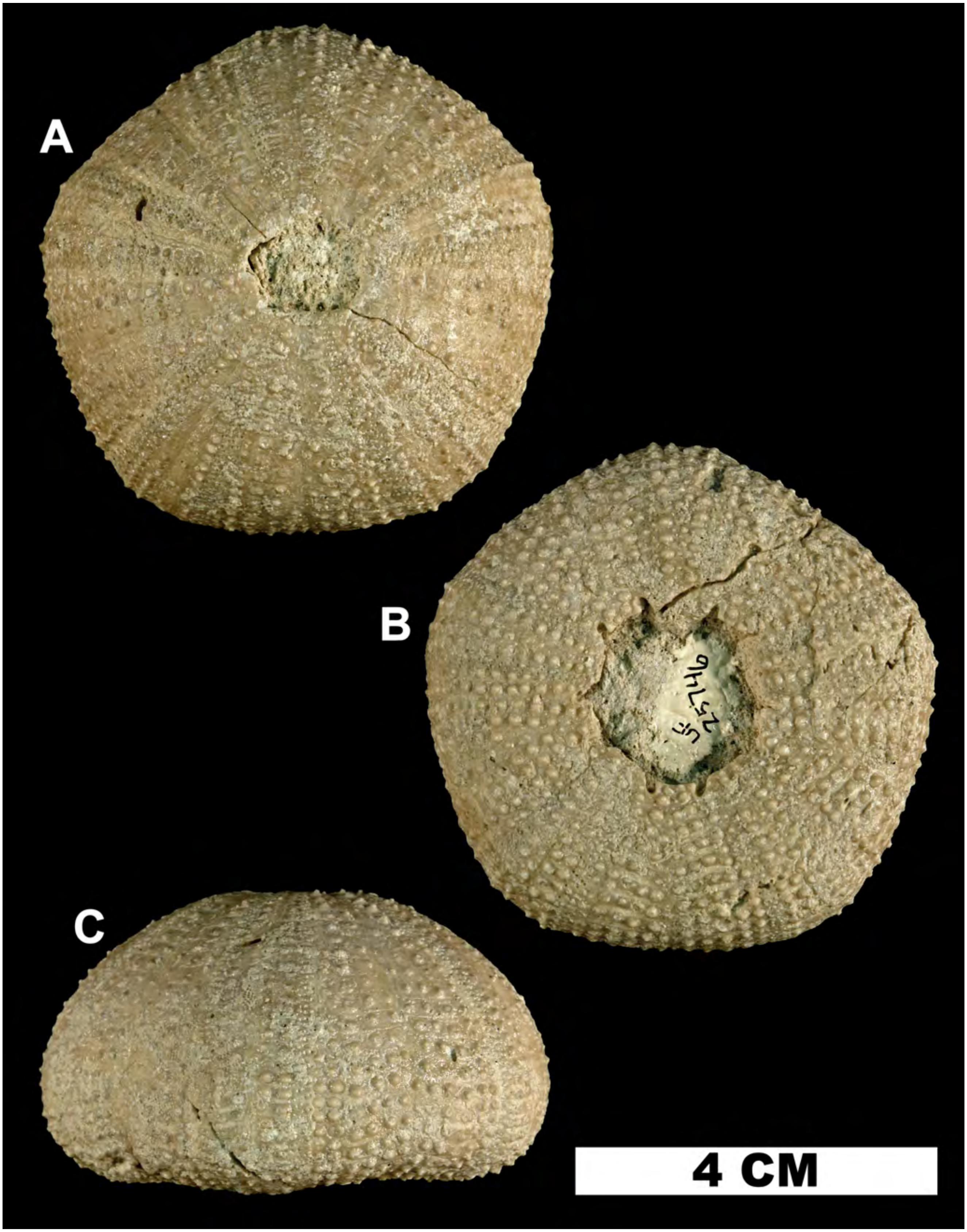


Figure 28. *Lytechinus variegatus* (UF 25746), Caloosahatchee Formation (FM locality HN004). A. aboral view, B. oral view, C. lateral view.

tional quarries south of Fort Myers, Lee County. The spination of these late Pliocene specimens is indistinguishable from that of the modern representatives of the species, though the individuals are, on average, smaller in size, rarely exceeding 35 mm TD in the Tamiami Formation (UF 289216; Fig. 27). This decrease in average size in the late Pliocene specimens of Lee County is not consistent in populations of the late Pliocene throughout the region, as *L. variegatus* often exceeds 75 mm TD in the correlative upper Pliocene Goose Creek Limestone of northeastern South Carolina. Specimens from the lower Pleistocene Caloosahatchee Formation are typically larger than those from the Tamiami Formation; a specimen (UF 64825) from Palm Beach County (FM locality PB014) is 60 mm TD, and another from the Cochran Shell Pit (FM locality HN004) (UF 25746; Fig. 28) is 57 mm TD.

Kier (1963) described the subspecies, *L. variegatus pluritaberculatus*, from the Caloosahatchee and Tamiami Formations of southern Florida. He distinguished it from *L. variegatus variegatus*, which he did not document in these units, by the more numerous tubercles in its ambulacra. Kier (1963) recognized that this subspecies is identical in all its characters with *L. variegatus variegatus* except in the number and arrangement of the secondary tubercles in the ambulacra and the lateral

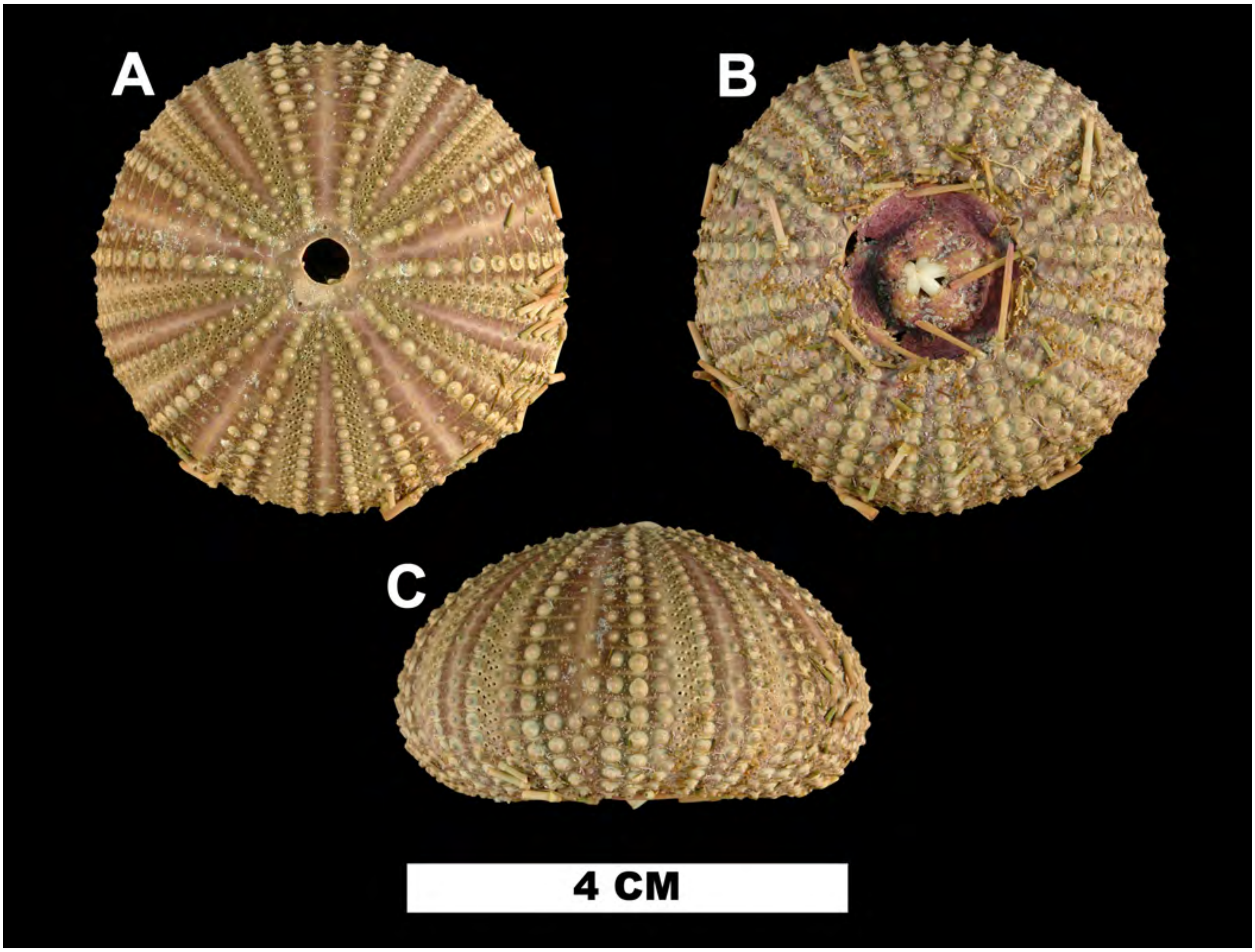


Figure 29. *Lytechinus variegatus* (UF-IZ 18898), modern specimen for comparison (St. Andrew Bay, Panama City, at 1 m depth in seagrass, Bay County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

distance between the primary ambulacral tubercles. However, tuberculation in the dozens of specimens of *L. variegatus* described herein from the Tamiami Formation of Florida is highly variable.

Kier (1963) admitted that there is overlap in the characters of his subspecies and the typical *L. variegatus*, which is why he did not elevate his taxon to species. Mortensen (1943:440) reported that specimens with a double series of secondary tubercles are rare, but do occur in Recent populations of *L. variegatus*. Although the occurrence of specimens with a double row of secondary tubercles is more prevalent in *L. variegatus plurituberculatus* Kier, 1963, we do not believe this warrants subspecific designation, and herein treat these specimens as *L. variegatus*.

Family **ECHINOMETRIDAE** Gray, 1855

Genus ***ECHINOMETRA*** Gray, 1825

ECHINOMETRA LUCUNTER (Linnaeus, 1758)

Figures 30–33

Echinus lucunter Linnaeus, 1758, p. 665.
Echinometra lucunter (Linnaeus). Cooke, 1941, p. 18.
Echinometra lucunter (Linnaeus). Mortensen, 1943, p. 357. (includes a very extensive additional synonymy).
Echinometra lucunter (Linnaeus). Dartevelle, 1953, p. 38.
Echinometra lucunter (Linnaeus). Cooke, 1959, p. 25, pl. 6, figs. 1, 2.
Echinometra lucunter (Linnaeus). Gordon, 1963, pp. 632–635.
Echinometra lucunter (Linnaeus). Kier, 1963, p. 19. pl. 3, fig. 2; pl. 4, figs. 1–3.
Echinometra lucunter (Linnaeus). Kier and Grant, 1965, pp. 18, 20, pl. 16, figs. 1–4.
Echinometra lucunter (Linnaeus). Kier, 1966, p. 6, pl. 1, fig. 2. pl. 2, fig. 4.
Echinometra lucunter (Linnaeus). Kier, 1975, p. 17.
Echinometra lucunter (Linnaeus). Lewis and Storey, 1984, pp. 207–211.
Echinometra lucunter (Linnaeus). Gordon, 1991, pp. 37–41, fig. 2.
Echinometra lucunter (Linnaeus). Kier, 1992, p. 17, pl. 4, figs. 1–4.
Echinometra lucunter (Linnaeus). Donovan, 1993, pp. 381–382, fig. 8.
Echinometra lucunter (Linnaeus). Donovan, 1994, pp. 166–169, fig. 1c.
Echinometra lucunter (Linnaeus). Donovan and Jones, 1994, pp. 109–111, fig. 1.
Echinometra lucunter (Linnaeus). Hendler et al., 1995. pp. 225–225, figs. 117, 134F.
Echinometra lucunter (Linnaeus). Oyen and Portell, 2001, pp. 193–218, pl. II, fig. 2.
Echinometra lucunter (Linnaeus). Pomory, 2003, pp. 23–25, fig. 9.
Echinometra sp. cf. *E. lucunter* (Linnaeus). Donovan et al., 2005, pp. 104–105, pl. 1.13, pl. 2, 1–7, pl. 7, 2, 3, 6.

Occurrence.—*Echinometra lucunter* is rare as a fossil in Florida, but it is present in the lower Pleistocene Caloosahatchee Formation, especially in the vicinity of LaBelle, where Kier (1963) noted its occurrence in the old Denaud pits, in NW¼ sec. 14, T. 43 S., R 28 E., Sears Quadrangle, Hendry County. *Echinometra lucunter* was also collected from the Caloosahatchee Formation in the Cochran Shell Pit near LaBelle, Hendry County (FM locality HN004), and in Collier County (FM locality CR006). The species is also documented from the Miami Limestone near Buena Vista, Miami (USGS locality 4867).

This species is widespread in the Caribbean: Jamaica (Miocene[?] [Donovan et al., 2005] – Pleistocene [Donovan, 1993, 1994]), Dominican Republic (Pliocene [Kier, 1992]), Angola (Pleistocene [Dartevelle, 1953]), Puerto Rico (late Oligocene? [Gordon, 1963]), Bermuda (Pleistocene [Donovan and Jones, 1994]).

Discussion.—*Echinometra lucunter* occurs in the Recent fauna from Florida to Brazil and Bermuda, and the western coast of Africa (Hendler et al., 1995). It is especially common in shallow-water rocky habitats of the Florida Keys and throughout the Caribbean. Hendler et al. (1995) stated that *E. lucunter* can exceed 150 mm in size, though we suspect this includes spines, as Mortensen (1943) indicated that Clarke's (1912) specimen from Bermuda, at 94 mm TD, was the largest ever documented. A more typical size is up to 65 mm TD, but it is usually smaller. The species test is exceptionally variable, so much so that Mortensen (1943) stated that if the known variation occurred in fossils as well, they would undoubtedly be regarded as distinct.

Donovan (1994) noted that while *E. lucunter* is a common element of modern nearshore environments in the Caribbean, its fossil record is poor, likely due to environmental and taphonomic factors. Gordon (1991) discussed the poor fossil record of the genus *Echinometra* in the region, and Greenstein's (1991, 1993a, b) studies on the taphonomy of this species and other regular echinoids of the region provided evidence that although *E. lucunter* is very common in the nearshore habitats

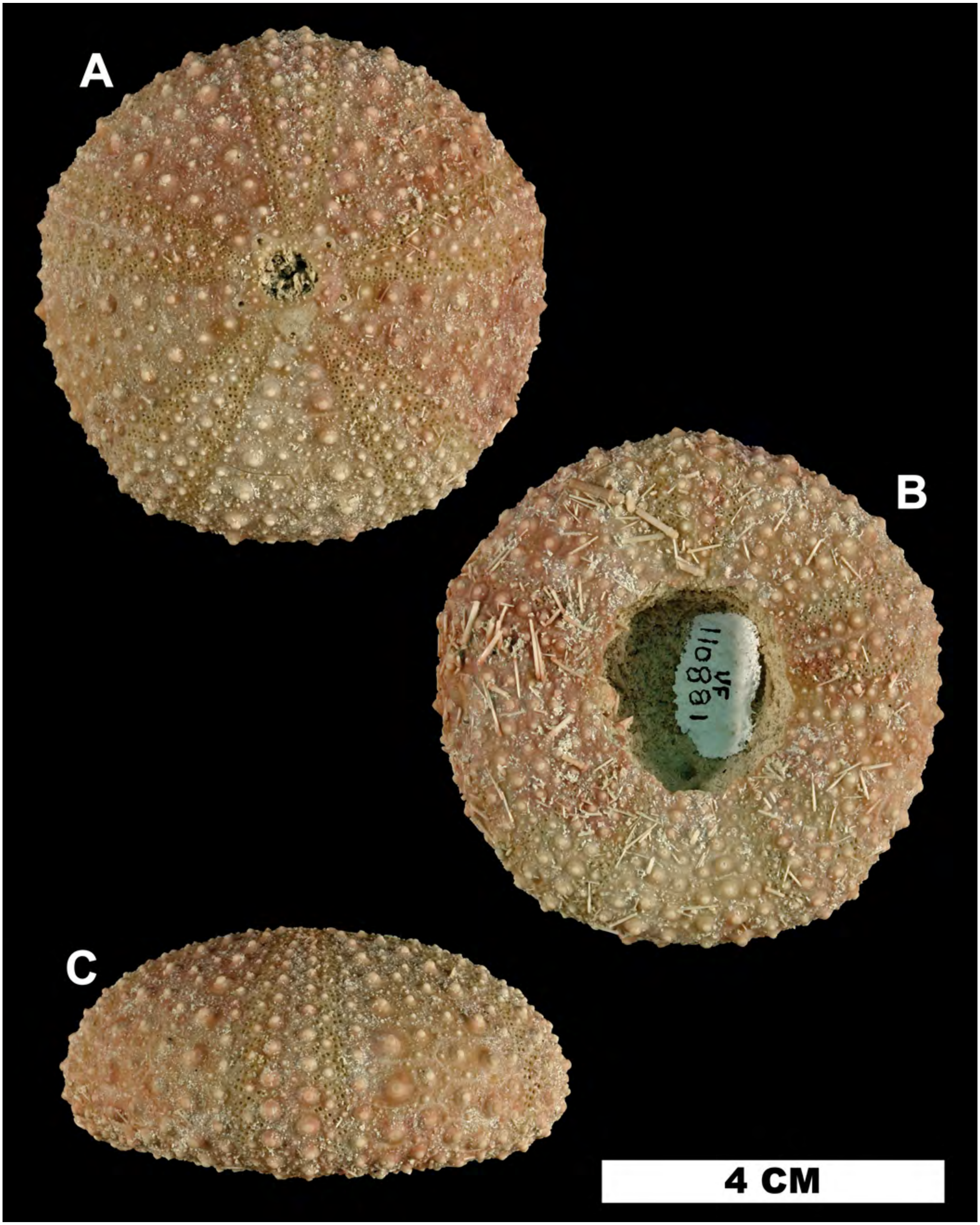


Figure 30. *Echinometra lucunter* (UF 110881), Caloosahatchee Formation (FM locality HN004). A. aboral view, B. oral view, C. lateral view.

of the region today, its relative scarcity in at least the Pleistocene deposits should not imply that it was not equally as widespread and abundant at that time.

Kier (1963) was the first to document fossil *E. lucunter* in the region when he noted the limited occurrence of *E. lucunter* in the lower Pleistocene Caloosahatchee Formation of south Florida. The fossil specimens described by Kier (1963) are only slightly elongated, whereas in most of the Recent specimens the test is greatly elongated. Kier (1963) did not consider this difference to be significant, and according to Clark (1954:374, footnote), Recent specimens are commonly circular in outline in the western part of the Gulf of Mexico.

This tendency for the Caloosahatchee Formation specimens to be more circular in outline than is typical for the modern examples is exemplified in a specimen (UF 110881) from the Cochran Shell Pit, Hendry County (FM locality HN004) (Fig. 30). This specimen is very large, and very nearly circular, being 63.8 mm TD at the point of greatest width, and 63.3 mm TD orthogonal to this axis. A specimen of roughly the same size (UF 12937; Fig. 31) from Collier County (64 mm TD at the point of greatest width, 60.4 mm TD orthogonal to this axis,

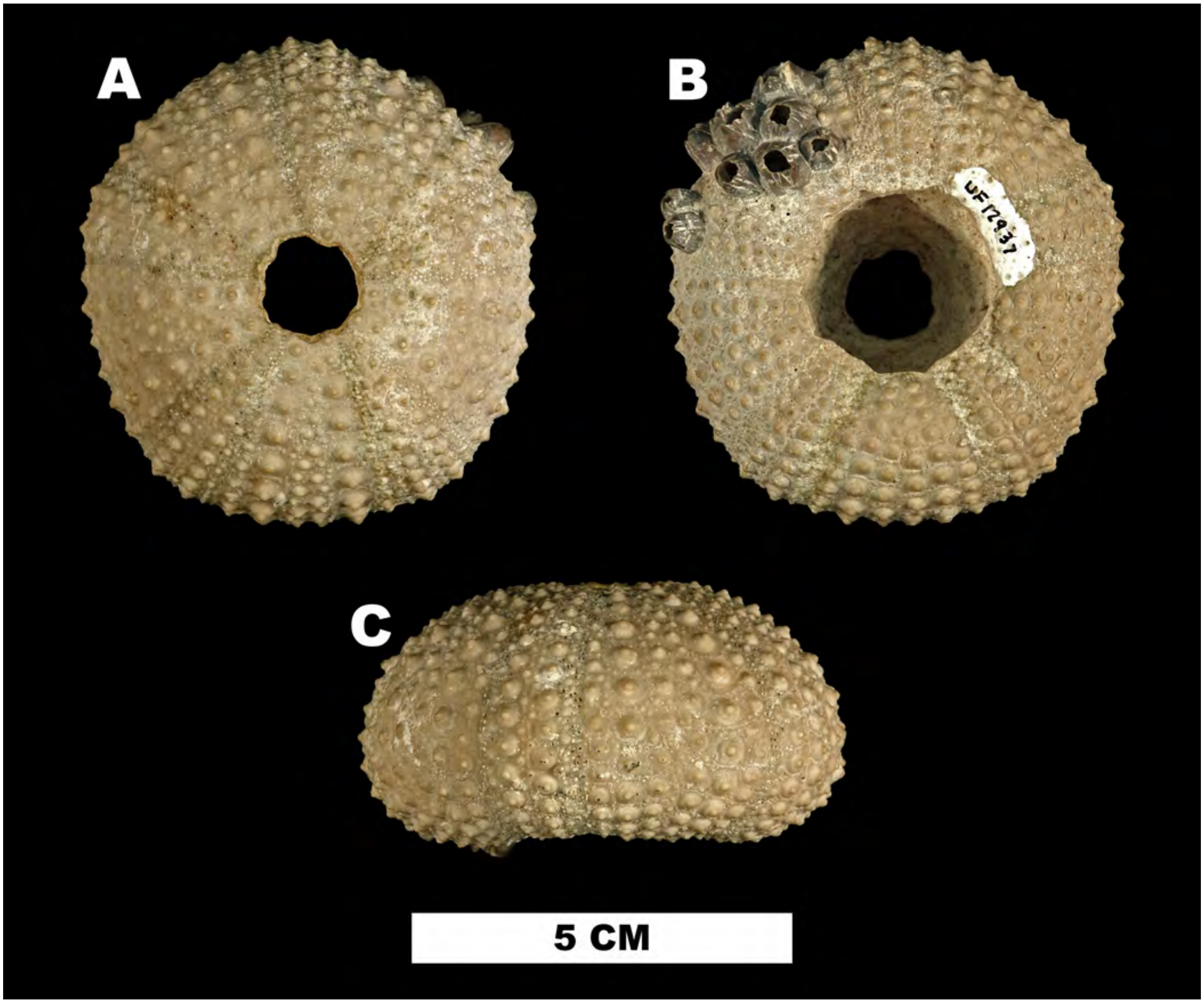


Figure 31. *Echinometra lucunter* (UF 12937), Caloosahatchee Formation (FM locality CR006). A. aboral view, B. oral view, C. lateral view.

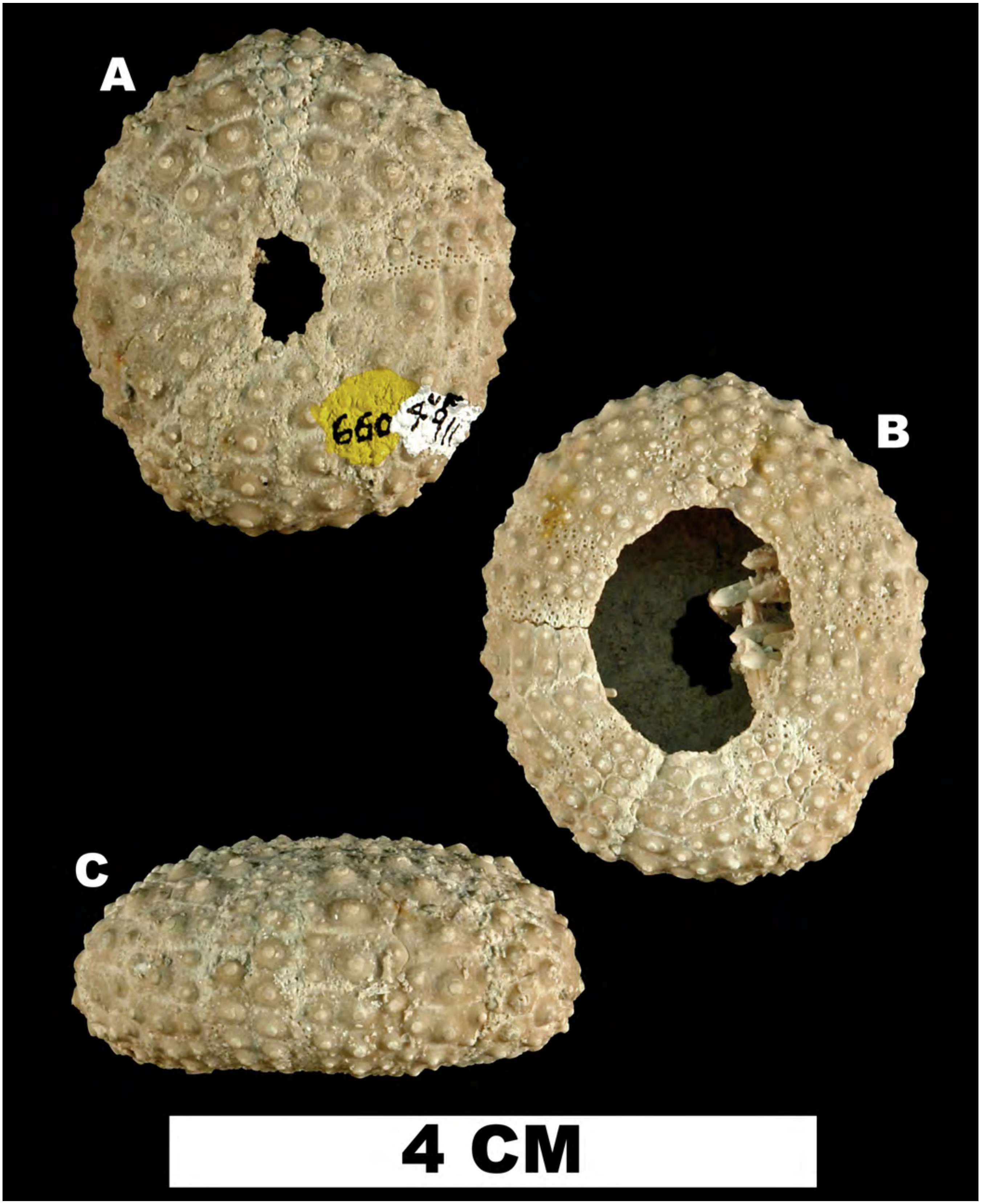


Figure 32. *Echinometra lucunter* (UF 4911), Caloosahatchee Formation (FM locality 2879). A. aboral view, B. oral view, C. lateral view.

and 34.7 mm TH) is slightly more ovate. Although the tendency for a more circular test is more common in larger specimens, this is not always the case as smaller specimens from the Caloosahatchee Formation (e.g., UF 4911; Fig. 32) are typically ovate and more typical of modern representatives of the species.

Infraclass **IRREGULARIA** Latreille, 1825

Order **ECHINOLAMPADOIDA** Kroh and Smith, 2010

Family **ECHINOLAMPADIDAE** Gray, 1851

Genus ***ECHINOLAMPAS*** Gray, 1825

ECHINOLAMPAS LYCOPERSICUS Guppy, 1866

Figures 34–35

Echinolampas lycopersicus Guppy, 1866, p. 300, pl. 19, fig. 8.

Echinolampas lycopersicus (Guppy). Cotteau, 1875, p. 21, pl. 3, figs. 22–26.

Echinolampas anguillae Cotteau, 1875, p. 24, pl. 4, figs. 5–8.

Echinolampas lycopersicus (Guppy). Jackson, 1922, pp. 64–66, pl. 11, figs. 3–6.

Echinolampas anguillae (Cotteau). Jackson, 1922, p. 66, pl. 11, figs. 7–9.

Echinolampas lycopersicus (Guppy). Arnold and Clark, 1927, p. 50.

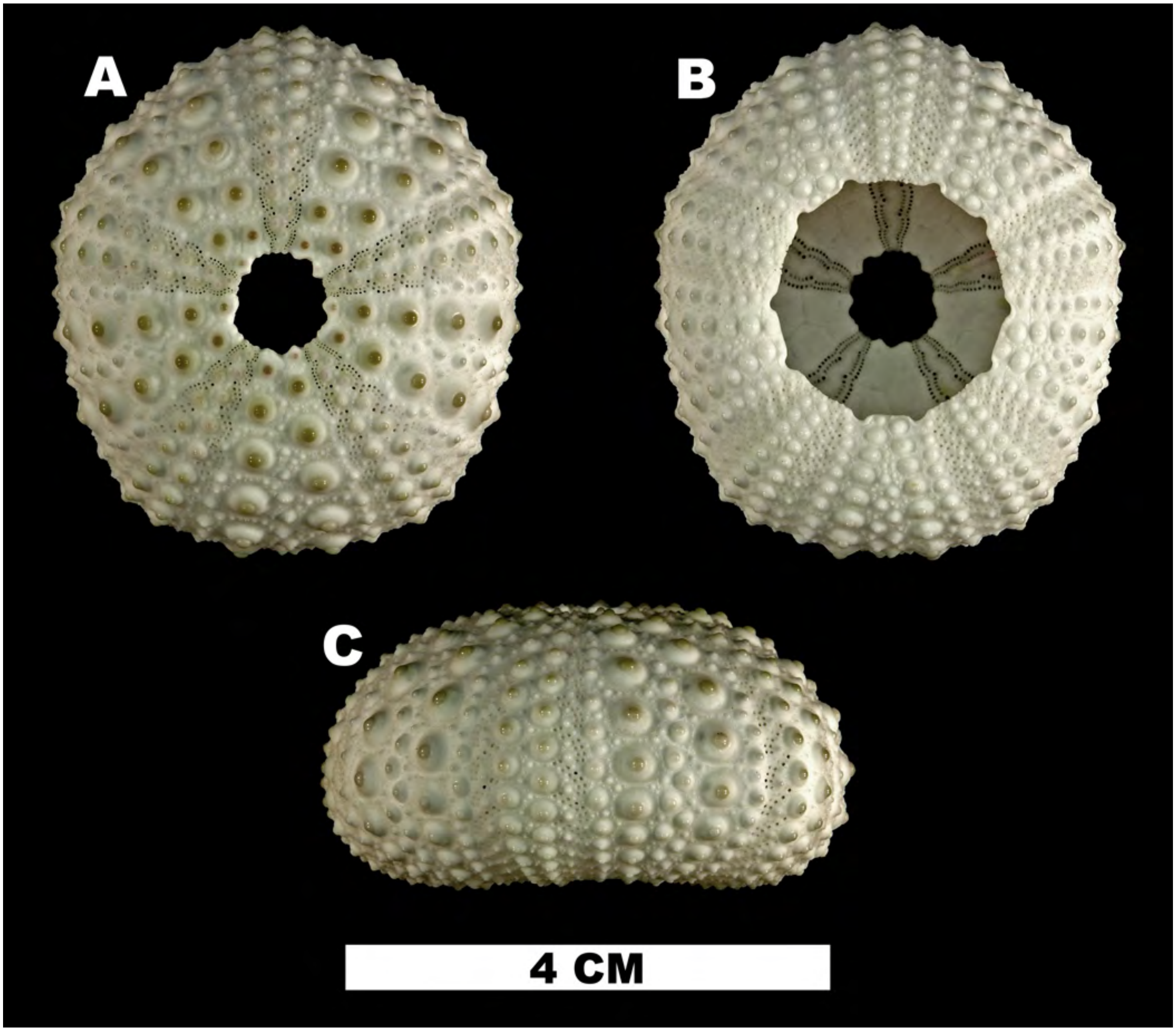


Figure 33. *Echinometra lucunter* (UF-IZ 18899) modern specimen for comparison (Marathon Key, 1 m depth amongst rocks, Monroe County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

Echinolampas brachytoma Arnold and Clark, 1927, p. 49, pl. 9, figs. 5, 6.

?*Echinolampas* sp. Jeannett, 1928, p. 35, text fig. 11.

Echinolampas lycopersicus (Guppy). Cooke, 1961, pp. 21–22, pl. 9, figs. 3–5.

Echinolampas lycopersicus (Guppy). Gordon, 1963, pp. 637, 640, text fig. 3, 4. pl. 80, figs. 8, 9. (includes additional references).

Echinolampas (*Progonolampas*) *torrense*, Sánchez-Roig, 1953, p. 152, pl. 5, figs. 5, 6.

Echinolampas? *lycopersicus* (Guppy). Donovan, 1993, pp. 393, 394.

Occurrence.—Occurs rarely with *Clypeaster petersonorum* n. sp. in the lower indurated beds of the lower Miocene Chipola Formation along the Chipola River, below Tenmile Creek, southwest of Altha, Calhoun County, Florida.

Echinolampas lycopersicus is widespread in the Caribbean Region, documented from the following: Jamaica? (Eocene [Arnold and Clark, 1927; Donovan, 1993]), Cuba (Jackson, 1922), Trinidad (middle Miocene [Cooke, 1961]), Venezuela (middle Miocene [Cooke, 1961]), Anguilla (Miocene type locality for the species [Jackson, 1922]) and Puerto Rico (late Oligocene [Gordon, 1963]). Cotypes consist of six specimens (USNM 115387a), one of which was figured by Guppy (1866) from the Miocene Anguilla Formation, Anguilla. The holotype of another Miocene species that does not occur in Florida, *E. anguillae*, USNM 115372, is also from the Anguilla Limestone of Anguilla.

Discussion.— *Echinolampas lycopersicus* was described by Guppy (1866) from the Miocene Anguilla Formation on the island of Anguilla. It has since been shown to be a consistent element of the late Oligocene-Miocene faunas of the West Indies. Jackson (1922) noted that it is very abundant in Puerto Rico and Anguilla, and he described many localities for each of these islands, as well as a lesser number in Cuba. Cooke (1961) documented *E. lycopersicus* in the middle Miocene of Trinidad and Venezuela and Gordon (1963) discussed the occurrence of this species in the upper Oligocene Cibao Marl and Lares Limestone of Puerto Rico where it occurs with *Clypeaster concavus* Cotteau, 1875 in both units.

Donovan (1993) discussed the presence of this species in the Eocene of Jamaica as documented by Arnold and Clark (1927), and cast doubt on this record. Donovan (1993) asserted that the specimens attributed to this species by Arnold and Clark (1927) should be ascribed to the more oval *Echinolampas strongyla* Arnold and Clark, 1927, so this Eocene occurrence of the species should be treated with caution.

Jackson (1922) noted that *E. lycopersicus* is very uniform in character and varies principally in that most specimens are quite low, some, especially from Puerto Rico, are much higher and dome-shaped. Cooke (1961) also remarked that this species varies considerably in size and degree of inflation, but the shape of the petals is relatively constant. He noted that the specimens from Trinidad and Venezuela are much more highly inflated than the one he figured from Anguilla (Cooke 1961: pl. 9, figs. 3–5) but that others from Anguilla are as inflated as those from Trinidad and Venezuela.

Gordon (1963) stated that the species is moderately variable with some specimens being broad and flat and others more nearly hemispherical. Of the 152 specimens measured from the Lares Limestone of Puerto Rico, Gordon found a tendency for there to be a relative, but slight increase in TW as TL increases so that the tests varied from almost circular to more elongate and sub-pentagonal. Gordon (1963) also stated that many of the species Arnold and Clark (1927) placed in *E. paragoga* Arnold and Clark, 1927, from the Miocene of Jamaica, should be placed in *E. lycopersicus*.

This is the first documented occurrence of an *Echinolampas* in the Miocene of Florida and the first report of *E. lycopersicus* in North America. Specimens of *E. lycopersicus* are very rare in the Chipola Formation and have thus far only been documented in the stratotype area of the unit along the Chipola River south of the mouth of Tenmile Creek in Calhoun County. The specimens available are all incomplete. However, when all of the material is examined (UF 222583–222585, UF 228992–228993, and UF 289231), sufficient information is revealed to ascertain the characteristics of the test and it becomes clear that the material represents *E. lycopersicus*. Cooke (1961) stated that the species varies considerably in size and degree of inflation.

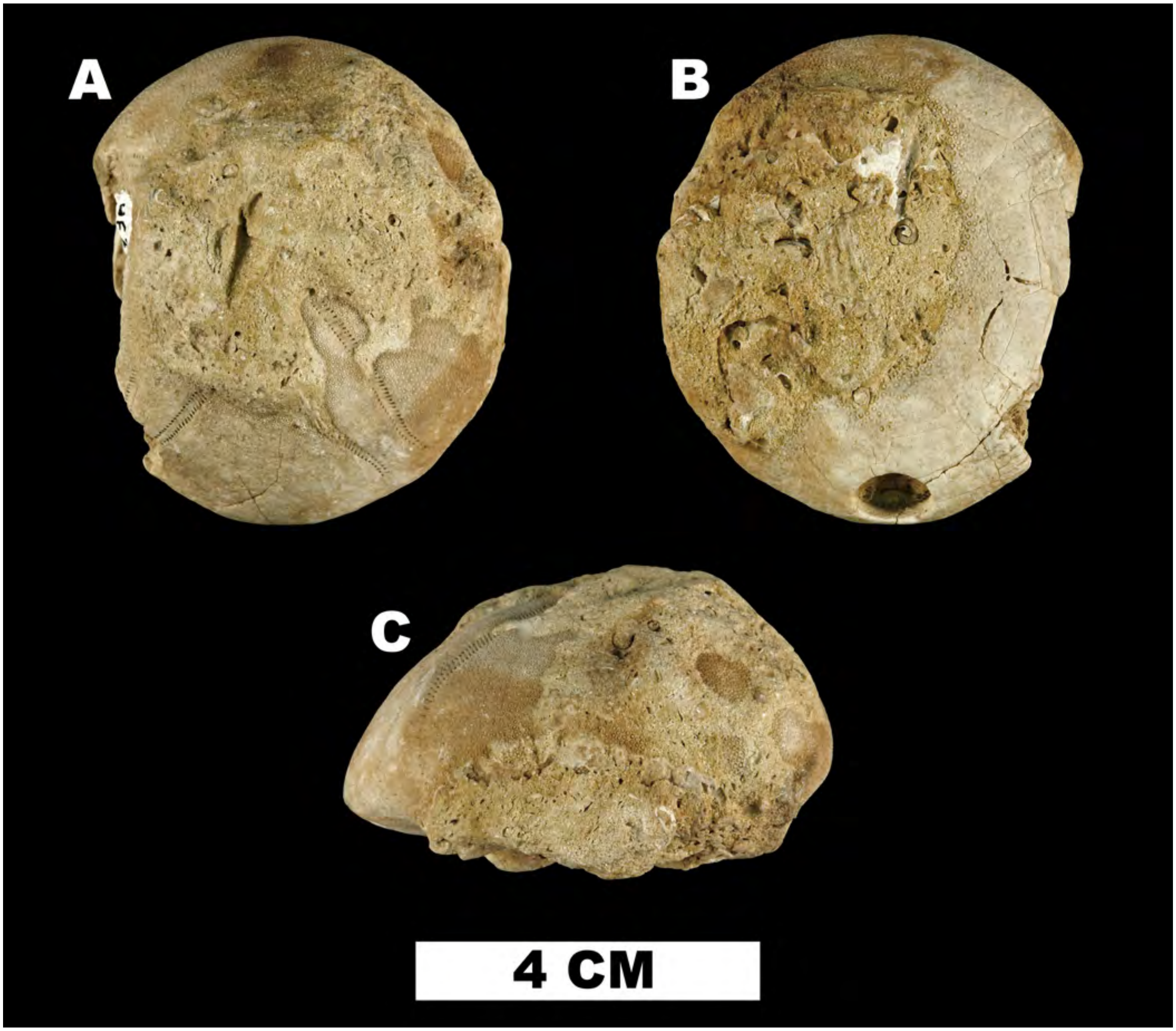


Figure 34. *Echinolampas lycopersicus* (UF 222584), Chipola Formation (FM locality CA036). A. aboral view, B. oral view, C. right lateral view.

Specimen UF 222584 exhibits the best-preserved oral surface (Fig. 34) and specimen UF 289231 is well preserved but missing its posterior margin (Fig. 35).

As mentioned in Osborn et al. (2016:48) there are approximately 300 nominal taxa in the genus *Echinolampas*, and this has invited attempts to subdivide the genus into several genera or subgenera. These attempts have largely failed due to the lack of consistently applicable criteria. It is a regrettable fact that in many cases, many species have themselves been described without a firm basis for their diagnosis, strongly suggesting that the diversity within the genus is vastly overestimated. It would at first glance seem that there are few justifiable criteria for description of yet another species within the genus. Therefore, in spite of the variation in overall test morphology of *E. lycopersicus*, we do not find discriminating features among the Chipola Formation specimens by which to describe a new species. Nevertheless, the species is unique among the North America *Echinolampas*, and the first representative of the genus documented from the Miocene of the eastern United States.

Order **CASSIDULOIDA** Claus, 1880
Family **CASSIDULIDAE** L. Agassiz and Desor, 1847
Genus ***RHYNCHOLAMPAS*** A. Agassiz, 1869
RHYNCHOLAMPAS AYERSI Kier, 1963
Figure 36

Rhyncholampas ayersi Kier, 1963, pp. 45–48, pl.16, figs. 3–6; text figs. 43–46.

Occurrence.—*Rhyncholampas ayersi* appears to be restricted to the Caloosahatchee Formation (Bee Branch Member sensu DuBar, 1958) where it is most common near LaBelle, Hendry County, Florida. Kier (1963) listed the following localities: north bank of Caloosahatchee River and pits on north bank in SE¼ sec. 12, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 23082/USGS locality 23083); north bank of Caloosahatchee River west of Three Way Rock Company pits in SW¼ sec. 6, T. 43 S., R. 29 E., LaBelle Quadrangle, Hendry County (USGS locality 23085), and the type locality at the Denaud pits in NW¼ sec. 14, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 22373). It

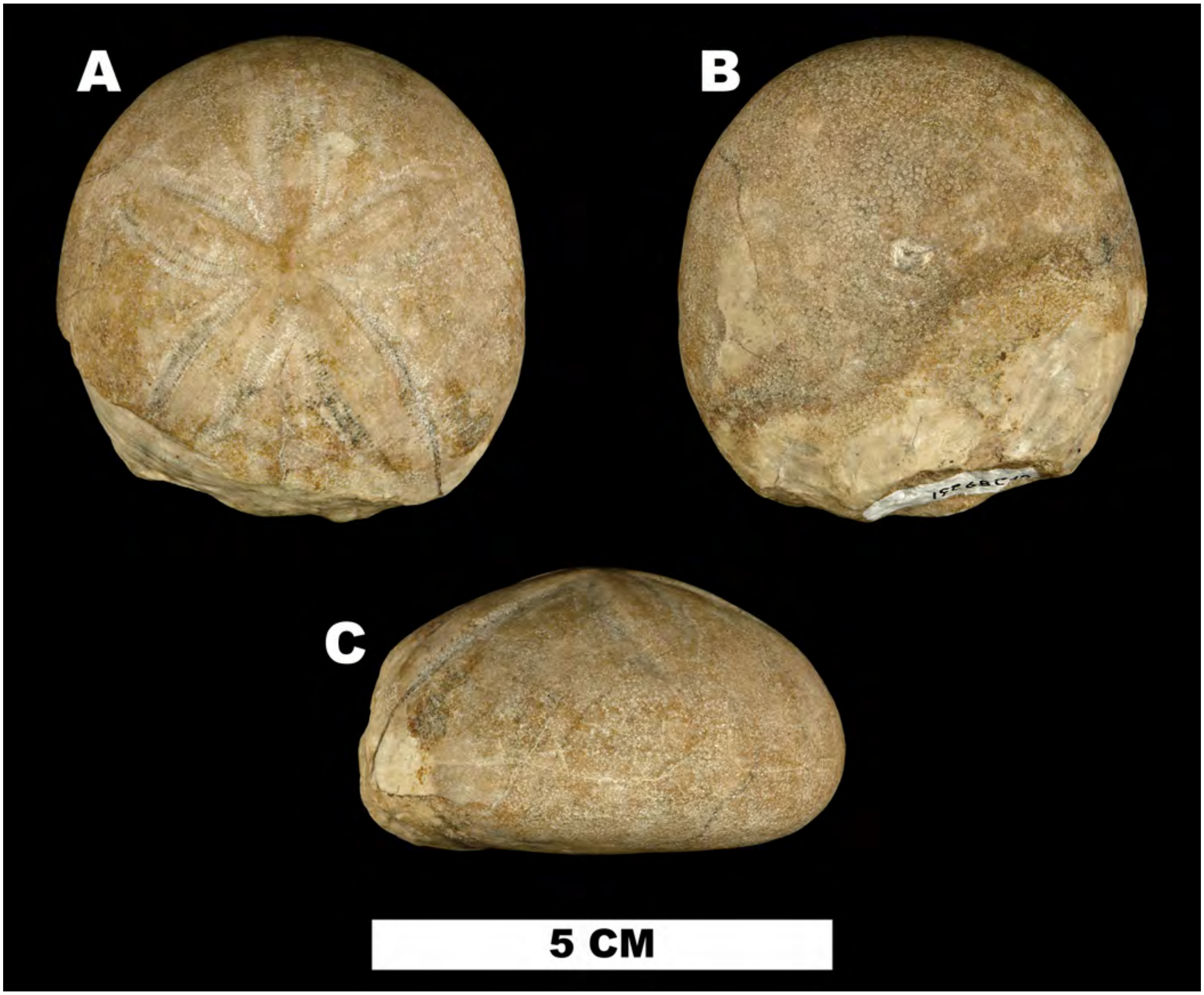


Figure 35. *Echinolampas lycopersicus* (UF 289231), Chipola Formation (FM locality CA036). A. aboral view, B. oral view, C. right lateral view.

is found at most exposures of the Caloosahatchee Formation in southern Florida, including at Moorehaven, Glades County; the borrow pit northwest of LaBelle on the north side of Caloosahatchee River, Hendry County; the now inactive Cochran Shell Pit, Hendry County (FM locality HN004); and the Star Ranch Quarry in Palm Beach County (FM locality PB014).

Discussion.—*Rhyncholampas ayersi* has not been documented outside of the Caloosahatchee Formation of southern Florida. Kier (1963) distinguished *R. ayersi* from *R. evergladensis*, which occurs in slightly older strata of the upper Pliocene Tamiami Formation of south Florida, by having more of its adapical surface inflated, by its steeper sloping sides, less pointed adapical surface, and less angular marginal outline. Kier further clarified that the oral surface in *R. ayersi* is less depressed, the naked zone in interambulacrum 5 is narrower, and phyllode III is narrower. These two species can be readily differentiated in the field even in incomplete specimens or those partially obscured by adhering matrix by the overall lower form of *R. evergladensis* and the more inflated, "swollen" appearance of *R. ayersi*.

Kier (1963) remarked that *R. sabistonensis*, which is, in part, a contemporary of *R. ayersi* from the Carolinas, is intermediate in general form between *R. ayersi* and *R. evergladensis*. We support this suggestion because *R. ayersi* is more similar in form to *R. sabistonensis* than *R. evergladensis*, and differentiating *R. ayersi* from *R. sabistonensis* has caused some confusion in the literature. DuBar et al. (1980) documented the presence of *R. ayersi* in the Waccamaw Formation along the Intracoastal Waterway in North Myrtle Beach, Horry County, South Carolina. Examination of specimens from this site reveals many representatives of *R. sabistonensis*, but none approaches the overall inflated appearance, steeper sloping sides and flatter adapical surface of *R. ayersi*. The inflated oral surface and high test with steep sides also readily distinguish *R. ayersi* from *R. meansi* n. sp. Once these defining characters are fully considered, *R. ayersi* becomes one of the most readily recognizable species of the genus in the regional Neogene strata.

RHYNCHOLAMPAS CHIPOLANUS Oyen and Portell, 1996
Figures 37–39

Rhyncholampas chipolanus Oyen and Portell, 1996, pp. 59–66.
Rhyncholampas chipolanus (Oyen and Portell). Oyen and Portell, 2001, pp. 193–218, pl. I, fig. 13.
Rhyncholampas sp. cf. *R. chipolanus* (Oyen and Portell). Oyen, 2001, pp. 132, 133, figs. 3–17 a, b.
Rhyncholampas sp. Oyen, 2001, pp. 133–134, fig. 3–17c.
Rhyncholampas aff. *chipolanus* (Oyen and Portell). Osborn and Ciampaglio, 2010, p. 207.

Occurrence.—*Rhyncholampas chipolanus* has not been documented outside of Florida, where it is now recorded from four Miocene age units: Chipola Formation (FM locality CA025—the type locality of the species, and FM locality CA067); bed of the Apalachicola River, Jackson County (FM locality JA041); Peace River Formation in the bed of the Peace River above Zolfo Springs, Hardee County (Osborn and Ciampaglio, 2010); Arcadia Formation (upper Portion) at the Fort Green 13 dragline, Polk County (FM locality PO002); Torreya Formation, Taft Pit, near Crawfordville, Wakulla County (FM locality WA001).

Discussion.—*Rhyncholampas chipolanus* was described from a single specimen (UF 66633; Fig. 37) obtained from the lower Miocene Chipola Formation on the west bank of the Chipola River 0.5 miles upstream from mouth of Four Mile Creek, Calhoun County (FM locality CA025) (Oyen and Portell, 1996). Species within the genus *Rhyncholampas* are often highly variable, so it is difficult to ascertain the full range of variation in this species without additional material from, or near, the type locality. Although additional specimens have not been collected from that area, specimens from additional Miocene age exposures in the state have provided specimens that we attribute to *R. chipolanus*.

As noted by Osborn and Ciampaglio (2010), specimens of *R. chipolanus* collected in the upper Miocene, Peace River Formation above Zolfo Springs, Hardee County, agree with the type of *R. chipolanus*. However, these are less peaked at the apical area and generally more rounded in appearance (Fig. 38). Oyen (2001) documented the occurrence of *R. chipolanus* in the Arcadia Formation at

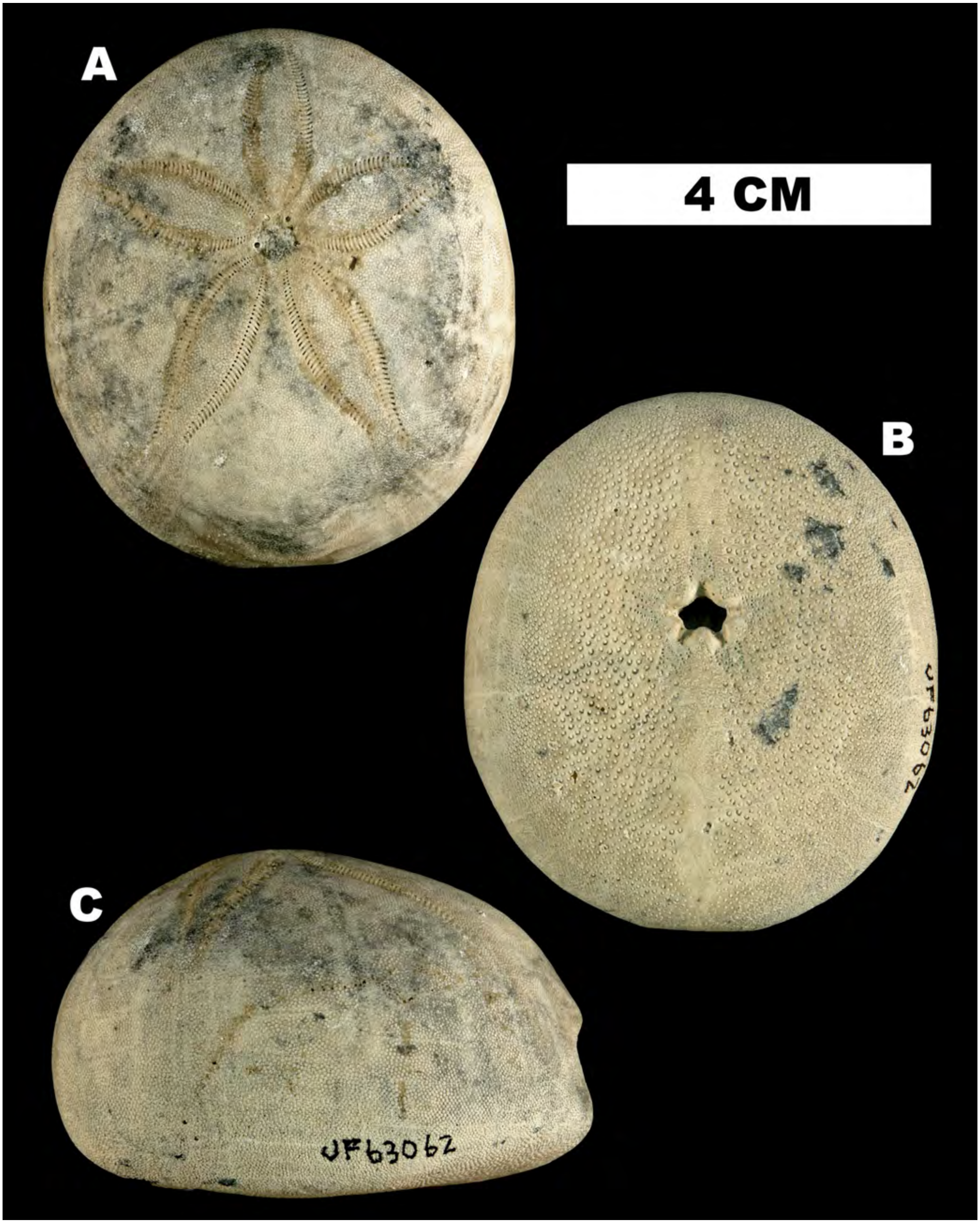


Figure 36. *Rhyncholampas ayersi* (UF 63062), Caloosahatchee Formation (FM locality PB014). A. aboral view, B. oral view, C. lateral view.

Fort Green 13 Dragline in Polk County, Florida (FM locality PO002). Here in the lower Miocene portion of the deposit, *R. chipolanus* occurs with moldic *Abertella* that are similar in form to *A. floridana*. The latter are undoubtedly not their more alate (sensu Mooi et. al., 2016), widened congener, *A. dengleri*, of the overlying, upper Miocene, Peace River Formation (see below).

Rhyncholampas specimens from the Taft Pit, Wakulla County (FM locality WA001) noted above consist of incomplete material. However, the specimens available cannot be distinguished from *R. chipolanus*. In the Torreya Formation, *R. chipolanus* occurs with cidarid spines, which are often indistinguishable from *Prionocidaris cookei*. However, some of the spines within the assemblage have spinules that are much longer than that documented in *P. cookei* by Cutress (1976, 1980).

Oyen (2001:133–134) documented a poorly preserved specimen of *Rhyncholampas* from the Peace River Formation above Zolfo Springs, Hardee County (FM locality HR013). He suggested it to be *R. chipolanus*, but the material was too incomplete to be certain. As discussed above, additional specimens from this site have confirmed the presence of *R. chipolanus* there (Osborn and

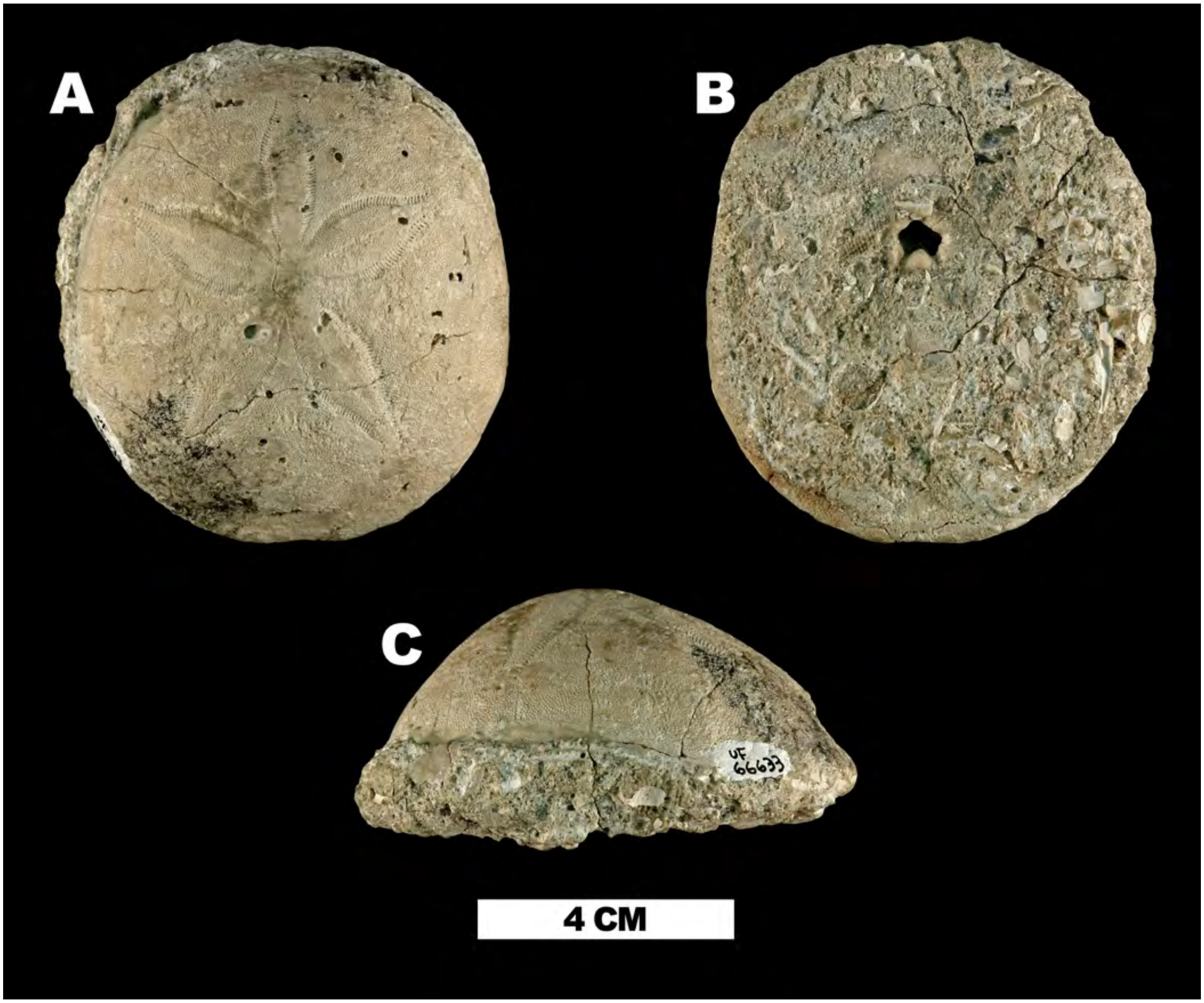


Figure 37. *Rhyncholampas chipolanus* holotype (UF 66633), Chipola Formation (FM locality CA025). A. aboral view, B. oral view, C. lateral view.

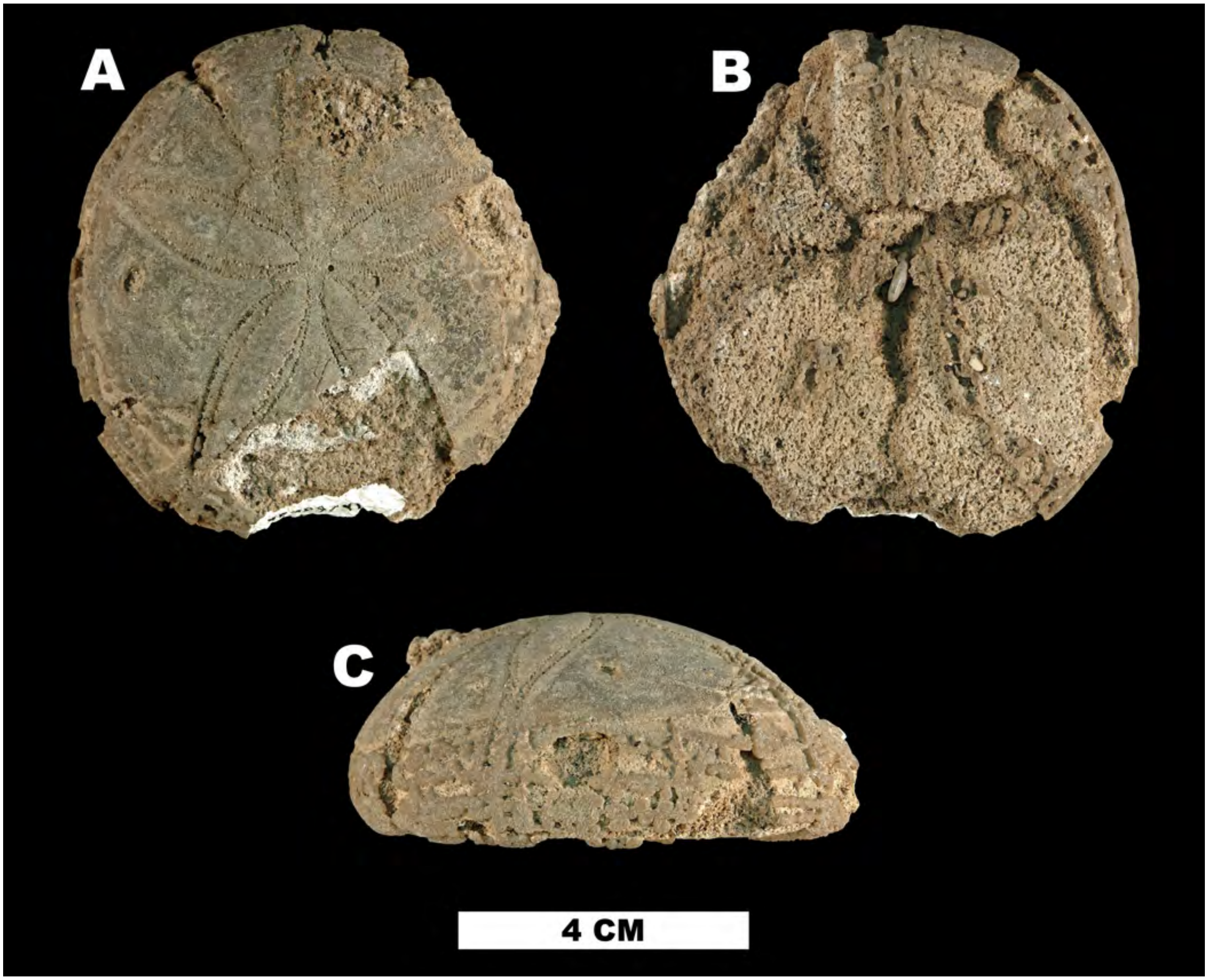


Figure 38. *Rhyncholampas chipolanus* (UF 289221), Peace River Formation (FM locality HR013). A. aboral view, B. oral view, C. lateral view.

Ciampaglio, 2010). In addition, specimens of *R. chipolanus* have been collected from the Chipola Formation in the Apalachicola River in Calhoun County (FM locality CA067); specimen UF 112039 is an example (Fig. 39).

When documenting the species, Oyen and Portell (1996) noted that *R. chipolanus* is most similar to *R. evergladensis*. They differentiated the two species by showing that the petals of *R. chipolanus* terminate slightly further from the test margin and are nearly closed distally, whereas the petals of *R. evergladensis* are distinctly open and extend further toward the test margin. Oyen and Portell (1996) noted that the periproct is transversely oriented in both species, but in *R. chipolanus* it is subpentagonal in outline with the apex of the pentagon pointing upward, whereas it is more elliptical in *R. evergladensis*. They also indicated that *R. chipolanus* is more peaked at the apical system, while most *R. evergladensis* do not achieve this more conical form. However, as they noted, some specimens of *R. evergladensis* do rarely display a similarly conical test.

The upwardly pointed periproct of the holotype is conspicuous. However, it appears there is variation in the degree of accentuation in this fea-

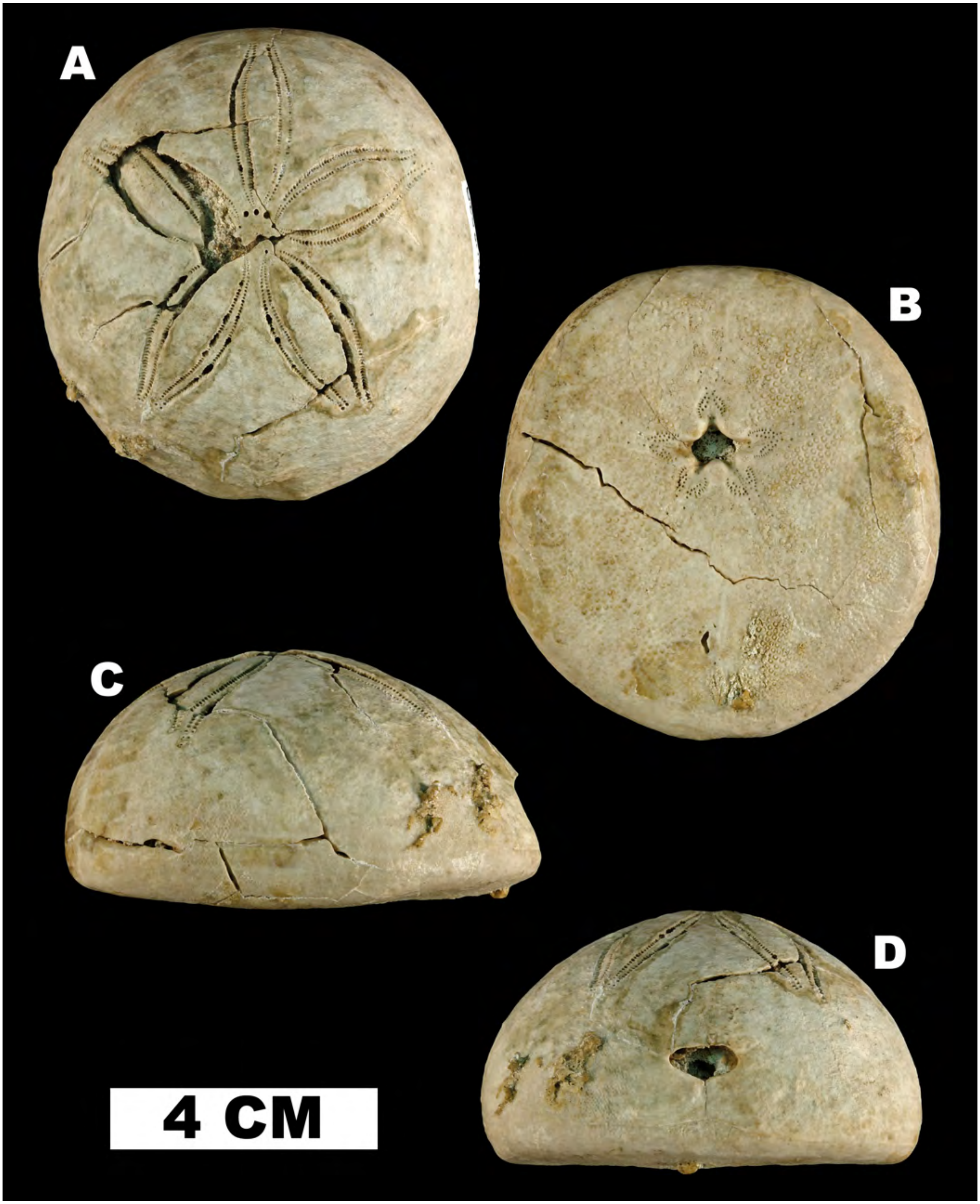


Figure 39. *Rhyncholampas chipolanus* (UF 112039), Chipola Formation (FM locality CA067). A. aboral view, B. oral view, C. lateral view, D. posterior view.

ture. Additional specimens of *R. chipolanus* from the Peace River, Torreya, and Arcadia Formations that otherwise agree well with those documented above have a more elliptical periproct that lacks the acuteness of the upper vertex.

RHYNCHOLAMPAS EVERGLADENSIS
(Mansfield, 1932)
Figures 40–42

Cassidulus (*Rhynchopygus*) *evergladensis* Mansfield, 1932, p. 48, pl. 18, figs. 1–10.

Cassidulus (*Cassidulus*) *evergladensis* (Mansfield). Cooke, 1942, p. 30, pl. 8, figs. 5, 6.

Cassidulus sabistonensis (Kellum). Cooke, 1959*,* p. 57, pl. 22. figs. 5, 6. (in part: Cooke figured and described *R. sabistonensis* from NC, but considered *R. sabistonensis* and *R. evergladensis* synonymous).

Rhyncholampas evergladensis (Mansfield). Kier, 1963, pp. 48–52, pl. 17, figs. 1–5. text figs. 42, 47–50.

Rhyncholampas evergladensis (Mansfield). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—*Rhyncholampas evergladensis* is common in the upper Pliocene Tamiami Formation throughout much of southwestern Florida, occurring in both the sand facies and Ochopee Limestone members of the unit. Notable localities include the Quality Materials Quarry, Charlotte County (FM locality CH080); pits east of Burnt Store Road, south of Port Charlotte (FM localities CH046, CH047, CH048, CH079); Lomax King Pit, Charlotte County (FM locality CH003), and quarries near Copeland, Collier County (FM locality CR041).

Discussion.—Cooke (1959) considered *R. evergladensis* to be a subjective junior synonym of *R. sabistonensis*. However, Kier (1963) had more than 100 specimens of *R. evergladensis* available for comparison and asserted that the higher, narrower test of *R. sabistonensis* distinguished it from *R. evergladensis*, and we concur. Kier (1963) also differentiated *R. evergladensis* from his newly described *R. ayersi* by the more pointed adapical surface, more gently sloping sides, more angular marginal outline, more depressed adoral surface, wider naked zone in interambulacrum 5, and wider phyllode III. As mentioned above in the discussion of *R. ayersi*, even suboptimal material of these two species can be readily differentiated in the field. See the discussion for *R. meansi* n. sp. for characters distinguishing it from this, and other *Rhyncholampas*.

Kier (1963:fig. 47) documented specimens of *R. evergladensis* up to 97 mm TL, though the species is usually much smaller. Of 101 specimens, the smallest he observed was 35 mm TL. As Kier (1963) noted, TH varies from 44% to 58% TL, and larger specimens had a relatively lower TH.

Rhyncholampas evergladensis is commonly associated with *Encope tamiamiensis*. Both species appear to be restricted to the Tamiami Formation in southwestern Florida. Missimer (1992) divided the complicated lithologies of the Tamiami Formation into numerous members, two of which contain notable occurrences of *R. evergladensis* and other echinoids: the Ochopee Limestone member and the sand facies. Though the pale sandy limestone of the Ochopee Limestone member, well exposed in Collier County, contains an abundance of echinoids, the concentrations are virtually monospecific, often consisting of dense accumulations of *E. tamiamiensis*, with *R. evergladensis* also present, though much less common.

Rhyncholampas evergladensis is much more abundant within the sand facies, which was well-exposed in multiple quarries in Charlotte County, notably a series of small pits along Burnt Store Road south of Punta Gorda, and the Quality Materials Quarry, Charlotte County (FM locality CH080). Twelve echinoid species from the Tamiami Formation have been collected in the Quality Materials Quarry, with representatives of most species retaining their spines, including *R. evergladensis*. The spination of *R. evergladensis* consists of a rather uniform covering of short, glassy spines aborally, with thicker, stouter spines suited for burrowing and locomotion on the oral surface (UF 289219; Fig. 40). The spination is similar to that discussed and illustrated by Mortensen (1948) for *Rhyncholampas pacificus* A. Agassiz, 1863, the extant type species of the genus, and for the closely related *Cassidulus caribaearum* (Telford and Mooi, 1996:fig. 2). We herein figure a typical specimen of *R. evergladensis* (UF 24524) from the Tamiami Formation (Fig. 42), and a very large representative from the Tamiami Formation in the Lomax King Pit (FM locality CH003) (UF 21050; Fig. 41).

RHYNCHOLAMPAS SABISTONENSIS
(Kellum, 1931)
Figure 43

Cassidulus (*Pygorhynchus*) *berryi* Kellum, 1926, p. 15, pl. 1, figs. 4–7. (not *Cassidulus berryi* Twitchell in Clark and Twitchell, 1915).

Cassidulus (*Pygorhynchus*) *sabistonensis* (Kellum), 1931, p. 51. (new name for *C. berryi* Kellum).

Cassidulus (*Cassidulus*) *sabistonensis* Kellum. Cooke, 1942, p. 31.

Cassidulus sabistonensis (Kellum). Cooke, 1959, p. 57, pl. 23, figs. 6–14.

Rhyncholampas sabistonensis (Kellum). Kier, 1962, pp. 174, 180.

Rhyncholampas sabistonensis (Kellum). Ciampaglio et al., 2009, fig. 2.

Rhyncholampas sabistonensis (Kellum). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Lower Pleistocene Nashua Formation, East Coast Aggregates Quarry, St. Johns County (FM locality SJ007). This species is

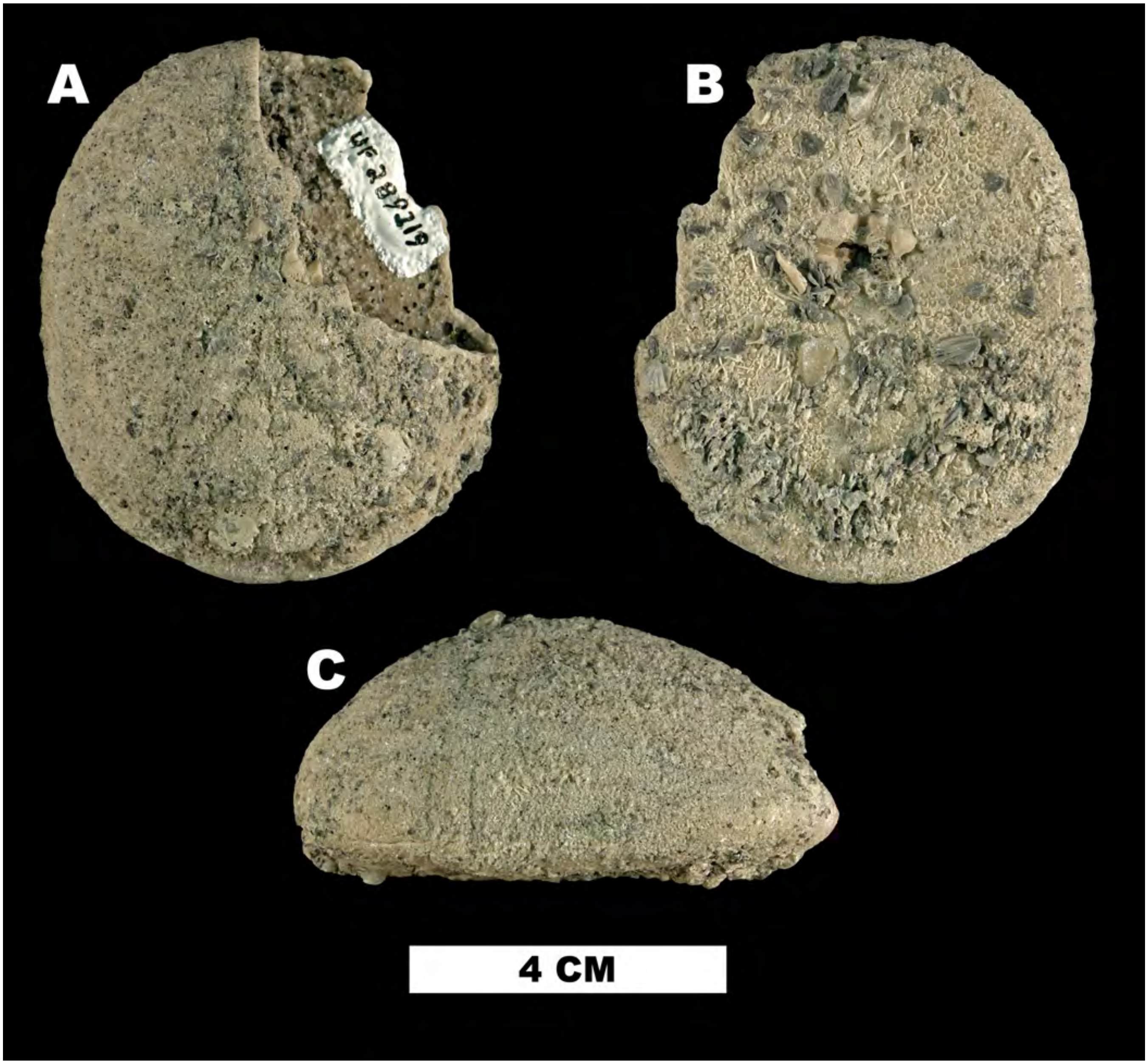


Figure 40. *Rhyncholampas evergladensis* with spines (UF 289219), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

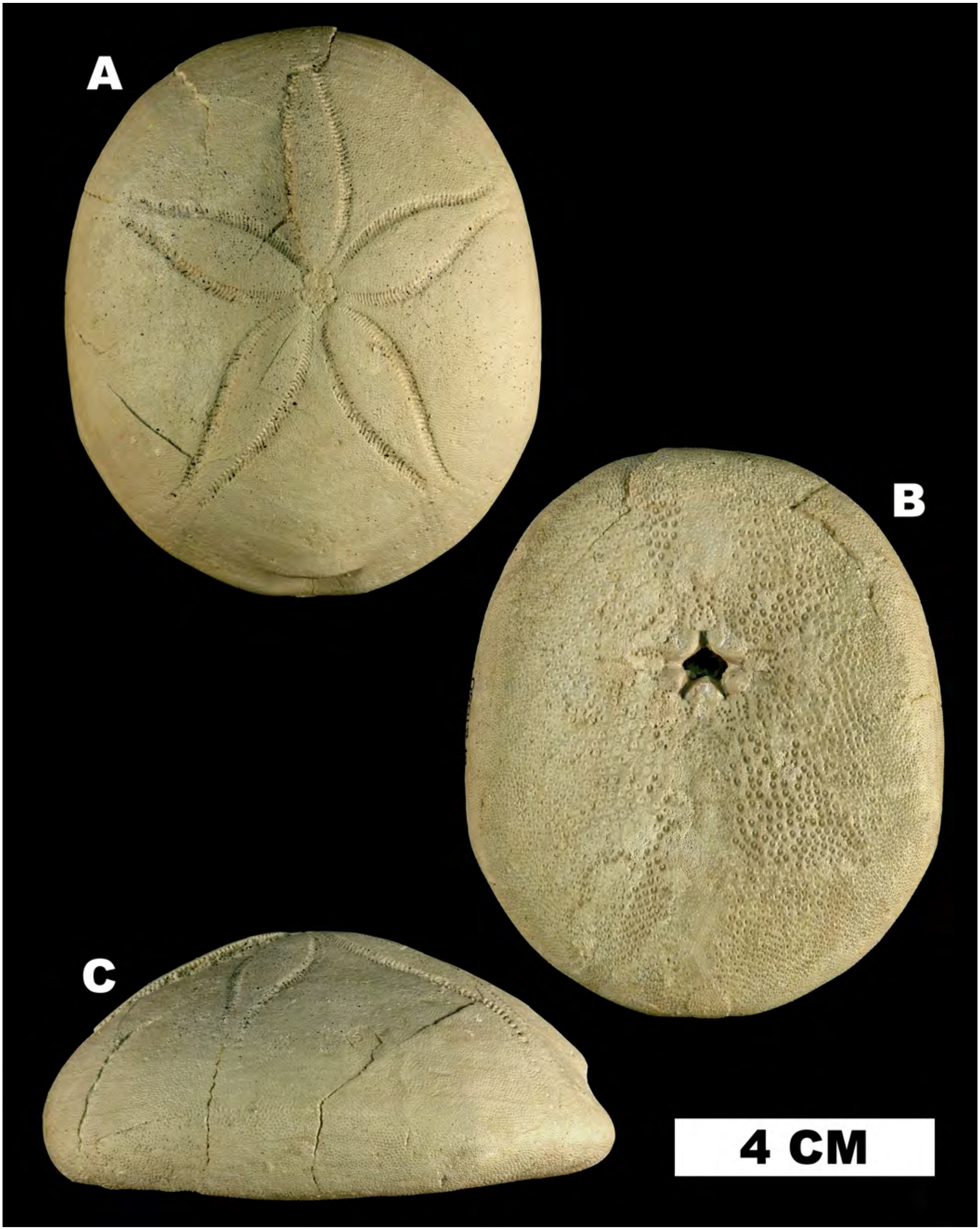


Figure 41. *Rhyncholampas evergladensis* (UF 21050), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

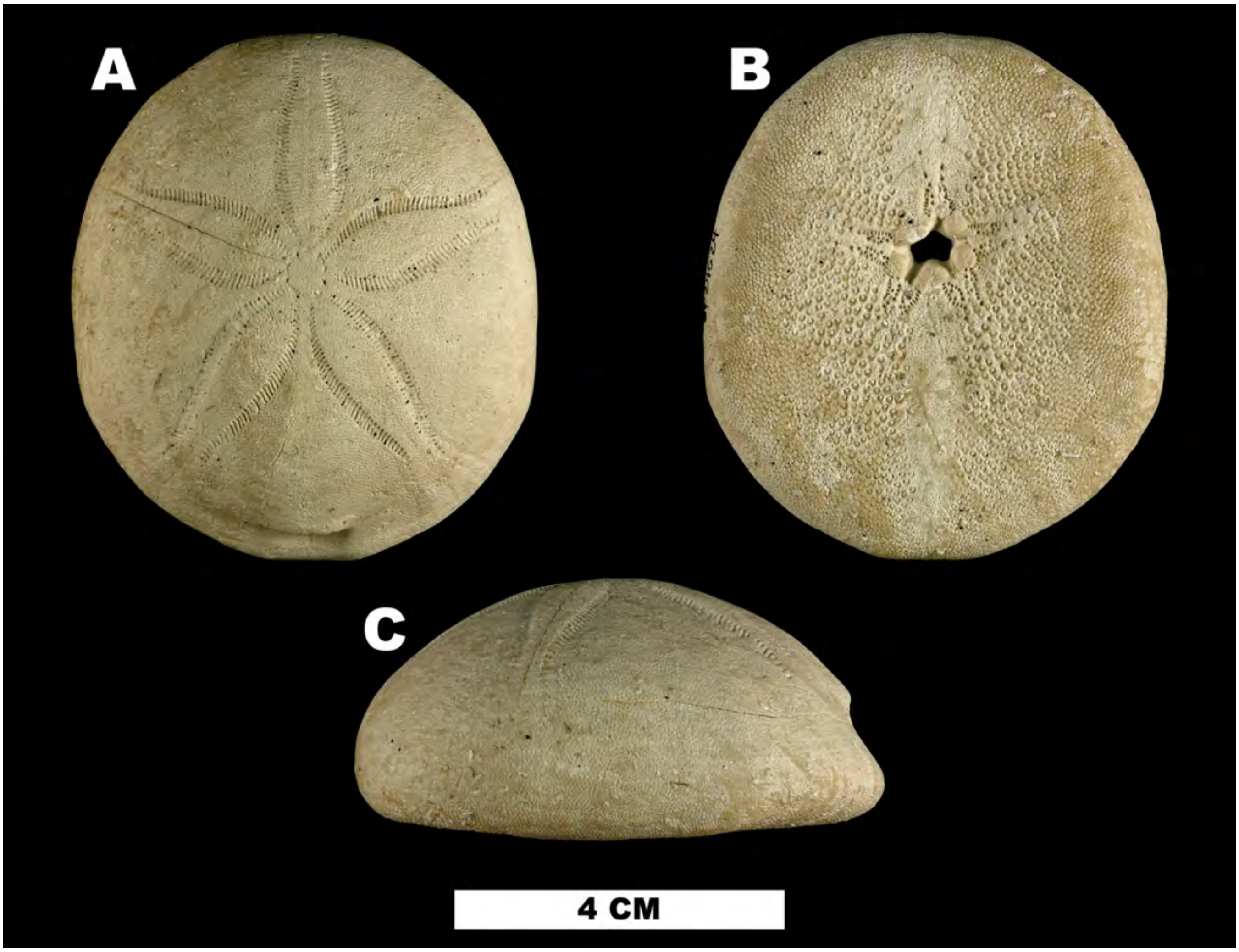


Figure 42. *Rhyncholampas evergladensis* (UF 24524), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

more abundantly represented in the late Pliocene (upper Goose Creek Limestone) to early Pleistocene (Waccamaw Formation) of the Carolinas. Souto et al. 2019 (table 2) placed this species in the middle to late Eocene in error. The type locality is the farm of E. W. Sabiston, 2 miles north of Jacksonville, Onslow County, North Caarolina (USGS locality 10637, L. B. Kellum).

Remarks.—This is the first documented occurrence of *R. sabistonensis* in Florida. The Nashua Formation contains a well-documented late Pliocene to early Pleistocene fauna that shares affinities with both the Waccamaw Formation of the Carolinas and the Caloosahatchee Formation of southern Florida (Huddlestun, 1988:133–134; Petuch, 2004:210). Given the geographic location of Nashua Formation exposures in western St. Johns County and eastern Putnam County, in the vicinity of Palatka and Hastings, which is nearly midway between the south Florida exposures of the Caloosahatchee Formation and the Waccamaw Formation exposures of South Carolina, it is not surprising to find *R. sabistonensis* in the Nashua Formation.

Cooke (1942) stated that the petals of *R. sabistonensis* are more like those of *R. evergladensis* than of any other American species, being rounder and less spatulate. Cooke (1959) subsequently considered *R. evergladensis* to be a junior synonym of *R. sabistonensis*, though he did not provide an explanation for this change.

With more than 100 measured specimens of *R. evergladensis* available for comparison, Kier (1963) asserted that the higher and narrower test of *R. sabistonensis* distinguished it from *R. evergladensis*. He recognized the two morphotypes as distinct species, as do we. As noted above, Kier (1963) recorded a range for TH of 44% to 58% TL. The holotype of *R. sabistonensis* (USNM 353233), likely from the Waccamaw Formation (precise stratigraphy is uncertain) in North Carolina has a TH 63% TL. Although there is overlap in TH ranges of the species, *R. sabistonensis* has a consistently higher and narrower test than *R. evergladensis*.

A specimen of *R. sabistonensis* (UF 289382; Fig. 43) from the East Coast Aggregates Quarry, St. Johns County (FM locality SJ007) measures 44 mm TL, 38 mm TW, and 31 mm TH, for a height nearly 70% TL. This specimen and others are indistinguishable from both the holotype of *R. sabistonensis* and a substantial reference collection of *R. sabistonensis* from the early Pleistocene, basal shell bed of the Waccamaw Formation along the

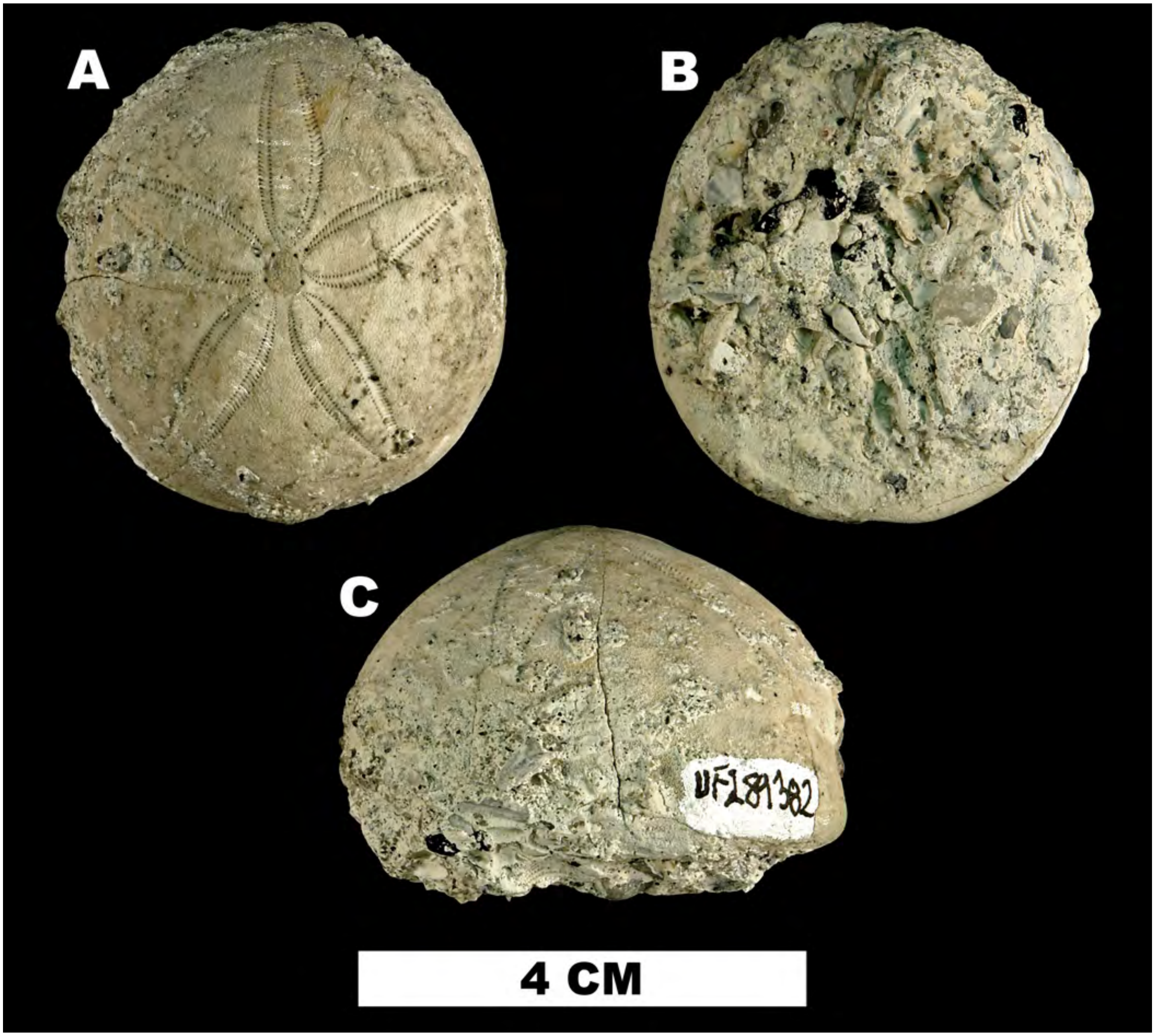


Figure 43. *Rhyncholampas sabistonensis* (UF 289382), Nashua Formation (FM locality SJ008). A. aboral view, B. oral view, C. lateral view.

Intracoastal Waterway, North Myrtle Beach, Horry County, South Carolina.

Rhyncholampas sabistonensis is most abundant in the lower Pleistocene Waccamaw Formation of the Carolinas, where it is associated with *Mellita caroliniana* and *Arbacia waccamaw* Cooke, 1941, as well as other, rarer echinoid species.

RHYNCHOLAMPAS MEANSI n. sp.
Figures 44–48

Rhyncholampas evergladensis (Mansfield). Petuch, 2004, p. 232, pl. 86, fig. J. (not *R. evergladensis*).

Rhyncholampas cf. *evergladensis* (Mansfield). Petuch and Roberts, 2007, p. 162, fig. 6.8B.

Diagnosis.—*Rhyncholampas* of large size, up to 88.9 mm TL, width on average 90.2% TL, height on average 50.9% TL; test with gently rounded upper surface that is not at all pointed; greatest width adjacent to, or just posterior to, apical area; greatest height slightly anterior of apical area; oral surface flat to slightly concave; base of periproct opening on average situated 24.8% TH above ambitus.

Description.—Description based UF 289232 (Fig. 44), paratypes UF 289233 (Fig. 45) and UF 289234 (Fig. 46), as well as six additional specimens from the uppermost Caloosahatchee Formation, UF 156410 (Fig. 47), UF 116227 (Fig. 48), and four additional specimens from the Anastasia Formation. Test large, TL 63.7 mm to 88.9 mm, TW 57.5 mm to 78.6 mm, and TH 30.6 mm to 48.9 mm; (holotype UF 289232: 70.5 mm TL, 63.7 mm TW, 34.6 mm TH); test broadly ovate to subcircular; TW on average 90.2% TL (TW ranges 87.8–95% TL), greatest width adjacent to, or just posterior of, apical area. Test low, only moderately inflated, TH on average 50.9% TL (ranges 46.4–55% TL); greatest height slightly anterior to apical system; gently rounded upper surface not pointed, sides steeply sloping up from ambitus then gently rounded to aboral surface; posterior slightly truncated; oral surface slightly concave to nearly flat, not inflated. Apical system anterior, center on average 45.7% TL from anterior margin, monobasal with four genital pores. Ambulacra not observed in entirety on any single specimen; petals lanceolate, converging distally, not closed, long, extending nearly to ambitus; petaloid III narrowest. Periproct supramarginal, base of opening on average situated 24.8% TH above ambitus, wider than high, height on average 68.5% width; shallow subanal sulcus extending from opening to posterior margin. Peristome anterior, anterior edge on average 39.8% TL from anterior margin, pentagonal, depressed, wider than high, peristome width on average 71.9% length. Phyllodes well developed, broad; buccal pores present; bourrelets prominent. Tubercles much larger on oral surface than adorally; prominent naked zone in interambulacrum 5 on oral surface.

Zoobank Nomenclatural Act.—50E79D8C-BE56-4F0A-9138-D015B0875FE0.

Occurrence.—*Rhyncholampas meansi* occurs in the uppermost portion of the lower Pleistocene Caloosahatchee Formation, middle Pleistocene Bermont Formation, and middle to upper Pleistocene Anastasia Formation of Florida. The type locality for the species is the upper bed of the Caloosahatchee Formation, in a small pit just north of Highway 80 east of LaBelle (FM locality 6022) dug for roadfill used during Highway 80 improvements east of LaBelle, Hendry County. The species is found in greatest abundance in strata referred to the Anastasia Formation in the Dickerson Quarry, St. Lucie County (FM locality SL004), and also occurred in the Bermont Formation in Glades County (FM locality GL007).

Petuch (2004) and Petuch and Roberts (2007) recorded a specimen of *Rhyncholampas* that is likely this species from the Bermont Formation (Holey Land Member) in the Griffin Brothers Quarry, Holey Land Wildlife Management Area, Palm Beach County, Florida.

Discussion.—Extensive collecting in the latter part of the 20th century to the present has revealed the persistent presence of a species of *Rhyncholampas* in various uppermost lower to late Pleistocene deposits of southern Florida. This form is distinguishable from the other representatives of the genus in the Neogene strata of the region: *R. chipolanus* in the Miocene of Florida, *R. sabistonensis* in the early Pleistocene of Florida and late Pliocene to early Pleistocene of the Carolinas, *R. evergladensis* in the late Pliocene, and *R. ayersi* in the early Pleistocene. The distinct new form is here described as *R. meansi* n. sp.

With a latest early to late Pleistocene age, this is the youngest *Rhyncholampas* in the fossil record of the Americas. The genus is not represented in the modern regional faunas, and is represented in the global modern fauna only by *R. pacificus*, which occurs in the tropical eastern Pacific Ocean. At its type locality east of LaBelle, *R. meansi* occurs in an indurated limestone brought up from beneath water level with Fort Thompson and Bermont shell, indicating it occurs in the uppermost bed of the Caloosahatchee Formation in the area. This is above the occurrence of *R. ayersi*, which is documented from the Bee Branch Member (sensu DuBar, 1958) of the lower portion of the Caloosahatchee Formation.

Members of the genus *Rhyncholampas* are often highly variable, with ecophenotypic variation in TH, TW, degree of test slope, and numer-

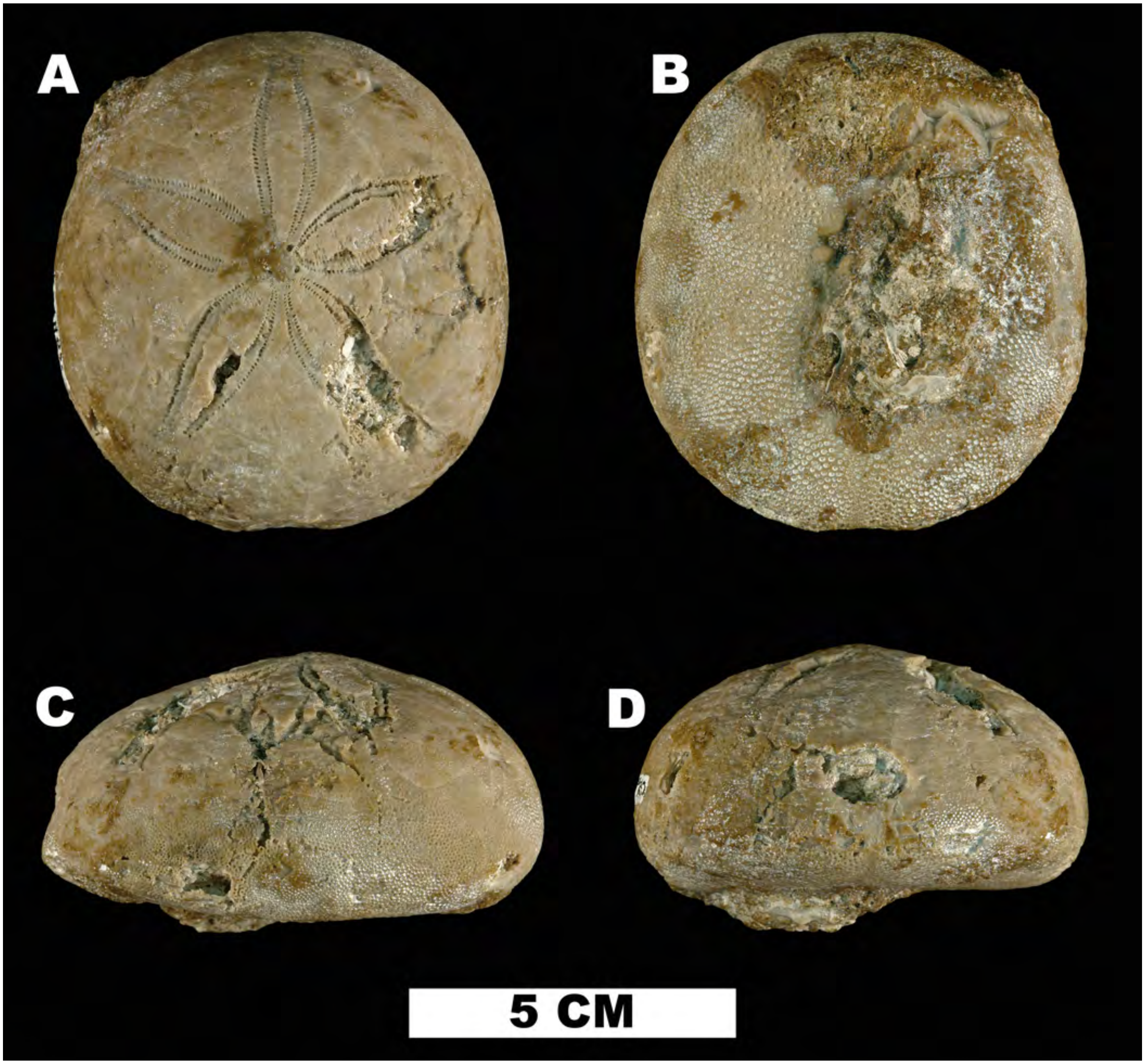


Figure 44. *Rhyncholampas meansi* n. sp., holotype (UF 289232), Caloosahatchee Formation (FM locality 6022). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

ous other features. This variability is seen not only among geographically separated populations (McKinney et al., 2014), but also within populations in the same geological horizon at the same locality. This variation, coupled with the already oversplit global fossil faunas, creates challenges when describing a new *Rhyncholampas*. We certainly recognize these difficulties. However, although the genus is strongly represented in both worldwide and regional Eocene faunas (Lambert and Thiéry, 1909–1925; Kier and Lawson, 1978; Kroh, 2010), Pleistocene age species are rare outside of Florida both regionally and globally (*R. ayersi* in the lower Caloosahatchee Formation and *R. sabistonensis* of lower Pleistocene in northern Florida and the Carolinas are the only exceptions). We can find no documentation of other described species of *Rhyncholampas* in the worldwide Pleistocene faunas outside of the regional *R. ayersi* and *R. sabistonensis* (Lambert and Thiéry, 1909–1925; Kier and Lawson, 1978; Kier, 1962; Kroh, 2010).

The available specimens of *R. meansi* n. sp. are not perfectly preserved. The most abundant occurrence of this species is in the Anastasia For-

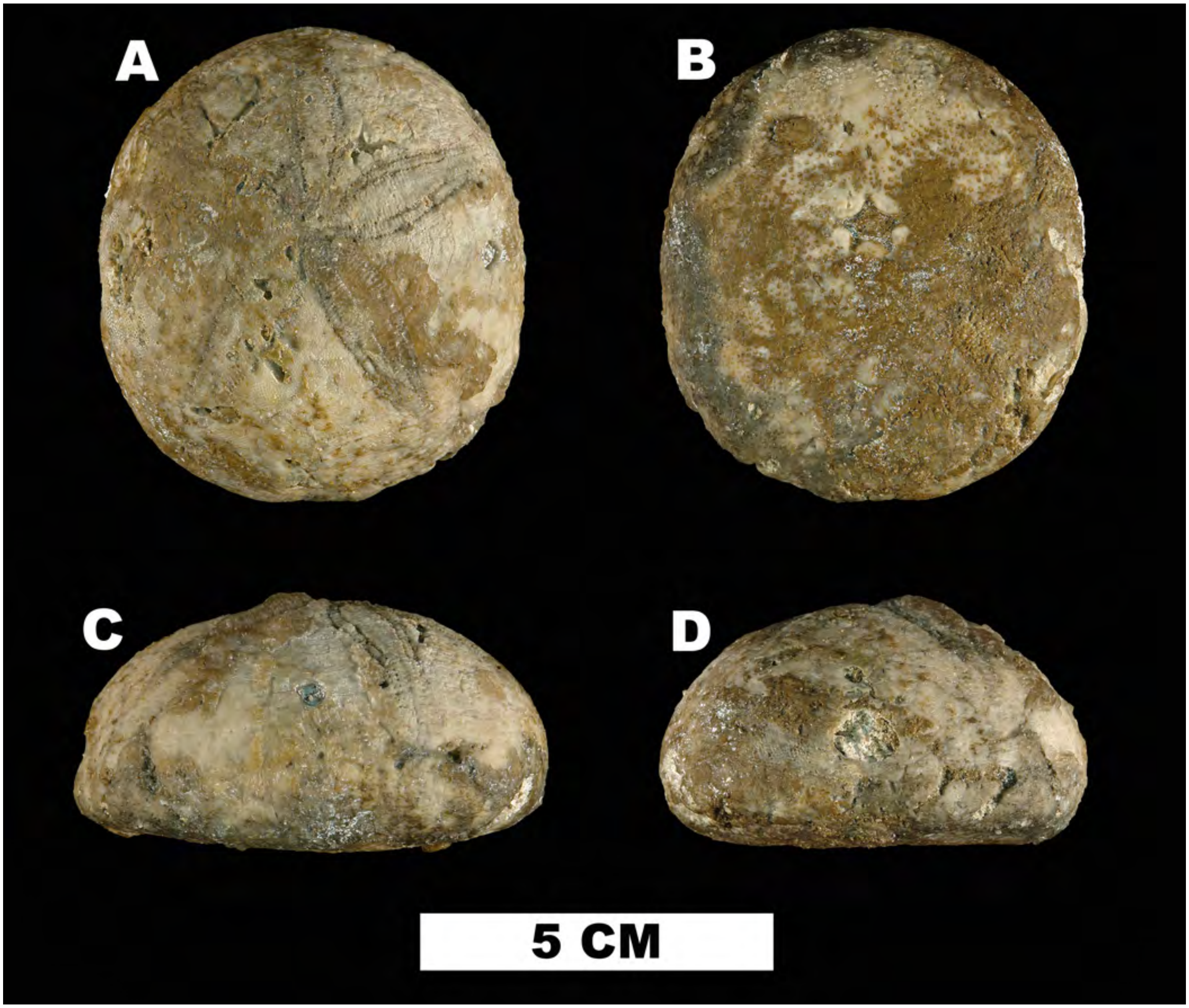


Figure 45. *Rhyncholampas meansi* n. sp., paratype (UF 289233), Caloosahatchee Formation (FM locality 6022). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

mation in the former Dickerson Quarry, St. Lucie County (FM locality SL004). However, these specimens are especially troublesome because they are invariably encrusted with a very tough, sandy coquina limestone (Figs. 47–48). This matrix is much harder than the tests of the *Rhyncholampas* within and precludes full preparation of the specimens to reveal important details.

Specimens from the uppermost, indurated horizon of the Caloosahatchee Formation east of LaBelle (Figs. 44–46) are embedded in a very hard limestone and encrusted with calcite that is often at least partially dissolved into the test, making preparation of the specimens exceptionally difficult. However, enough specimens from the Caloosahatchee Formation are available with sufficient detail to make a determination of the distinguishing features of the species. In addition, abundant

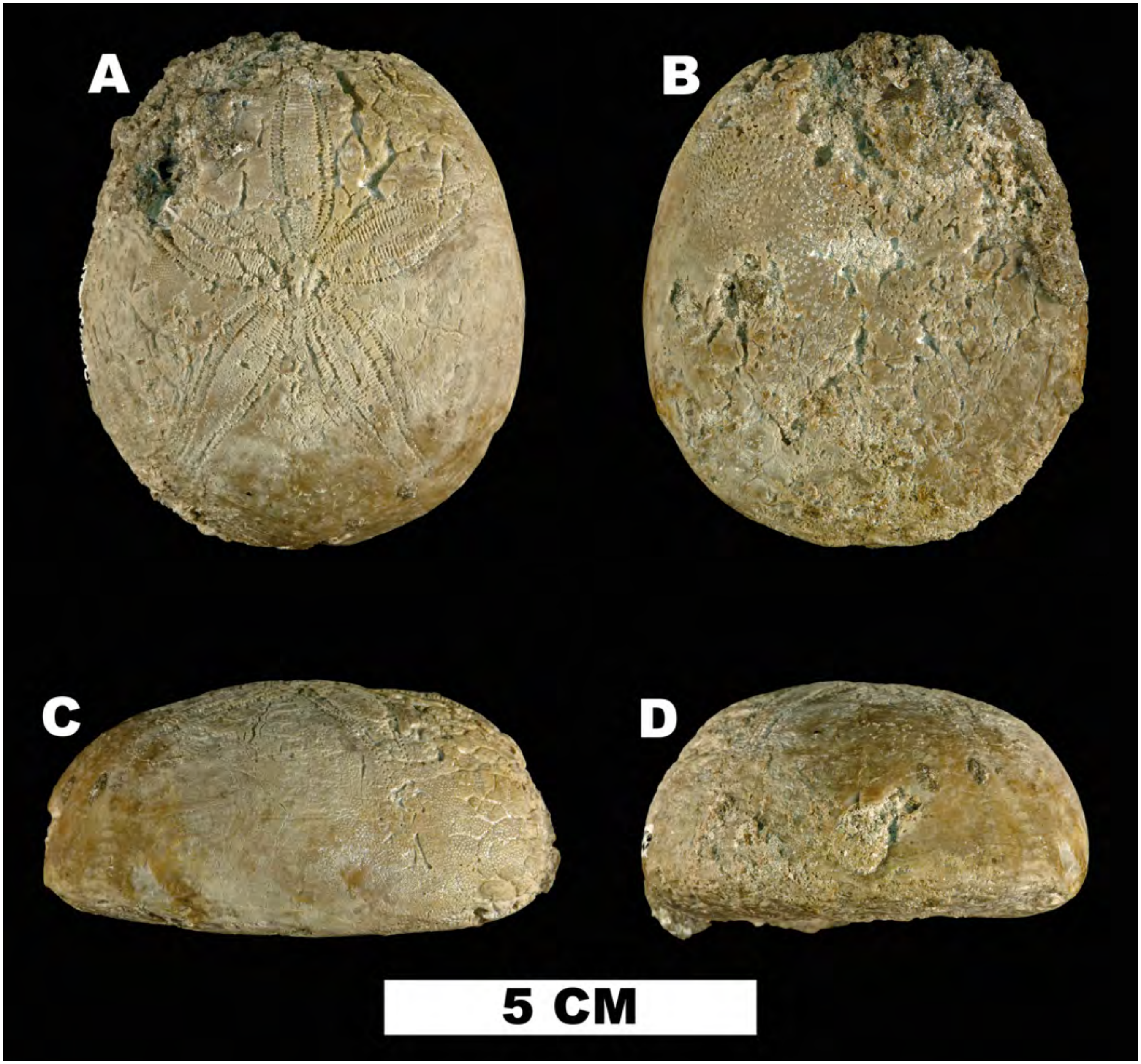


Figure 46. *Rhyncholampas meansi* n. sp., paratype (UF 289234), Caloosahatchee Formation (FM locality 6022). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

specimens from the Dickerson Quarry, although at least partially encrusted with matrix, permit determination that they are conspecific with the Caloosahatchee material, allowing us to determine that it represents a new species, particularly as there are no additional, regional Pleistocene *Rhyncholampas* currently documented. Although global comparisons with all currently described species (especially Paleogene counterparts) are not feasible, we name the new species to draw attention to a previously unrecognized, important taxon from the latest early to late Pleistocene of Florida. It is the youngest documented species of the genus outside of the extant *R. pacificus*.

Petuch (2004) and Petuch and Roberts (2007) figured a *Rhyncholampas* from the Holey Land Member of the Bermont Formation in southern Florida that is likely *R. meansi*. Petuch and Roberts (2007) recognized that it does not match the characteristics of *R. evergladensis* and designated it as *Rhyncholampas* cf. *evergladensis*. However, the overall morphology of *R. meansi* is most similar to *R. evergladensis*.

Rhyncholampas meansi n. sp. can be readily differentiated from *R. evergladensis* in that the upper surface of the former is more gently rounded and the test is proportionately wider. Kier (1963) reported an average TW to TL ratio of 83% for 101 specimens of *R. evergladensis*. In *R. meansi*, the test is much broader, with the TW ranging from 87.8 to 95% TL (average 90.2%, based on 14 specimens with measurable ratios). No specimens of

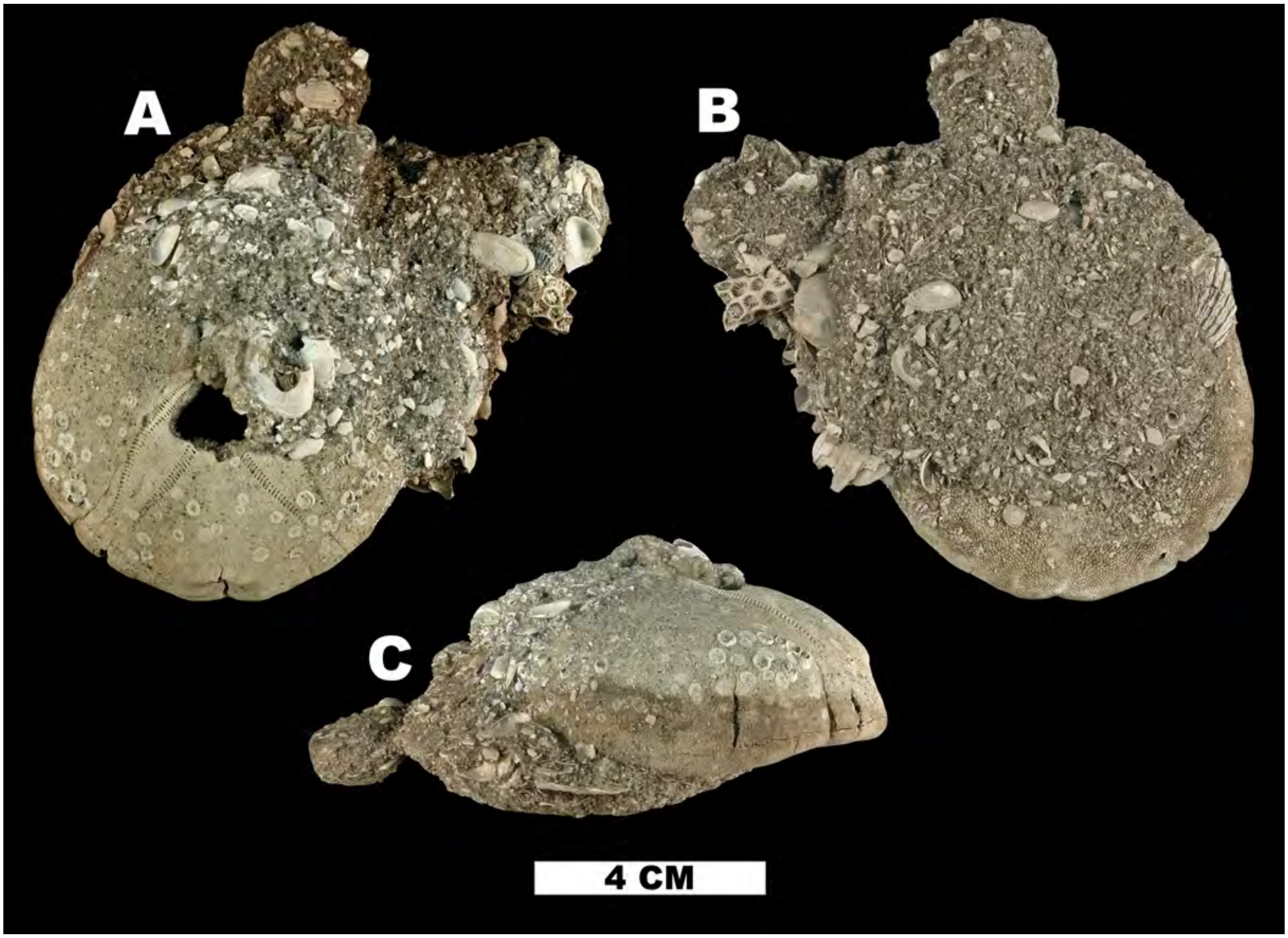


Figure 47. *Rhyncholampas meansi* n. sp., paratype (UF 156410), Anastasia Formation (FM locality SL004). A. aboral view, B. oral view, C. lateral view.

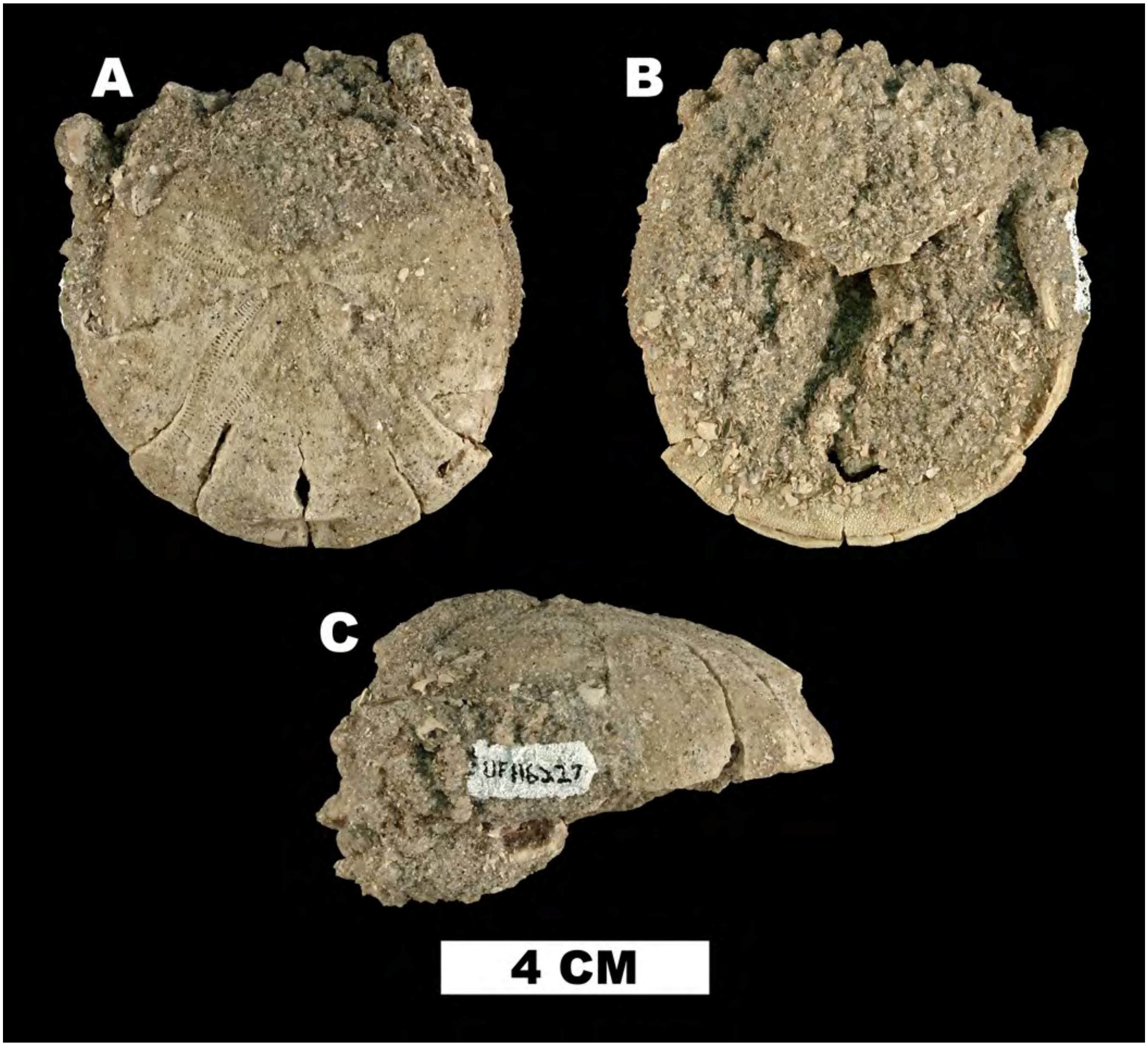


Figure 48. *Rhyncholampas meansi* n. sp., paratype (UF 116227), Anastasia Formation (FM locality SL004). A. aboral view, B. oral view, C. lateral view.

R. meansi are as narrow as the average of the 101 specimens of *R. evergladensis* measured by Kier (1963).

Kier (1963) noted that *R. evergladensis* has a TH that varied from 44 to 58% TL. TH of *R. meansi* ranges from 46.4–55% TL. Although this range is similar to that of *R. evergladensis*, *R. meansi* has a much more gently rounded upper surface than is typical of *R. evergladensis*, which Kier (1963) described as "more pointed". Also, the margin of *R. meansi* is never sharply curved, as is typical for *R. evergladensis*, but is more gently rounded. The oral surface of *R. evergladensis* is concave, whereas in *R. meansi* it is flat or only slightly concave. The distinctly broad test, with a gently rounded aboral surface that is never pointed, and flat oral surface readily distinguish *R. meansi* from *R. evergladensis*.

Rhyncholampas ayersi, which occurs below *R. meansi* in the Caloosahatchee Formation, is a somewhat smaller (TL 54–65 mm *sensu* Kier,

1963) and higher (TH on average 55% TL *sensu* Kier, 1963) species than *R. meansi* with much steeper sides (Fig. 36) and a more rounded margin that gives it a swollen or inflated appearance — much more so than the lower, aborally gently rounded test of *R. meansi*. The lower and wider test of *R. meansi* readily differentiates it from *R. sabistonensis* (Fig. 43).

Etymology.—Named in honor of Florida's Assistant State Geologist Guy Harley Means for his many significant contributions to the Florida Museum of Natural History and to the advancement of paleontology of the state.

Material.—Holotype UF 289232 and paratypes UF 289233 and UF 289234, as well as non-type specimens (UF 289235, UF 289236, and UF 308033) from the uppermost Caloosahatchee Formation, all from a small quarry dug for road fill used during the widening of Highway 80 east of LaBelle (FM locality 6022).

Order **CLYPEASTEROIDA** A. Agassiz, 1872
Family **CLYPEASTERIDAE** L. Agassiz, 1836
Genus ***CLYPEASTER*** Lamarck, 1801
CLYPEASTER ROMANI Kier, 1964
Figure 49

Clypeaster subdepressus (not Gray), Cooke, 1942, p. 11, pl. 4, fig. 5.
Clypeaster subdepressus (not Gray), Cooke, 1959, p. 36, pl. 11, figs. 2–4. (in part, figured specimen is *C. romani*).
Clypeaster crassus Kier, 1963, pp. 30–32, pl. 11, figs. 1–3. text fig. 24. tbl. 1.
Clypeaster romani Kier, 1964, p. 610 (new name for *C. crassus*).
Clypeaster romani (Kier). Ciampaglio et al., 2009, fig. 2.
Clypeaster romani (Kier). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Within Florida, *C. romani* has not been documented outside of the upper Pliocene Tamiami Formation: Sunniland Rock Company quarries west of Florida Rt. 29, Sunniland, Collier County (type locality); float from pits west side of Rt. 29, 1.3 miles south of Sunniland, Collier County (Kier, 1963). The species is more abundant in the lower Pleistocene Waccamaw Formation in the Carolinas (Ciampaglio et al., 2009; Ciampaglio and Osborn, 2011).

Discussion.—Kier (1964) recognized that the name *C. crassus* Kier, 1963 was preoccupied, and replaced the junior homonym *C. crassus*, with *C. romani*.

Cooke (1959:36) referred specimens of this species from the intercoastal waterway in South Carolina to *C. subdepressus*. However, *C. romani* has a much thicker margin and the area between its margin and the ends of its petals is flat or depressed, whereas it slopes towards the margin in *C. subdepressus*. Furthermore, in *C. romani*, petal III is more widely open and not as long relative to the other petals, and the test is less elongate than in *C. subdepressus* (Kier, 1963).

The correlation between the Florida and Carolina occurrences of *C. romani* is noteworthy. In Florida, Kier (1963) documented this species in the typical, upper Pliocene Tamiami Limestone (Ochopee Limestone member) near Sunniland, Collier County. *Clypeaster romani* has not been found in the overlying lower Pleistocene Caloosahatchee Formation (which does contain *C. subdepressus*) in southern Florida. However, in the Carolinas, *C. romani* is present in the lower portion of the lower Pleistocene Waccamaw Formation, (time correlative of the Caloosahatchee Formation).

In Florida, this species has not been documented outside of the Ochopee Limestone member of the Tamiami Formation near the type locality for the species in Collier County, where Kier (1963) documented it with *E. tamiamiensis* and *R. evergladensis*. We have not found *C. romani* in the sand facies (echinoid/barnacle facies *sensu* DuBar, 1958) westward in Charlotte County where the Tamiami Formation has a very rich and diverse echinoid fauna.

CLYPEASTER ROSACEUS (Linnaeus, 1758)
Figures 50–54

Echinus rosaceus Linnaeus, 1758, p. 665.
Clypeaster rosaceus (Linnaeus). Lamarck, 1801, p. 349.
Clypeaster ellipticus Michelin, 1861, pp. 101–148, pls. 9–36.
Diplothecanthus rosaceus (Lamarck). Clark and Twitchell, 1915, p. 219, pl. 102, figs, 1a–b; pl. 103, figs. 1a, b.
Diplothecanthus dalli Twitchell in Clark and Twitchell, 1915, p. 218, pl. 99, figs. 2a, b; pl. 100, figs. la, b.
Clypeaster dalli (Twitchell). Jackson, 1922, p. 37, pl. 4, fig.1.
Clypeaster rosaceus (Linnaeus). Jackson, 1922, p. 33.
Clypeaster kugleri Jeannet, 1928, p. 19, pl. 2, figs. 4–6.
Clypeaster rosaceus (Linnaeus). Cooke, 1942, p. 11.
Clypeaster rosaceus (Linnaeus). Mortensen, 1948, p. 40, pl. 1, figs. 2–4; pl. 64, figs. 1–5. (includes additional synonymy).

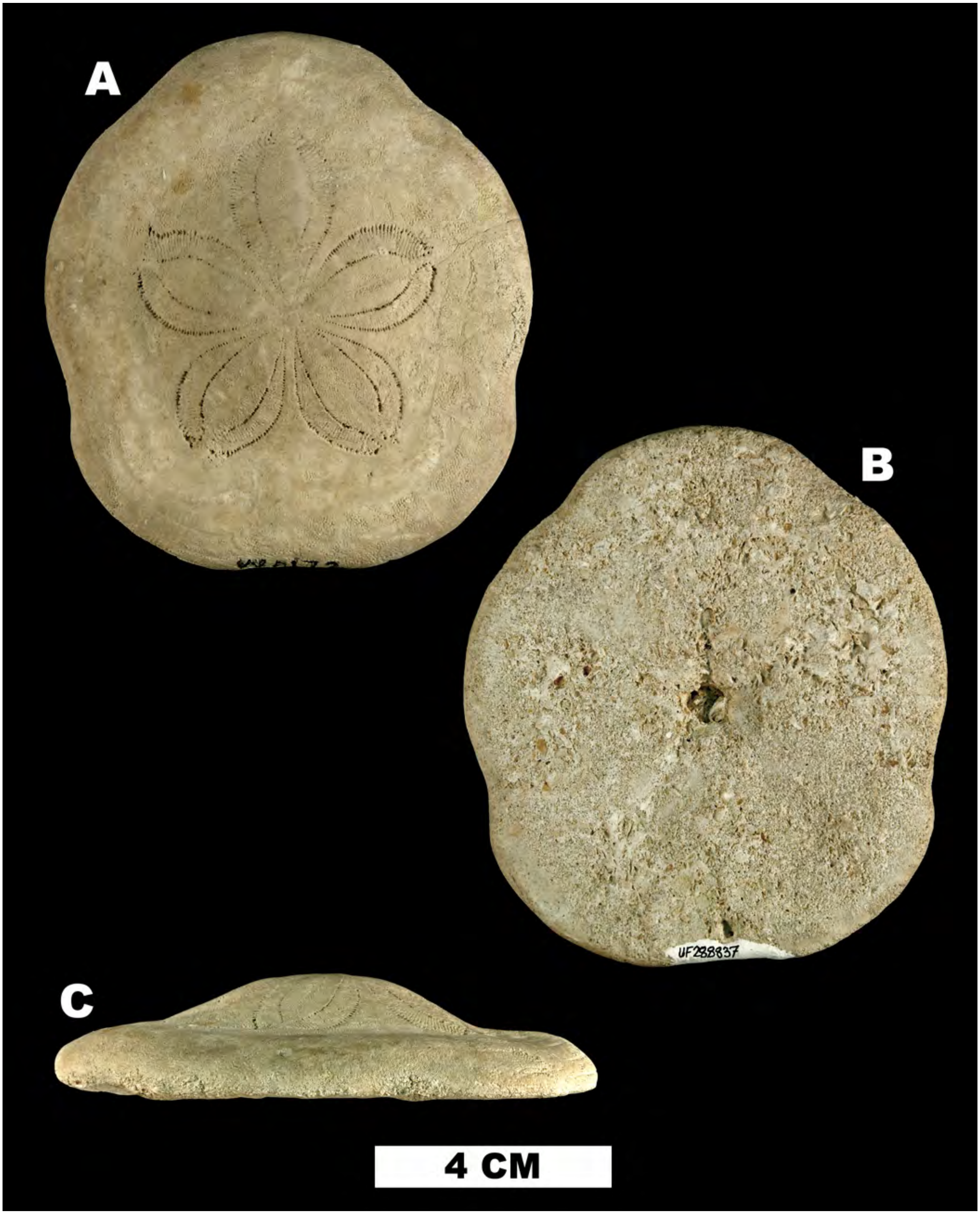


Figure 49. *Clypeaster romani* (UF 288837), Waccamaw Formation of South Carolina (FM locality ZS041). A. aboral view, B. oral view, C. lateral view.

Clypeaster rosaceus (Linnaeus). Sánchez-Roig, 1949, p. 78.
Clypeaster rosaceus (Linnaeus). Durham, 1955, text figs. 15a, 25a.
Clypeaster rosaceus (Linnaeus). DuBar, 1958, p. 209, pl. 12, fig. 17.
Clypeaster rosaceus (Linnaeus). Cooke, 1959, p. 34, pl. 10, figs. 1–3.
Clypeaster rosaceus (Linnaeus). Engel, 1961, p. 2.
Clypeaster rosaceus (Linnaeus). Cooke, 1961, pp. 16, 17, pl. 5, fig. 3.
Clypeaster rosaceus rosaceus (Linnaeus). Kier, 1963, p. 26.
Clypeaster rosaceus dalli (Twitchell). Kier, 1963, pp. 26–30, pl. 10; text figs. 19–23.
Clypeaster rosaceus (Linnaeus). Kier and Grant, 1965, pp. 26–28, pl. 4, #1–7. pl. 6, #7. text fig. 6.
Clypeaster rosaceus (Linnaeus). Serafy, 1971, pp.783–785, figs. 1, 2b, tbl. 2.
Clypeaster rosaceus (Linnaeus). Kier, 1975, p.18, pl. 12.1, 12.2.
Clypeaster rosaceus (Linnaeus). Poddubiuk, 1985, pp. 76–78, figs. 1a, 2 tbl. 1.
Clypeaster rosaceus dalli (Twitchell). Poddubiuk, 1985, tbl. 2.
Clypeaster rosaceus duchassingi (Michelin). Poddubiuk, 1985, tbl. 2.
Clypeaster rosaceus (Linnaeus). Hopkins, 1988, p. 338, tbl. 1, figs. 1, 2.
Clypeaster rosaceus (Linnaeus). Mooi, 1989, fig. 34.
Clypeaster rosaceus (Linnaeus). Donovan, 1993, pp. 386–388, figs. 10.1, 10.2.
Clypeaster rosaceus (Linnaeus). Donovan et al., 1994, p. 354.
Clypeaster rosaceus (Linnaeus). Hendler et al., 1995, pp. 229–230, figs.121, 134I.
Clypeaster rosaceus (Linnaeus). Oyen and Portell, 2001, pp.193–218, pl. II, fig. 5.
Clypeaster rosaceus (Linnaeus). Pomory, 2003, pp. 19–20, fig. 7.
Clypeaster rosaceus subspecies (Linnaeus). Petuch, 2004, p. 232, pl. 85, fig. D.
Clypeaster rosaceus subspecies (Linnaeus). Petuch and Roberts, 2007, p. 162, fig. 6.9C.
Clypeaster rosaceus (Linnaeus). Mihaljevic et al., 2010, pp. 5, 6, fig. 5.1.
Clypeaster rosaceus (Linnaeus). Mihaljevic et al., 2011, figs. 1g, h. 4, 5, 8f.

Occurrence.—*Clypeaster rosaceus* is documented from the lower Pleistocene Caloosahatchee Formation (represented by the morphotype attributed to *C. rosaceus dalli* by Kier, 1963), middle Pleistocene Bermont Formation, and upper Pleistocene Miami Limestone of south Florida. Only a few representative localities are listed here: Caloosahatchee Formation (Bee Branch Member sensu DuBar, 1958) as float from north bank of the Caloosahatchee River and LaBelle pits on the north bank in SE¼ sec. 12, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS localities 23082, 23083); as float in the Denaud pits, in NW¼ sec. 14, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS 22373) (Kier, 1963); Caloosahatchee River 2.5 miles below LaBelle (USGS locality 4955 [Cooke, 1959]); Bermont Formation as float from a road metal pit on the south side of Florida route 80 southwest of Belle Glade, Palm Beach County (USGS locality 22704 [Kier, 1963]); Griffin Quarries on the Palm Beach-Broward County line south of Belle Glade (Petuch, 1992); Four-mile Hammock between Fort Thompson and Denaud (USGS locality 2094, type locality of *Diplothecanthus dalli* Twitchell in Clark and Twitchell, 1915); Miami Limestone, Buena Vista, near Miami (USGS locality 4867).

This species is also present throughout the Caribbean Region: Jamaica (Plio-Pleistocene [Donovan, 1993, 1994]); Cuba (Pleistocene [Sánchez-Roig, 1949]); Venezuela (Miocene-Pleistocene [Cooke, 1961; Mihalijevic et al., 2010]); Dominican Republic (Miocene or Pliocene? ref. for *C. dalli* [Jackson, 1922]); Guadeloupe? (occurrence of *C. rosaceus duchassingi* [Michelin, 1861]); St. Kitts (Pleistocene [Engel, 1961]).

Discussion.—*Clypeaster rosaceus* is perhaps the most distinctive representative of *Clypeaster* in the modern faunas of the Caribbean region. Although it is the type species of the genus, it is not typical in its living habits relative to most of its congeners, as it is essentially a surface dweller with a preference for sea grass beds (Telford et al., 1987), whereas most extant members of the genus are shallow burrowers (Seilacher, 1979).

Adults of living specimens are a rich, dark brown, covered with an even carpet of short, stout spines. The test is distinctively shaped, with a strongly developed oral infundibulum, at the top of which is situated the peristome, and in which copious amounts of sea grass can be stored prior to ingestion (Telford et al., 1987). The species is typically about 130 mm TL (Kier and Grant, 1965).

The very swollen, strongly convex upper surface, concave lower surface that is deeply invaginated around the peristome, inflated petals, and thick strong "double walled" test readily distinguish this species from any other species in the modern fauna. This internal "double wall" structure is nearly unique to *C. rosaceus*, where a single

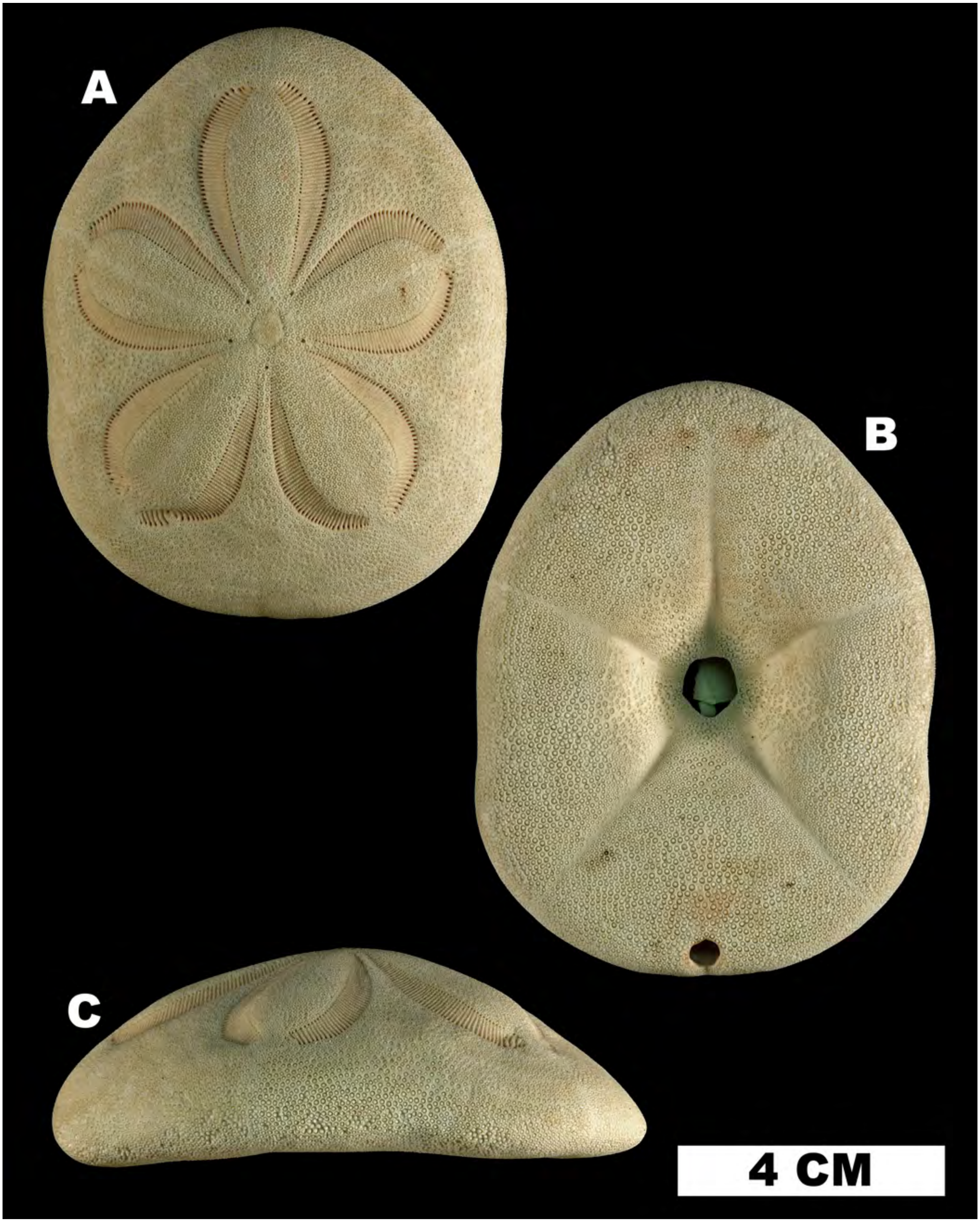


Figure 50. *Clypeaster rosaceus* (UF-IZ 18900), modern specimen (off Marathon Key at 2 m depth, Monroe County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

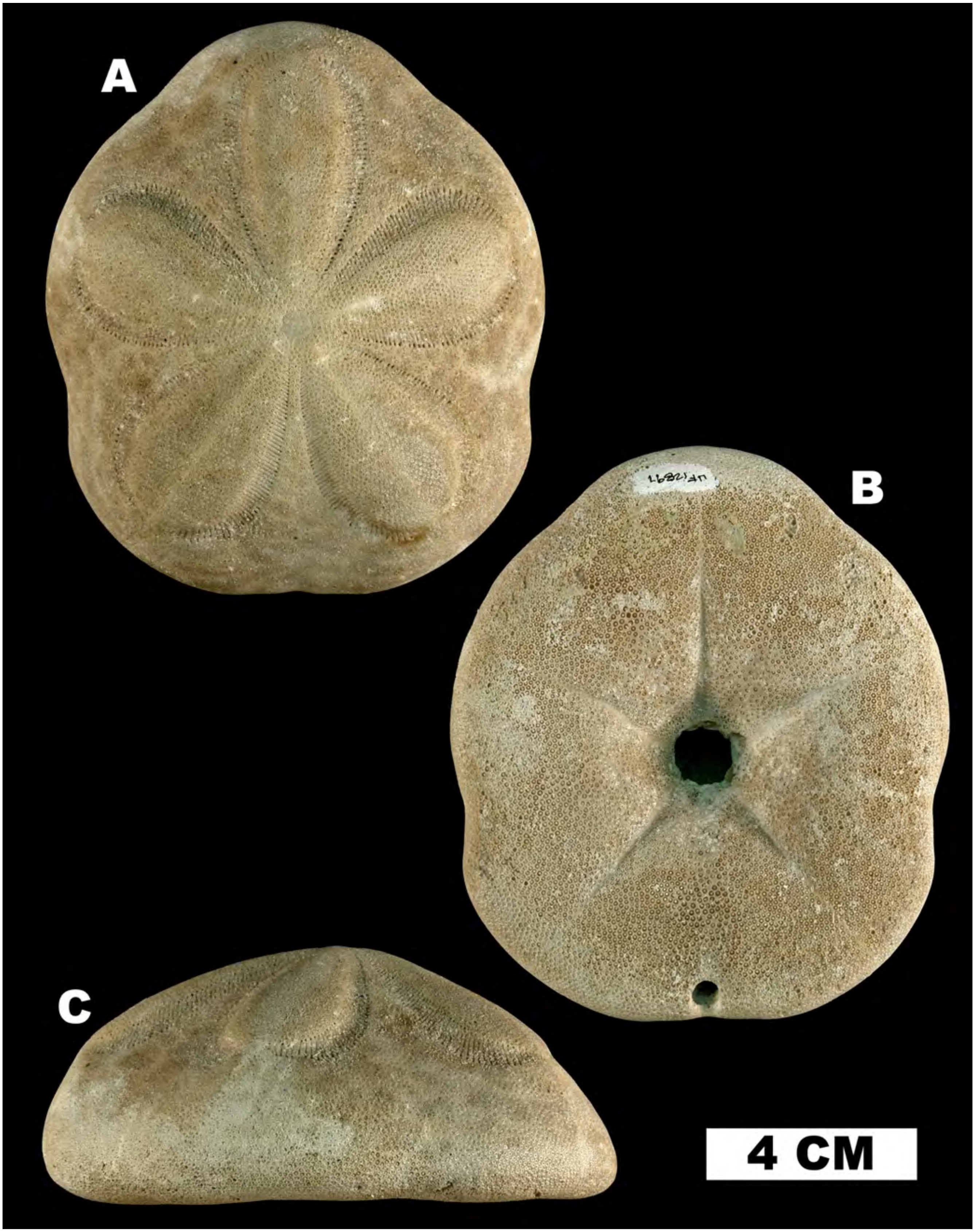


Figure 51. *Clypeaster rosaceus* (UF 12897), Caloosahatchee Formation (FM locality HN004). A. aboral view, B. oral view, C. lateral view.

buttress wall is not merely present at the periphery, as it is in most species of the genus, but in *C. rosaceus* it extends orally and aborally, forming what Mortensen (1948) referred to as a "double wall". Mortensen (1948) and Poddubuik (1985) considered this double-wall characteristic of this species, and this feature can be used to readily identify even partial specimens in the fossil record.

Clypeaster rosaceus is well documented in the fossil record of southern Florida, from the lower Pleistocene Caloosahatchee Formation (Kier, 1963); middle Pleistocene Bermont Formation (Kier, 1963; Petuch, 2004; Petuch and Roberts, 2007), and upper Pleistocene Miami Limestone. Some authors have referred this morphotype from the fossil record of Florida (slightly wider than the extant specimens) to *C. dalli* (Twitchell in Clark and Twitchell, 1915; Jackson, 1922) or *C. rosaceus dalli* (Kier, 1963; Poddubiuk, 1985). As discussed below, we see no value in distinguishing the Florida fossil morphotype of *C. rosaceus* as a subspecies.

Twitchell in Clark and Twitchell (1915) first documented a variation of *C. rosaceus* in Pleistocene deposits of Florida and called it *Diplothecanthus dalli*. He differentiated it from *C. rosaceus* by its relatively high test, apex slightly eccentric posterior and acute, with a straighter slope anteriorly and a steeper slope posteriorly, in having the apical system sloping downward anteriorly, and its interporiferous areas being more tumid. Jackson (1922) stated that *C. dalli* was also distinguishable due to its more swollen petal areas. However, even he cautioned that some specimens of *C. rosaceus* also have noticeably swollen petals. Nevertheless, he disregarded this similarity as simply being two allied species taking on each others characteristics, a consistent mechanism for which was never suggested. Given the great variation among modern *C. rosaceus*, these traits, linked to the dubious taxonomic history of *C. dalli*, are not considered diagnostic.

Cooke (1959) stated that two of the three fossil specimens from the Caloosahatchee River named *Diplothecanthus dalli* Twitchell in Clark and Twitchell (1915) have somewhat more inflated petals than the other, which Twitchell identified as *C. rosaceus*. However, Cooke asserted that all three specimens were *C. rosaceus* and that they are Pleistocene rather than Pliocene, as had been supposed previously. Cooke (1959) therefore considered *D. dalli* synonymous with *C. rosaceus*. Engel (1961) supported Cooke (1959) in this synonymy.

Kier (1963) had 69 specimens of *D. dalli* available for comparison and noted that the test varies in shape, from low to highly inflated, with angular to rounded marginal outline. The petals could be highly inflated or only slightly inflated. In the apical system, all the genital pores may be widely separated from the madreporite, or any number of them may be in contact with the madreporite, a feature seen within modern populations of *C. rosaceus* (Andreas Kroh, personal communication, and RM, unpublished observations). The characters that do not vary are the outline of the petals, the position and size of the periproct, and the extent of the depressed area around the peristome (Kier, 1963).

In his study of this material, Kier (1963) disagreed with Cooke (1959) and did not consider the two species to be synonymous. Instead, he considered *D. dalli* a subspecies of *C. rosaceus*. When he recognized *C. rosaceus dalli* in the Pleistocene of Florida, he stated that *C. rosaceus rosaceus* had not been found in the Pliocene or Pleistocene of Florida and that occurrences in the Pleistocene fossil record of the state are attributable to *C. rosaceus dalli*.

Kier (1963) distinguished *C. rosaceus dalli* from *C. rosaceus rosaceus* primarily by its wider test. He stated that in all other features, these specimens are indistinguishable from *C. rosaceus rosaceus*, asserting at the same time that although some specimens of *C. rosaceus rosaceus* are as wide as certain *C. rosaceus dalli*, most of them are narrower. Kier also examined the specimen from the Dominican Republic, which Jackson (1922) had referred to *C. dalli,* and stated that it cannot be distinguished from the material in the Caloosahatchee Formation. Jackson attributed the Dominican Republic specimen tentatively to the Miocene or Pliocene.

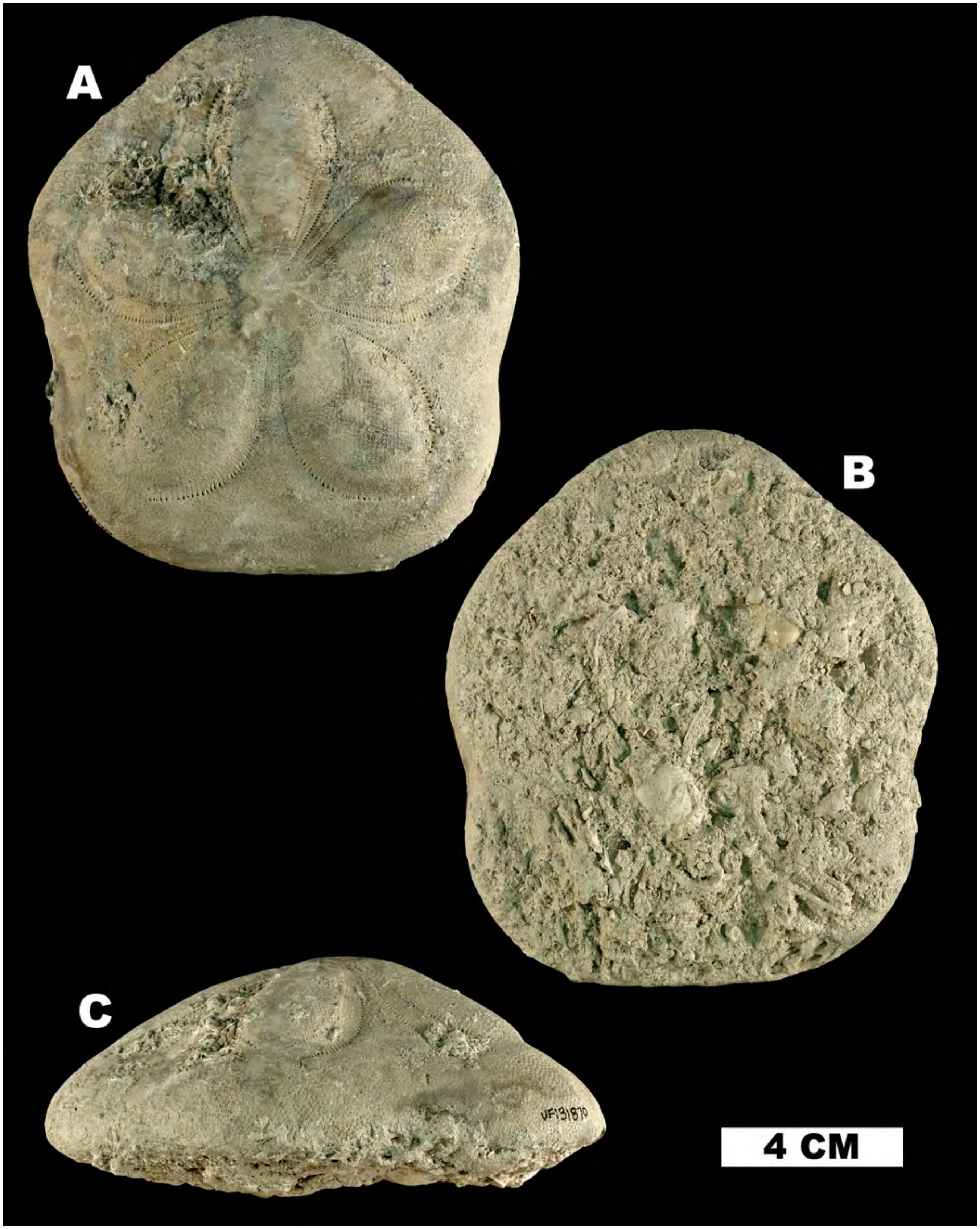


Figure 52. *Clypeaster rosaceus* (UF 131870), Bermont Formation (FM locality PB014). A. aboral view, B. oral view, C. lateral view.

Figure 53. *Clypeaster rosaceus* (UF 131871), Bermont Formation (FM locality PB014). A. aboral view, B. oral view, C. lateral view.

Figure 54. *Clypeaster rosaceus* (UF 42000), Bermont Formation (FM locality PB001). A. aboral view, B. oral view, C. lateral view.

Oyen and Portell (2001:214) stated that *C. rosaceus dalli* was likely a case of taxonomic splitting, and questioned the validity of the subspecies. Given the great variation in *C. rosaceus*, we likewise do not recognize either of the above mentioned subspecific designations of *C. rosaceus*. However, we do point out that the Pleistocene occurrences of *C. rosaceus* from Florida have a tendency towards a wider test, as documented by Kier (1963), but all other traits are too variable and not useful in differentiating the Recent and fossil forms.

CLYPEASTER SUBDEPRESSUS (Gray, 1825)
Figures 55–56

Echinanthus subdepressa Gray, 1825, p. 427.
Clypeaster subdepressus (Gray). A. Agassiz, 1874, p. 306, pl. 116, figs. 1, 2; pl. 12d, fig. 4; pl. 13, figs. 10–18.
Clypeaster subdepressus (Gray). H. L. Clark, 1914, p. 38, pl. 123, figs. 11, 12.
Clypeaster subdepressus (Gray). Cooke, 1942, p. 11, pl. 4, fig. 5.
Clypeaster (*Stolonoclypus*) *subdepressus* (Gray). Mortensen, 1948, p. 112, pl. 23, figs. 1–3; pl. 24, fig. 3; pl. 25, fig. 6; pl. 26, figs. 1, 6; pl. 27, fig. 4; pl. 45, figs. 4, 11, 14, 15. (includes additional synonymy).
Clypeaster subdepressus lobulatus Bernasconi, 1956, p. 122, pl. 1, figs. 4a–c.
Clypeaster subdepressus (Gray). Cooke, 1959, p. 36, pl. 11, figs. 2–4.
Clypeaster subdepressus (Gray). Engel, 1961, pp. 1–6.
Clypeaster subdepressus (Gray). Kier, 1963, pp. 25, 26, pls. 8, 9, text fig. 18.
Clypeaster subdepressus (Gray). Kier and Grant, 1965, pp. 28, 30, 31, pl. 5 #1–6, pl. 6, #1–10. pl. 15, #8. text fig. 6.
Clypeaster subdepressus (Gray). Kier, 1975, p. 18, pl. 6.4.
Clypeaster subdepressus (Gray), Serafy, 1979, pp. 65–67, fig. 28.
Clypeaster subdepressus (Gray). Hopkins, 1988, p. 340, figs. 1, 2. tbl. 1.
Clypeaster subdepressus (Gray). Mooi, 1989, fig. 4a.
Clypeaster subdepressus (Gray). Donovan et al., 1994, p. 354.
Clypeaster subdepressus (Gray). Hendler et al., 1995, pp. 231, 232, figs. 122, 134J.
Clypeaster subdepressus (Gray). Mihaljevic et al., 2010, pp. 6–8, fig. 5.3.
Clypeaster subdepressus (Gray). Mihaljevic et al., 2011, figs. 3j, 4d, 9b.

Occurrence.—*Clypeaster subdepressus* is known from the Caloosahatchee Formation (early Pleistocene), Bermont Formation (middle Pleistocene), and Miami Limestone (late Pleistocene) in southern Florida. Kier (1963) reported this species in the following Caloosahatchee Formation (Bee Branch Member sensu DuBar, 1958) localities: outcrops along north bank of Caloosahatchee River and in road metal (LaBelle) pits on north bank in SE¼ sec. 12, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 23083); float in Denaud pits, in NW¼ sec. 14, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 22373); float from north bank of Caloosahatchee River west of Three Way Rock Company pits, in SW¼ sec. 6, T. 43 S., R. 29 E., LaBelle Quadrangle, Hendry County (USGS locality 23085). It also occurs in the Miami Limestone at Buena Vista, near Miami (USGS locality 4867) and the Bermont Formation near South Bay, Palm Beach County (FM locality PB007).

This species is well known in the fossil record of the Caribbean: Cuba (Pleistocene [Sánchez-Roig, 1949:82]); Jamaica (Pleistocene [Donovan, 1994]), and Venezuela (Pleistocene [Mihaljevic et al., 2010]).

Discussion.—*Clypeaster subdepressus* is one of the most abundant nearshore members of the genus in the modern fauna of the region. Hendler et al. (1995) reported it from North Carolina southward around the Florida Keys, in the Gulf of Mexico, and throughout the Caribbean to Rio de Janeiro, Brazil. It is found commonly on sand fields or shelly sediments that are free of sea grass (Telford et al., 1987), and though it has been reported as deep as 210 m, it is most commonly documented at depths from five to 50 m (Hendler et al., 1995).

Live individuals of *C. subdepressus* are tan to yellow-brown, and covered aborally by short, densely distributed spines, with longer locomotory spines on the oral surface (Telford et al., 1987). Hendler et al. (1995) documented tests of this species up to 300 mm TL, though these are exceptionally large. Serafy (1979) reported specimens from the eastern Gulf of Mexico up to 190 mm TL. The petals are of equal size, and the test markedly flattened on the oral surface, which has a very shallow infundibulum localized around the peristome. Also, characteristic of this striking and easily recognized species is that the aboral surface is flattened towards the margin of the test, rising to form a low hump at the center to accommodate the large Aristotle's lantern.

Cooke (1959) stated that the fossil specimens

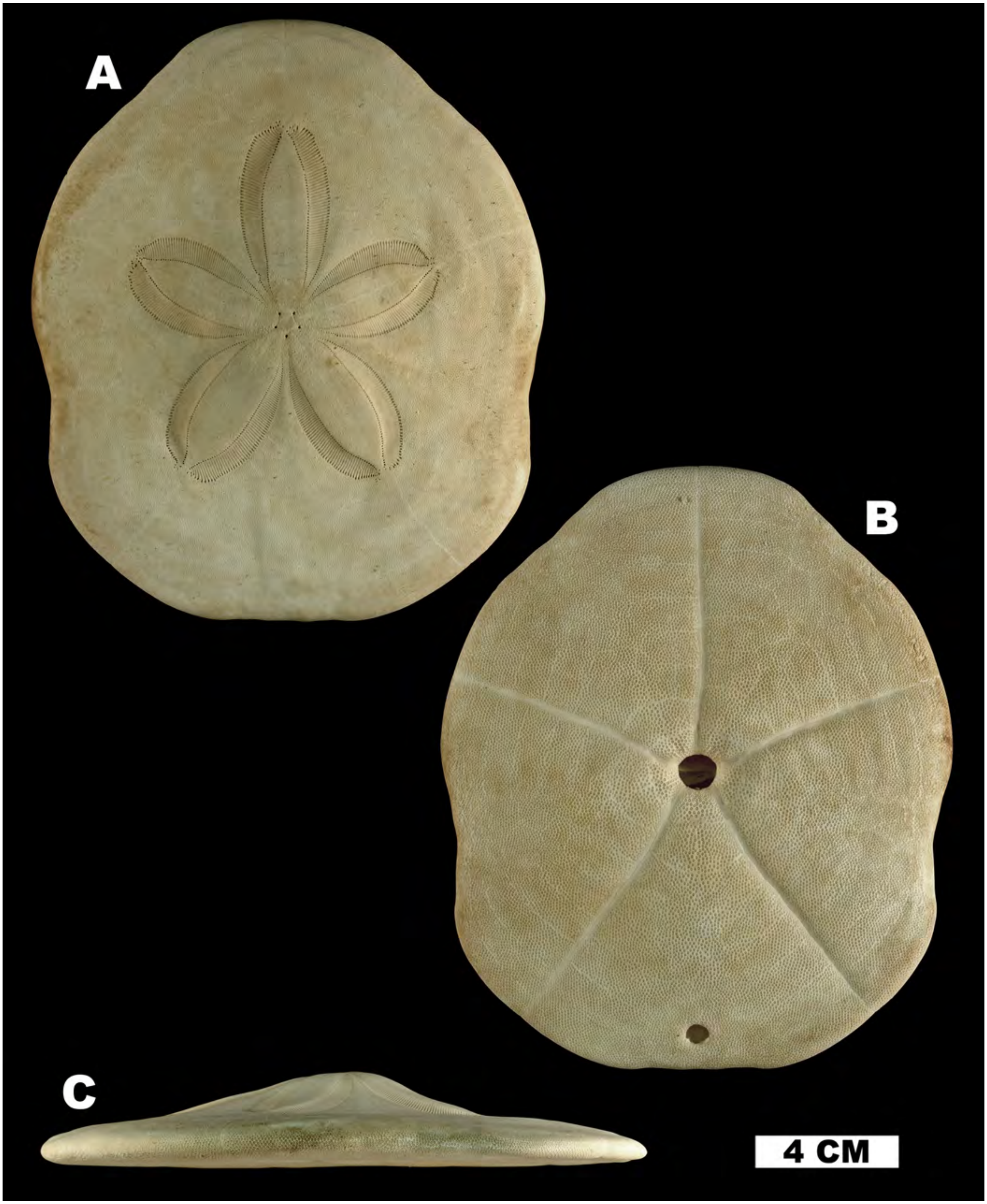


Figure 55. *Clypeaster subdepressus* (UF-IZ 18901), modern specimen (off the Dry Tortugas at 10 m depth, Monroe County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

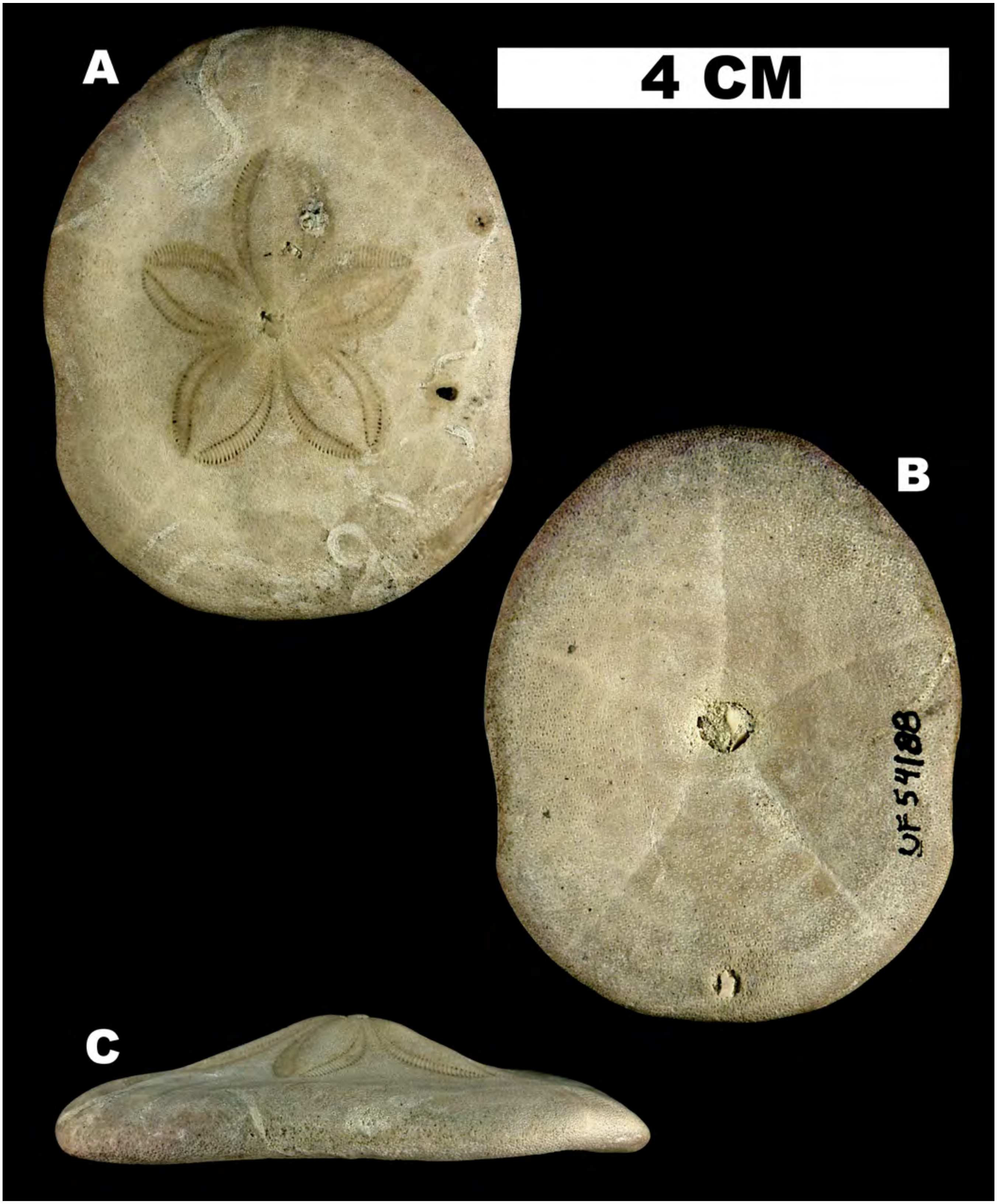


Figure 56. *Clypeaster subdepressus* (UF 54188), Bermont Formation (FM locality PB007). A. aboral view, B. oral view, C. lateral view.

from the Intracoastal Waterway in Horry County, South Carolina appear to have no consistant differences from modern *C. subdepressus*, which can vary in test shape. However, Kier (1963) asserted that the differences between *C. subdepressus* and the fossil specimens from the Waccamaw Formation in North and South Carolina, as well as the upper Pliocene Tamiami Formation of southern Florida, warranted erection of a new species he initially described as *C. crassus*, and subsequently redesignated as *C. romani* (Kier, 1964). *Clypeaster romani* has a much thicker test margin and the area between its margin and the ends of its petals is flat or depressed, whereas it slopes in *C. subdepressus*. Furthermore, in *C. romani*, ambulacrum III is more widely open and shorter than the other petals, and the test is less elongate (Kier, 1963).

Kier (1963) discussed and figured this species from the lower Pleistocene Caloosahatchee Formation of southern Florida where it occurs with *C. rosaceus* and numerous other species in the Bee Branch Member sensu DuBar (1958), along the Caloosahatchee River and pits adjacent to the river near LaBelle, Hendry County. Kier (1963: pls. 8, 9) illustrated a beautiful representative from this unit.

It is easy to confuse specimens of the late Pliocene *Clypeaster sunnilandensis* Kier, 1963, with *C. subdepressus*. However, when Kier (1963) described *C. sunnilandensis*, he remarked that it is identical in all characters to *C. subdepressus* except that its anterior, unpaired petal is open, whereas in *C. subdepressus* it is closed, this feature seems to readily distinguishable in these taxa.

CLYPEASTER SUNNILANDENSIS Kier, 1963

Figures 57–59

Clypeaster sunnilandensis Kier, 1963, pp. 32, 33, pl. 3, fig, 3. pls. 12, 13.

Clypeaster cf. *C. sunnilandensis* (Kier). Kier, 1992, p. 19, pl. 6, figs. 1, 2.

Clypeaster sunnilandensis (Kier), Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Within Florida, *C. sunnilandensis* appears to be restricted to the late Pliocene, where it occurs in both the Tamiami and Intracoastal Formations of Florida. A few occurrences reported within the Tamiami Formation are the type locality Sunniland Rock Company pits west of Florida route 29, Sunniland, Collier County and float from pits west side of Rt. 29, 2 km south of Sunniland, Collier County (Kier, 1963). This species is also abundant in certain horizons of the sandy limestone of the echinoid/barnacle facies in the Quality Materials Quarry, Charlotte County (FM locality CH080). *Clypeaster sunnilandensis* attains considerable size in the upper Pliocene Intracoastal Formation in the Langston Quarry, Liberty County (FM locality LI005) (Ciampaglio and Osborn, 2011); see below for further remarks on this population. Kier (1992) also documented *C. sunnilandensis* in the upper Miocene Cercado Formation of the Dominican Republic.

Discussion.—*Clypeaster sunnilandensis* was only recorded from the Tamiami Formation of southern Florida until Ciampaglio and Osborn (2011) noted its presence in the upper Pliocene Intracoastal Formation of Liberty County. As discussed below, specimens from the Intracoastal Formation are larger, but otherwise indistinguishable from those in the Tamiami Formation.

Kier (1963) examined 35 specimens of *C. subdepressus*, and in all, the anterior petal was closed. However, in all 12 specimens of *C. sunnilandensis* available to him, petal III was open. This trait is also consistent in specimens from the Intracoastal Formation of Liberty County (UF 289223; Fig. 57).

Maximum size of 14 specimens from the Tamiami Formation was 157 mm TL (Kier, 1963). The species is now known to attain even greater sizes, up to 180 mm TL in the Intracoastal Formation. In the sand facies of the Tamiami Formation of Charlotte County, the species rarely exceeds 100 mm TL.

The type locality for *C. sunnilandensis* is in the Ochopee Limestone member of the Tamiami Formation (a pale sandy limestone), but it is very rare in that member. A specimen 116.3 mm TL from the type locality in Collier County is figured (UF 98692; Fig. 58). *Clypeaster sunnilandensis* is far more prevalent in the sand facies of the Tamiami (sensu Missimer, 1992), which contains a rich and diverse echinoid fauna in a gray, very sandy limestone with sporadic concentrations of large

Figure 57. *Clypeaster sunnilandensis* (UF 289223), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

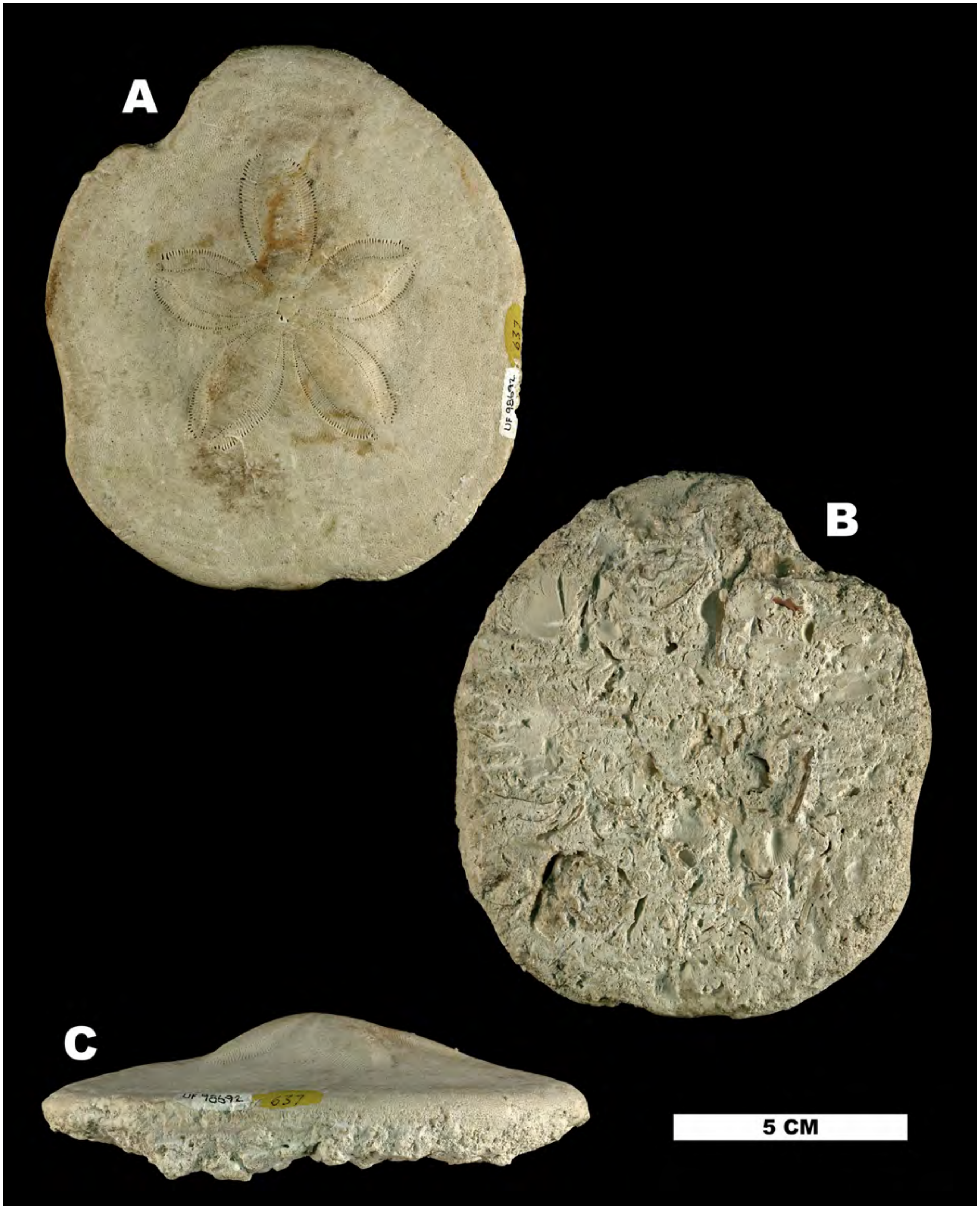


Figure 58. *Clypeaster sunnilandensis* (UF 98692), Tamiami Formation (FM locality 2601). A. aboral view, B. oral view, C. right lateral view.

barnacles (UF 289222; Fig. 59). This facies is perhaps best exposed in the Quality Materials Quarry, Charlotte County, Florida (FM locality CH080). In the Intracoastal Formation, the species occurs in a sandy biocalcarenite facies.

CLYPEASTER PETERSONORUM n. sp.
Figures 60–61

not *Clypeaster gatuni* (Jackson) Cooke. 1942, p. 13, pl. 1, fig. 15 (in part, Cooke referred this species to *C. gatuni*)

not *Clypeaster concavus* (Cotteau) Cooke. 1959, pp. 35, 36, pl. 11, fig 5 (in part, Cooke referred this species to *C. concavus*)

Diagnosis.—*Clypeaster* of moderate size (largest specimen 111 mm TL); oral surface generally flat, inflated proximal to ambitus, gentle depression inward towards shallow infundibulum; aboral surface moderately inflated, TH on average 21.5% TL; petaloid area slightly swollen, ambulacra faintly depressed, petals broad, lanceolate, nearly closed distally; petals extend about two-thirds distance to ambitus; petals I and V extend on average 59.5% distance from apical system to ambitus; petals II and IV extend on average 63.4% distance from apical system to ambitus, petal III extends on average 66.3% distance from apical system to ambitus.

Description.—Based on the holotype (UF 283993; Fig. 60) and paratypes (UF 283994, UF 283995; Fig. 61, UF 283996). Additional paratypes are UF 283997–283999. All specimens from the lower Miocene Chipola Formation, Chipola River, Calhoun County (FM locality CA001).

Test medium-sized, holotype 103.7 mm TL, 85.2 mm TW, 23.7 mm TH; largest specimen 111.1 mm TL, 99.2 mm TW, 22.5 mm TH, TW on average equals 86.5% TL; widest point slightly anterior, adjacent to ambulacra II and IV; outline oval to subpentagonal, subtruncate posteriorly in one specimen (UF 283994); aboral surface moderately inflated, not depressed, highest point at apical system; TH on average 21.5% TL. Margin rounded, thicker at anterior ambitus than at posterior, posterior margin on average 5.6% TL, anterior margin on average 7.5% TL; test thickens at margin with increasing TL, smallest specimen (84 mm TL, 73 mm TW [estimated due to test fractures]) has posterior marginal thickness of 4.2% TL, anterior margin 6% TL. Oral surface generally flat, inflated proximally to ambitus, gentle depression inward towards shallow infundibulum. Periproct subcircular, slightly wider than long, width on average 5.5% TL, length on average 4.7% TL; near the margin, on average posterior edge of periproct 2.8% TL from ambitus. Peristome subcentral, posterior edge of peristome on average 45% TL from posterior ambitus; anterior edge of peristome on average 47% TL from anterior ambitus; depressed, nearly circular, width on average 8.3% TL, length on average 7.9% TL. Apical system pentagonal, central; five genital pores at the corners of madreporite. Petaloid area slightly swollen, ambulacra faintly depressed. Petals broad, lanceolate, nearly closed distally; ambulacrum III longest (on average 33.6% TL), II and IV shortest (on average 28.8% TL) ambulacra I and V on average 31.7% TL; petals extend about two-thirds distance to ambitus; ambs I, V extend on average 59.5% distance from apical system to ambitus; ambs II and IV extend on average 63.4% distance from apical system to ambitus, amb III extends on average 66.3% distance from apical system to ambitus. Poriferous zones broad, inner pores small, circular, outer pores larger, elongate, pores conjugate, interporiferous zones more than twice as wide as poriferous at widest part (complete pore pair counts not available for any specimen). Interambulacra inflated on aboral surface between petals towards apical system. Tubercles crowded, sunken, smaller on upper surface than on lower.

Zoobank Nomenclatural Act.—9805E4BA-DE48-49AE-91B9-F9F7D88ADD22.

Occurrence.—Lower portion of the lower Miocene Chipola Formation, along the Chipola River, below the mouth of Tenmile Creek, Calhoun County, Florida. This species has not been definitively identified from outside of the type locality. Fragments of *Clypeaster* from the Miocene Torreya Formation in the FM-IP collections are likely referable to this species, though the material is insufficient to warrant positive identification.

Discussion.—The existence of a new species of *Clypeaster* in the lower Miocene Chipola Formation along the Chipola River, Calhoun County,

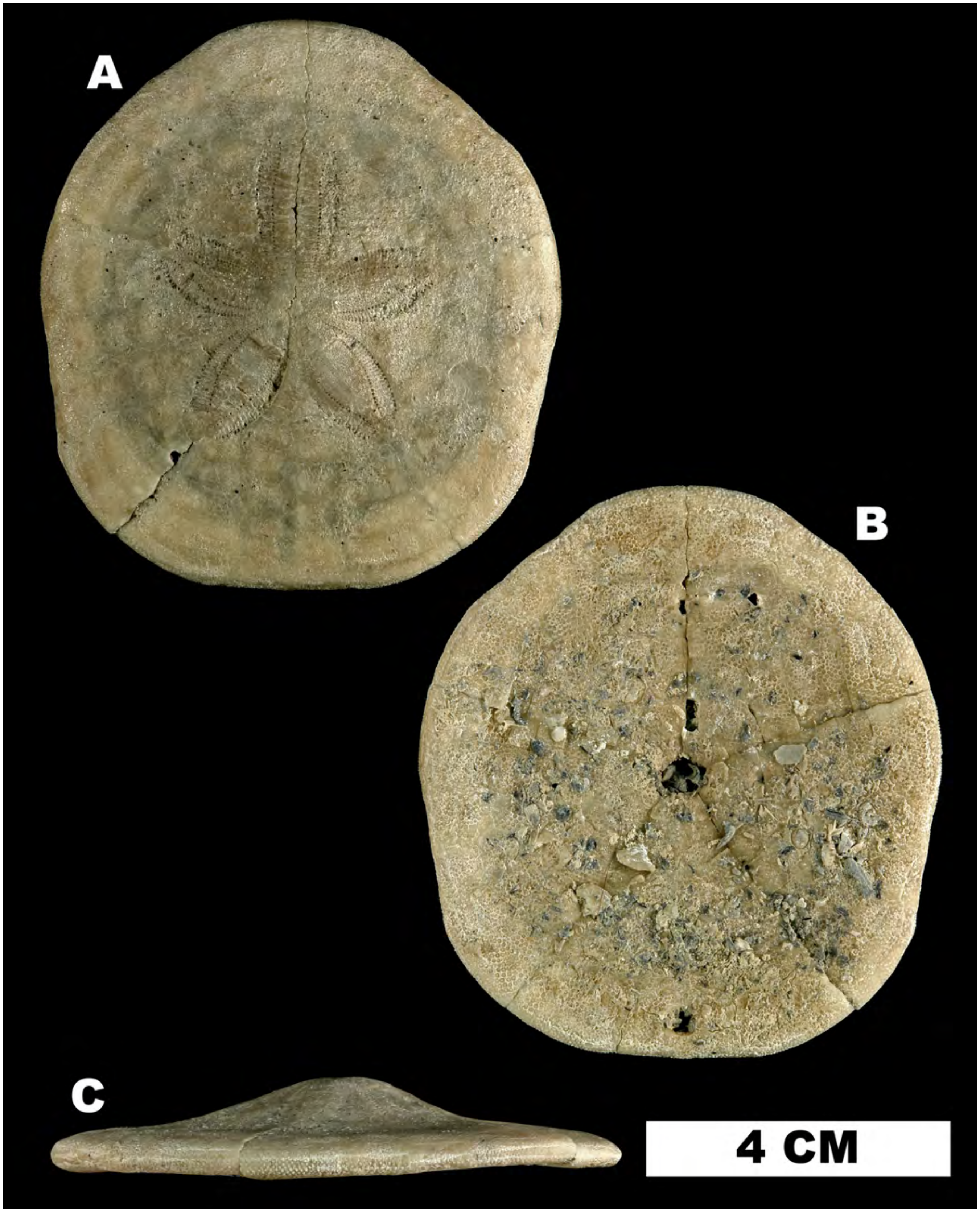


Figure 59. *Clypeaster sunnilandensis* (UF 289222), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

Florida, was first postulated by Cooke (1942), who documented an incomplete specimen (USNM 164671) collected by Frank Burns, one mile below Bailey's Ferry (which was near the mouth of Tenmile Creek). Cooke (1942) attributed the lone specimen to *Clypeaster gatuni* Jackson, 1917, which was described from, and until that time had not been documented outside of, the lower Miocene Gatun Formation, near Gatun Dam, Panama. Cooke (1942) did not name a new species, stating only that it is half as large as the type specimen of *C. gatuni*, and is the only specimen of its kind from Florida.

Cooke (1959) subsequently redesignated this specimen as *C. concavus* Cotteau, 1875, from the Miocene Anguilla Limestone of Anguilla, and placed *C. gatuni* in synonomy. Cooke (1959) did not discuss the reasons for this, or for assigning the single specimen (USNM 164671) from the Chipola Formation to *C. concavus*, beyond stating that like most species in the genus, *C. concavus* is highly variable. Additional examination of the type material of *C. gatuni* and additional specimens from the type locality is required to determine if *C. gatuni* is synonymous with *C. concavus*. That analysis is outside the scope of this work, so we herein treat *C. concavus* and *C. gatuni* as distinct species and compare the Chipola Formation specimens to both.

Jackson (1917) provided plates of the well-preserved *C. gatuni* holotype (USNM 324453). He stated that two additional specimens, much worn and incomplete, could also be referred to *C. gatuni*. The holotype is 146 mm TL, 122 mm TW, and 35 mm TH. Jackson stated that *C. gatuni* is elongate to moderately subpentagonal in outline, the widest point being across ambulacra II and IV, with a deeply concave underside that is flat on the border with a deeply sunken peristome and petals that are nearly equidistant from the margin (petals III, I and V are a few millimeters longer than petals II and IV), highly elevated, and open distally with the interambulacra between the petals being strongly elevated as if "pinched up" (Jackson, 1917). The Chipola Formation specimens differ from *C. gatuni* in lacking the deep infundibulum and distinct inflation of the interambulacra on the dorsal surface between the petals shown so well by Jackson (1917). In addition, the petals of *C. petersonorum* n. sp. are nearly closed distally and not as open as in *C. gatuni*.

Clypeaster concavus is widespread in the Miocene and late Oligocene of the Caribbean, documented from its type locality in Anguilla, as well as Mexico, Cuba, the Dominican Republic, Panama, and Puerto Rico. Cooke (1959) and Gordon (1963) stated that *C. concavus* shows considerable variation in size, shape, degree of flatness of the underside, and the depth of the infundibulum.

This well documented variability of *C. concavus* makes comparison to *C. petersonorum* n. sp. problematic. Although the aboral surface may share similarities with *C. concavus* and the two species share overall test dimensions, in all available specimens of *C. petersonorum*, the infundibulum is not as deep.

Although *C. gatuni* and *C. concavus* are the two species Cooke (1942, 1959) associated with the Chipola Formation, the Cenozoic faunas of the Caribbean contain an abundance of additional species of *Clypeaster*, with which presumably Cooke (1959) was familiar. However, he did not consider any similar enough to warrant comparison with the Chipola Formation specimen he had at hand. However, in an effort to rule out as many of the Caribbean Neogene species as feasible, we have compared *C. petersonorum* n. sp. to as many of these as possible. This is arduous considering that many species named by Sánchez-Roig (1949–1953) are poorly described and figured.

In addition, global comparisons start to be impractical, given that there are approximately 400 nominal taxa in the genus *Clypeaster*, only about 40 of which are extant (Mortensen, 1948; Durham, 1955; inter alia). Historically, attempts have been made to subdivide the genus, mainly on the basis of test structure (Mortensen, 1948). However, these subgenera have are generally recognized as being of little taxonomic value (Durham, 1966; Hopkins, 1988; Mihaljevic et al., 2011). With this many taxa in the global fauna, it is likely that even more regional faunas (especially the poorly documented ones from Cuba) have not been spared over-split-

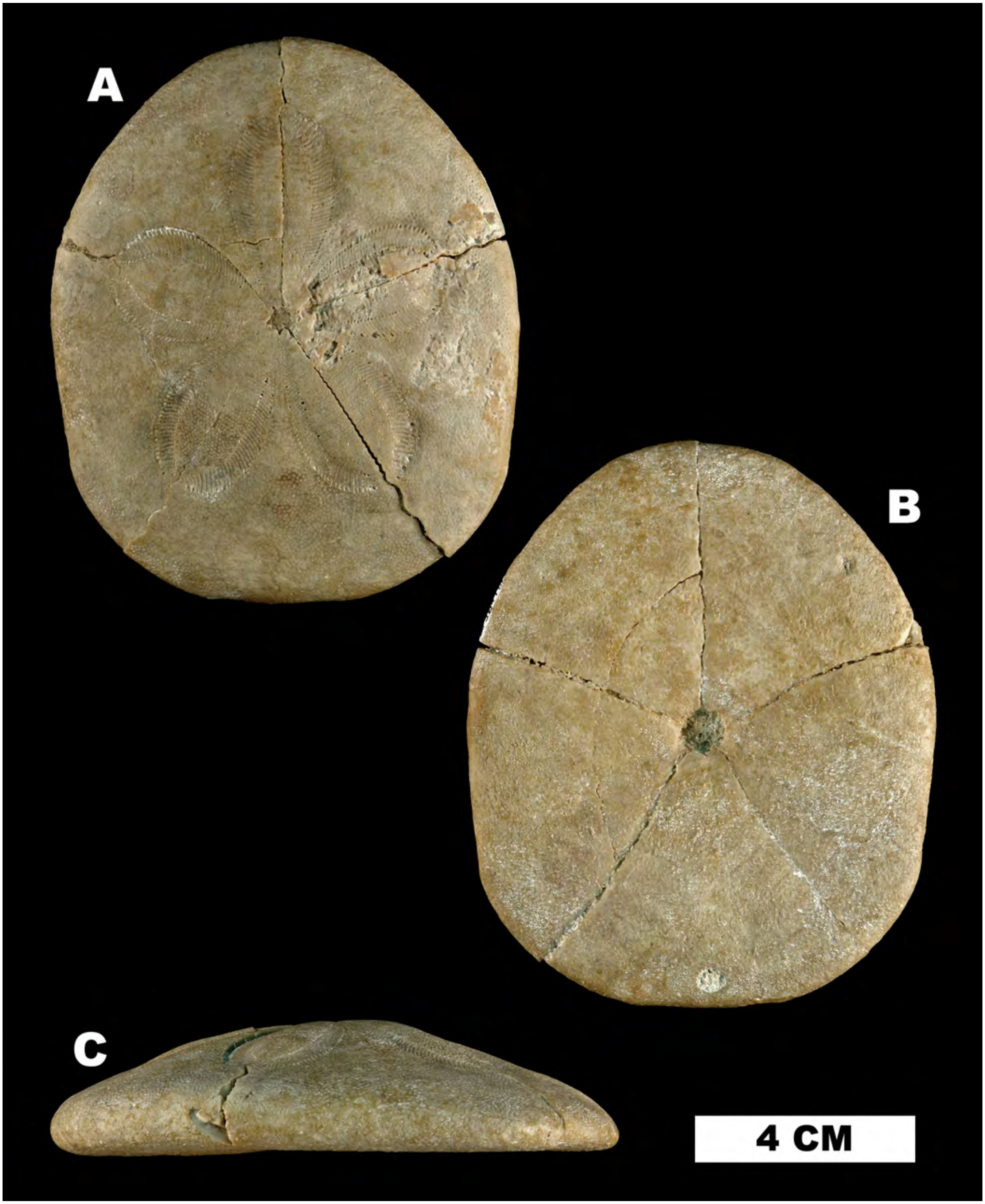


Figure 60. *Clypeaster petersonorum* n. sp., holotype (UF 283993), Chipola Formation (FM locality CA001). A. aboral view, B. oral view, C. lateral view.

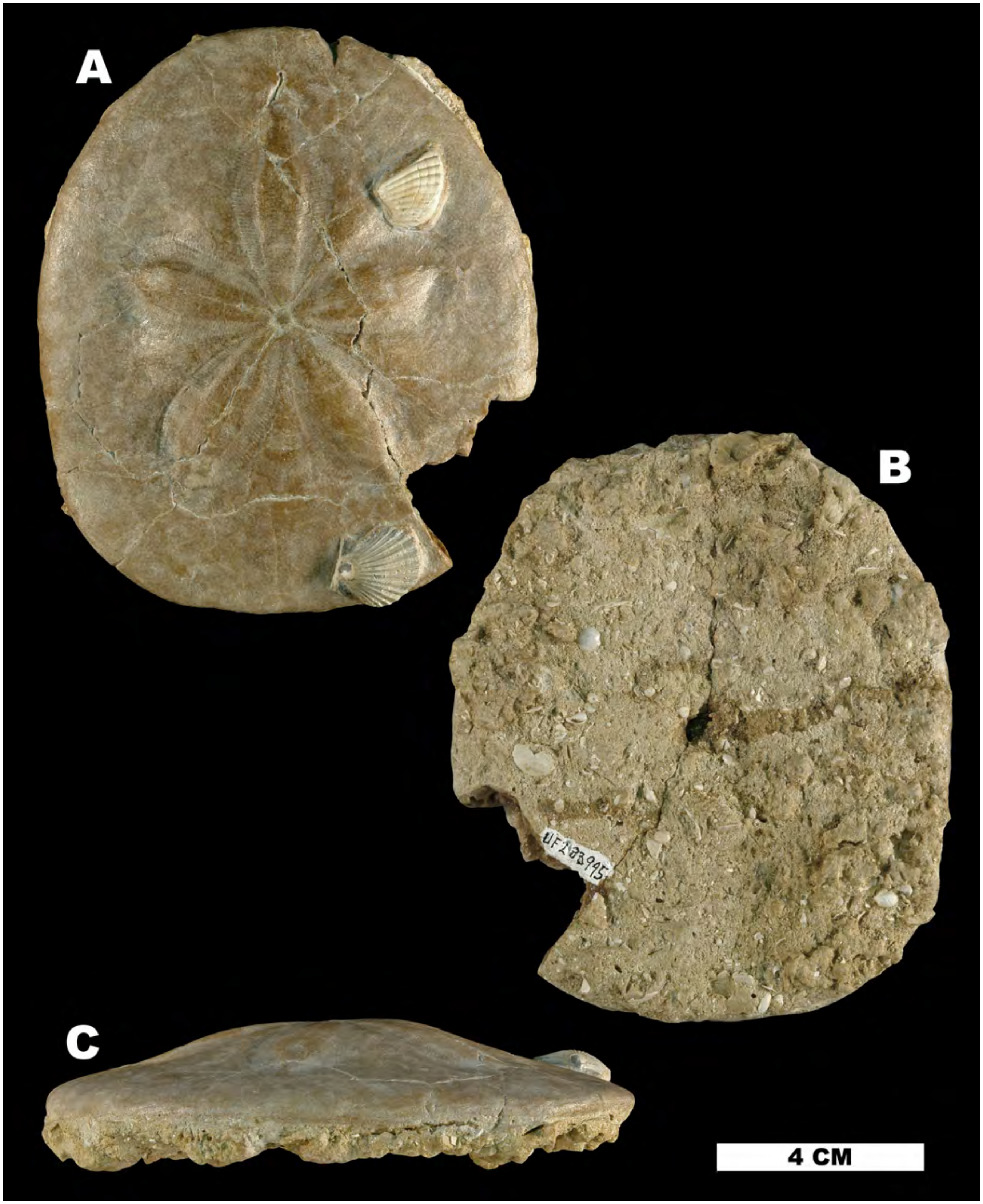


Figure 61. *Clypeaster petersonorum* n. sp., paratype (UF 283995), Chipola Formation (FM locality CA001). A. aboral view, B. oral view, C. lateral view.

ting and over-estimates of diversity.

For example, Sánchez-Roig (1949) alone documented 35 species of *Clypeaster* in the Cenozoic of Cuba, as well as two species he assigned to the genus *Anomalanthus*, which Durham (1966) reassigned to the genus *Clypeaster*. Sánchez-Roig (1951–1953) subsequently documented another 23 *Clypeaster*, as well as several new genera he erected, such as *Herrerasia*, *Rojaster*, *Zanolettia*, all of which Durham (1966) also placed into synonymy with *Clypeaster*. This creates a challenging total of nearly 60 species of *Clypeaster* within Oligocene to Pleistocene strata of Cuba alone. The majority of these species were referred questionably to Oligocene-Miocene strata, are poorly figured, often insufficiently described, with type material poorly designated and largely unavailable for study. The task of comparing any new material such as that of *C. petersonorum* n. sp. to even a small percentage of these is nearly impossible.

In order to perform a taxonomically rigorous analysis of the group, all name-bearing types of these taxa will have to be re-examined. However, other fossil echinoid faunas of the West Indies are better documented and understood, and some of the Cuban species of *Clypeaster* also occur outside of Cuba, making comparisons such as the ones that follow more feasible. We endeavored to utilize more recent works that treated variability of the species and occasionally provided better figures. We resorted to earlier descriptions and figures only when necessary, due to their often less accurate nature.

Poddubiuk (1985) asserted that the late Oligocene to Miocene species of *Clypeaster* from the Caribbean Islands should be grouped into no more than seven species: *C. batheri* Lambert, 1915; *C. caudatus* Jackson, 1922; *C. concavus* Cotteau, 1875; *C. cubensis* Cotteau, 1875; *C. julli* Roman, 1952; and *C. oxybaphon* Jackson, 1922. However, Poddubiuk did not fully elaborate on the implied and likely extensive synonymies. *Clypeaster petersonorum* n. sp. is readily differentiated from *C. caudatus, C. cubensis,* and *C. julli* by its much lower test. *Clypeaster oxybaphon*, which also occurs in the Oligocene Bridgeboro Limestone in Washington County Florida, has depressed submargins that characterize the species and readily distinguishes it from *C. petersonorum* n. sp. *Clypeaster batheri* is an Oligocene species that Poddubiuk (1985) considered a senior synonym of the very similar *C. cotteaui.* Therefore, we distinguish it from *C. petersonorum* n. sp. in the discussion below.

Donovan (1993) provided a key to the Cenozoic *Clypeaster* of Jamaica, which includes *C. cotteaui* Egozcue in Cotteau and Egozcue, 1897; *C. rosaceus*; *C. concavus*; *C. lanceolatus* Cotteau in Cotteau and Egozcue, 1897; and *C. eurychorus* Arnold and Clark, 1934. *Clypeaster petersonorum* n. sp. is readily distinguished from *C. cotteaui* (which also occurs in the Oligocene Bridgeboro Limestone in Washington County, Florida) by it much larger and thinner test, less swollen margin, and less concave oral surface. *Clypeaster petersonorum* n. sp. also has a more depressed test with a less concave oral surface than *C. lanceolatus*, which is well-figured by Cotteau and Egozcue (1897). *Clypeaster eurychorus* Arnold and Clark, 1934) has a high, swollen test that easily distinguished from that of *C. petersonorum* n. sp. Arnold and Clark (1927) considered two specimens from the Cenozoic of Jamaica as *C. antillarum* Cotteau, 1875. This species is very similar to *C. concavus*, and is differentiated from *C. petersonorum* n. sp. by the same features. *Clypeaster antillarum* has been considered a subjective junior synonym of *C. concavus* (Donovan, 1993:386; Poddubiuk, 1985:76). Donovan and Portell (1996) subsequently documented the occurrence of the modern *C. lamprus* H.L. Clark, 1914, in the lower Pleistocene strata of Jamaica.

Gordon (1963) described the fossil echinoids of the middle Tertiary of Puerto Rico, including *Clypeaster concavus puertoricanus* Gordon, 1963, from a Miocene specimen with an uncharacteristically less concave oral surface and greater inflated petaloid areas. This subspecies has a much higher test and more inflated petaloid regions than *C. petersonorum* n. sp.

Jackson (1922) provided a key to 19 species of *Clypeaster* from the Cenozoic strata of the West Indies. Of these species, *C. petersonorum* n.

sp. requires comparison with only a few species that are not readily distinct from it, or previously discussed above: *Clypeaster parrae* Des Moulins, 1835; discussed by Cotteau (1897) from Cuba, has a much higher test than *C. petersonorum* n. sp. *Clypeaster planipetalus* Cotteau, 1897, from the Miocene of Antigua (Jackson, 1922), has a low test with a relatively flat oral surface similar to that of *C. petersonorum* n. sp. However, its test is much narrower and ovate. *Clypeaster placentoides* Jackson, 1922, from the Oligocene of Cuba, has a depressed test, with a comparatively flat oral surface. It is described by Jackson (1922) as being "biscuit-like in shape"; a form that would not come to mind when describing *C. petersonorum* n. sp. *Clypeaster cryptopetalus* Jackson, 1922, from the Miocene of Antigua has a thicker margin, depressed submargin on the aboral surface, and indistinct petaloid ambulacra (thus the name). These features readily differentiate it from *C. petersonorum* n. sp. *Clypeaster platygaster* Jackson, 1922, was described from the Oligocene of Cuba. However, Cooke (1959) rightfully considers it to be a subjective junior synonym of *C. oxybaphon*.

Marchesini Santos (1958) described two new species from Miocene strata of Brazil: *Clypeaster lamegoi* Marchesini Santos, 1958 has a much straighter, flattened posterior margin that is not at all rounded as in *C. petersonorum* n. sp., and *Clypeaster pailinoi* Marchesini Santos, 1958, which is based on two very poorly preserved tests, is a much smaller species with comparatively thick margins, but the specimens are too poorly preserved to permit adequate comparison.

Clypeaster topilanus Jackson, 1937, from the Miocene of northeastern Mexico, has proportionately longer petals that reach much closer to the margin of the test than in *C. petersonorum* n. sp. Caso (1956) discussed *Clypeaster pileus* Israelsky, 1924, figuring a specimen from the Miocene of Veracruz that is similar in overall morphology to *C. petersonorum* n. sp. (Caso, 1956:fig. 15). However, the holotype of *C. pileus* has a far more inflated, nearly domed, apical area than *C. petersonorum* n. sp. *Clypeaster dondolii* Fischer, 1985, from the Miocene of Costa Rica, is similar to *C. petersonorum* n. sp. However, its apical area is more inflated and its anterior ambulacrum is much narrower. *Clypeaster caudatus* Jackson 1922 and *C. maoadentroensis* Kier, 1992, from the Pliocene of the Dominican Republic are readily distinguished from *C. petersonorum* n. sp. in having higher and more inflated tests with broader petals.

Clypeaster is even more strongly represented in the Miocene of Europe than in the Americas. However, considering the very low likelihood of *C. petersonorum* n. sp. extending into Europe or Asia (as no other fossil *Clypeaster* species of the region are documented outside of the Americas, nor do any of the modern nearshore species extend beyond American waters), and in view of the arguments above concerning the daunting task of comparing the entire global *Clypeaster* fauna, we have limited our examination to species within the eastern Americas.

Clypeaster petersonorum n. sp. is important as the only documented Miocene representative of the genus in the eastern United States, but we remain aware that improved access to material might increase our understanding of the nearly 60 Cuban Cenozoic species (Sánchez-Roig, 1949–1953). It is possible that *C. petersonorum* n. sp. could fall within the range of variability of one (or more) of these taxa. Therefore, it is with reluctance that we introduce *C. petersonorum* n. sp. to the Miocene fauna of the region, understanding that it highlights the problematic systematics of the entire genus.

Clypeaster petersonorum n. sp. has not been documented definitively outside of the type area along the banks of the Chipola River, where it occurs in the lowermost indurated bed of the lower Miocene Chipola Formation with *Echinolampas lycopersicus* Guppy, 1866.

Etymology.—Named in honor of Bernie and Carol Peterson for their contributions to the knowledge of the fossil faunas of Florida, guiding ASO on a trip to the type locality of *C. petersonorum* n. sp. and shedding light on the occurrence of this species within the Chipola Formation.

Material and Occurrence.—Holotype (UF 283993), paratypes (UF 283994, UF 283995, UF

283996), and less complete, non-type specimens collected from the lower portion of the lower Miocene Chipola Formation, along the Chipola River (FM locality CA001).

Order **SCUTELLOIDA** Mongiardino-Koch et al., 2018
Infraorder **LAGANIFORMES** Desor in L. Agassiz and Desor, 1847
Family **FIBULARIIDAE** Gray, 1855
Genus ***ECHINOCYAMUS*** van Phelsum, 1774
ECHINOCYAMUS CHIPOLANUS Cooke, 1942
Figure 62

Echinocyamus chipolanus Cooke, 1942, p. 29, pl. 1, figs. 9–11.

Echinocyamus chipolanus (Cooke). Cooke, 1959, p. 32, pl. 9, figs. 1–3.

Occurrence.—This species is only reported from the lower Miocene Chipola Formation, at the type locality: lower beds at Alum Bluff, Apalachicola River, Liberty County (USGS locality 2211).

Discussion.—*Echinocyamus chipolanus* is known only from the holotype (Fig. 62). It is more inflated than any other North American *Echinocyamus*, and its peristome is much larger (Cooke, 1942). The genital pores are farther apart than those of *Echinocyamus parvus* Emmons, 1858, and its poriferous zones appear to be more widely diverging (Cooke, 1959). Cooke (1959) reported that the type has been broken since figuring, revealing the auricles and the internal buttresses (Fig. 62), which support the placement of this species in the genus *Echinocyamus*.

Extensive screening of sediments at the type locality by RWP, as well as correlative sediments of the Chipola Formation along the Chipola River, Tenmile Creek, and Farley Creek by Emily and Harold Vokes and students of Tulane University has not provided any additional specimens of this species. Members of the genus *Echinocyamus* are typically gregarious and where one is found, many are often found; thus, if not for Cooke's confidence in describing this species and attributing it to this well-studied type locality, we would be tempted to cast doubt that it actually occurs in the Chipola Formation. This is the only documented occurrence of the genus *Echinocyamus* in the North American Neogene.

Infraorder **SCUTELLIFORMES** Haeckel, 1896
Family **MELLITIDAE** Stefanini, 1911
Genus ***ENCOPE*** L. Agassiz, 1840
ENCOPE ABERRANS Martens, 1867
Figures 64–68

Encope aberrans Martens, 1867, p. 112.

Encope michelini (Agassiz). A. Agassiz, 1872, p. 330 (in part); pl. 12b, fig. 4, pl. 12c, figs. 3, 4 (not pl. 12c, fig 1).

Encope michelini (Agassiz). Berry, 1941, (in part); pl. 63, figs. 2, 5, 8 (not pl. 63, figs. 1, 3, 7. pl. 64, figs. 1–6. pl. 65, figs. 1, 2).

Encope michelini (Agassiz). Mortensen, 1948, (description in part), p. 442 (only portion describing marginal indentations and the vortex of the test).

Encope michelini (Agassiz). Cooke, 1959, p. 49, pl. 18, figs 2, 3. (figured specimen is *E. aberrans*, not *E. michelini*).

Encope michelini (Agassiz). Cooke, 1961, pp. 17, 18, pl. 6, figs. 5, 6. pl. 7, fig. 5 (specimen is *E. aberrans* not *E. michelini*).

Encope michelini imperforata Kier, 1963, pp. 33–36, pl. 5, fig. 1, pl. 6, figs. 3, 4. text figs. 26–30 (not figure 25), table 2.

Encope aberrans (Martens). Phelan, 1972, pp. 125, 126, figs. 2C, 8, 9, 10. tbls. I, II.

Encope aberrans (Martens). Serafy, 1979, pp. 76–79, fig. 33.

Encope aberrans (Martens). Mooi, 1989, fig. 21h.

Encope aberrans imperforata (Kier). Kier, 1992, pp. 19, 20, pl. 6, fig. 3.

Encope aberrans (Martens). Hendler et al., 1995, p. 233, fig. 136C, (not fig.123 which is *E. michelini*).

Encope aberrans imperforata (Kier). Ciampaglio and Osborn, 2011, fig. 2.

Encope aberrans (Martens). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—This common nearshore, extant Florida species occurs as early as the late Pliocene within the state. It is present in the upper Pliocene Tamiami Formation, though rare, and is more common in the upper Pliocene Intracoastal Formation. *Encope aberrans* is also recorded from the upper Pliocene to lower Pleistocene Nashua Formation, the lower Pleistocene Caloosahatchee Formation, and the middle Pleistocene Bermont Formation. A few specific localities include: Tamiami Formation, Buckingham Marl member of Tamiami Formation, float from east side of marl pits, east side of Spanish Creek, 2 km east of Alva, just south of Rt. 78, Lee County (Kier, 1963); Intracoastal Formation, Langston Quarry, Liberty County (FM locality LI005) (Ciampaglio and Osborn, 2011); Nashua Formation, Cracker Swamp Ranch, Putnam County (FM locality PU004); Caloosahatchee Formation, Bee Branch Member sensu DuBar

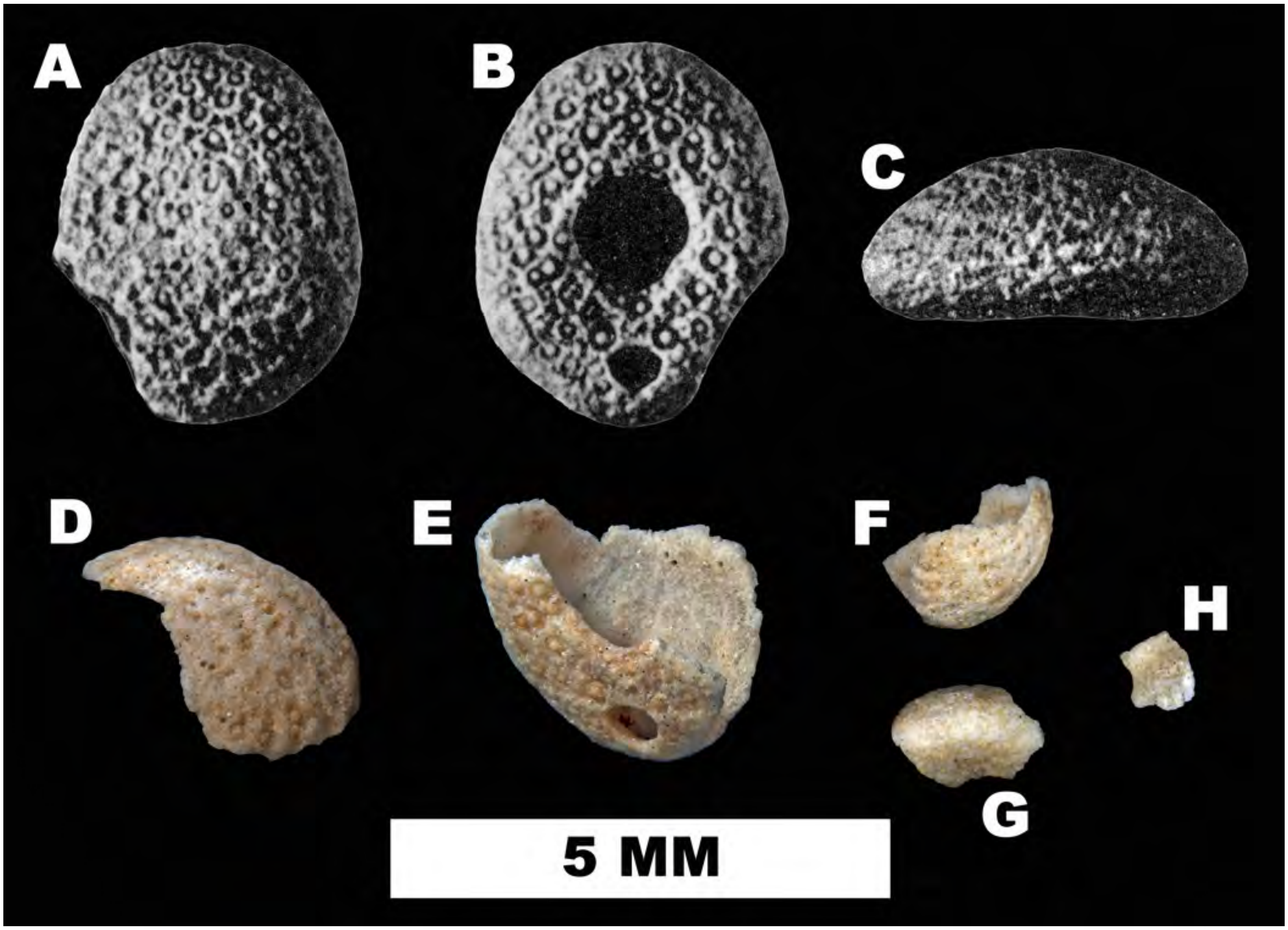


Figure 62. *Echinocyamus chipolanus* holotype (USNM 499003), Chipola Formation (FM locality LI003). A-C. from Cooke (1959), D-G. broken holotype.

(1958), as float from the north bank of the Caloosahatchee River and from the LaBelle pits on the north bank, in SE¼ sec. 12, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (type locality of *E. aberrans imperforata*, USGS locality 23082 [Kier, 1963]); north bank of Caloosahatchee River west of Three Way Rock Co. pits in SW¼ sec. 6, T. 43 S., R. 29 E., La Belle, Hendry County (USGS locality 23085 [Kier, 1963]); float in Denaud pits in NW¼ sec. 14, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 22373 [Kier, 1963]); Caloosahatchee Canal (south bank), 1.6 km east of bridge at LaBelle, Hendry County (USGS locality 22387 [Kier, 1963]); Clewiston, Hendry County (FM locality HN017); Bermont Formation, Belle Glade Rock Pit, Palm Beach County (FM locality PB001); float from pit on south side of Florida route 80 southwest of Belle Glade, Palm Beach County (USGS locality 22704 [Kier, 1963]).

Encope aberrans also occurs in the Caribbean: Venezuela (Pliocene [Cooke, 1961]) and the Dominican Republic (upper Miocene Rio Cana Section [Kier, 1992]).

Discussion.—This is a common, large, sand dollar in the modern fauna of the region from Cape Hatteras, North Carolina, southward to the Bahama Islands, and throughout the Gulf of Mexico (Hendler et al., 1995). References to *E. aberrans* and *E. michelini* prior to 1972 must be regarded with caution as the species were considered synonymous by many workers, with *E. michelini* regarded as extremely variable, as illustrated in the synonymy above.

Cooke (1959) discussed and figured *E. aberrans* as *E. michelini* and figured and discussed *E. michelini* as *E. emarginata*. Phelan (1972) clarified the status of all these species, but material can still be misidentified by using outdated nomenclature. For example, Hendler et al. (1995:fig. 123) included an image of *E. michelini* misidentified as *E. aberrans*, and we recommend caution when reviewing the literature.

As noted by Phelan (1972), the spadeshaped test of *E. aberrans* clearly lacks the deep marginal notches (sensu Mooi, 1989) of *E. michelini*. Instead, there are distinct, but shallow, posterior notches in each of the two posterior ambulacra and three indistinct ambulacral indentations in the anterior paired and unpaired ambulacra. The anal lunule (sensu Mooi, 1989) is very short, and typically much smaller than that of *E. michelini*.

When Kier (1963) described *E. michelini imperforata* Kier, 1963 from Neogene deposits of southern Florida, he indicated that this subspecies is similar in all respects to *E. michelini* except that its anal lunule is quite small or entirely absent, also noting that the ambulacral notches are very well developed in many specimens but completely absent in others. Although Kier (1963) originally assigned this subspecies to *E. michelini,* Phelan (1972) placed Kier's *E. michelini imperforata* in *E. aberrans*, stating that *E. aberrans imperforata* has more variation in lunule size than expected in a normal population of *E. aberrans*, but that he did not recognize the subspecies, nor regard it as typical of *E. michelini*.

Kier (1963:fig. 25) figured the holotype of *E. michelini imperforata* (=*E. aberrans* sensu Phelan, 1972). However, this specimen has deep notches characteristic of *E. michelini* and it appears that Kier actually included specimens of both *E. aberrans* and *E. michelini* (which were considered synonyms at the time) in his *E. michelini imperforata*, drawing attention to the well-developed notches in some of his material (Kier 1963:34, figs. 25, 30). A specimen of *E. michelini* (UF 183305) from the Bermont Formation has a greatly reduced anal lunule (Fig. 63). UF 193700, a large specimen of *E. aberrans* from the same locality, measures 135 mm TL, 137 mm TW, and has a reduced anal lunule (Fig. 64).

We do not recognize the subspecific designation of *imperforata*. As documented by Kier (1963), a missing, or greatly reduced anal lunule is uncommon in Recent populations of *E. aberrans*. However, considering that similar specimens occur within populations of otherwise typical specimens in the lower to middle Pleistocene strata of southern Florida, it is our opinion that lunule reduction represents variation within both *E. aberrans* and *E. michelini* that was more widespread in the fossil record of the lower to middle Pleistocene than among extant populations. Kier (1992) demonstrated that the tendency towards reduction of the anal lunule occurs in other Caribbean sand dollars while documenting their reduction or absence in *E. aberrans* from Neogene strata in the Dominican Republic, and even postulated that specimens from the Pliocene of Venezuela were *E. aberrans imperforata*.

A population of typical *Encope aberrans* with well-developed anal lunules occurs in the upper Pliocene Intracoastal Formation in Liberty County, Florida (Figs. 65–66). However, these specimens have a slightly thinner test margin and lack the conspicuously elevated region posterior to the apical system seen in typical *E. aberrans*. Otherwise, the specimens agree with *E. aberrans*.

ENCOPE MACROPHORA (Ravenel, 1842)
Figures 69–71

Scutella macrophora Ravenel, 1842, p. 334, text fig.
Encope macrophora (Ravenel). Ravenel, 1848, p. 3.
Encope macrophora (Ravenel). Tuomey and Holmes, 1855, p. 2, pl. 1, fig. 3.
Ravenellia macrophora (Ravenel). Lütken, 1864, p. 168.
Macrophora macrophora (Ravenel). Conrad, 1865, p. 74.
Macrophora raveneli Conrad, 1865, p. 74.
Encope macrophora (Ravenel). Grabau and Shimer, 1910, p. 594, fig. 1927.
Encope macrophora (Ravenel). Stefanini, 1911, p. 708.
Encope macrophora (Ravenel). Clark and Twitchell, 1915, p. 206, pl. 93, figs. 2a–e; pl. 94, figs. 1a–f, 2. (includes additional references).
Encope macrophora (Ravenel). Cooke, 1942, p. 20.
Encope macrophora (Ravenel). Cooke, 1959, p. 48, pl. 17, figs. 1, 2.
Encope macrophora (Ravenel). Kier, 1963, figs. 31, 33.

Figure 63. *Encope michelini* (UF 183305) (=*E. michelini imperforata* sensu Kier, 1963), Bermont Formation (FM locality CR017). A. aboral view, B. oral view, C. lateral view.

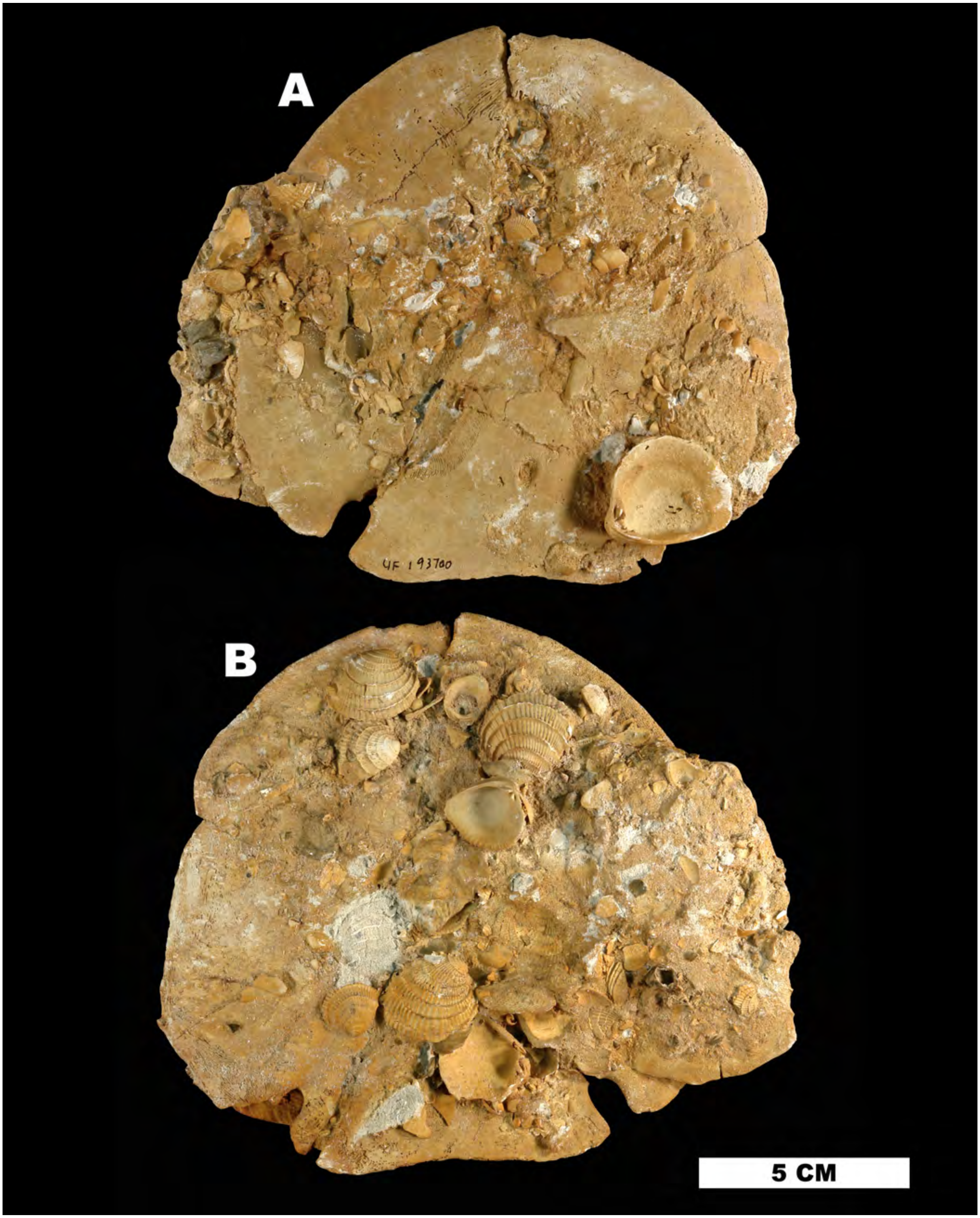


Figure 64. *Encope aberrans* with greatly reduced anal lunule (UF 193700), Bermont Formation (FM locality CR015). A. aboral view, B. oral view.

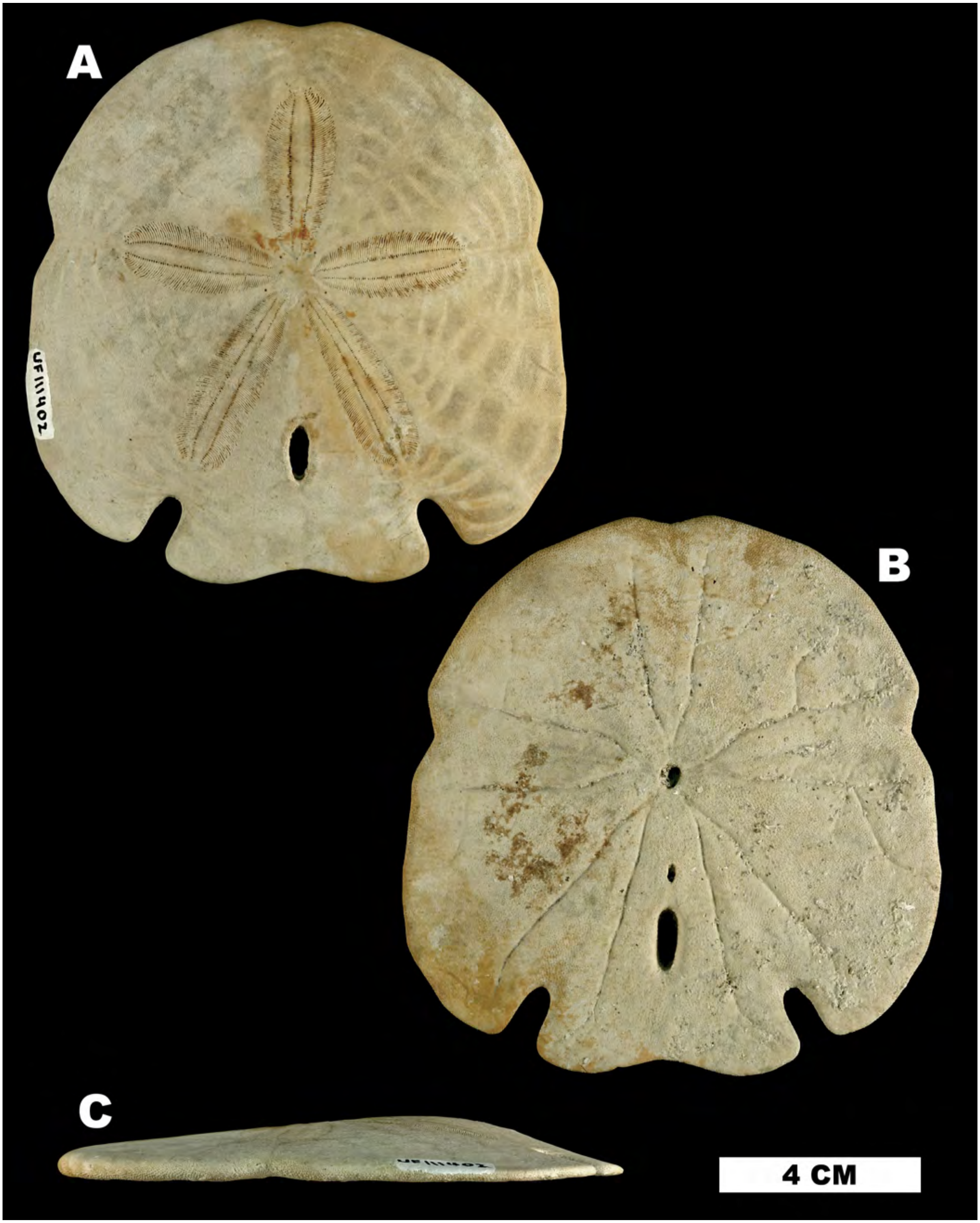


Figure 65. *Encope aberrans* (UF 111402), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

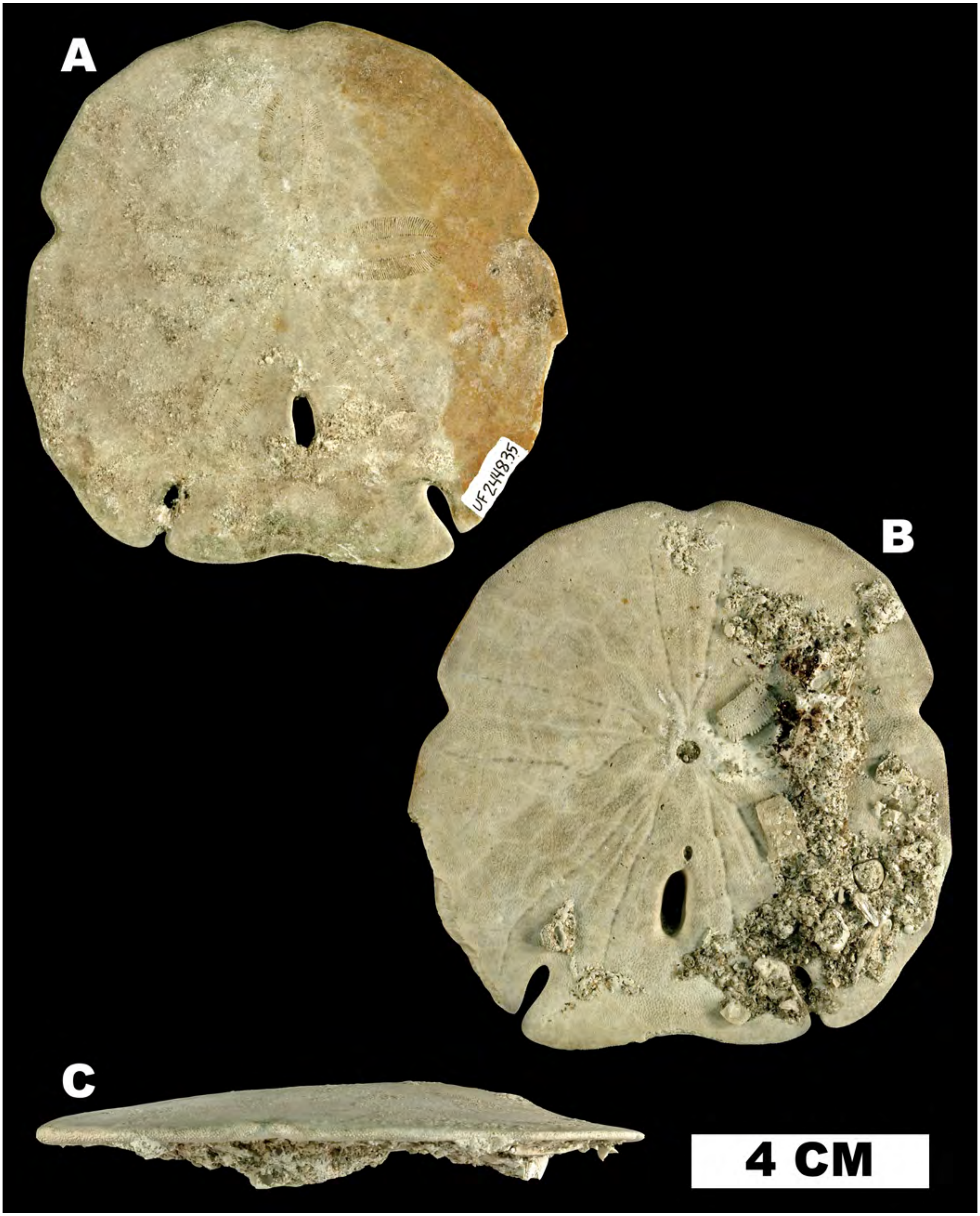


Figure 66. *Encope aberrans* (UF 244835), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

Encope macrophora (Ravenel). Smith and Ghiold, 1982, fig. 3.
Encope macrophora (Ravenel). Campbell, 1987, pp. 18, 19.
Encope macrophora (Ravenel). Campbell and Campbell, 1995, pp. 83–84, pl. 2, fig. 4. pl. 4, fig. 3.
Encope macrophora (Ravenel). Weaver et al., 2006, pp. 77–80, fig. 5.
Encope macrophora (Ravenel). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Specimens indistinguishable from *Encope macrophora* occur in the upper Pliocene Intracoastal Formation and the lower, likely late Pliocene portion of the Nashua Formation in northern Florida. Southward, it is replaced in the late Pliocene by *E. tamiamiensis*. A few specific localities are the Intracoastal Formation: Langston Quarry, Liberty County (FM locality LI005), and Nashua Formation, East Coast Aggregates Quarry, St. Johns County (FM locality SJ007).

This species is also documented from the Yorktown Formation (middle Pliocene) of North Carolina (Weaver et al., 2006), the lower Goose Creek Limestone (middle Pliocene), of South Carolina, which contains the type locality of the species at the Grove Plantation, Cooper River, 5 miles northwest of Wando, Berkeley County (type locality of Ravenel [1842], USNM 145411, 145410), as well as in the Yorktown Formation, middle Pliocene (zone 2) of Virginia (Campbell, 1987; Campbell and Campbell, 1995).

Discussion.—Ravenel (1842) described *Scutella macrophora* as well as *Scutella caroliniana* (=*Mellita caroliniana*) from specimens found on his plantation, "the Grove" on the Cooper River near Charleston, South Carolina. Ravenel (1848) subsequently redesignated *S. macrophora* as a member of the genus *Encope*. However, both Lütken (1863) (*Ravenellia*) and Conrad (1865) (*Macrophora*) founded new genera based on Ravenel's species. Twitchell in Clark and Twitchell (1915) stated there was no good basis for the retention of either of these genera, and they are not used today.

Mansfield (1932) described a population of late Pliocene *Encope* from southern Florida as *E. macrophora tamiamiensis*. He stated that his new subspecies appears to be intermediate in form between *E. macrophora* and the modern *E. grandis* of the west coast of the Americas. Mansfield further suggested that *E. macrophora tamiamiensis* differed from *E. macrophora* in having a proportionately wider and thinner test, a concave instead of convex posterior margin, and a much smaller interambulacral lunule. He also indicated that the margin of his new subspecies was thin, but did not have a sharp edge.

Cooke (1942) elevated *E. tamiamiensis* to species status and later (Cooke, 1959) distinguished *E. tamiamiensis* from *E. macrophora* by its smaller lunule, thinner margin, and shorter and wider test. Cooke (1959) also stated the anterior paired petals are more broadly lanceolate than those of *E. macrophora* and do not extend along a straight line across the test, but form an angle of approximately 154° with each other.

Kier (1963) reviewed the two species in detail, and concluded that they are distinct. Plots of TW versus TL for both species clearly illustrate that width to length ratio cannot be used to distinguish them (Kier, 1963:fig. 31). However, plots of the distance from the apical system to the anterior margin show that *E. macrophora* has a distinctly more anterior apical system (Kier, 1963:fig. 33), with this distinction becoming even more evident in larger specimens. Kier emphasized that *E. tamiamiensis* has a thinner margin, a smaller lunule, and anterior paired petals that are less curved posteriorly.

Encope macrophora is therefore differentiated from *E. tamiamiensis* by its more anteriorly located apical system and anterior ambulacra that form an angle with each other greater than 154° (Kier, 1963). *Encope macrophora* also possesses a typically thicker margin, and on average, a proportionately larger lunule. However, the use of lunule size as one of the characteristics to distinguish the two species is not recommended, as this is not a consistent differentiator (Cooke, 1959; Kier, 1963). Many specimens of *E. tamiamiensis* have a posterior interambulacral lunule that is equal to, or proportionately larger than, that displayed by the holotype of *E. macrophora*. Although Cooke (1959) and Kier (1963) also asserted that margin thickness could also serve to distinguish the species, variation in both taxa renders this feature equivocal as well. Differentiating these two species continues to be troublesome when examining isolated specimens.

Figure 67. *Encope aberrans* (UF 42001), Bermont Formation (FM locality PB001). A. aboral view, B. oral view, C. lateral view.

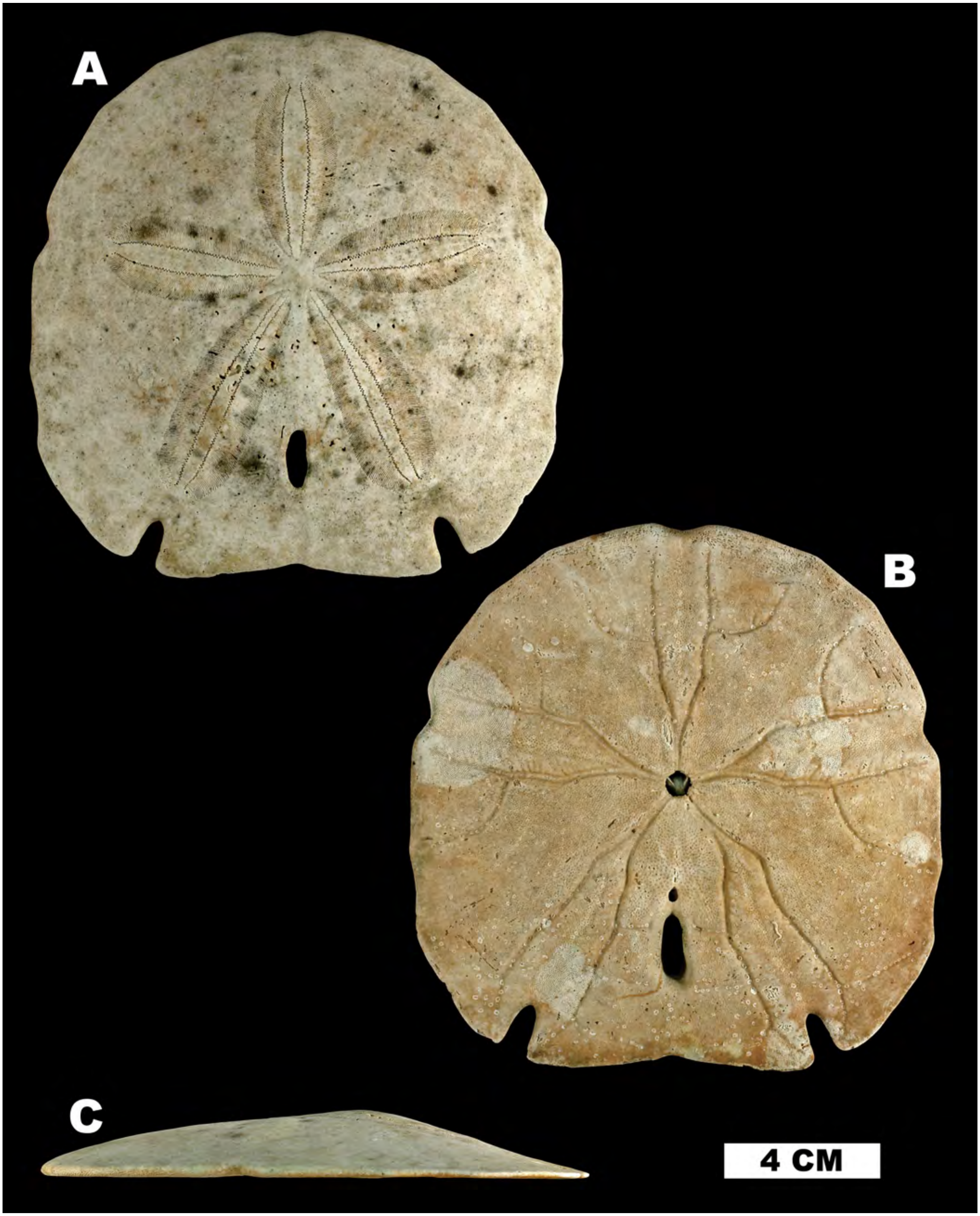


Figure 68. *Encope aberrans* (UF-IZ 18902), modern specimen (off Anna Maria Island at 10 m depth, Manatee County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

Figure 69. *Encope macrophora* (UF 289230), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. right lateral view.

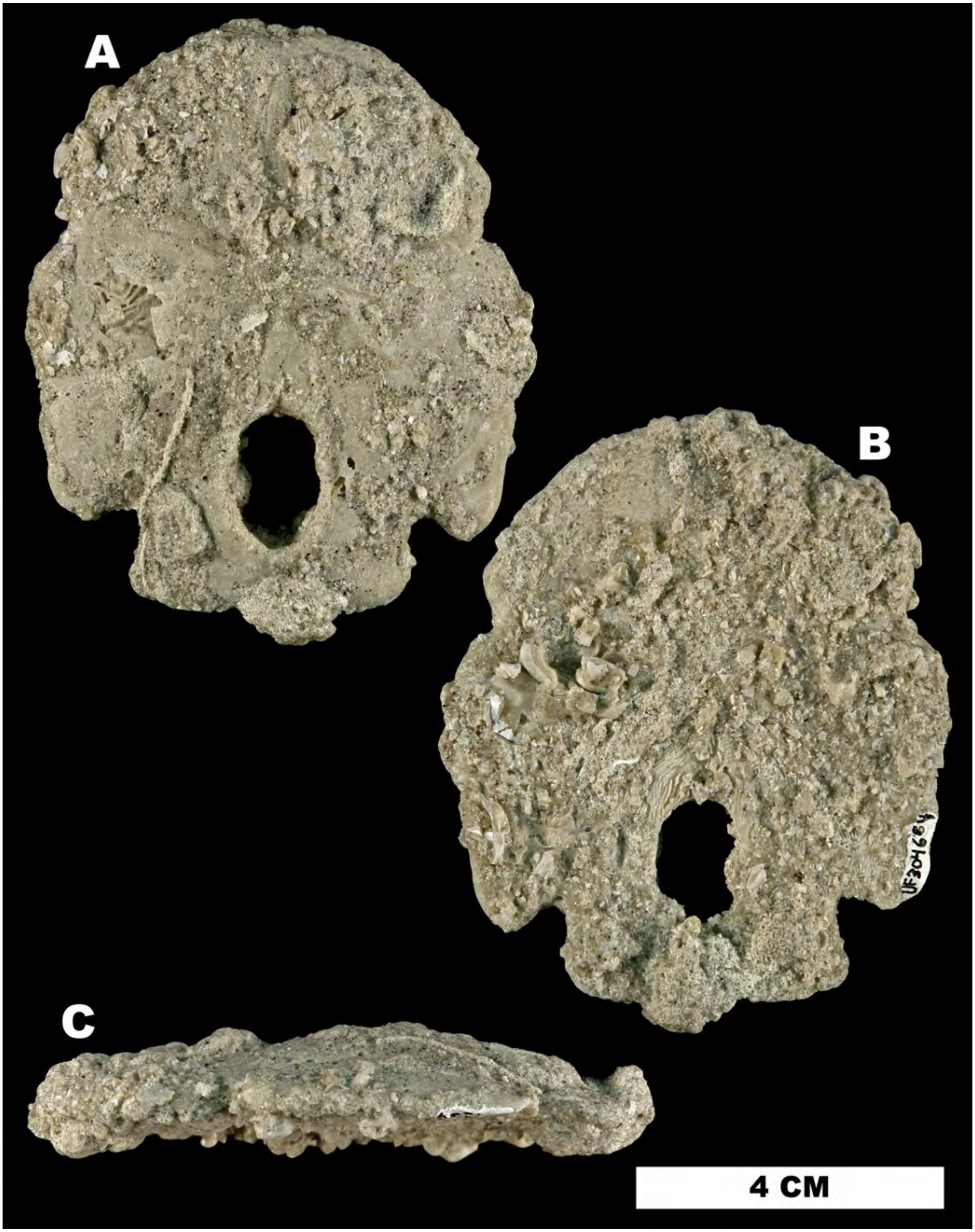


Figure 70. *Encope* aff. *macrophora* (UF 304684), Nashua Formation (FM locality SJ004). A. aboral view, B. oral view, C. lateral view.

A large assemblage of numerous specimens from a locality is required to better ascertain the variability of features within the population.

Campbell and Campbell (1995) recognized *E. macrophora* as a key indicator of the middle Pliocene, lower portion of the Goose Creek Limestone in South Carolina, stating that the average size of specimens within the Goose Creek Limestone is 30–35 mm TL and that they have a rounded margin that may thicken with increased size. They also indicated that the much larger sample size of specimens of *E. macrophora* available from the lower Goose Creek Limestone in Berkeley County, South Carolina showed a range of variation fully compatible with that of *E. tamiamiensis*. However, they did not quantify this assertion.

Ciampaglio and Osborn (2011) documented the occurrence of *E. macrophora* in the upper Plio-

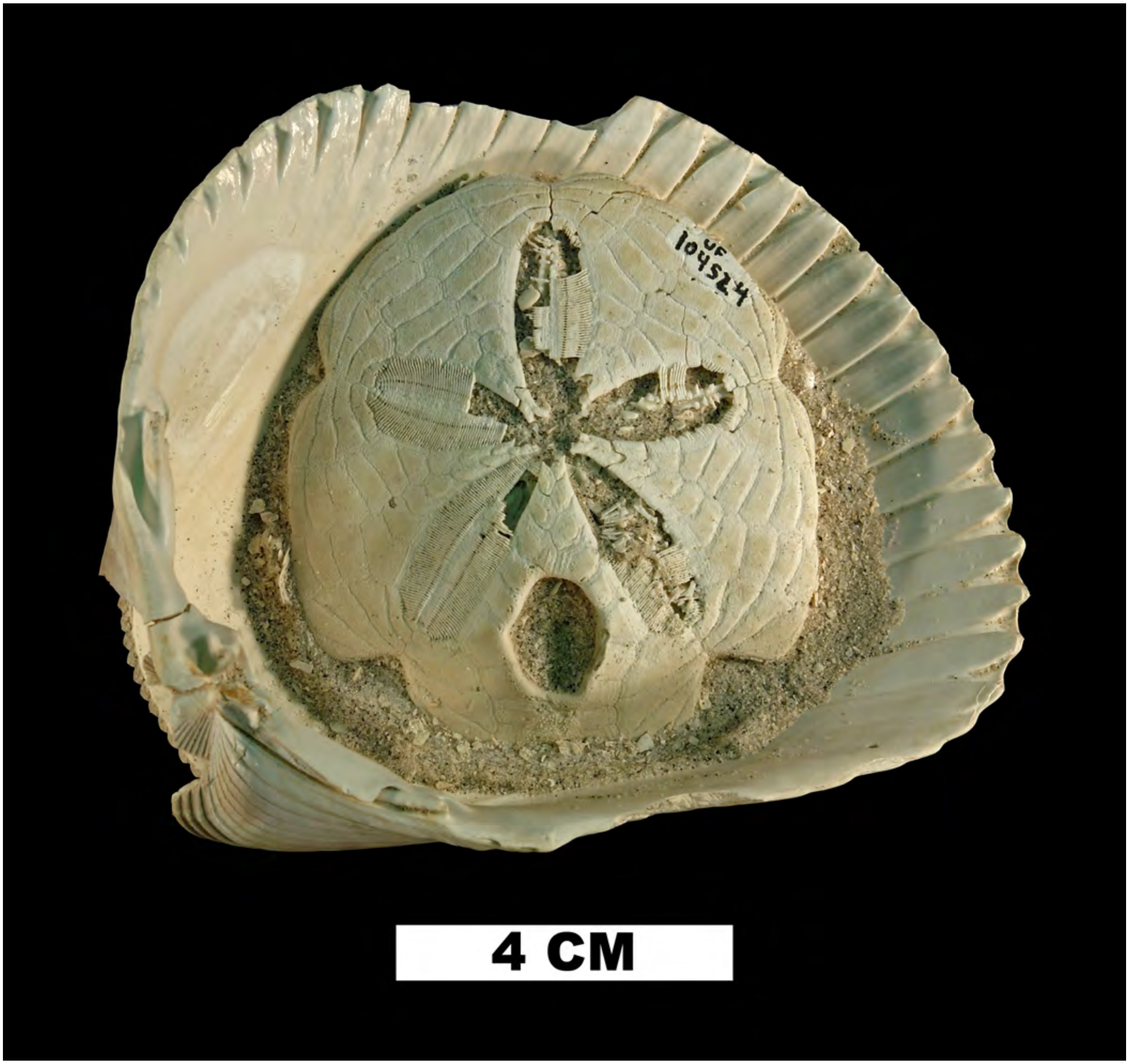


Figure 71. *Encope* aff. *macrophora* (UF 104524), Nashua Formation (FM locality PU004) in matrix inside large *Dinocardium* valve.

cene Intracoastal Formation in Liberty County, Florida. Specimens within this unit often achieve sizes closer to the maximum for the species, and are sympatric with specimens of *E. aberrans*.

Encope macrophora is also tentatively recognized in the Nashua Formation in St. Johns County. Here, specimens occur in a cemented, sandy limestone that precludes complete preservation with good surface detail. However, they look more like *E. macrophora* than *E. tamiamiensis*. The Florida exposures of the Nashua Formation are largely considered to reside within the Pleistocene. However, this lower, sandy, indurated horizon contains a fauna considered more typical of the late Pliocene (e.g., with occurrences of *Carcharocles megalodon* [Kittle et al., 2013]). The identification and stratigraphic placement are tentative, so this occurrence is not included in Figures 2–4.

ENCOPE MICHELINI L. Agassiz, 1841
Figures 63, 72–76

Encope michelini Agassiz, 1841, p. 58, pl. 6a, figs. 9, 10.

Encope michelini Agassiz. A. Agassiz, 1872, p. 329, pl. 12d, fig. 1. (not pl. 12c, figs. 3, 4. pl. 12d, fig. 4. These are *E. aberrans*).

Encope michelini (Agassiz). Berry, 1941, pl. 63, figs. 1, 3, 7. pl. 64, figs. 1–6. pl. 65 figs. 1, 2. (not pl. 63. fig. 2, 5, 8, these are *E. aberrans*).

Not *Encope michelini* (Agassiz). Cooke, 1942, p. 21, pl. 4; fig. 6 (=*Encope tamiamiensis* Mansfield).

Encope michelini (Agassiz). Mortensen, 1948, p. 442 (in part: portion referring to specimen from Charlotte Harbor only; not, pl. 70, fig. 23).

Not *Encope michelini* (Agassiz). Cooke, 1959, p. 42, pl. 18. figs. 2, 3 (these are *E. aberrans*).

Encope emarginata (Leske). Cooke, 1959, p. 49, pl. 17, fig. 5. pl. 18, fig. 1 (these are *E. michelini*).

Encope michelini (Agassiz). Caso, 1951, fig. 113.

Encope michelini imperforata Kier, 1963, pp. 33–36 (description in part, where referencing specimens with well developed marginal notches, also figs. 25, 30).

Encope michelini (Agassiz). Kier and Grant, 1965, pl. 5, fig. 7. pl. 6, figs. 9, 1. pl. 7, figs. 1–8. pl. 15, fig. 7. text fig. 7.

Encope michelini (Agassiz). Phelan, 1972, pp. 124, 125, figs. 1, 2B, 5, 6, 7, tbls I, II.

Encope michelini (Agassiz). Serafy, 1979, pp. 80–82, fig. 35.

Encope michelini (Agassiz). Smith, 1980, pp. 18, 20, figs.19c, d.

Encope michelini (Agassiz). Hendler et al., 1995, pp. 233, 234, figs. 123, 124, 134A, (fig. 123 is *E. michelini*, misidentified as *E. aberrans*).

Encope michelini (Agassiz). Oyen and Portell, 2001, pl. II, fig.6.

Encope michelini (Agassiz). Pomory, 2003, pp. 26, 27, fig. 10.

Encope michelini (Agassiz). Lawrence et al., 2004, p. 407, 408.

Encope michelini (Agassiz). Ciampaglio et al., 2009, fig. 2.

Encope michelini (Agassiz). Ciampaglio and Osborn, 2011, fig. 2.

Encope michelini (Agassiz). Ziegler et al., 2016, fig. 6b.

Occurrence.—*Encope michelini* is widely distributed in Florida in strata as old as the late Pliocene. The species occurs in the Tamiami, Caloosahatchee, Anastasia, Bermont, Nashua, and Fort Thompson Formations, as well as the Miami Limestone. A few specific locations follow: Tamiami Formation: uppermost indurated bed of the formation exposed at the Quality Materials Quarry, Charlotte County (FM locality CH080); Peace River, southwest of Arcadia, DeSoto County; Anastasia Formation at Vero Beach Landfill, Indian River County (FM locality IR003); Dickerson Quarry, St. Lucie County (FM locality SL003); Bermont Formation at101 Ranch Pit 02, Okeechobee County (FM locality OB013); Fort Thompson Formation at Glenwood Heights, Dade County (FM locality DA012); Caloosahatchee Formation, banks of the Caloosahatchee River near LaBelle. Miami Limestone at Buena Vista, near Miami (USGS locality 4867). This species also occurs in the middle Pleistocene Canepatch Formation of South Carolina.

Discussion.—*Encope michelini* is a common sand dollar in the modern faunas of the region, often occurring in significant numbers just offshore along the Atlantic and Gulf Coasts of Florida. It is documented from Cape Hatteras, North Carolina southward around the southern tip of Florida, throughout the Gulf of Mexico to Cozumel, Mexico. However, it has not been documented in the Bahamas (Serafy, 1979).

As discussed in the remarks for *E. aberrans* above, significant confusion persisted over the past century concerning the three species of *Encope* that occur in the Recent faunas of Atlantic Coast of the Americas. During this time, specimens of *E. michelini* were often identified as *E. emarginata* (Leske, 1778) and *E. aberrans* were typically identified as *E. michelini*. We recommend caution when working with older references to any of these species.

Encope michelini is readily distinguished from *E. aberrans* by its five, nearly equally sized ambulacral notches in the ambitus, and its larger anal lunule in the posterior interambulacrum.

Phelan (1972) and Serafy (1979:fig. 34) illustrated the difference in notch and lunule size of these two species. The spade-shaped test of *E. aberrans* noticeably lacks the deep ambulacral notches of *E. michelini*. See discussion for *E. aberrans* concerning details of how these notches differ in the two species. Phelan (1972) noted that juvenile specimens of *E. michelini* have a marginal outline similar to specimens of *E. aberrans* prior to the development of the three anterior notches. This was figured by Berry (1941). However, Phelan (1972) stated that except in the case of very small specimens, the smaller peristome in *E. michelini* can be used to distinguish juveniles of these two species.

A review of the material from the Pleistocene strata of southern Florida attributed to *E. michelini imperforata* by Kier (1963) (*E. aberrans* according to Phelan, 1972), and not recognized as a distinct subspecies herein (see discussions for *E. aberrans*) reveals that at least a portion of the material Kier examined was attributable to *E. michelini*, though the majority are *E. aberrans*. As recorded in the synonomy above, that portion of Kier's material, including figured specimens (Kier, 1963:figs. 25, 30), in which marginal notches are well developed are attributable to *E. michelini*. This is similar to the situations found in an *Encope* population in the middle Pleistocene Bermont Formation in the Longan Lakes Quarry (FM locality CR015) in which there exist examples of both *E. aberrans* and *E. michelini* with greatly reduced lunules. As stated in the remarks for *E. aberrans* above, it appears there was a greater tendency for reduction of the anal lunule in both *E. aberrans* and *E. michelini* in the Pleistocene of the region than is seen in modern populations of these two species. For example, contrast the size of the anal lunule between two specimens of *E. michelini* from the Bermont Formation, UF 183305 with a greatly reduced anal lunule, and UF 105638 with the larger anal lunule typical of the species (Figs. 63, 72).

Specimens of *E. michelini* occurring in the Anastasia Formation in the Dickerson Quarries (FM locality SL003), achieve great size, often exceeding 150 mm TL (e.g., UF 116331, UF 116145, and UF 116122). This locality produces the largest *E. michelini* specimens among the FM-IP collections. UF 111845 (Fig. 73) from the Dickerson Quarry measures 143 mm TL, 135 mm TW.

ENCOPE TAMIAMIENSIS Mansfield, 1932
Figures 77–83

Encope macrophora tamiamiensis Mansfield, 1932, p. 48, pl. 17, fig. 8.

Encope tamiamiensis (Mansfield). Cooke, 1942, p. 20.

Encope tamiamiensis (Mansfield). Cooke, 1959, pp. 48, 49, pl. 17. figs. 3, 4.

Encope tamiamiensis (Mansfield). Kier, 1963, pp. 36–40, pl.14, figs. 1–6. text figs. 31–35.

Encope tamiamiensis (Mansfield). Oyen and Portell, 2001, pp. 193–218, pl. II, fig. 4.

Encope tamiamiensis (Mansfield). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—*Encope tamiamiensis* has not been positively identified outside of the upper Pliocene Tamiami Formation, where it is ubiquitous in the unit throughout southwestern Florida. A few notable localities include the Quality Materials Quarry, Charlotte County (FM locality CH080); pits east of Burnt Store Road, south of Port Charlotte, Charlotte County; quarries near Copeland, Collier County, and Alligator Creek, east of Hwy 41, Charlotte County. Cooke (1959) provided the following localities: Tamiami Trail 5 miles east of Carnestown and about 11 km northeast of Everglades, Collier County (type, USGS locality 11177); Tamiami Trail 10 km west of Miami (USGS locality 13410); Tamiami Trail at Carnestown, 6 km north of Everglades (USGS locality 11180); pit east of road to Immokalee, 6 miles north of Tamiami Trail (USGS locality 15050); east side of State road 164, 15 km north of intersection with US 94 (Tamiami Trail) (USGS locality 15223); 8 km west of intersection of Tamiami Trail and west end of road to Pinecrest (USGS locality 14187).

Discussion.—Mansfield (1932) described this sand dollar from the upper Pliocene Tamiami Formation near Carnestown, Collier County, in southern Florida as *E. macrophora tamiamiensis*. Cooke (1942) elevated *E. tamiamiensis* to species status but did not figure either *E. tamiamiensis* or *E. macrophora*. Cooke (1959) distinguished *E. tamiamiensis* from *E. macrophor*a by the former's smaller lunule, thinner margin, and shorter and wider test. Furthermore, Cooke (1959) stated the

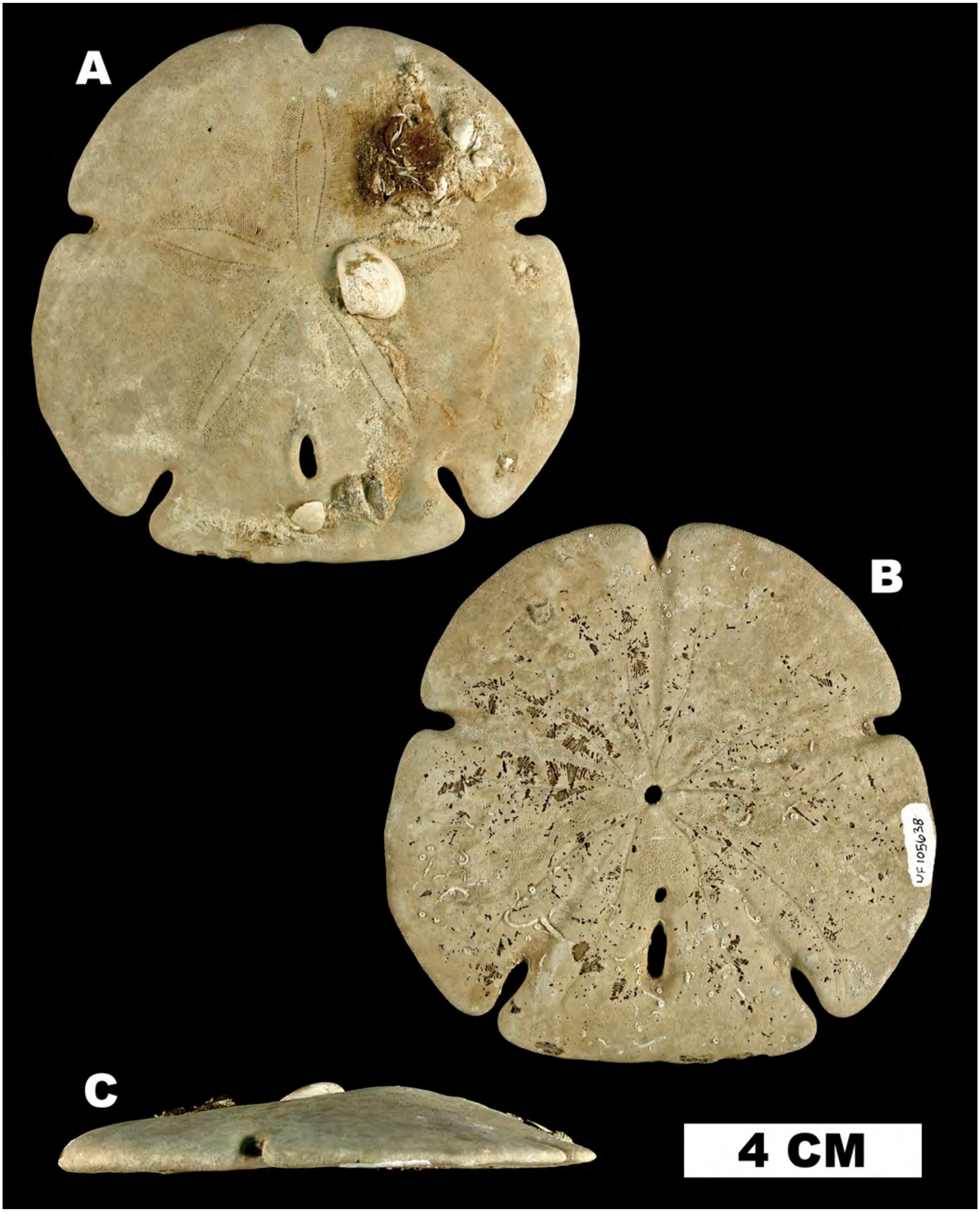


Figure 72. *Encope michelini* (UF 105638), Bermont Formation (FM locality OB013). A. aboral view, B. oral view, C. lateral view.

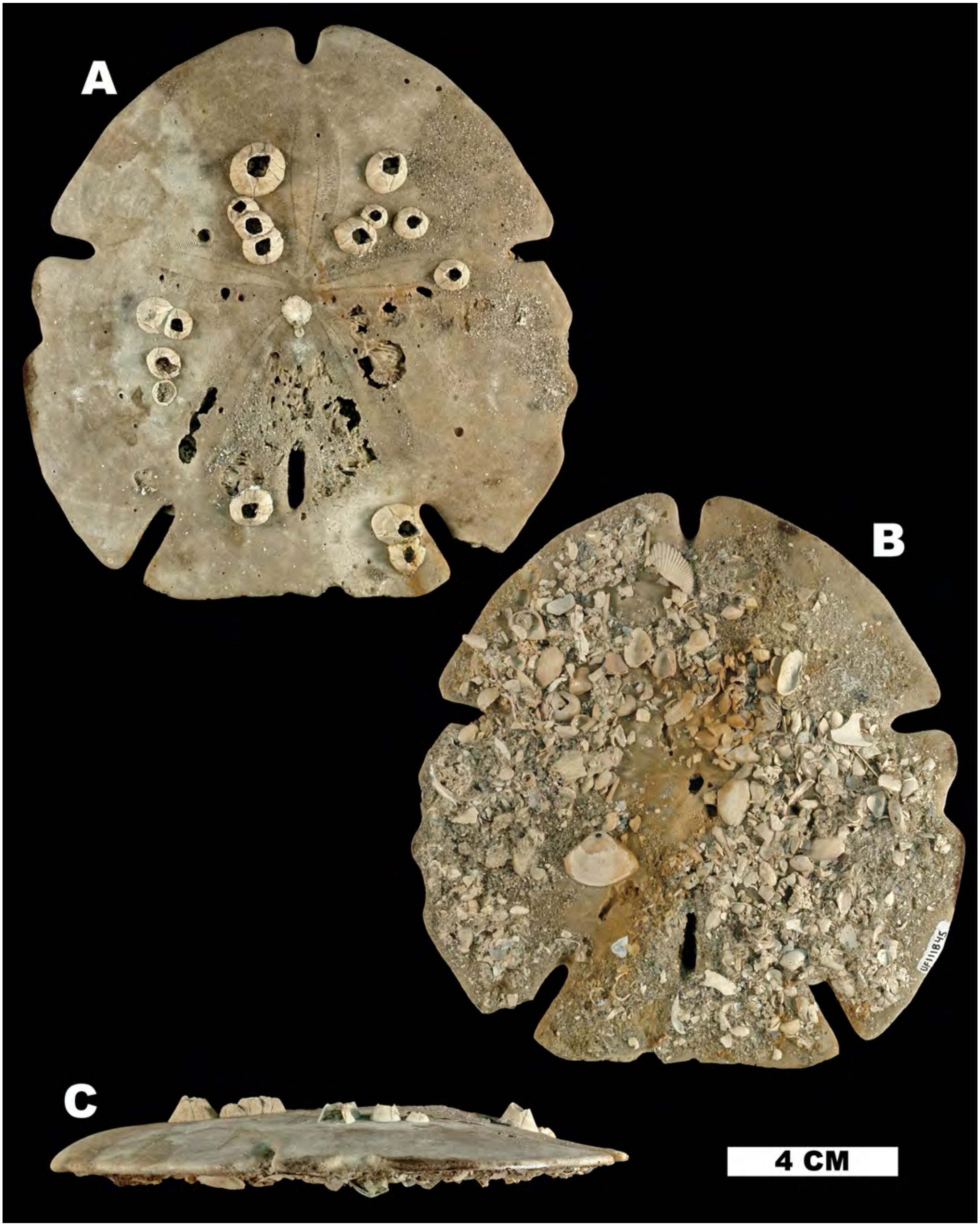


Figure 73. *Encope michelini* (UF 111845), Anastasia Formation (FM locality SL003). A. aboral view, B. oral view, C. lateral view.

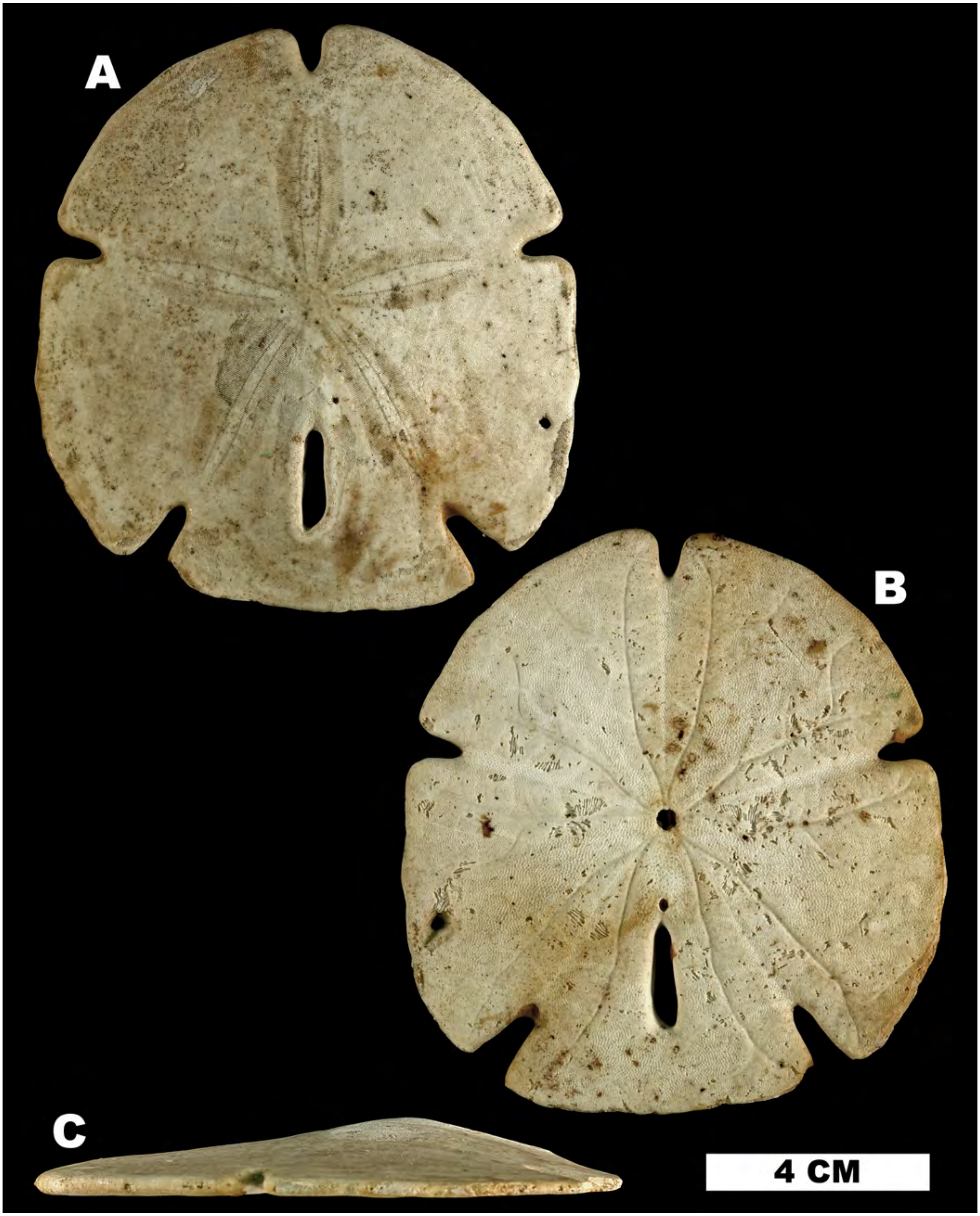


Figure 74. *Encope michelini* (UF-IZ 18903) modern specimen (Gulf of Mexico off Sarasota in 5 m depth, Sarasota County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

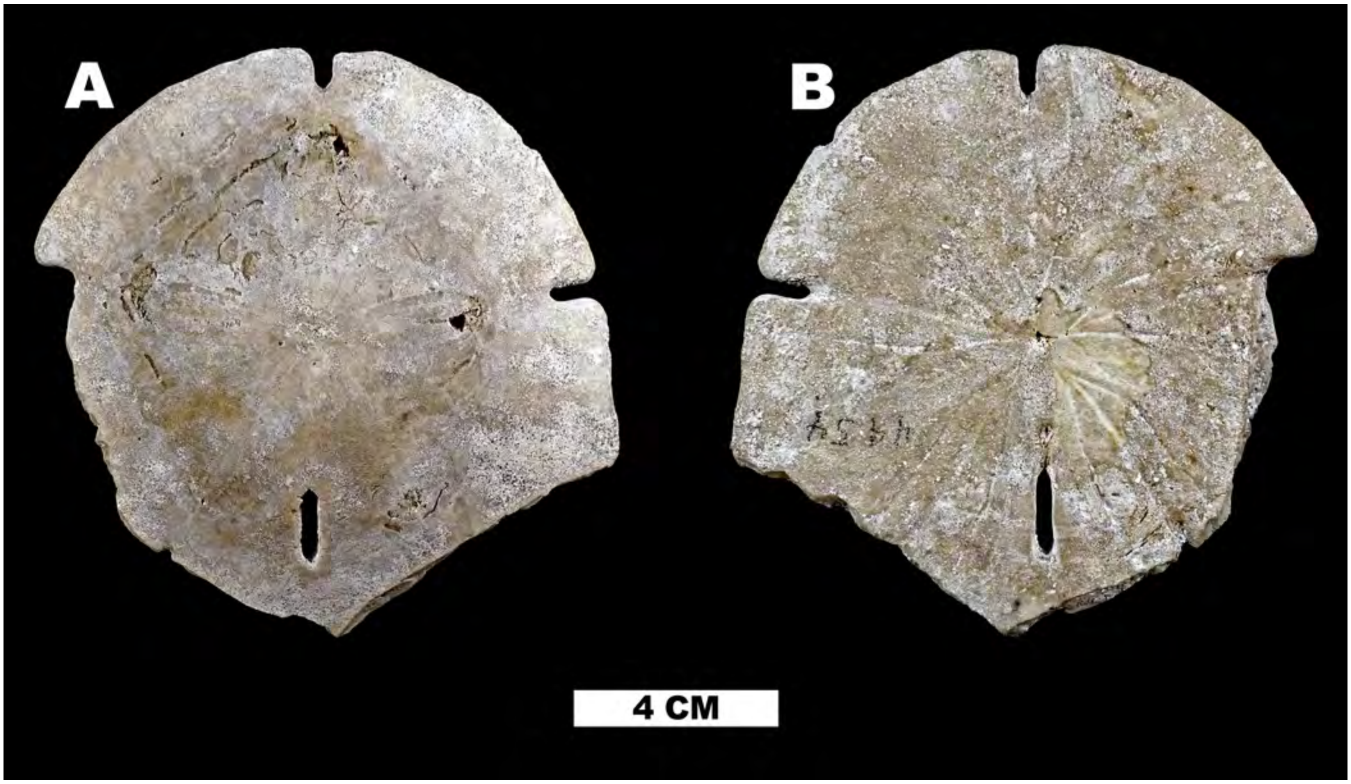


Figure 75. *Encope michelini* (USNM 316014), Miami Limestone (Big Pine Key on Railroad to Key West, Monroe County, Florida, USA). A. aboral view, B. oral view.

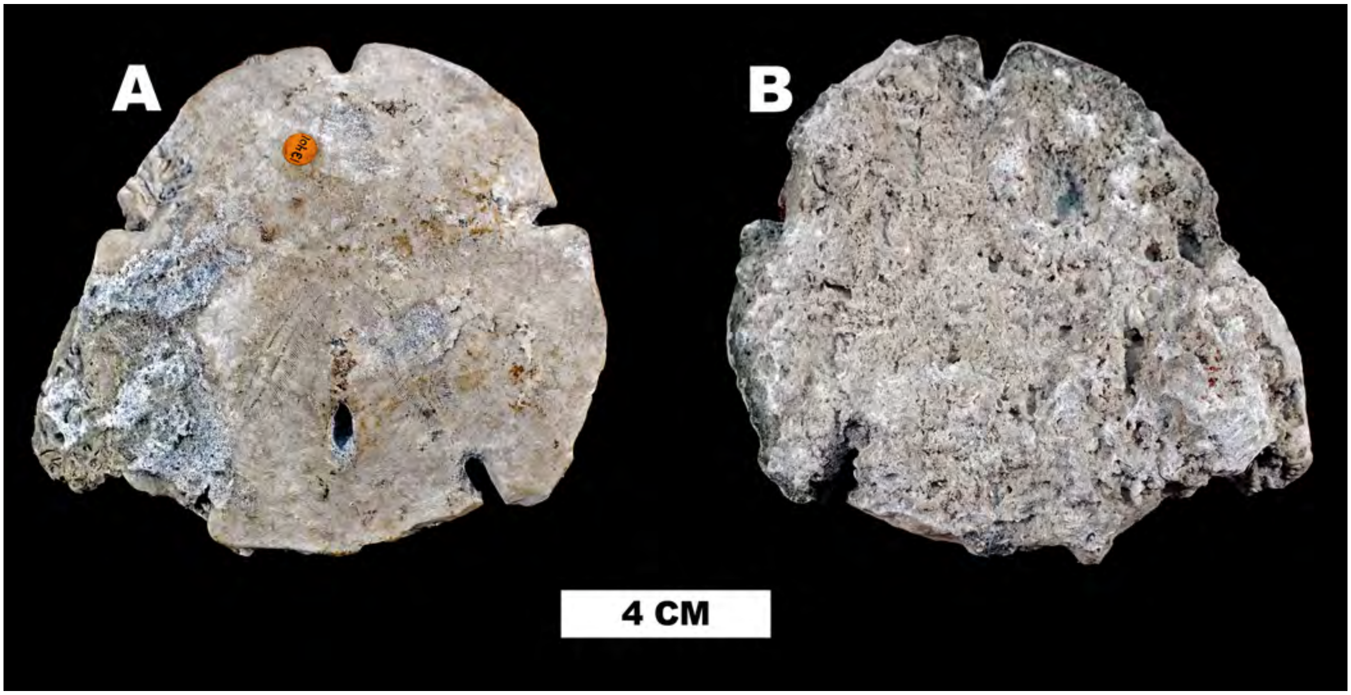


Figure 76. *Encope michelini* (USNM 316014), Miami Limestone (Big Pine Key on Railroad to Key West, Monroe County, Florida, USA). A. aboral view, B. oral view.

anterior paired petals are more broadly lanceolate than those of *E. macrophora* and do not extend across the test in a straight line, but form an angle with each other of approximately 154°.

Kier (1963:36) examined more than 1000 specimens of *E. tamiamiensis* and stated the largest specimen was 122 mm TL. Two Tamiami Formation specimens from the Lomax King Pit, Charlotte County (FM locality CH003) measure 125 mm and 134 mm TL respectively, providing a new upper limit for size of the species (Fig. 77).

Kier (1963:fig. 31) plotted TW against TL of both species and clearly illustrated that the species share bivariate space defined by these features (see *E. macrophora*, above), and that width to length ratio cannot be used to distinguish them. Kier did show that distance from the apical system to the anterior margin (Kier, 1963:fig. 33) in *E. macrophora* is clearly less than in *E. tamiamiensis*, particularly at large sizes. See the discussion for *E. macrophora*, above, for additional comments concerning differentiation of these two species. *Encope tamiamiensis* typically has a thinner margin, a smaller lunule, and anterior paired petals that are less curved posteriorly. Figure 78 shows an *E. tamiamiensis* specimen, UF 22146, with a broad anal.

Encope tamiamiensis is very common in the late Pliocene of the Tamiami Formation throughout southwestern Florida. The species occurs in a variety of lithologies, all of which are characterized by a high sand content; from the sandy, white Ochopee Limestone member of the unit in the more southwesterly exposures in Collier County to the sand facies (sensu Missimer, 1992) in Charlotte County. In both of these members, *E. tamiamiensis* often occurs in dense accumulations that are typically sorted by size, with concentrations of specimens of similar size (and therefore likely age) preserved in dense accumulations. This is not surprising, as Ebert and Dexter (1975) document populations of *E. grandis*, morphologically similar and likely closely related to, *E. tamiamiensis* that consist primarily of the same year (i.e., size) class. They also demonstrated that size classes were not uniformly distributed according to depth. Although large *E. grandis* were more abundant in the lower intertidal zone, small individuals were distributed throughout their study area. Therefore, attempts to use size distributions of any given *Encope* species to ascertain depths inhabited by a population occurring in the fossil record would likely be problematic.

The type locality of Mansfield's (1932) *E. macrophora tamiamiensis* is the Tamiami Trail, 5 miles east of Carnestown, 7 miles northeast of Everglades, in Collier County. This stratum is the typical white limestone of the Ochopee Limestone member of the Tamiami Formation (as defined by Missimer, 1992). Mansfield (1932) conspicuously excluded the specimens of *Encope* from Alligator Creek, near Punta Gorda, Charlotte County in his new subspecies. The specimens at Alligator Creek occur in the sand facies of the Tamiami Formation with a concentration of large barnacles (DuBar, 1962; Missimer, 1992). Mansfield (1932) stated that the *Encope* from Alligator Creek appear more closely related to *E. macrophora tamiamiensis* than to *E. macrophora*, but he did not place them within his new subspecies. Cooke (1942) included Alligator Creek as a site for *E. tamiamiensis* and not *E. macrophora*. However, Cooke (1959) reversed his earlier decision without discussion and included the Alligator Creek locality within his list of occurrences for *E. macrophora*, removing it from his records of *E. tamiamiensis*.

In his review of the Neogene biostratigraphy of the Charlotte Harbor area of southwestern Florida, DuBar (1962:21, 56) described a few exposures along Alligator Creek as containing *E. macrophora tamiamiensis*, including one exposure he documented as having "great masses of *E. tamiamiensis* fragments". Note that he used both the subspecies and specific designations of *E. tamiamiensis* interchangeably within this work. However, he clearly attributed the specimens to *E. tamiamiensis*, and not *E. macrophora*.

Investigations at the Alligator Creek site confirm DuBar's (1962) statement concerning the presence of a bed of test fragments. Complete specimens are not nearly as common, but the specimens are inseparable from *E. tamiamiensis*, but exhibit a tendency for the lunule to be broader than typical

Figure 77. *Encope tamiamiensis* (UF 303099), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

Figure 78. *Encope tamiamiensis* (UF 22146), Tamiami Formation (FM locality CR009). A. aboral view, B. oral view, C. lateral view.

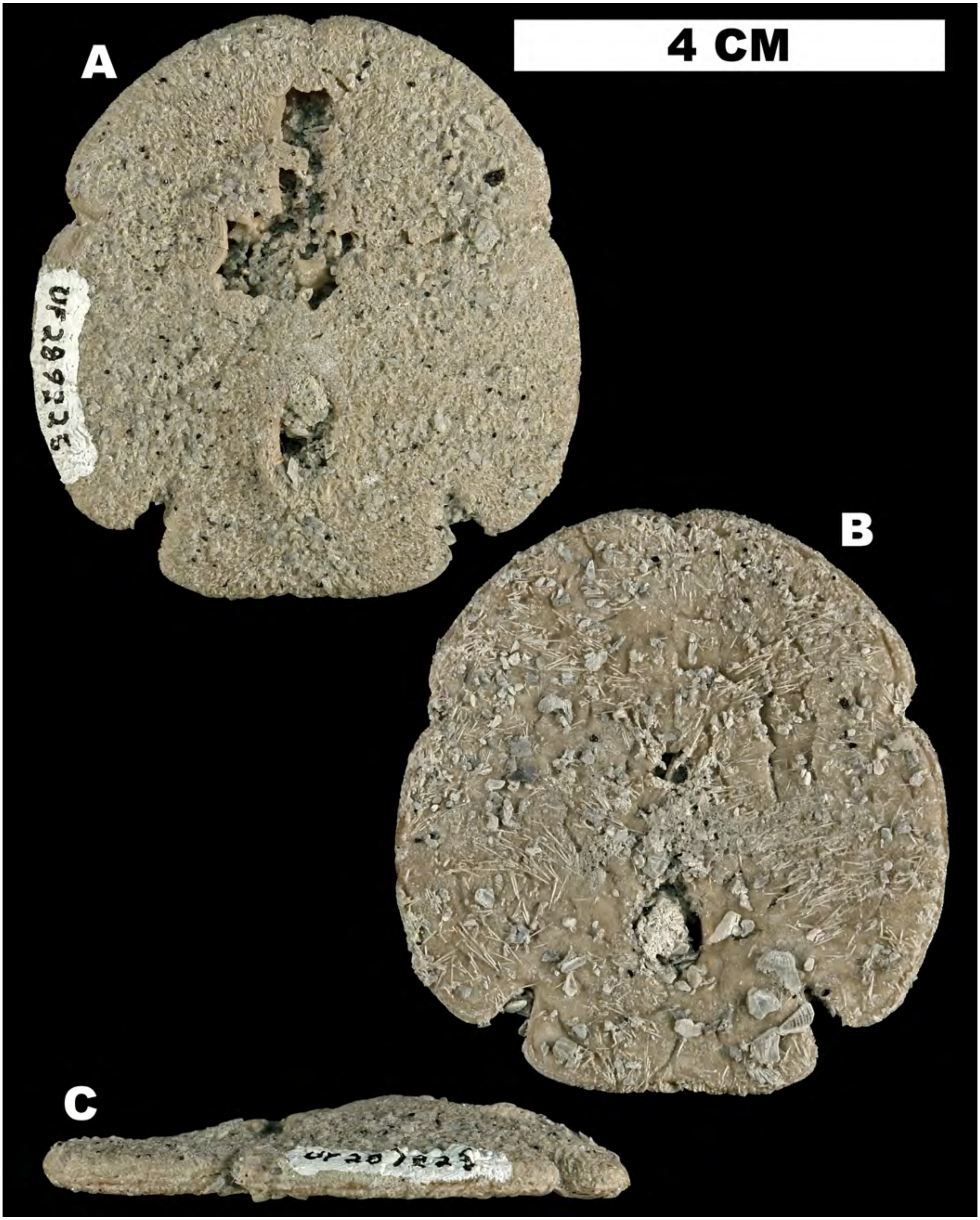


Figure 79. *Encope tamiamiensis* with spines (UF 289225), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

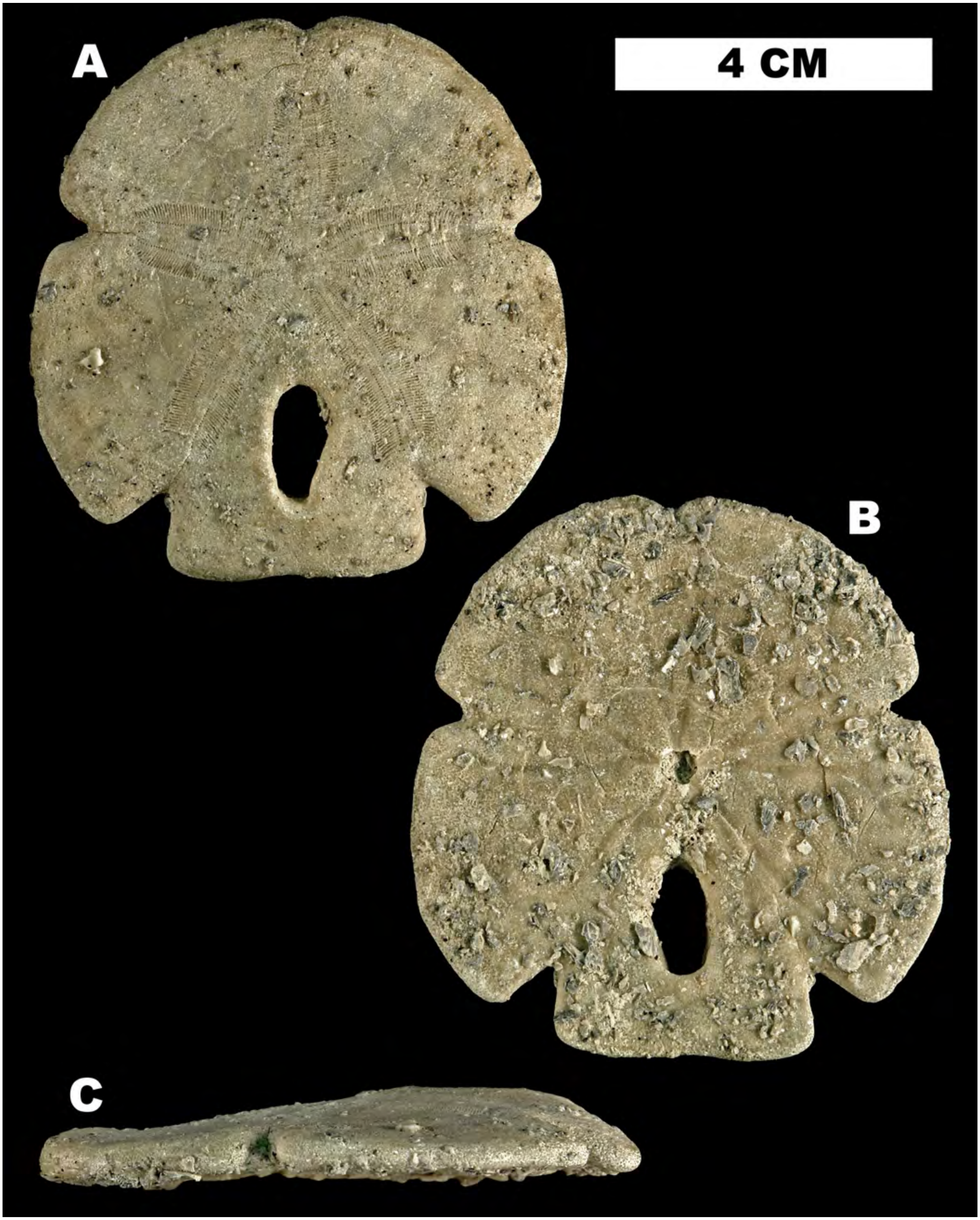


Figure 80. *Encope tamiamiensis* (UF 289228), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view.

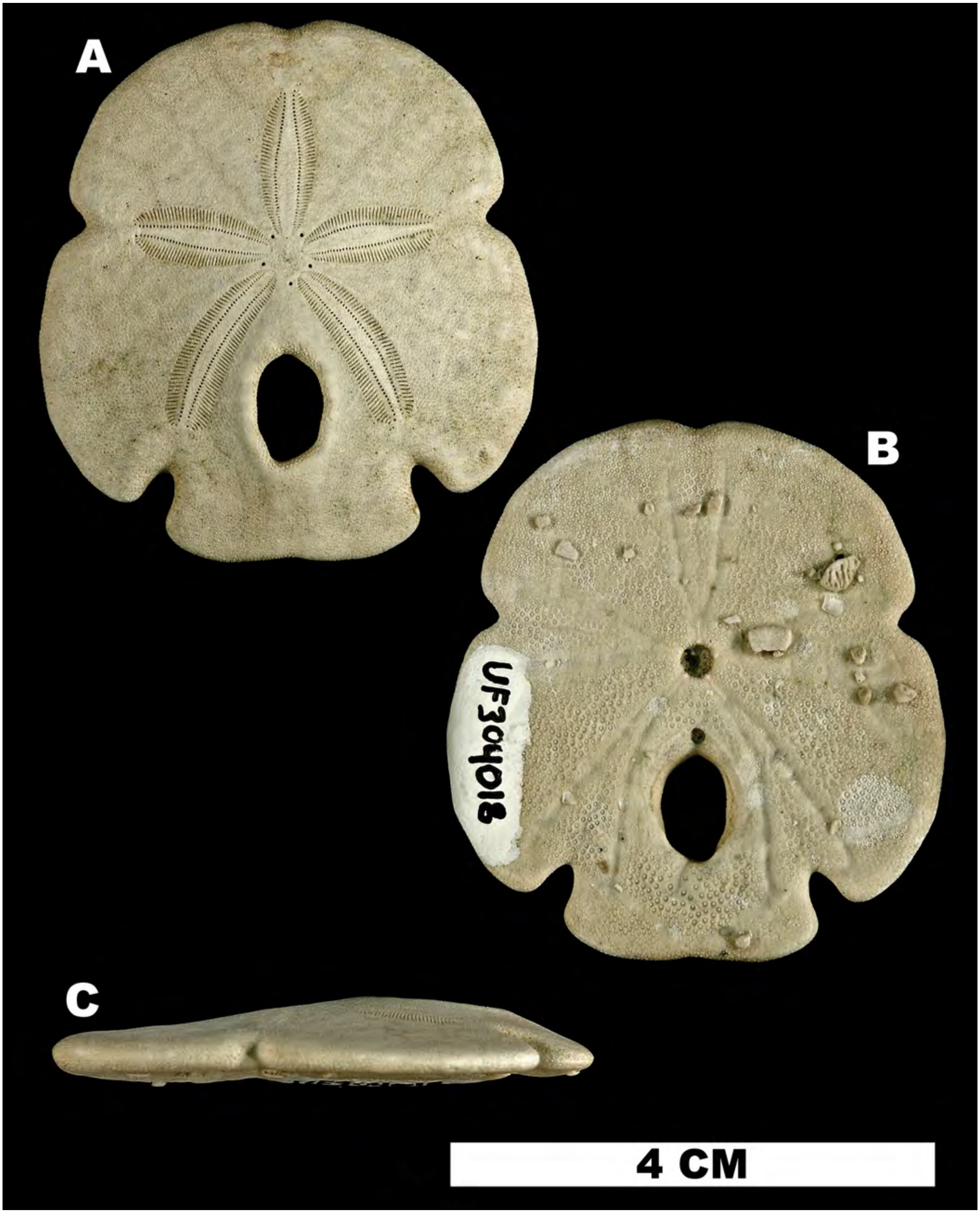


Figure 81. *Encope tamiamiensis* (UF 304018), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

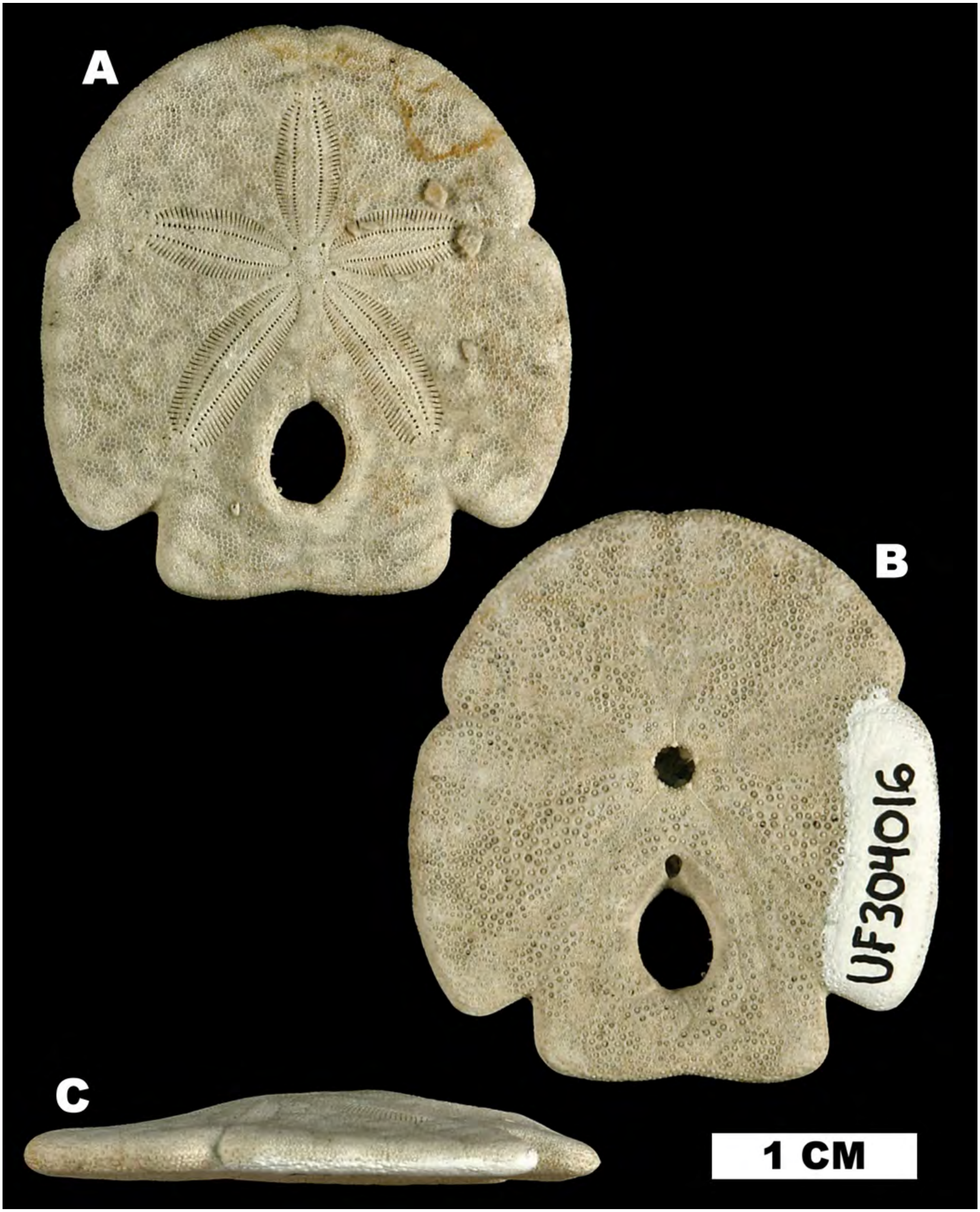


Figure 82. *Encope tamiamiensis* (UF 304016), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

for *E. tamiamiensis*. Nevertheless, specimens with a range of lunule types, from narrow to broad, are present, and as noted above, this feature does not consistently differentiate the two species. Therefore, this population is herein not included among the occurrences of *E. macrophora*. We do not recognize *E. macrophora* south of St. Johns County, Florida, nor are we aware of an occurrence of *E. tamiamiensis*, which appears to be restricted to the Tamiami Formation, north of Charlotte County, Florida.

Rare specimens retaining spines occur in the Tamiami Formation, Quality Materials Quarry, Charlotte County (FM locality CH080) (UF 289225; Fig. 79). Spines similar to those of modern representatives of the genus are more typically found on the oral surface of these fossils.

Genus ***LEODIA*** Gray, 1851

LEODIA SEXIESPERFORATA (Leske, 1778)

Figures 84–85

Echinodiscus sexies perforatus Leske, 1778, p. 199, pl. 50, figs. 3, 4.
Echinus hexaporus Gmelin, 1788, p. 3189.
Scutella sexforis Lamarck, 1816, p. 9.
Mellita hexapora (Gmelin). L. Agassiz, 1841, p. 41, pl. 4, figs. 4–7; pl. 4e, figs. 11–12.
Mellita similis L. Agassiz, 1841, p. 43, pl. 4, figs.1–3.
Leodia richardsonii Gray, 1851, p. 36.
Mellita sexforis (Lamarck). A. Agassiz, 1872, 1873, pp. 141, 536, pl. 11, figs. 1–12; pl. 11d, fig. 3.
Mellita sexiesperforata (Leske). Crozier, 1920, pp. 435–442.
Leodia sextiesperforata (sic) (Leske). Lambert and Thiéry, 1921, p. 324.
Mellita sexiesperforata (Leske). Clark, 1942, p. 382.
Leodia sexiesperforata (Leske). Cooke, 1942, p. 22.

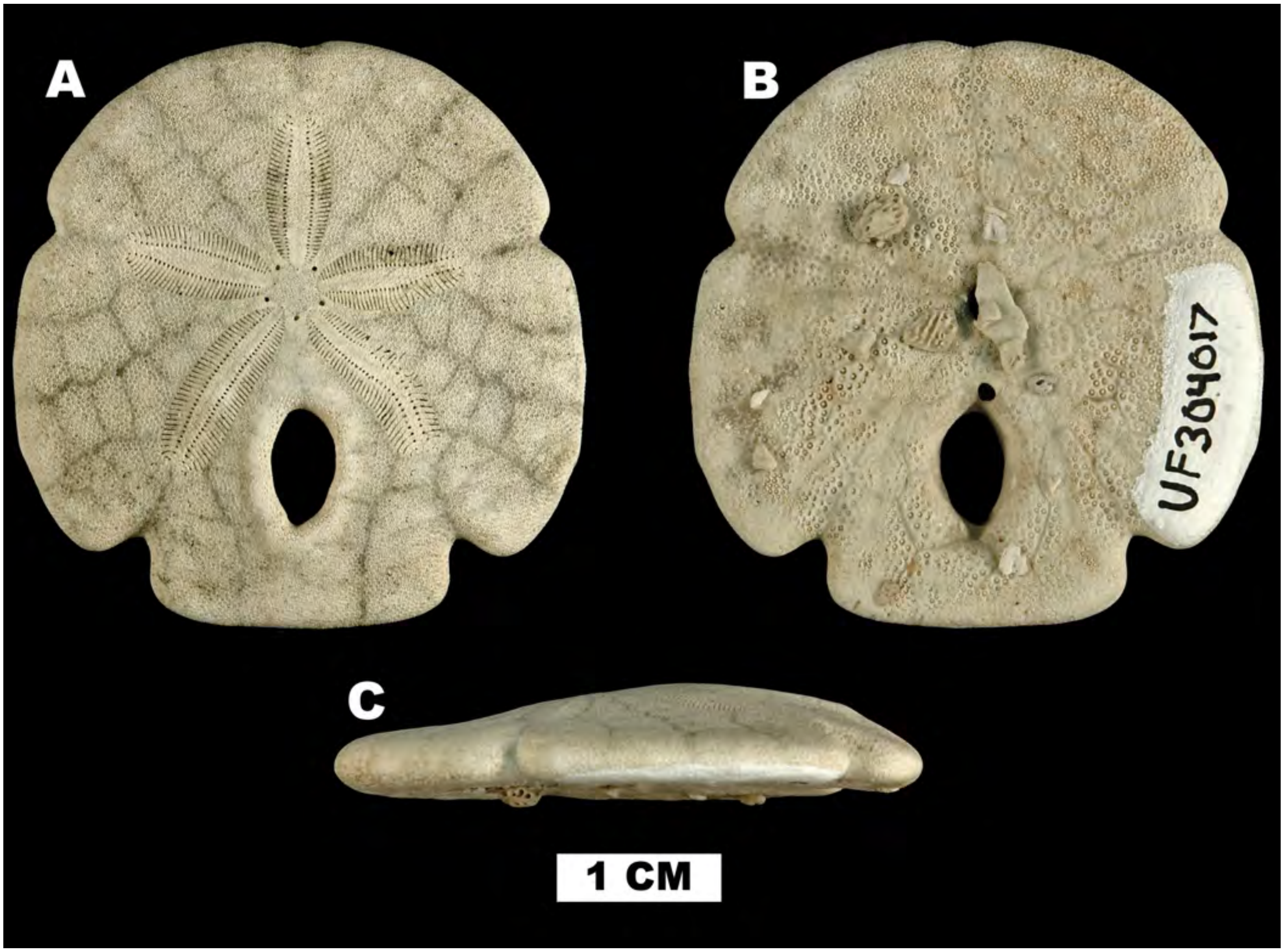


Figure 83. *Encope tamiamiensis* (UF 304017), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

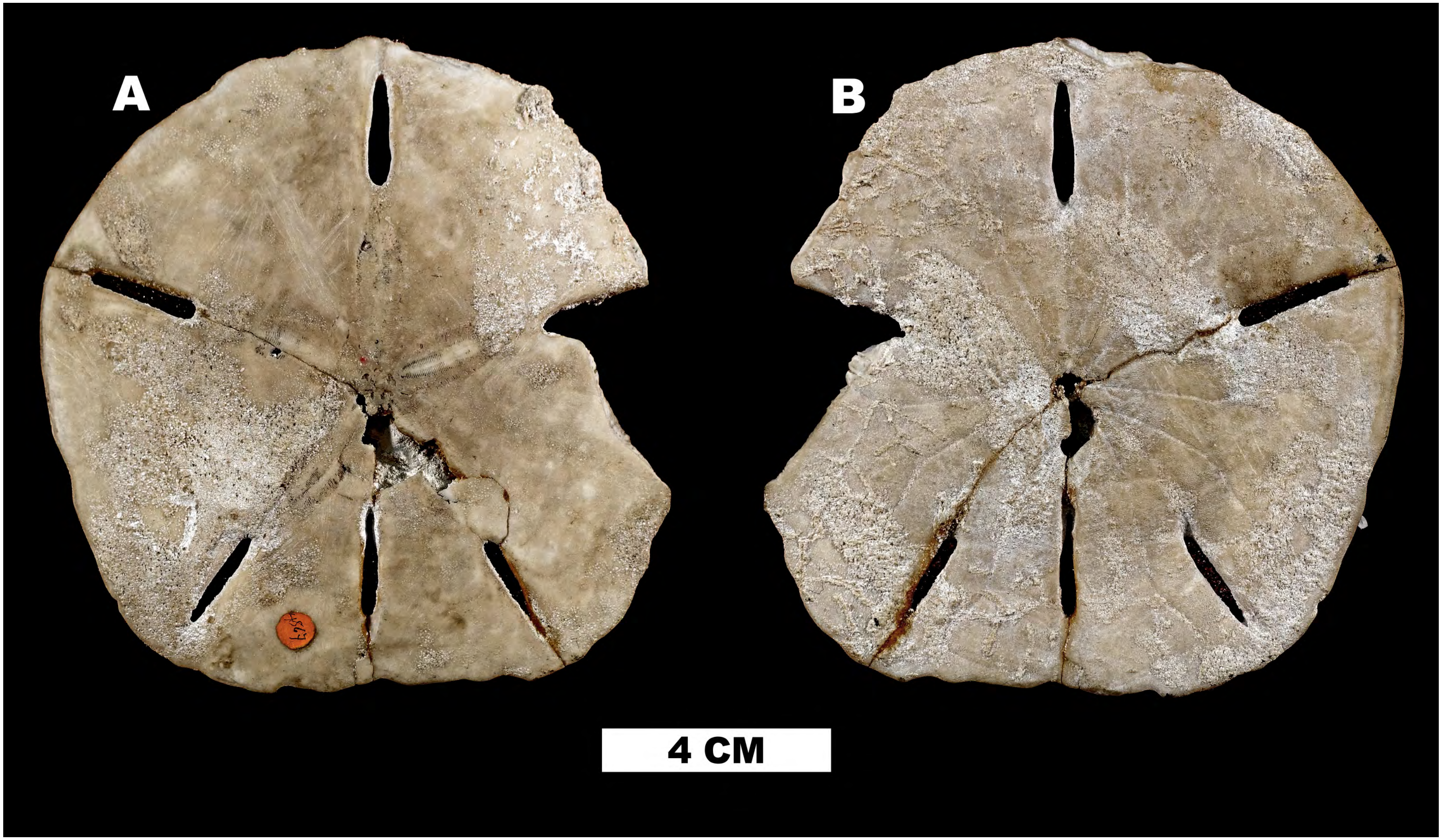


Figure 84. *Leodia sexiesperforata* (USNM 316004), Miami Limestone (Golf Grounds, Buena Vista, Miami, Miami-Dade County, Florida, USA). A. aboral view, B. oral view.

Mellita (Leodia) sexiesperforata (Leske). Mortensen, 1948, p. 429, pl. 58, fig. 4; pl. 61, fig. 7; pl. 72, fig. 19. (includes additional synonymy).

Leodia sexiesperforata (Leske). Cooke, 1959, pp. 46, 47, pl. 19. figs. 4, 5.

Leodia sexiesperforata (Leske). Kier, 1963, p. 8.

Leodia sexiesperforata (Leske). Kier, 1975, p.18, pl. 9.7.

Leodia sexiesperforata (Leske). Serafy, 1979, pp. 74, 75, fig. 32.

Leodia sexiesperforata (Leske), Smith, 1980, pp. 21–24, fig. 64d.

Leodia sexiesperforata (Leske). Mooi, 1989, figs. 11c, 25L, 26p, 27n, 29f.

Leodia sexiesperforata (Leske). Hendler et al., 1995, pp. 234, 235, figs. 125, 135B.

Leodia sexiesperforata (Leske). Mooi and Peterson, 2000, figs. 1, 3.4, 4.4, 5, 6.

Leodia sexiesperforata (Leske). Francisco and Pauls, 2008, p. 224, figs. 2E–F. tables 1, 2.

Leodia sexiesperforata (Leske). Coppard et al., 2013, figs. 1, 2a, 3. tbl. 1.

Leodia sexiesperforata (Leske). Donovan et al., 2015, pp. 10, 11, fig. 7.

Leodia sexiesperforata (Leske). Coppard, 2016, fig. 1.

Leodia sexiesperforata (Leske). Ziegler et al., 2016, figs. 6 k–o.

Occurrence.—Mooi and Peterson (2000) discussed questionable occurrences of *L. sexiesperforata* in the upper Pleistocene Miami Limestone and Fort Thompson Formation in Florida. However, we have been unable to validate the presence of this species in the Fort Thompson Formation. The species does occur in the Miami Limestone at Buena Vista, near Miami (USGS locality 4867). Considering the abundance of this species throughout the Caribbean region as far north as the Florida Keys (though it does more rarely occur farther north to the Carolinas), its near absence in the fossil record of the region is surprising. Donovan et al. (2015) documented the occurrence of this species in the Pleistocene of the Cayman Islands.

Discussion.—This is a common sand dollar of the Caribbean, recorded from the coasts of the Carolinas (where it is rare), south around Florida, and northward into the Gulf of Mexico to Sanibel Island, also the Caribbean and Atlantic south to Uruguay (Hendler et al., 1995). The species has a very characteristic, thin, flattened test through which pass one anal and five ambulacral lunules, an almost perfectly central apical system, and short, straight petals that are nearly equal in length.

Leodia sexiesperforata often buries itself in broad patches of sand free of vegetation. Although Telford and Mooi (1986) and Mooi (1989) suggested its restriction to biogenic, carbonate sands, Martinez and Mooi (2005) documented its occurrence in Uruguay on terrigenous-sourced sands. Mooi and Peterson (2000) had predicted that it could occur on terrigenous-sourced, siliceous sands at the fringes of its range.

Mortensen (1948) and Kier (1963) discussed differences between *Leodia* and *Mellita*, including the fact that ambulacral lunules in the former develop by direct perforation, but start as open notches that close as the animal matures in the latter. Harold and Telford (1990) used this character in their phylogenetic analysis, as did Mooi and Peterson (2000).

Cooke (1959) suggested that *L. sexiesperforata* occurred in the Pleistocene but indicated that no specimens complete enough for accurate identification were available for study in USNM collections. Cooke (1959:47) documented a *Leodia* 113 mm TL from the Pleistocene Miami Formation near Miami, Florida that he suggested was more likely *Mellita caroliniana*. This was probably USNM 316004, which we can confirm is indeed *L. sexiesperforata* (Fig. 84). It is the only corroborated specimen of *L. sexiesperforata* from the fossil record of Florida. Searches of the very extensive collections of the FM-IP have failed to reveal additional specimens of *L. sexiesperforata* from the fossil record of the state. It should be noted that large specimens of *M. caroliniana* have been confused with *L. sexiesperforata*, which could account for sporadic reports in the literature prior to the present work.

As discussed in the remarks for *M. caroliniana*, large specimens attributed to *L. sexiesperforata* from the Nashua Formation of Florida by Oyen (2001:175) are *M. caroliniana*.

Genus ***MELLITA*** L. Agassiz, 1841

MELLITA ACLINENSIS Kier, 1963

Figures 86–87

Mellita aclinensis Kier, 1963, pp. 40–45, pl. 15, figs. 1–3. text figs. 36–41; tables 3, 4.

Mellita cf. *M. aclinensis* (Kier). Kier, 1983, pp. 502, 503, pl. 2, figs. 1–3.

Occurrence.—*Mellita aclinensis* has not

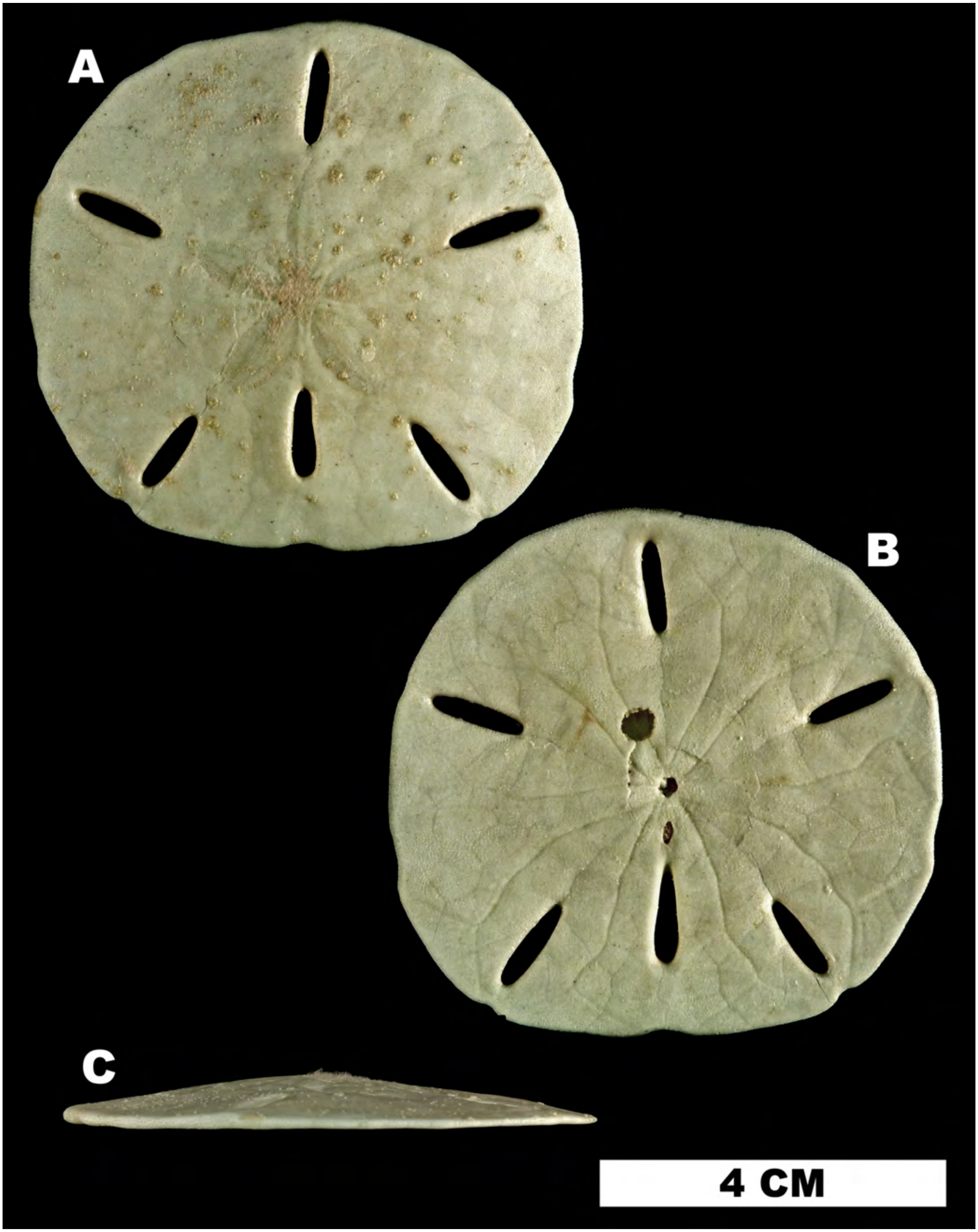


Figure 85. *Leodia sexiesperforata* (UF-IZ 18904), modern specimen for comparison (off Chub Cay at 2 m depth, Bahamas). A. aboral view, B. oral view, C. lateral view.

been documented outside of the Tamiami Formation of southwestern Florida. A few notable occurrences include: quarry east of Burnt Store Road, south of Punta Gorda, Charlotte County; Quality Materials Quarry, Charlotte County (FM locality CH080); small pits in sec. 29, T. 41 S., R. 23 E., 1 mile southwest of Acline, Charlotte County (type locality *M. aclinensis*); Lomax-King Pit, Charlotte County (FM locality CH003).

Discussion.—Kier (1963) described *M. aclinensis* from the upper Pliocene Tamiami Formation, near Acline, Charlotte County, Florida, but did not compare it to *M. caroliniana*. He stated that other than having five ambulacral lunules, it has all the other characters of *Mellita* that distinguish the genus from *Leodia*, and that it seemed reasonable to consider this a species of *Mellita*. He therefore broadened the concept of the genus to include species having five ambulacral lunules, even though it had already long been known that *M. caroliniana* was a *Mellita*, and that it had five ambulacral lunules.

The 11 specimens of *M. aclinensis* Kier (1963) had available from the type, and only known locality at the time, ranged from 16.5 mm to 73.0 mm TL. However, Kier did not provide additional measurements for the larger specimen. The next largest specimen he measured was 44.0 mm TL. Had Kier (1963) examined specimens of *M. caroliniana*, it is unlikely he would have overlooked the strong similarities between his new *M. aclinensis* and the well-known *M. carolinensis*, and at least looked for differences to distinguish the two species.

Nevertheless, Kier (1972) discussed the occurrence of *M. aclinensis* in the middle Pliocene Yorktown Formation of Virginia; specimens that we would assert are *M. caroliniana*. He insisted that the specimens from Virginia differed from the Florida material only by their size: specimens from Florida were less than 73 mm TL whereas the Virginia specimens were 128–147 mm TL, leading him to suggest that the Florida population represented juvenile specimens. Kier (1972) stated that the Florida population also has wider lunules, but assumed that this was because they still exhibited the relatively shorter lunules normally seen in younger specimens. Considering similarities of the large specimen he figured as *M. aclinensis* (Kier, 1972: pl. 6) and the large specimen of *M. caroliniana* figured by Clark and Twitchell (1915), it remains puzzling that Kier (1972) still did not make comparisons of large *M. caroliniana* with his large specimens from Virginia.

However, Kier (1972) finally did mention *M. caroliniana* in his discussion of *M. aclinensis*. He stated the test of *M. aclinensis* is much flatter than that of *M. caroliniana* and the lunules of *M. caroliniana* are often, but not always, narrower than *M. aclinensis*. This directly contradicted his placement of the Yorktown Formation specimens in *M. aclinensis*, as they have narrow lunules and proportionately flatter tests indistinguishable from those in large specimens of *M. caroliniana* from the type locality.

Kier (1972) further confirmed that there are many specimens of *M. caroliniana* in the USNM collections from locations near the type locality in South Carolina that are conspecific with Ravenel's holotype. He stated that they are variable in the shape of their petals and lunules, and include specimens that have longer, curved posterior petals with narrow lunules (as in Ravenel's holotype) as well as those with straight, posterior petals and short lunules, similar to the specimen figured by Tuomey and Holmes (1855).

Kier (1983) documented the occurrence of *M. aclinensis* in the lower Pleistocene Croatan Formation, in the PCS Phosphate Mine in Aurora, Beaufort County, North Carolina. This stratum is currently referred to the lower Pleistocene James City Formation. In this later work, it appears Kier was having difficulty with the diagnostic characters of his own *M. aclinensis*. He designated these specimens as *Mellita* cf. *M. aclinensis*, stating that they appeared to be intermediate between *M. aclinensis* and *M. caroliniana*. He indicated that *M. aclinensis* was distinguished from *M. caroliniana* by its flatter test and narrower lunules, even though he had earlier noted that the lunules of *M. caroliniana* are highly variable (Kier, 1972). Kier (1983) described flat test of the Croatan Formation specimens, but noted that in some specimens, the lunules are more rounded. At that point, he speculated that *M. caro-*

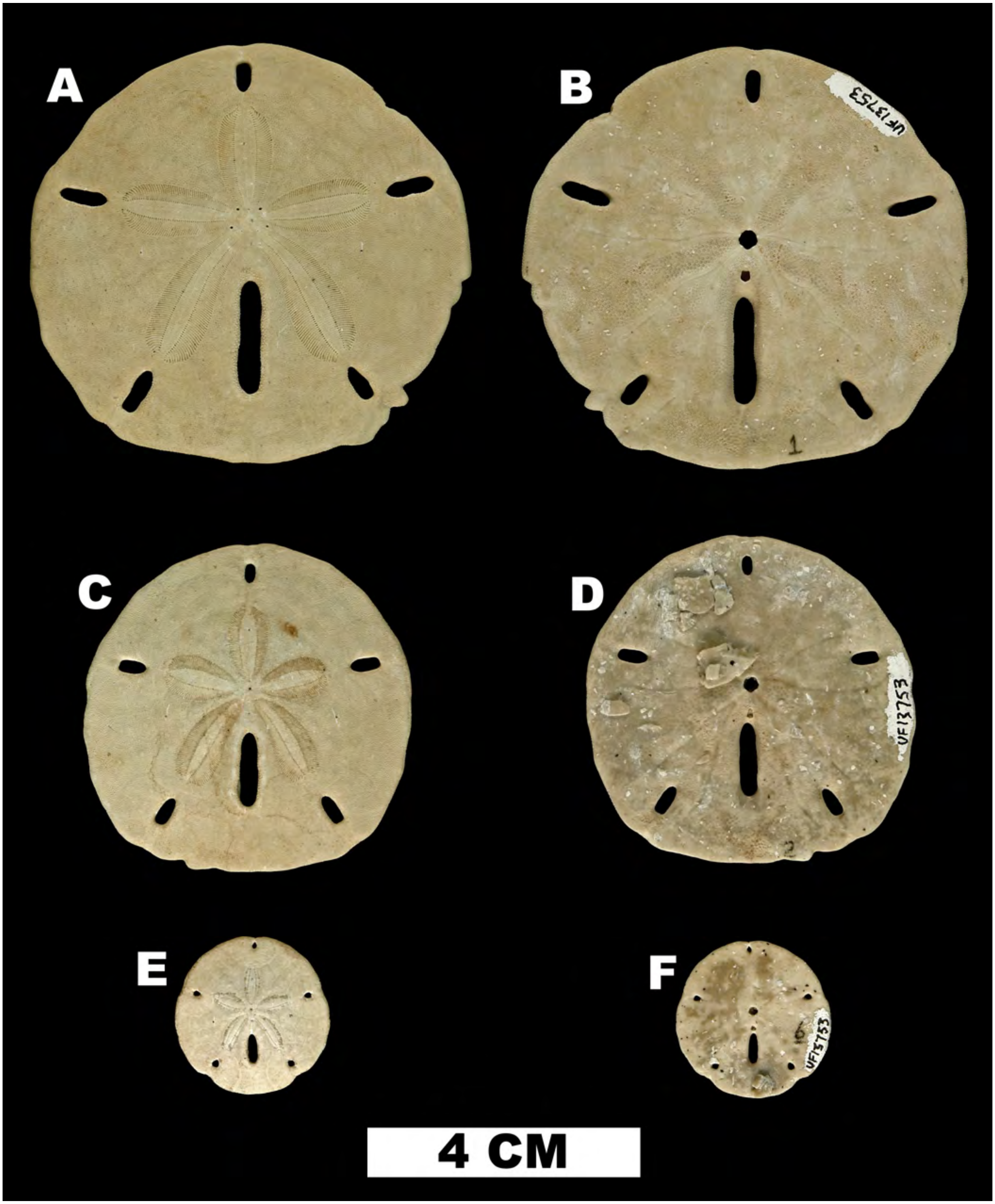


Figure 86. *Mellita aclinensis* (UF 13753), Tamiami Formation (FM locality CH003). Three specimens showing changes in growth.

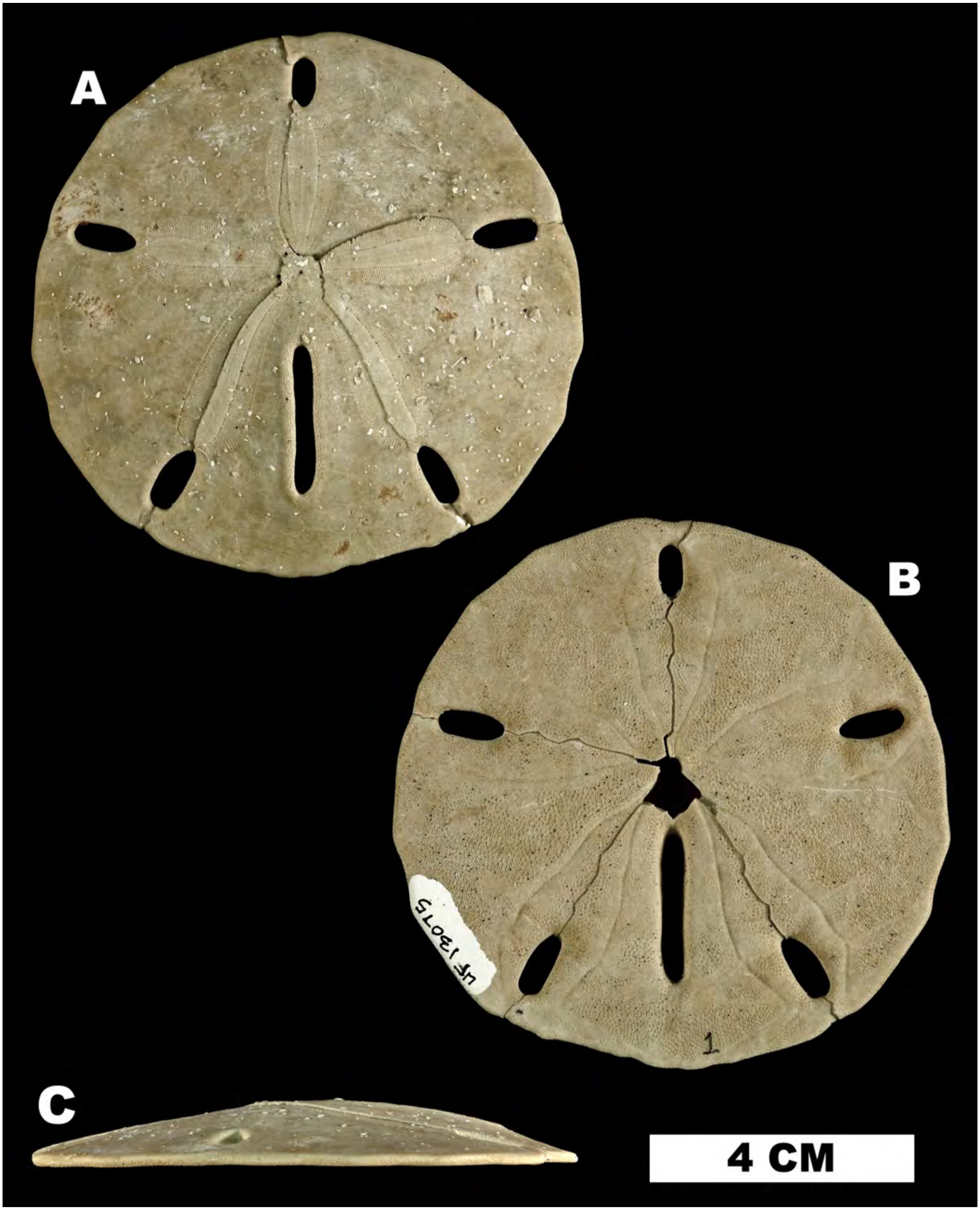


Figure 87. *Mellita aclinensis* (UF 13075), Tamiami Formation (FM locality CH003). A. aboral view, B. oral view, C. lateral view.

liniana and *M. aclinensis* were synonyms.

The variation in lunule shape is evident in a series of specimens of *M. caroliniana* from various populations from late Pliocene to early Pleistocene of the Carolinas. Also evident is the pronounced variation in test thickness, with thinner and thicker specimens even within the same population. For these reasons, unambiguous features to distinguish *M. cariolininana* and *M. aclinensis* remain elusive. We maintain both taxa here in order to highlight problems in the systematics of *M. aclinensis* and until such work as that indicated in Muníz Tirado and Mooi (2018) can be published with full synonymies of the taxa involved.

MELLITA CAROLINIANA (Ravenel, 1842)
Figures 88–90

Scutella caroliniana Ravenel, 1842, p. 333, text fig.
Mellita caroliniana (Ravenel). Ravenel, 1848, p. 4.
Mellita caroliniana (Ravenel). Tuomey and Holmes, 1855, p. 3, pl. 1, figs. 4, 4a, b.
Mellita caroliniana (Ravenel) Grabau and Shimer, 1910, p. 593, fig. 1926.
Mellita caroliniana (Ravenel). Clark and Twitchell, 1915, p. 204, pl. 91, figs, 1a, b; pl. 92, figs. 1a, b.
Leodia caroliniana (Ravenel). Cooke, 1942, p. 23.
Encope emarginata (Leske). Cooke, 1942, pl. 3, figs. 14, 15. (not *E. emarginata*, this is *M. caroliniana*).
Leodia caroliniana (Ravenel). Cooke, 1959, p. 47, pl. 19. figs. 1–3.
Mellita cf. *caroliniana* (Ravenel). Smith and Ghiold, 1982, figs. 1c, 6d.
Mellita caroliniana (Ravenel). Mooi, 1989, p. 41.
Mellita caroliniana (Ravenel). Campbell and Campbell, 1995, pl. 4. fig. 4.
Mellita sp. cf. *M. caroliniana* (Ravenel). Oyen, 2001, pp. 173–175, fig. 3–29c, d.
Not *Leodia sexiesperforata* (Leske). Oyen, 2001, pp. 175, 176, fig. 3–30a. (not *L. sexiesperforata*, this is *M. caroliniana*).
Mellita caroliniana (Ravenel). Ciampaglio et al., 2009, fig. 2.
Mellita caroliniana (Ravenel). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—*Mellita caroliniana* occurs in the lower Pleistocene Nashua Formation along Florida's east coast from the central peninsula to the north border: Cracker Swamp Ranch, Putnam County (FM locality PU004); F & W Mine, Orange County (FM locality OR002); East Coast Aggregates Quarry, St. Johns County (FM locality SJ007); Orange County (FM locality OR002); Brevard County (FM locality BR007).

This species also occurs in the middle Pliocene to early Pleistocene of North Carolina, South Carolina (type locality is the Grove Plantation of Dr. Edmund Ravenel, Cooper River, 5 miles northwest of Wando, South Carolina), Thompkins Quarry, east of Conway, South Carolina, and in the Yorktown Formation of Virginia (Kier, 1972).

Discussion.—In his discussion of *Leodia*, Oyen (2001:175–176) described a very large specimen (UF 31969; Fig. 88) he attributed to *Leodia sexiesperforata* from the Nashua Formation. Zoologists to whom he showed the specimen considered it to be *Mellita* (either *M. aclinensis* or *M. caroliniana*). However, Oyen doubted their conclusion because he could find no representatives of *M. aclinensis* that were that large. Examination of the specimen in the FM-IP collections reveal that this specimen was actually collected in the Tamiami Formation in a quarry off Burnt Store Road (FM locality LE009), south of Acline in Charlotte County, in strata correlated with, and very near the type locality of *M. aclinensis*. The matrix adhering to the oral side of the specimen is a gray limestone similar to that of the Tamiami Formation in that area. As Oyen noted, it is much larger than any specimens typical of *M. aclinensis* that have been documented from the unit. However, it is very representative of the large specimens of *M. caroliniana* known from South Carolina, and we do not hesitate in identifying it as such.

Survey of the FM-IP collections revealed an extremely large specimen of *M. caroliniana* from the Nashua Formation in Orange County, Florida (UF 12901; Fig. 89) that is 142 mm TL and 138 mm TW. A smaller specimen from the Nashua Formation, 75 mm TL and 75 mm TW, is also figured (UF 80503; Fig. 90). Additional collecting in the East Coast Aggregates Quarry, St. Johns County (FM locality SJ007), revealed *M. caroliniana* with *E.* aff. *macrophora* in an indurated sandy limestone facies of the lower Nashua Formation. This horizon has a fauna with strong Pliocene affinities, and likely represents a late Pliocene portion of the unit.

See the discussion for *M. aclinensis* above for a discussion of the previously proposed distinctions between *M. caroliniana* and *M. aclinensis*; *M. aclinensis* is likely a subjective junior synonym of

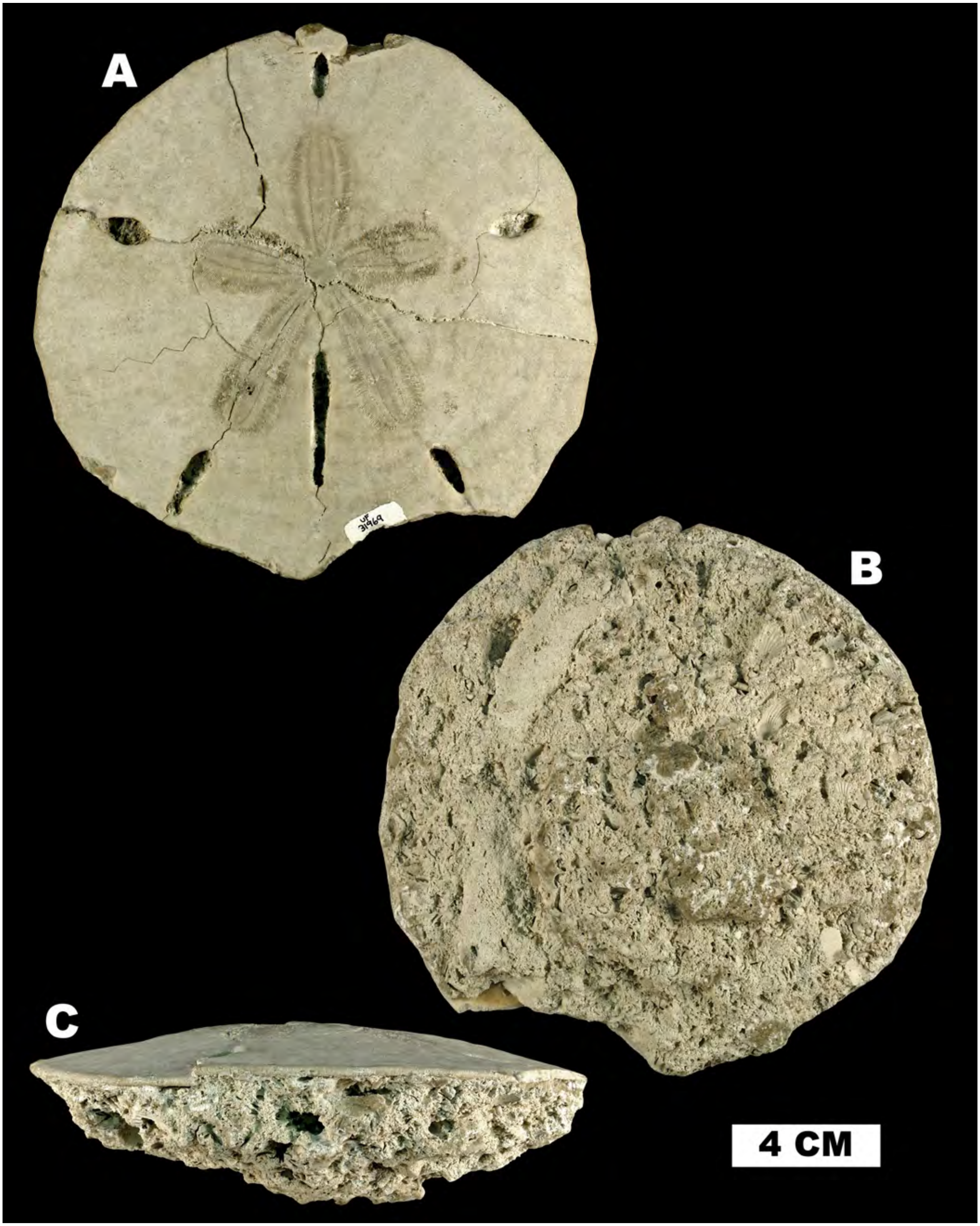


Figure 88. *Mellita caroliniana* (UF 31969), Tamiami Formation (FM locality LE009). A. aboral view, B. oral view, C. lateral view.

M. caroliniana.

MELLITA ISOMETRA Harold and Telford, 1990

Figures 91–94

Mellita quinquefora (Lamarck). Ravenel, 1848, 4 p.
Mellita ampla Ravenel. 1848, p. 4, no. 8.
Mellita nummularis Michelin, 1858, pp. 2–7.
Mellita quinquefora ampla Holmes, 1860, p. 3, pl. 1, figs. 6^a, b.
Mellita testudinata Agassiz, 1872, pp. 322–324, pl. 11, figs. 13–22. pl. 12, figs. 1, 2.
Mellita quinquiesperforata (Leske). W. Berry, 1941. p. 443, pl. 65, fig. 5.
Mellita quinquiesperforata (Leske). Cooke, 1942. p. 22, pl. 3, figs. 12, 13.
Mellita quinquiesperforata (Leske). Cooke, 1959, pp. 44, 45, pl. 19, figs. 6, 7.
Mellita quinquiesperforata (Leske). Cerame-Vivas and Gray, 1964, fig. 1. (discusses populations of *Mellita* from North Carolina that are referable to *M. isometra*).
Mellita quinquiesperforata (Leske). Serafy and Fell, 1985, pp. 20, 22, 23, fig. 30.
Mellita isometra Harold and Telford, 1990, pp. 1002–1005. figs. 11–13. (includes additional synonymy).
Mellita isometra (Harold and Telford). Hendler et al., 1995, pp. 236–238, figs. 126, 136B.
Mellita isometra (Harold and Telford). Ciampaglio et al., 2009, fig. 2.
Mellita tenuis (Clark). Coppard et al., 2013, pp. 1033–1042, figs. 4, (text in part).
Mellita isometra (Harold and Telford). Coppard et al., 2013, (text in part, they consider the two species to be synonymous.
Mellita isometra (Harold and Telford). Ziegler et al., 2016, fig. 7 f–j.

Occurrence.—In Florida, *Mellita isometra* occurs in the upper Pleistocene Anastasia and Satilla Formations; Satilla Formation: Rose's Bluff, Nassau County (FM locality NA002). Anastasia Formation: Beaches in Brevard County (FM locality BR008) where specimens of *M. isometra* often are encrusted in coquina limestone. The FM-IP collection also contains two specimens of *M. isometra* (UF 14778 and UF 2425) from an undifferentiated upper Pleistocene deposit in Manatee County (FM locality MA004). *Mellita isometra* also occurs in the upper Pleistocene Satilla Formation of Georgia and Canepatch Formation of the Carolinas.

Discussion.—Harold and Telford (1990) described *M. isometra* to include the populations of *Mellita* previously referred to *M. quinquiesperforata* that occur along the Atlantic Coast of North America from Massachusetts to Fort Lauderdale, Florida. They distinguished it by its circular to slightly pentangular outline (hence the name) with its point of maximum thickness being just anterior to the apical system. They suggested that *M. isometra* was replaced by *M. tenuis* westward in the eastern Gulf of Mexico, separated by the biogenic coralline sands of the reef areas around the southern tip of Florida where *Mellita* of any kind were not known to occur. Harold and Telford (1990) distinguished *M. tenuis* from *M. isometra* by the central to posterior position of maximum test thickness, and other, somewhat more equivocal characteristics.

Large specimens of *M. tenuis*, especially near Tampa Bay, tend to develop an angular outline more reminiscent of what Harold and Telford (1990) referred to as *M. isometra* than the typical, more nearly circular to ovate shape of *M. tenuis*. There remains confusion as to how to distinguish these two forms by morphology alone, and indeed, Coppard et al. (2013) produced cogent molecular arguments to synonymize the two forms, but did not do so formally. We continue to find that the point of greatest height just anterior of the apical system a reliable trait in differentiationg *M. isometra* from *M. tenuis*. In addition, differentiation of the two taxa is consistent with morphospecies concepts used elsewhere in this paper, and can still be helpful in understanding the evolution of the genus.

Most previous accounts of *M. quinquiesperforata* in the fossil record of the Carolinas and Georgia, as well as the Atlantic coastal areas of northern Florida are attributable to *M. isometra* where it is the dominant clypeasteroid of both the Recent nearshore fauna and most middle to upper Pleistocene deposits of the coastal areas. Mooi and Harold (1994) designated a neotype of *M. quinquiesperforata*, and confirmed the absence of the species from the Recent of the east and west coasts of Florida, a finding further supported by Coppard et al. (2013). However, Coppard et al.'s documented range of the species is incorrect as they neither cite Mooi and Harold (1994) nor record the original and subsequently redesignated type locality (Veracruz) along the Gulf Coast of Mexico.

Although *M. isometra* is common along the modern Atlantic Coast of Florida and the Carolinas,

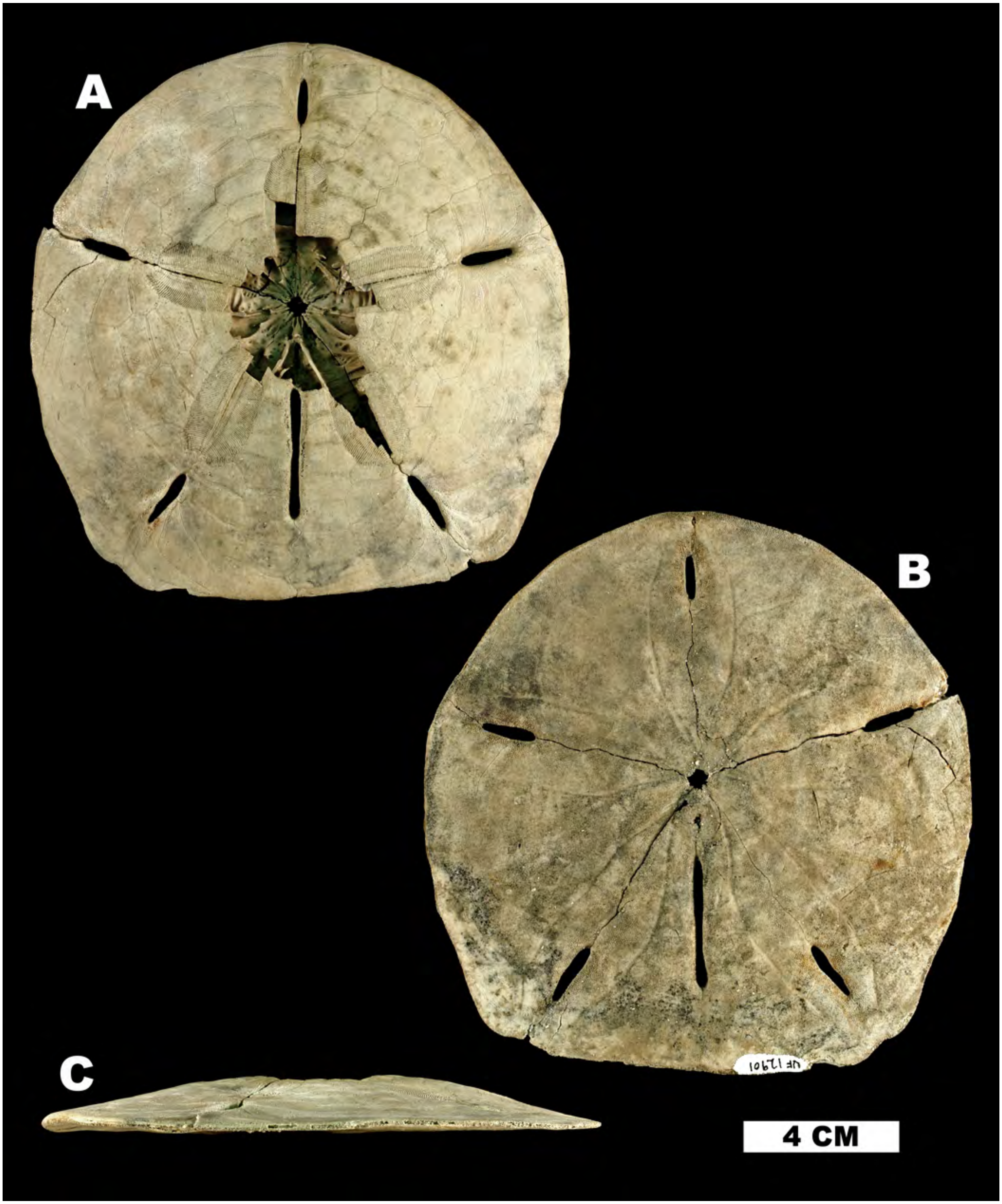


Figure 89. *Mellita caroliniana* (UF 12901), Nashua Formation (FM locality OR002). A. aboral view, B. oral view, C. lateral view.

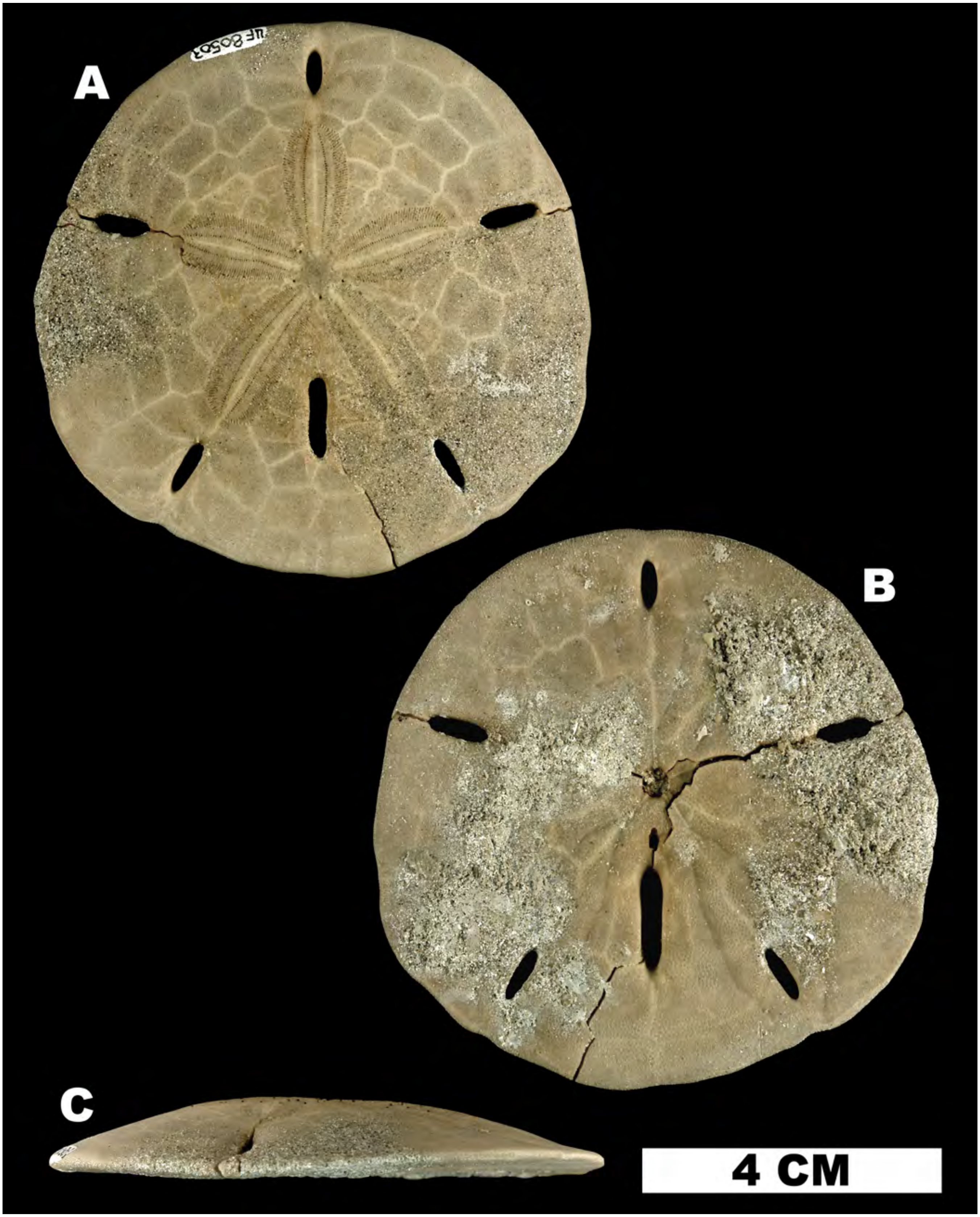


Figure 90. *Mellita caroliniana* (UF 80503), Nashua Formation (FM locality BR007). A. aboral view, B. oral view, C. lateral view.

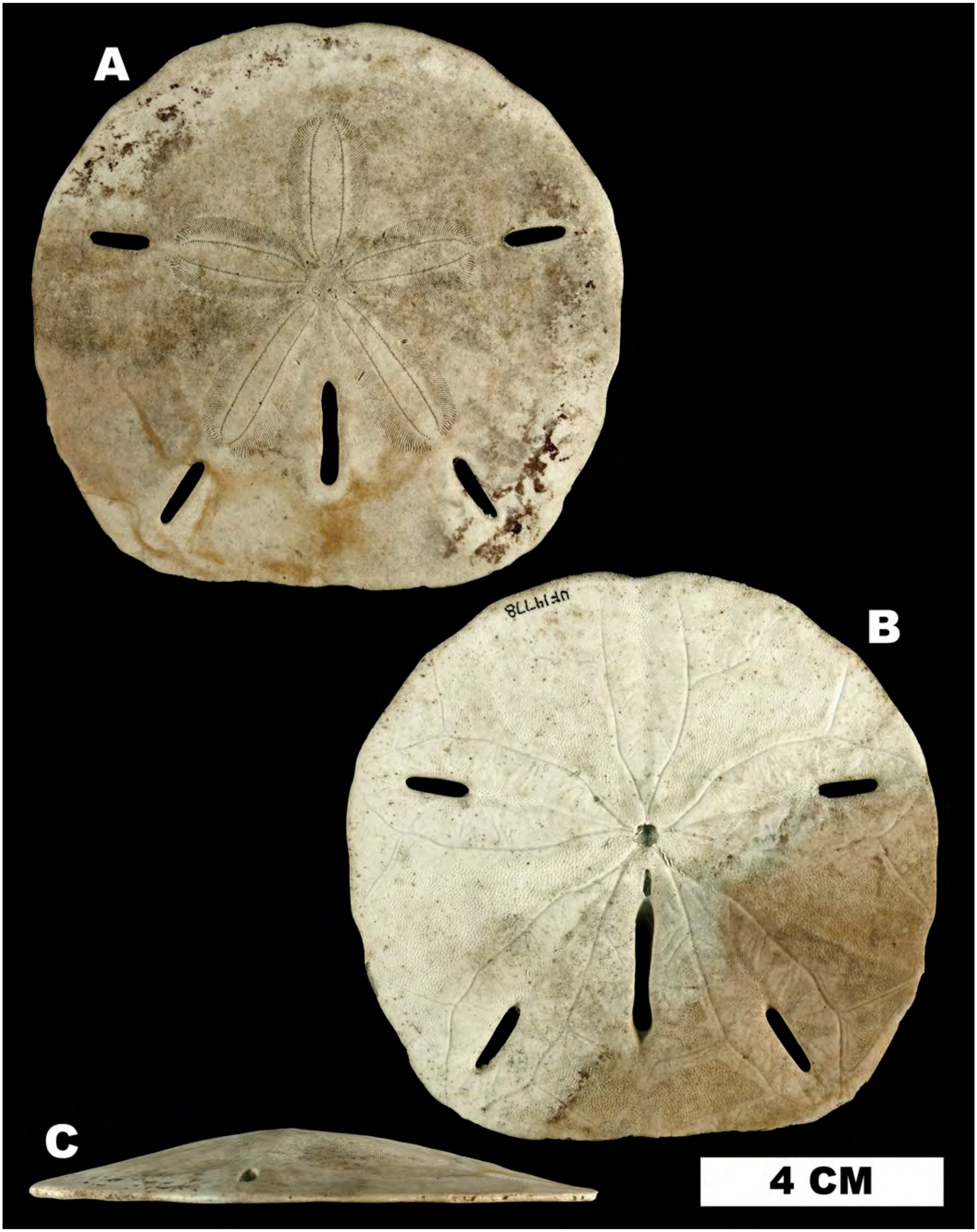


Figure 91. *Mellita isometra* (UF 14778), undifferentiated Pleistocene strata (FM locality MA004). A. aboral view, B. oral view, C. lateral view.

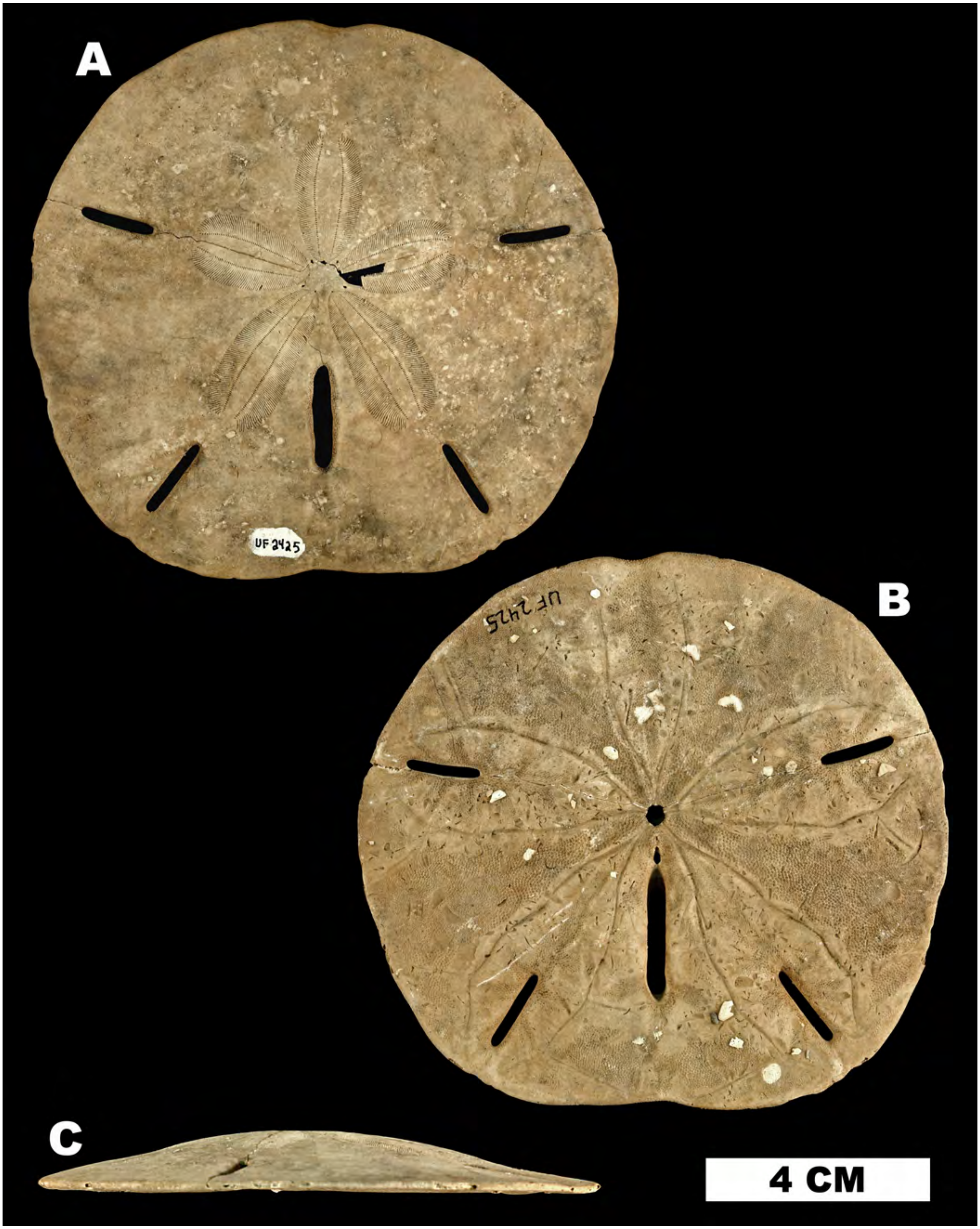


Figure 92. *Mellita isometra* (UF 2425), undifferentiated Pleistocene strata (FM locality MA004). A. aboral view, B. oral view, C. lateral view.

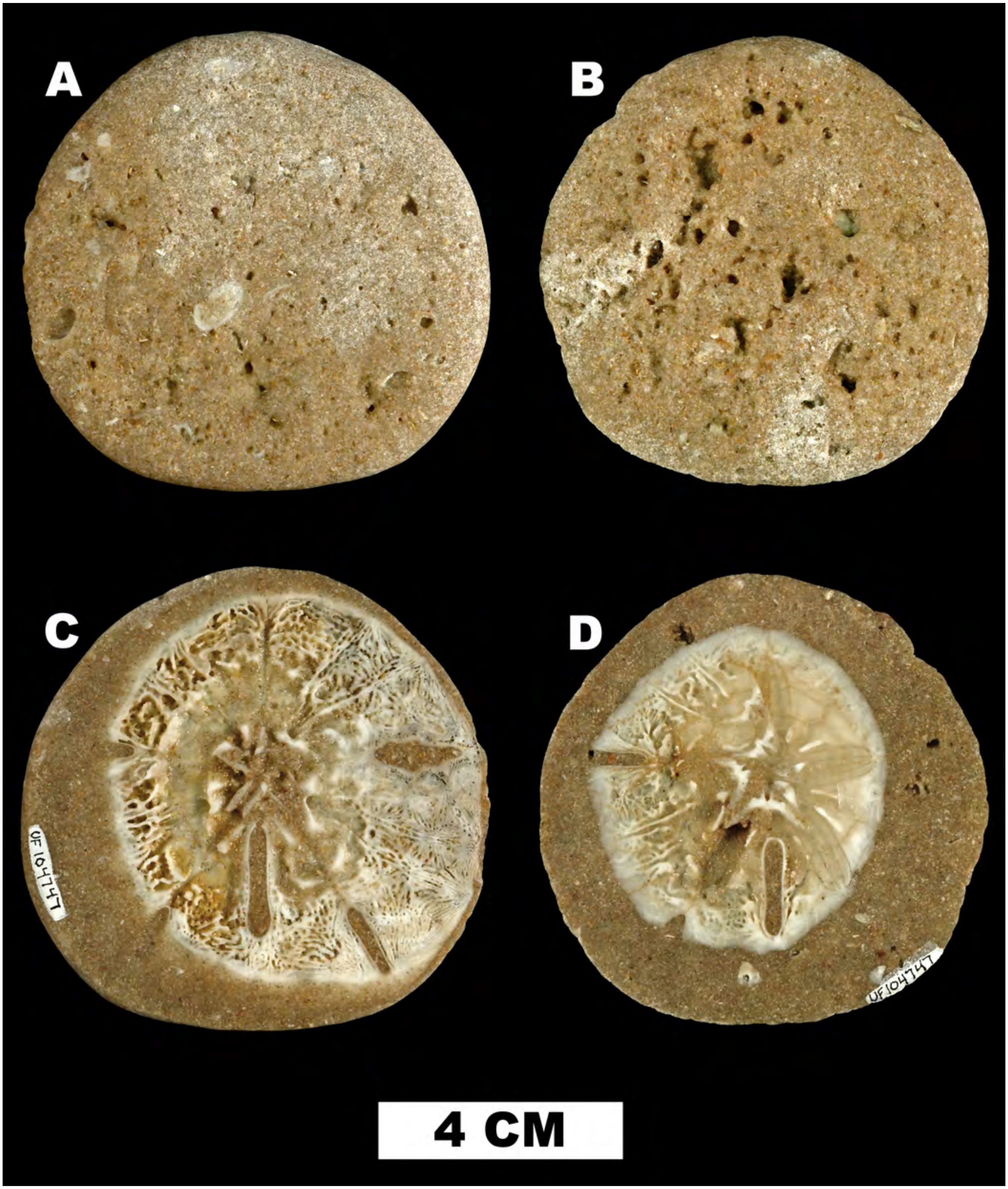


Figure 93. *Mellita isometra* (UF 104747), Anastasia Formation (FM locality BR008). Sectioned test. A, C. outer and inner sides of aboral portion of matrix encrusted test; B, D. outer and inner sides of oral portion of matrix encrusted test.

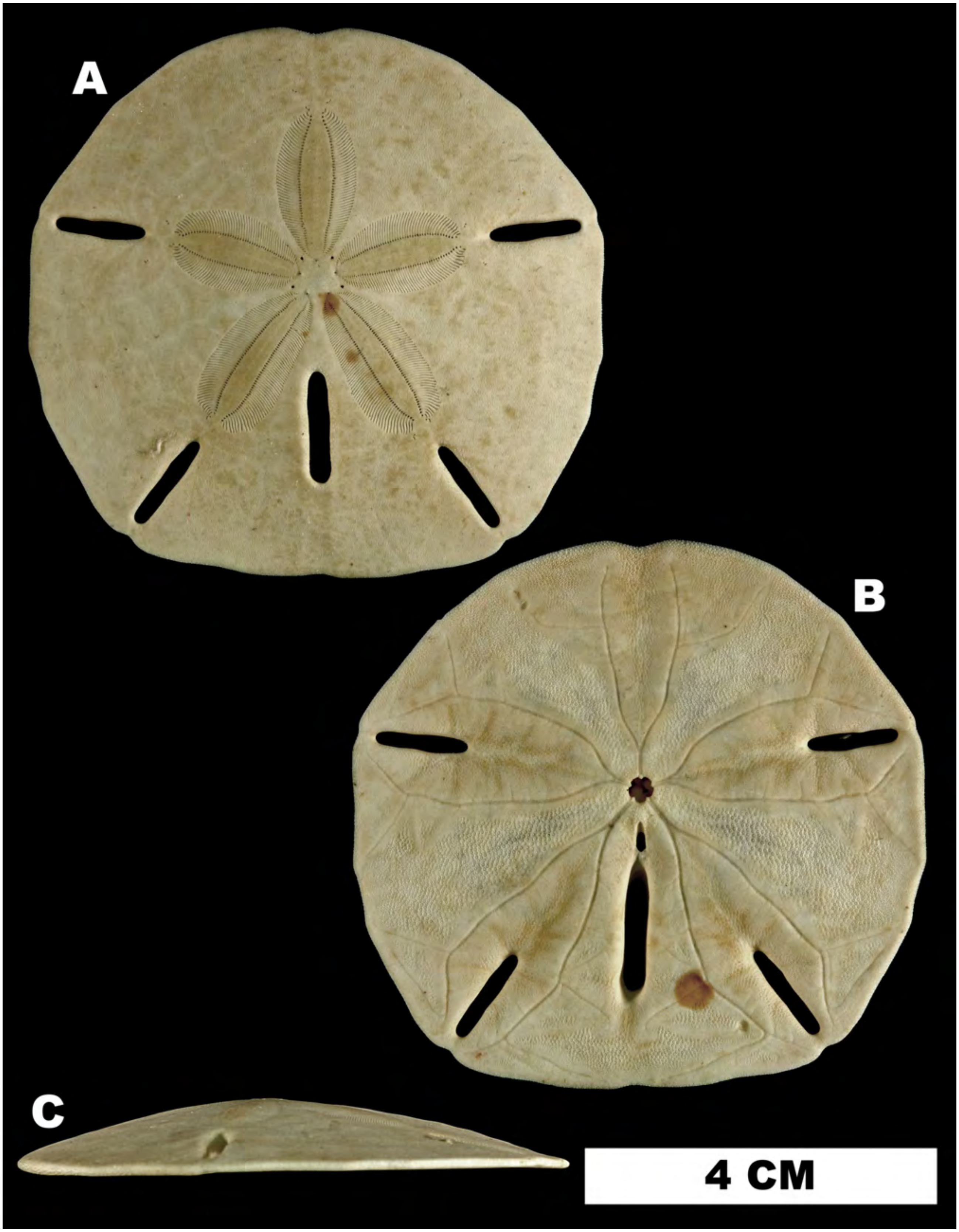


Figure 94. *Mellita isometra* (UF-IZ 18905), modern specimen for comparison (Beach of Saint Simons Island, Glynn County, Georgia). A. aboral view, B. oral view, C. lateral view.

occurring as far north as Massachusetts, it is rarely found in Pleistocene strata of the region. Its greatest abundance might be in the middle Pleistocene Canepatch Formation of Horry County, northeastern South Carolina, where it occurs with numerous *E. michelini*. *Mellita isometra* appears to be limited to sporadic occurrences in both the Satilla and Anastasia Formations, as well as an isolated occurrence in the west central Florida Gulf Coast in Manatee County. This occurrence of *M. isometra* in an undifferentiated upper Pleistocene sand deposit in Manatee County (FM locality MA004) is notable because it is within the range of extant *M. tenui*s as described by Harold and Telford (1990). *Mellita isometra* is otherwise not documented from the Gulf of Mexico except in the sense of the species employed by Coppard et al. (2013), but the anterior placement of greatest TH and almost equal TL and TW seem to indicate that this is *M. isometra* (UF 14778 and UF 2425; Figs. 91–92).

Mellita isometra occurs along the beaches of Brevard County (FM locality BR008) where specimens are often cemented in coquina and washed up on Atlantic beaches. The identity of these specimens can only be revealed by cutting parallel to the plane of the test, exposing the interior (e.g., UF 104747; Fig. 93).

MELLITA TENUIS H.L. Clark, 1940
Figures 95–96

Mellita quinquiesperforata var. *tenuis* H. L. Clark, 1940, p. 442, pl. 60, fig. 2; pl. 61, fig. 2.
Mellita quinquiesperforata tenuis (Clark). Cooke, 1942. p. 22.
Mellita quinquiesperforata tenuis (Clark). Mortensen, 1948, p. 426.
Mellita quinquiesperforata tenuis (Clark). Cooke, 1959, p. 46.
Mellita quinquiesperforata (Leske). Salsman and Tolbert, 1965, pp. 152–155, (*M. tenuis* off Panama City, Florida).
Mellita quinquiesperforata (Leske), Serafy, 1979, p. 68, fig. 29 (in part, discussed and illustrated specimen is *M. tenuis*).
Mellita tenuis (Clark). Harold and Telford, 1990, pp. 999–1002, figs. 8–10.
Mellita tenuis (Clark). Pomory et al., 1995, pp. 778–783.
Mellita tenuis (Clark). Lawrence and Tan, 2001, pp. 50–54, fig. 1.
Mellita tenuis (Clark). Swigart and Lawrence, 2008, pp. 46–56.
Mellita tenuis (Clark). Ziegler et al., 2016, fig. 7o.

Occurrence.—*Mellita tenuis* occurs along the eastern Gulf of Mexico from southern Florida to western Louisiana, and has not yet been documented in the fossil record of the region. However, we include it here because there remains the possibility, based on the results of Coppard et al. (2013) that *M. tenuis* will become a senior subjective synonym of *M. isometra*, in which case the occurrence data give herein for the latter species will become relevant to a treatment of *M. tenuis.*

Discussion.—This species, though widespread along the modern Gulf Coast of Florida, is not currently documented in the fossil record of the region. We include it here because of potential for *M. tenuis* to occur in additional exposures of middle to upper Pleistocene deposits, especially along the Gulf Coast of Florida. In addition, the points discussed here will become even more relevant if taxonomic changes are warranted that place *M. isometra* as a junior subjective synonym of *M. tenuis* (see discussion for *M. isometra* above).

Cooke (1959:46) stated that "H. L. Clark (1940:436) characterizes this variety as having a test more or less pentagonal, rather stout, the apex tending toward the anterior; periproct little or moderately elongated". Although this is directly from the key to *Mellita* provided by Clark (1940), it is incorrectly attributed by Cooke (1959). Cooke (1959) confused Clark's (1940) characters for *M. quinquiesperforata* with those of *M. quinquiesperforata* var. *tenuis*. The key for *M. tenuis* provided by Clark (1940) is actually: "Test nearly or quite circular, light and thin, the apex tending to be posterior; periproct very long and narrow." Clark's selection of the name *tenuis* for this variant references the thin test.

Clark (1940) discussed the significant size *M. tenuis* can attain, especially in southwestern Florida, with specimens 129 mm TL from Sanibel Island. However, Clark (1940:444), in recognizing variation among some larger specimens that are noticeably thicker than typical for the species, "prove that *tenuis* is not a well defined species yet", implying that differentiation of the species was evolutionarily nascent. However, he went on to explain that the typical examples are so conspicuously different from ordinary *M. quinquiesperforata* (by which he meant the Floridian east coast form) that they represent a different species char-

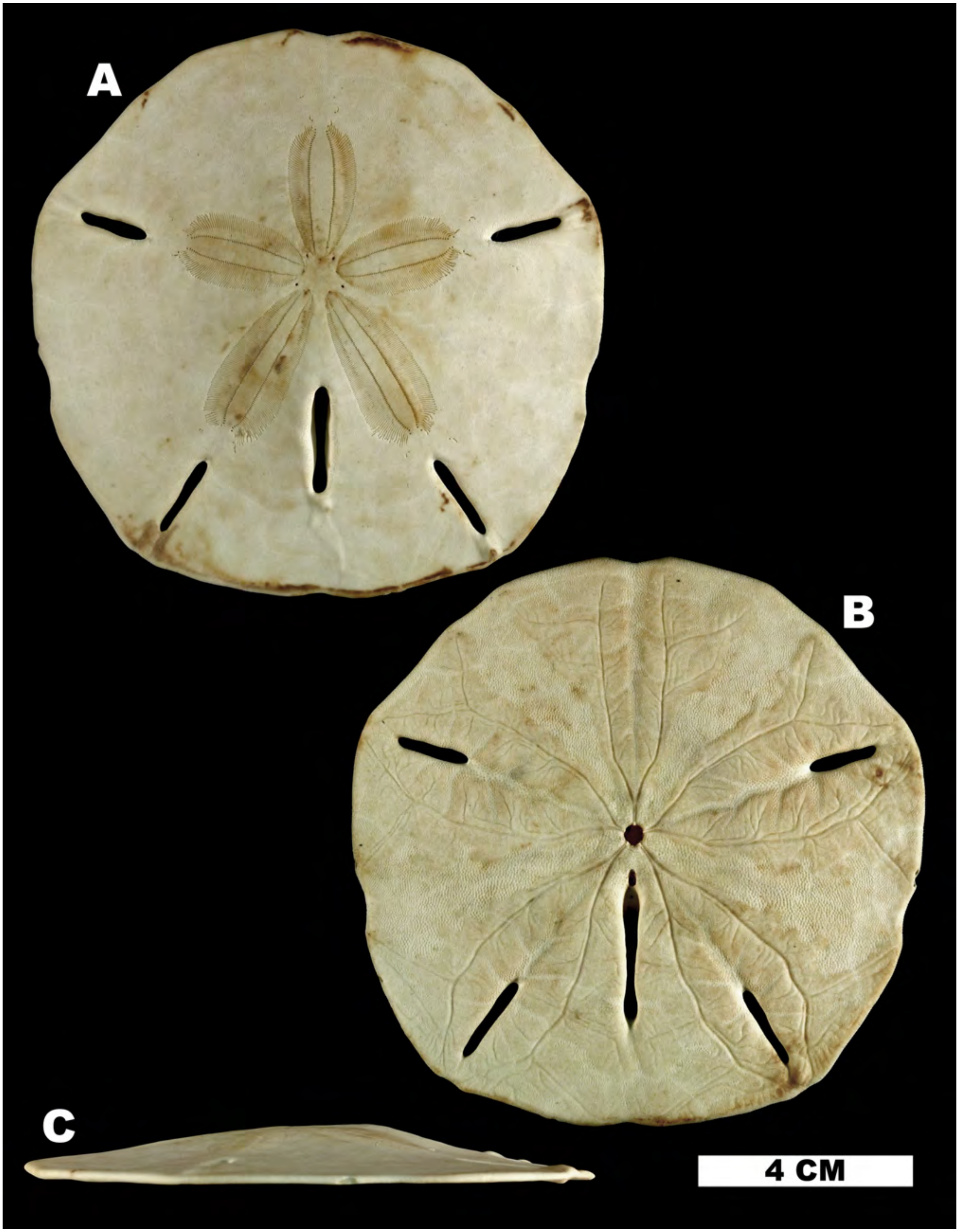


Figure 95. *Mellita tenuis* (UF-IZ 18906b), modern specimen for comparison (off Rattlesnake Key, Tampa Bay, Manatee County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

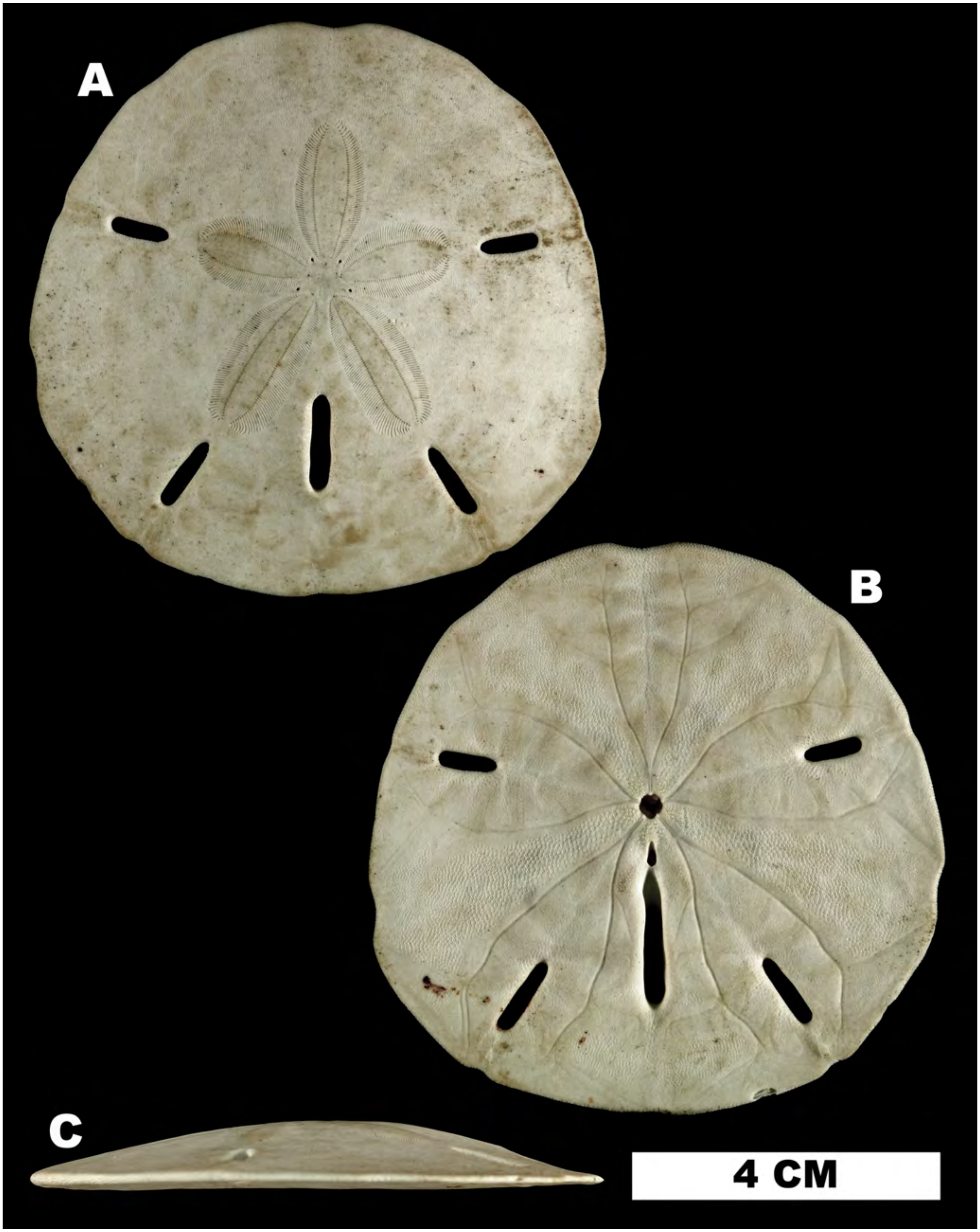


Figure 96. *Mellita tenuis* (UF-IZ 18906a), modern specimen for comparison (off Rattlesnake Key, Tampa Bay, Manatee County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

acteristic of the west coast of Florida.

Harold and Telford (1990) agreed with Clark (1940) in clarifying diagnostic traits of this form, and raised it to full species. In their key to Recent *Mellita*, they distinguish *M. tenuis* by its circular test that has its highest point at or posterior to the apical system, in a broad aboral plateau. They expanded the range of the species from Clark (1940) westward to western Louisiana. However, they indicated that some confusion may occur when identifying specimens of *M. tenuis* that possess an anterior ambital notch or small open lunule in ambulacrum III. This feature is sporadic throughout the range of the species, but more prevalent in a population near the western edge of its range at Dulac Beach, Terrebonne Parish, Louisiana, at which all specimens have an anterior notch varying from a shallow indentation to a nearly closed lunule.

Large specimens of *M. tenuis*, especially near Tampa Bay, tend to develop an angular outline (Fig. 95) more reminiscent of *M. isometra* than the typical, more nearly rounded shape of *M. tenuis* (Fig. 96). However, the point of greatest TH being at or just posterior to the apical system seems to be a more reliable trait in differentiating *M. tenuis* from *M. isometra*, in which the point of greatest TH is always distinctly anterior to the apical system.

Family **ABERTELLIDAE** Durham, 1955
Genus ***ABERTELLA*** Durham, 1953
ABERTELLA DENGLERI Osborn and Ciampaglio, 2010
Figures 97–101, 106

Abertella aberti (Conrad). McKinney, 1985, fig. 3. (in part, figured specimen is *A. dengleri*).

Abertella dengleri Osborn and Ciampaglio, 2010, pp. 207–217, text figs. 1–7, tables 1, 2.

Abertella dengleri (Osborn and Ciampaglio). Kroh et al., 2013, pp. 375, 377.

Occurrence.—*Abertella dengleri* has not been documented outside of the upper Miocene, lower portion of the Peace River Formation, within the bed of the Peace River, upriver from Zolfo Springs, Hardee County, Florida.

Discussion.—Specimens of *A. dengleri* occur in a dense accumulation of largely fragmented specimens in a horizon of sandy, siliclastic dolostone less than 20 cm in thickness, within the upper Miocene Peace River Formation. The locality occurs in the bed of the Peace River above Zolfo Springs, Hardee County, Florida (FM localities HR001, HR005, HR013).

The horizon in which *A. dengleri* occurs contains a profusion of *Abertella* fragments. Juvenile specimens are frequently found intact, while complete adult specimens are rare. Tests are often corroded, abraded, and chipped as they weather free from the very resistant, silica-rich matrix in the riverbed, typically obscuring surface details. Specimens of *Abertella* from this region of Florida were referred to in earlier literature as *A. aberti* (McKinney, 1985; Oyen, 2001). However, as discussed by Osborn and Ciampaglio (2010), these specimens are *A. dengleri.*

Abertella dengleri is readily distinguished from *A. aberti* Conrad, 1842, and all other described species of *Abertella*, by its greatly widened test (Kroh et al., 2013). Osborn and Ciampaglio (2010:tables 1–2; fig. 2) calculated that for ten specimens of *A. dengleri* and 21 specimens of *A. aberti* from the Scientists Cliffs of Maryland, the average TW:TL of *A. dengleri* was 1.37, whereas for *A. aberti* it is 1.03. Additional traits used to distinguish *A. dengleri* from *A. aberti* include its narrower posterior notch (not to be confused with the ambulacra notches of certain *Mellita* species), the tendency for petal III to be 88–91% of the length of the either of the anterior paired ambulacra (petal III is typically the same length as petal II and IV in *A. aberti*), and that petal I and V are 10% longer than the other petals in *A. aberti*.

In resurrecting *A. floridana* (Cooke, 1942), which has a test that is wider than that of *A. aberti*, we note that it fails to attain the strongly alate, laterally exaggerated morphology seen in *A. dengleri*. See the discussion of *A. floridana* below for additional taxonomic characters.

An abundance of *A. dengleri* tests is now available in the FM-IP collections that enable study of the ontogeny of the species. Typical adult specimens are shown in Figures 97–98. A juvenile specimen, UF 289213 (Fig. 99), is 17 mm TL, 18 mm TW. UF 289217 (Fig. 100) is a small slab with two juvenile specimens, one 5 mm TL, 5 mm TW, and the other 13.6 mm TL, 14.3 mm TW. As the juveniles are nearly circular (Fig. 101), ongoing study of these specimens, and more in the collections, can bring insights into the ontogeny of this strongly alate species. Greatly widened, alate forms occur within other genera of sand dollars, so it would appear that under certain circumstances, extreme widening is advantageous enough to occur convergently (Osborn et al., 2013; Mooi et al., 2016; Mooi et al., 2017).

ABERTELLA FLORIDANA (Cooke, 1942)
Figs. 102–107, 113

Scutella floridana Cooke, 1942, p. 19, pl. 4, figs. 9, 10.

Abertella aberti (Conrad). Cooke, 1959, pp. 44, 45, (in part, Cooke considered *A. floridana* a subjective junior synonym of *A. aberti*).

Emended Diagnosis.—An *Abertella* very similar to *A. aberti* in attaining large sizes (in excess of 120 mm TL); relatively narrow, gracile oral interambulacral plate columns; slightly tapered petaloids less blunt than in most other species; anal notch sharp and deep, depth generally greater than in either *A. dengleri* or *A. aberti*; test alate, width approximately 112% TL, relatively wider than in *A. aberti*, but much narrower than *A. dengleri*.

Occurrence.—Sopchoppy Limestone Member of the lower-middle Miocene Torreya Formation, Sopchoppy River, 5 km northwest of Sopchoppy, Wakulla County, Florida (type locality). Specimens we attribute to *A.* cf. *floridana* from the Chipola Formation, from the bed of the Apalachicola River (FM locality CA067), Calhoun County, are also likely this species.

Discussion.—Cooke (1942) described *A. floridana* from an incomplete holotype (USNM 498980) collected from the Sopchoppy Limestone along the banks of the Sopchoppy River, 3 miles west of Sopchoppy, Wakulla County. He stated that the petals of *A. floridana* appear to be blunter at the ends than those of *A. aberti*, its posterior notch is narrower, its periproct nearer the margin, and its plates more firmly joined together, with less conspicuous sutures (though see below).

Cooke (1959) subsequently considered his *A. floridana* to be a subjective junior synonym of *A. aberti*. He stated that the specimens from Florida have a narrower posterior notch than many of those from Maryland, but he believed the shape of the notch in specimens from both states to be variable. He noted that the madreporic plate in the apical system of the specimens from Florida is more distinctly raised than those from Maryland, but attributed this to corrosion of the Maryland specimens.

The holotype of *A. floridana* is not complete, as it is missing portions of both left and right margins. Therefore, Cooke (1942) was unable to make observations of the general outline of the species for direct comparison with *A. aberti*. However, after examining additional, complete specimens of *A. floridana* from the type locality (Figs. 102–105), it is evident that a clear distinction between *A. floridana* and *A. aberti* exists, warranting the resurrection of *A. floridana* and its removal from synonymy with *A. aberti*.

Abertella floridana can be distinguished from *A. dengleri*, which has a much wider test, or with the much smaller *A. carlsoni* n. sp., in which even the largest specimens have a narrower test relative to TL of the largest specimens of other species (Fig. 101). *Abertella floridana* is most similar to *A. aberti.*

Additional specimens from the type locality of *A. floridana* affirm some of the features Cooke (1942) used to differentiate *A. floridana* from *A. aberti*. The posterior notch of *A. floridana* is noticeably deeper and narrower (Fig. 106), giving the lobes a sharper, more prominent aspect. In addition, the periproct of *A. floridana* is nearer the margin: the posterior edge of the periproct of *A. aberti* is on average 4.5% TL from the ambitus within the anal notch, whereas in *A. floridana* the posterior edge of the periproct is on average 2.6% TL from the ambitus within the anal notch. Cooke (1942) attributed this to the deeper anal notch in *A. floridana*, which results in the posterior ambitus being closer to the periproct. However, this does not necessarily follow, as notch depth and periproct position are likely phylogenetically independent. Position of the periproct is, at least in part, determined by the plates between which it is located, and is therefore more likely influenced by sizes and shapes of the

Figure 97. *Abertella dengleri* (UF 116702), Peace River Formation (FM locality HR005). A. aboral view, B. oral view, C. lateral view.

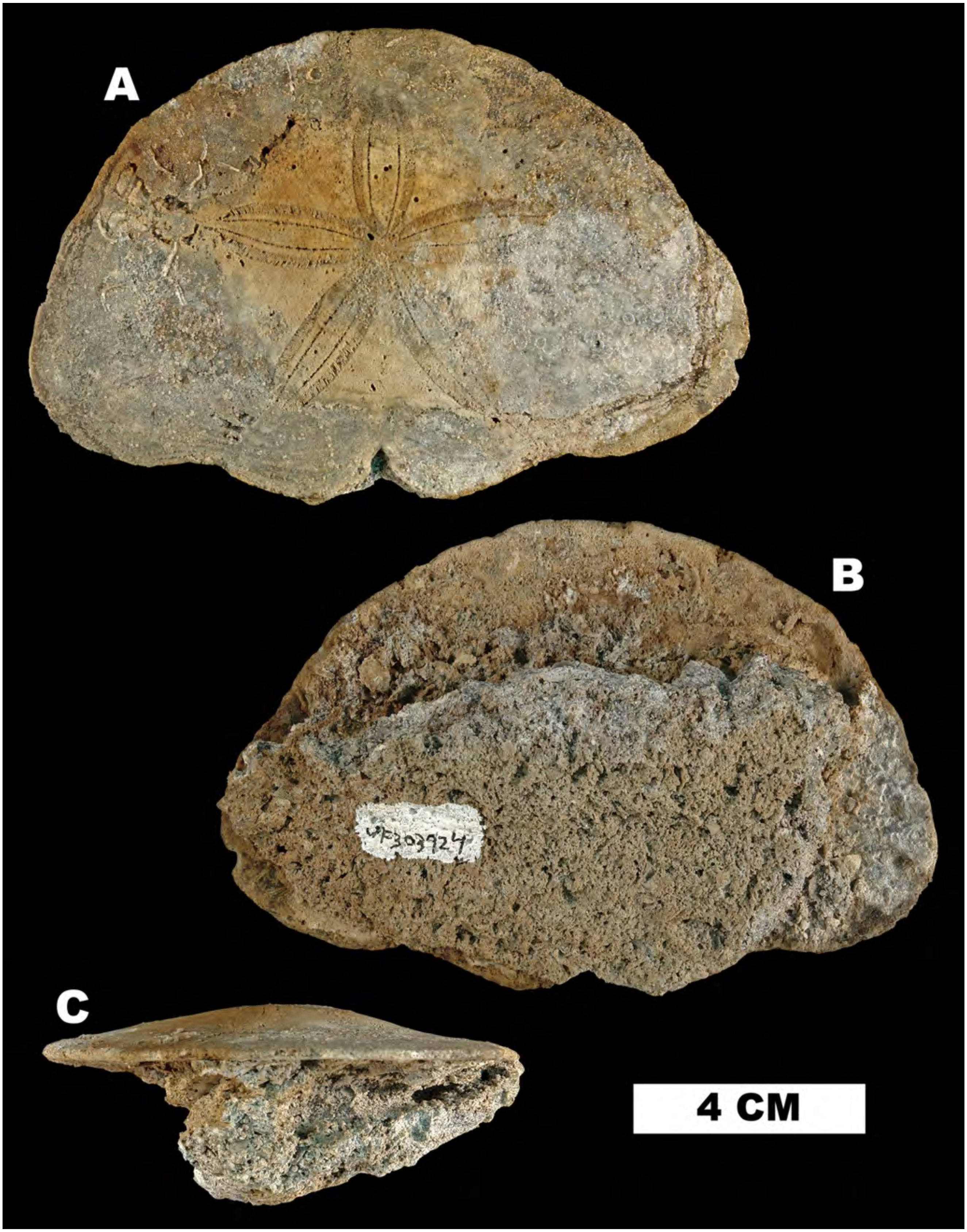


Figure 98. *Abertella dengleri* (UF 303924), Peace River Formation (FM locality HR013). A. aboral view, B. oral view, C. lateral view.

plates in the posterior interambulacrum than by the depth of the notch alone.

Cooke (1942) also asserted that the petals of *A. floridana* appear to be blunter at the ends than those of *A. aberti*. Our additional material of *A. floridana* (Figs. 102–105) show that the petals of this species are more tapered distally, whereas they are abruptly terminated and indeed "blunter" in *A. aberti*. Finally, Cooke (1942) stated that the plates of *A. floridana* are more firmly joined together and have less conspicuous sutures. However, Cooke (1942) was likely referencing an artifact of preservation most prevalent at the type locality of *A. aberti* (Drum Cliff, St. Marys County, Maryland), in which specimens are frequently broken or distorted along suture lines, and not a diagnostic morphological feature of the organisms themselves.

Cooke (1959) stated that the madreporic

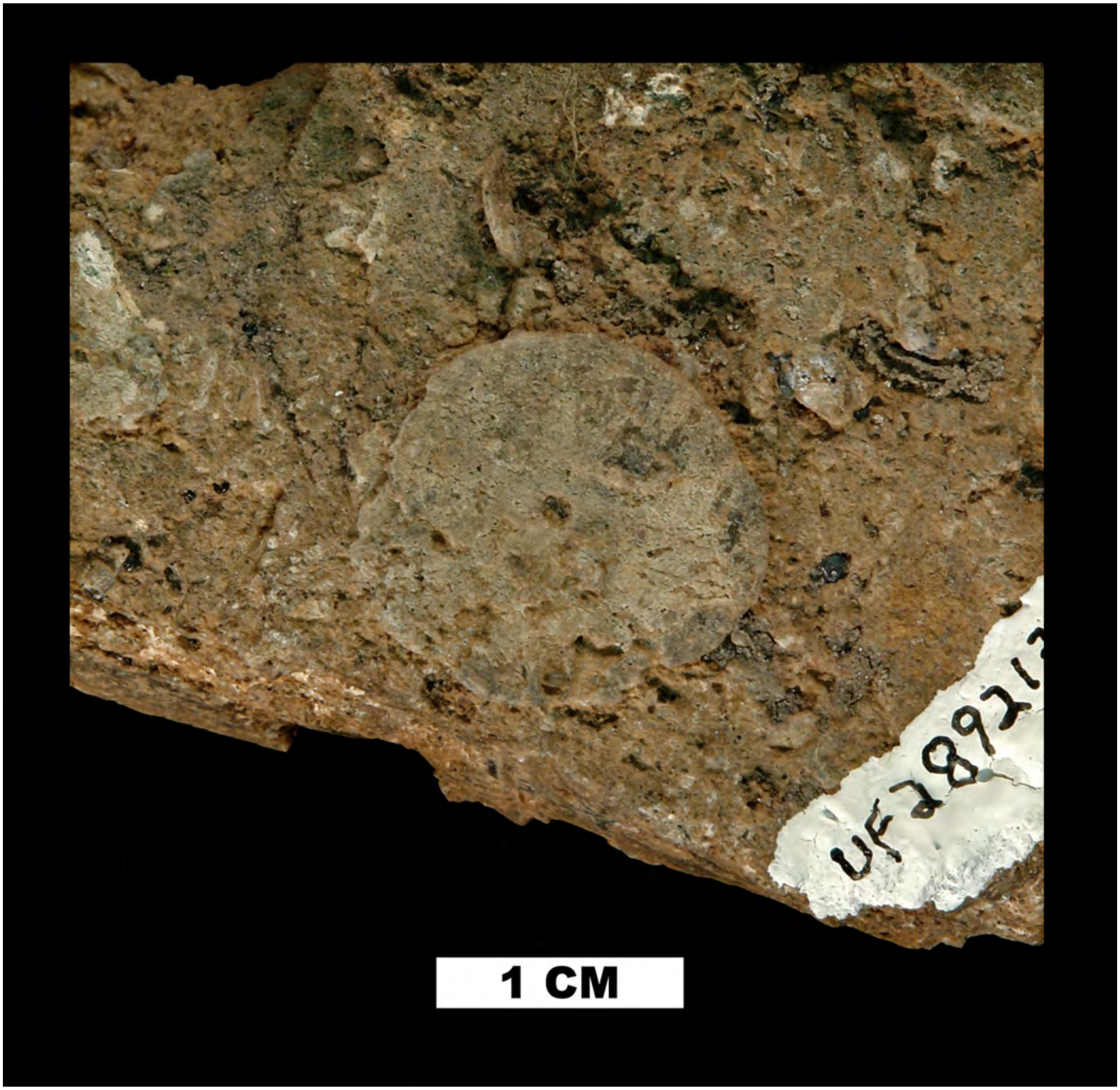


Figure 99. *Abertella dengleri* juvenile (UF 289213), Peace River Formation (FM locality HR013).

plate of specimens from Florida is more distinctly raised than those from Maryland. He attributed this to corrosion of the Maryland specimens, undoubtedly in reference to the very corroded nature of the specimens from the type locality. However, specimens from the Scientists Cliffs, Maryland are usually not corroded, and are typically well preserved. In these specimens, the madreporic plate is plainly visible but is not distinctly raised. In contrast, specimens of *A. floridana* from the type locality have a very distinct madreporic plate that is often, though not always, raised slightly above the surrounding test surface. However, this trait is variable, inconsistent in other scutelline taxa as well, and cannot be considered diagnostic for *A. floridana*.

As mentioned, Cooke (1942, 1959) did not

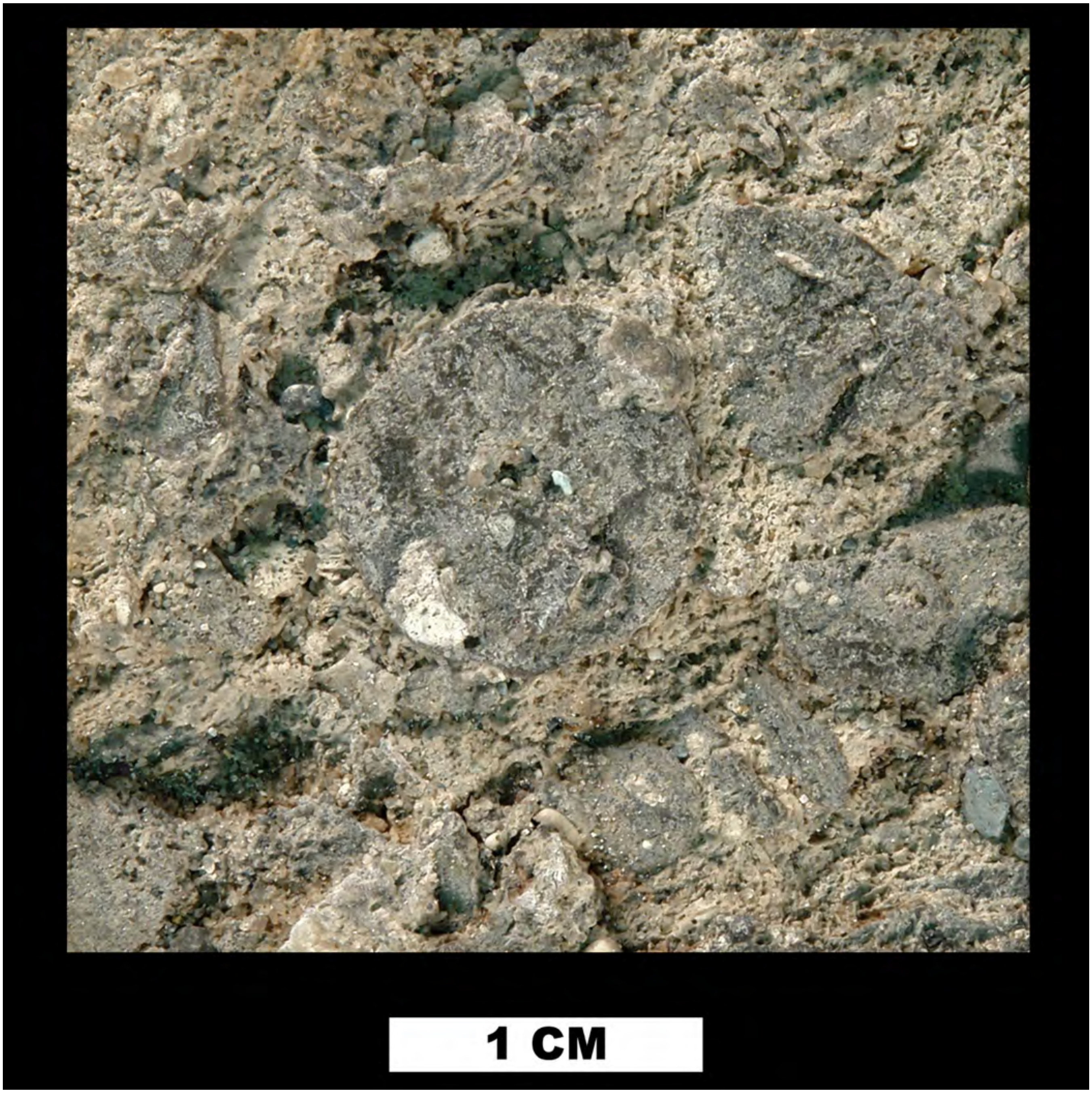


Figure 100. *Abertella dengleri* juvenile (UF 289217), Peace River Formation (FM locality HR013).

have access to complete specimens of *A. floridana*, so he was unable to make complete measurements for the species, notably for width. *A. floridana* is differentiated from *A. aberti* by its wider test (Fig. 101) which is on average 112% TL. Osborn and Ciampaglio (2010:215:table 2) measured 21 specimens of *A. aberti* from the Choptank Formation of Maryland, indicating a width on average 103% TL. Osborn and Ciampaglio (2010:215:table 1) demonstrated that in ten measured specimens of *A. dengleri*, the TW averaged 137% TL. Data obtained for the present study supports these findings (Fig. 101), showing that in terms of TW, *A. floridana* is consistently wider than *A. aberti*, but narrower than *A. dengleri*. In addition, the point of greatest width in *A. floridana* is more posterior than in *A. aberti*, giving it a more alate morphology. *Abertella floridana* is also distinguished from *A. aberti* by its narrower, more gracile, interambulacra on the oral surface (Fig. 107).

We concur with Cooke (1942) and consider *A. floridana* a separate species distinguished from *A. aberti* by its proportionately wider test, deeper anal notch, more marginal periproct, and narrower (more gracile) oral interambulacra. *Abertella floridana* is distinguished from *A. dengleri* by the much wider test of *A. dengleri* and is readily distinguished from *A. carlsoni* n. sp., by its much larger, proportionately wider test, and deeper anal notch.

Although *A. floridana* is not definitively

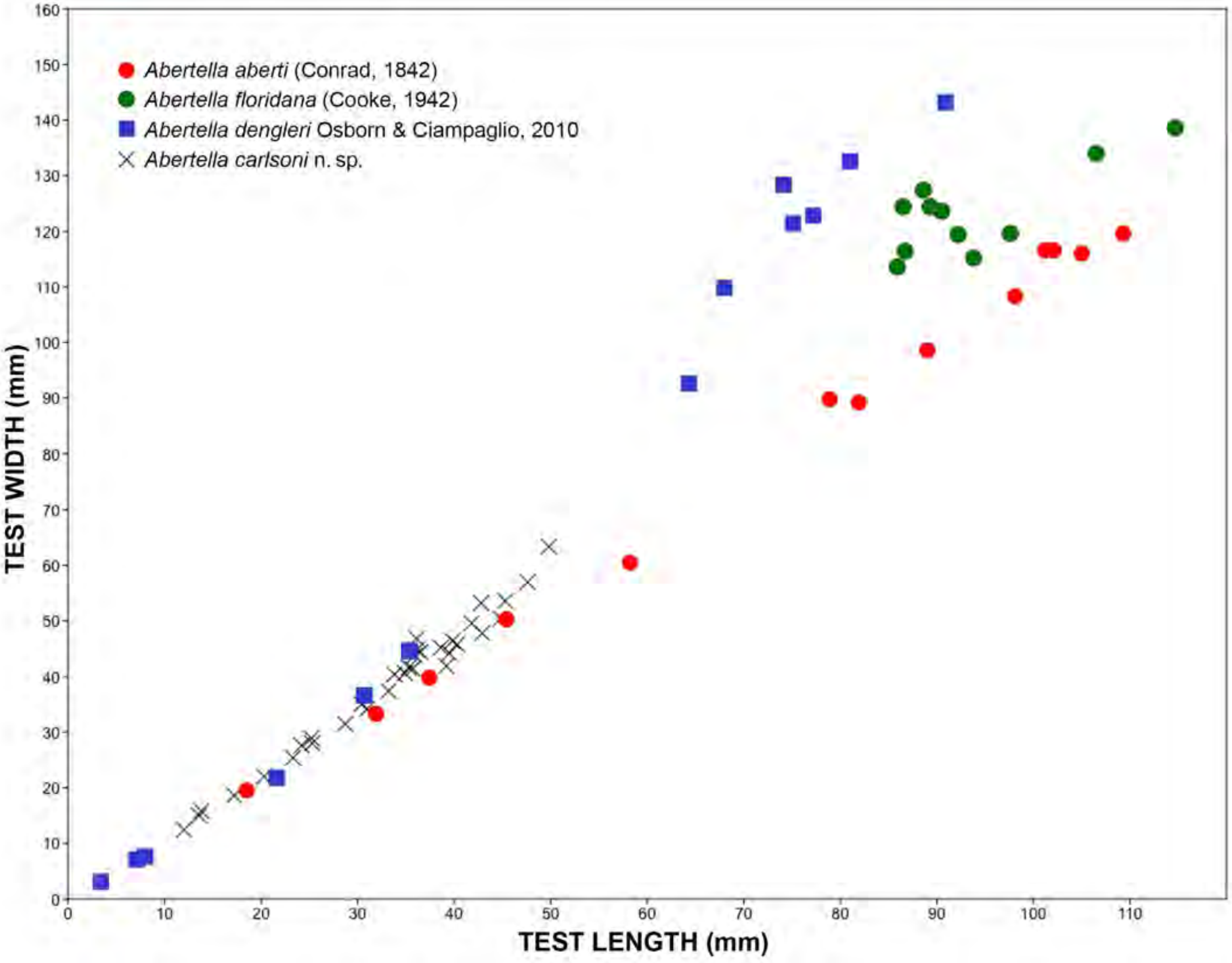


Figure 101. *Abertella,* graph of TW versus TL for specimens of *Abertella aberti, A. floridana, A. dengleri,* and *A. carlsoni* n. sp.

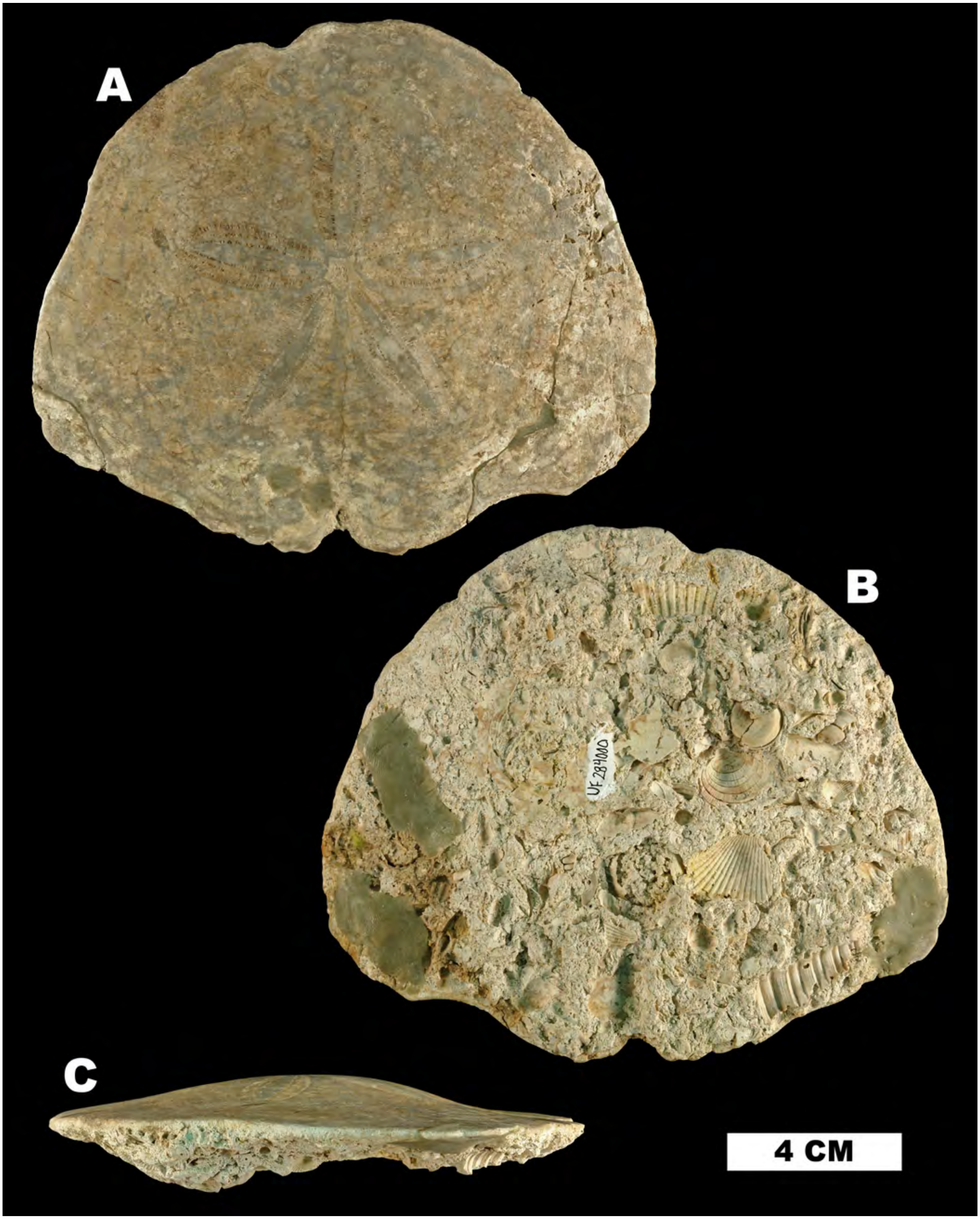


Figure 102. *Abertella floridana* (UF 284000), Sopchoppy Limestone (FM locality WA013). A. aboral view, B. oral view, C. lateral view.

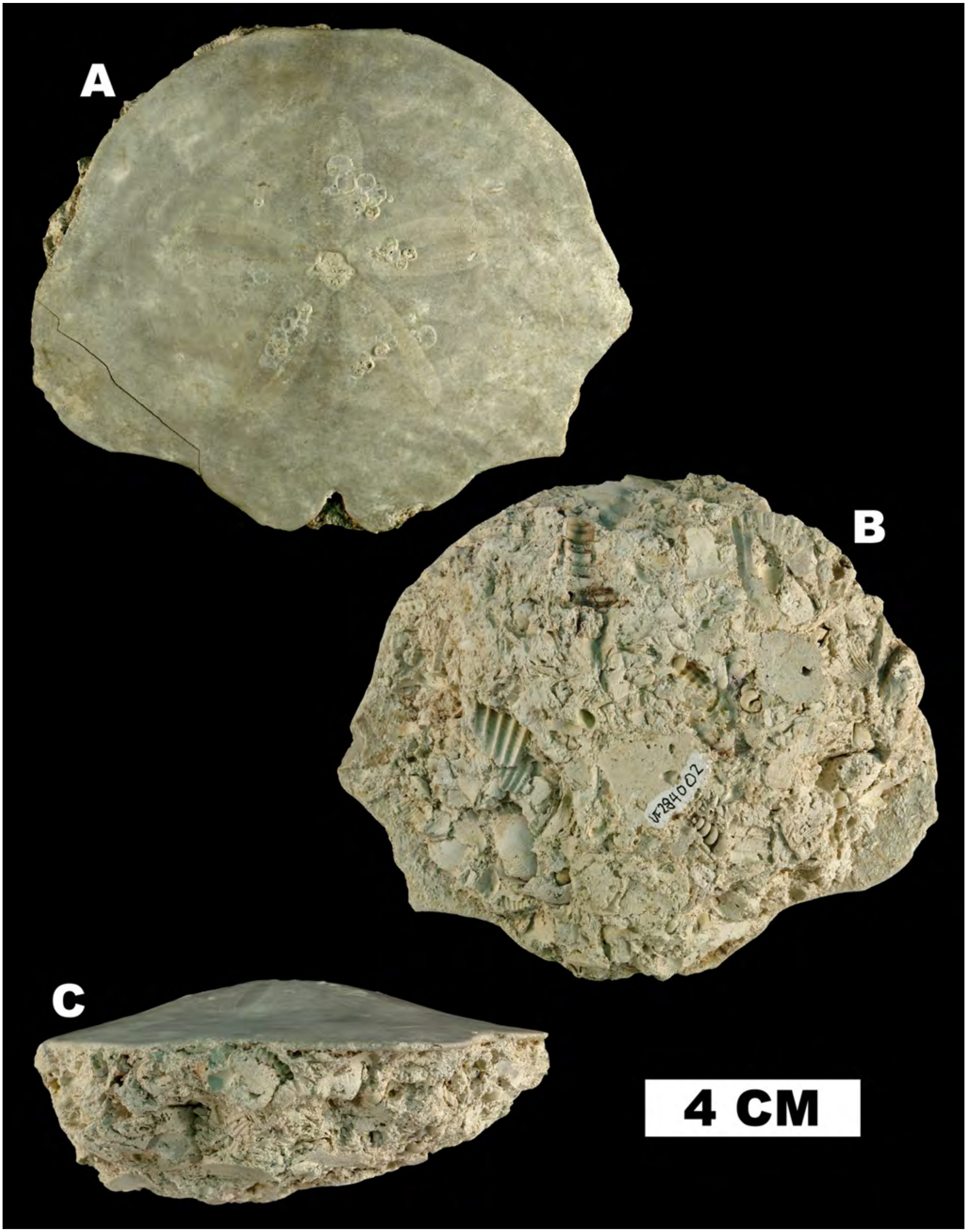


Figure 103. *Abertella floridana* (UF 284002), Sopchoppy Limestone (FM locality WA013). A. aboral view, B. oral view, C. lateral view.

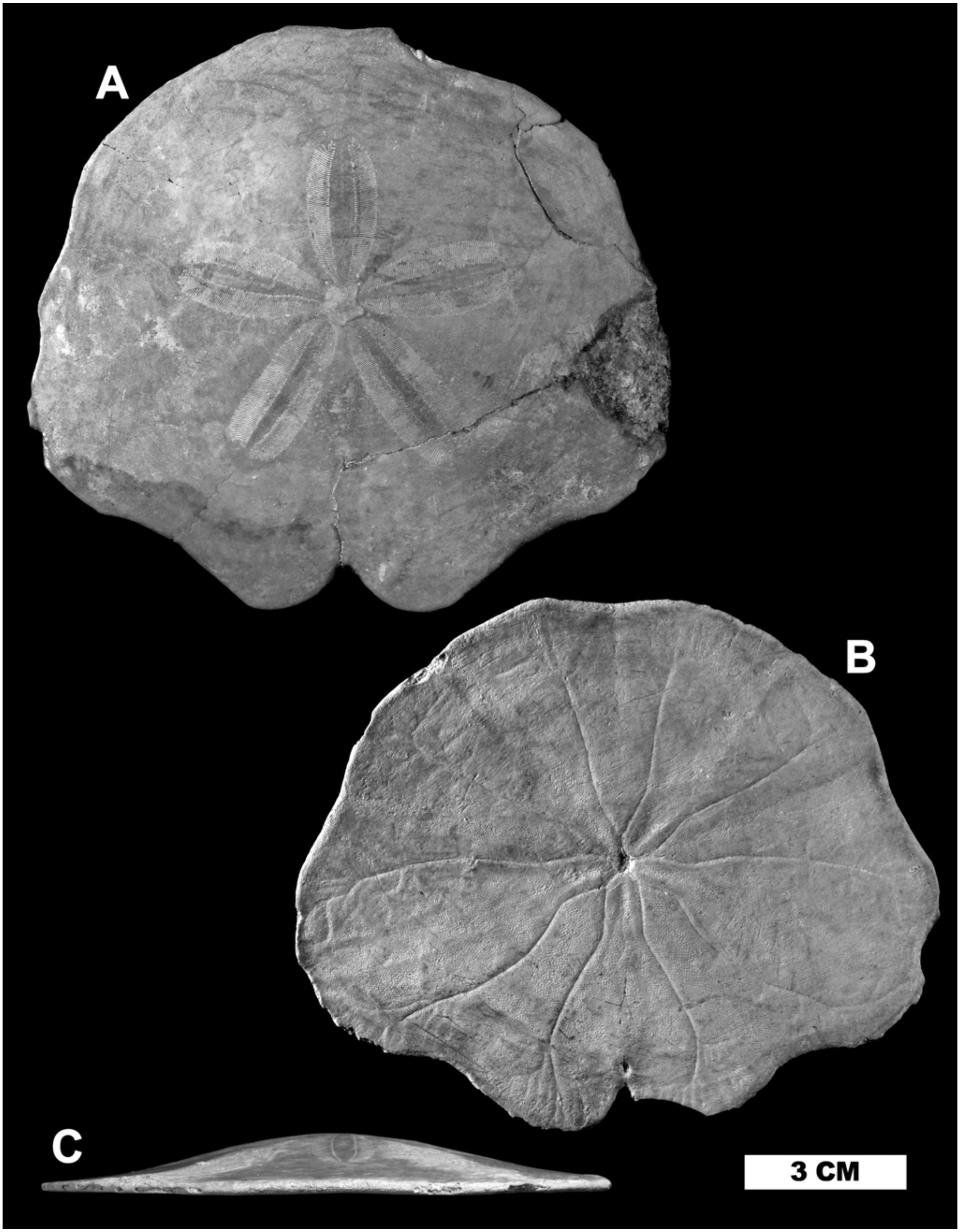


Figure 104. *Abertella floridana*, A, aboral view of CASG 91744. B, oral view with strong side lighting to show food grooves on CASG 91743. C, lateral view. Sopchoppy Limestone (FM locality WA013).

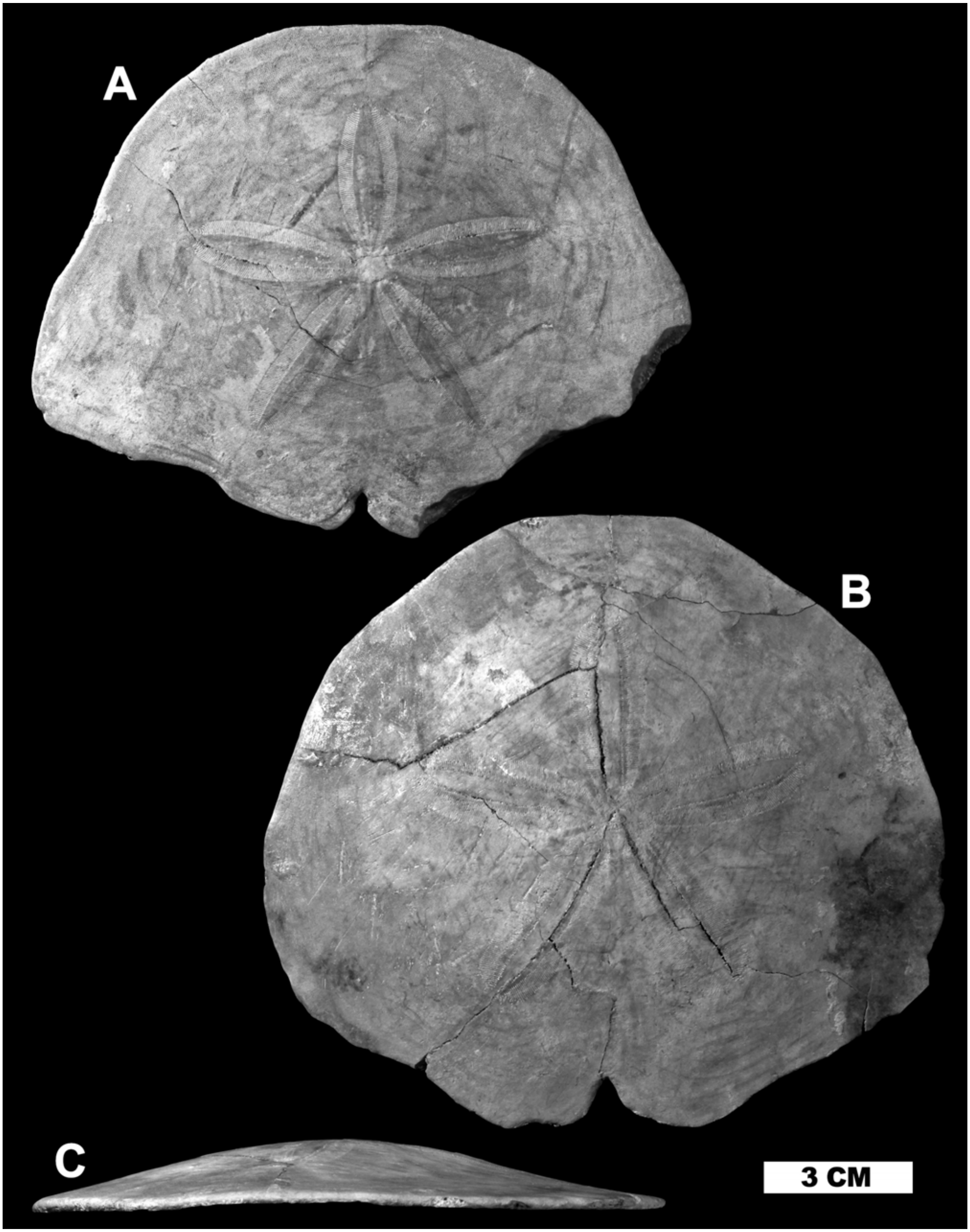


Figure 105. *Abertella floridana*, A, aboral view of strongly alate specimen, CASG 91742. B, aboral view of largest measured specimen, CASG 91745. C, view of left side of specimen in B. Sopchoppy Limestone (FM locality WA013).

documented outside of the type area, additional incomplete tests of *Abertella* within the Miocene of Florida are likely attributable to this species. Specimens of *Abertella* from the Chipola Formation collected in the Apalachicola River, Calhoun County (FM locality CA067), best represented in the FM-IP collections by UF 116696 (Fig. 108), are smaller than any known specimens of *A. floridana*. These specimens do not have completely preserved ambulacra, are wider than *A. aberti*, but not nearly as wide as *A. dengleri*. The Apalachicola River specimens have a much shallower anal notch, but this could be attributed to their smaller size. Comparable specimens approaching the size of the Apalachicola River fossils from the type locality of *A. floridana* are not available, and the former specimens are best referred to as *A.* cf. *floridana*.

Specimens in the FM-IP collections from the lower Miocene portion of the Arcadia Formation of Polk County, Florida, best represented in the collections by UF 5363 (Fig. 109), have poorly preserved surface detail, but they are more similar to *A. floridana* in that they are wider than typical *A. aberti*. Identification of this material is complicated by the fact that although UF 104448 does not have a well-preserved anal notch, UF 5363 has a much shallower anal notch than is typical of *A. floridana*. The notch of UF 5363 is more reminiscent

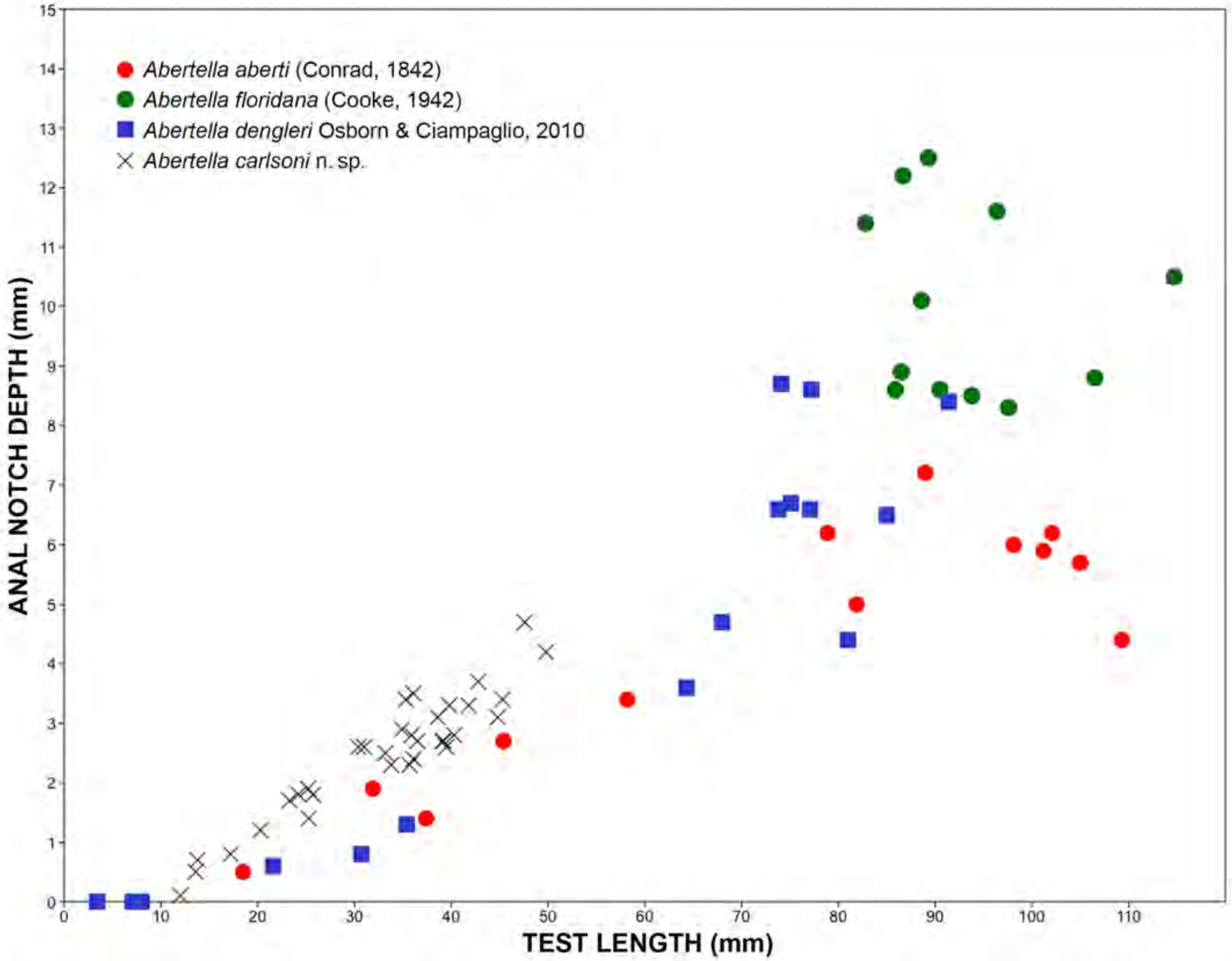


Figure 106. *Abertella,* graph of anal notch depth versus TL for specimens of *Abertella aberti*, *A. floridana*, *A. dengleri*, and *A. carlsoni* n. sp.

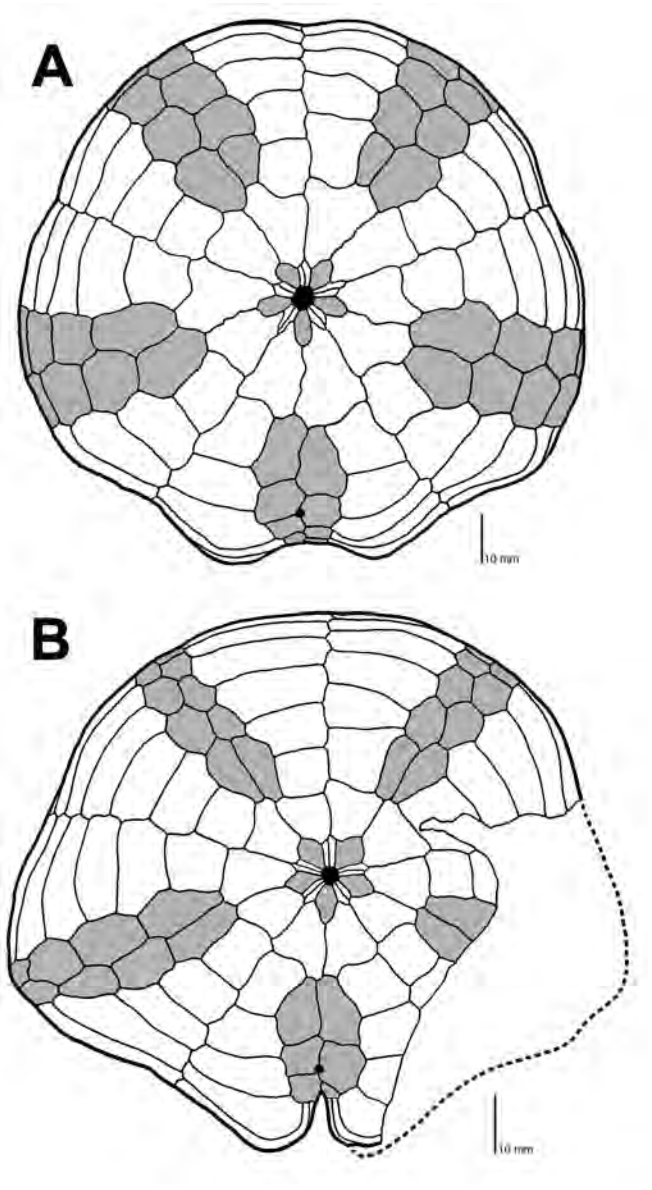


Figure 107. Comparison of oral plate architecture in A, *Abertella aberti* (CASG 91747) and B, *A. floridana* (CASG 91729). Anterior is towards top of page, peristome and periproct are in solid black, interambulacral plates are shaded. Outline of left side of test reconstructed with dotted line for *A. floridana*.

of *A. aberti* than either *A. floridana* or *A. dengleri*. However, this specimen is wider than typical for *A. aberti*, with its width 113% TL. These specimens are probably best referred to as *A.* cf. *floridana*, pending collection of additional, more complete, non-moldic material.

Additional specimens discussed herein as *Abertella* sp. could belong to *A. floridana*. As additional, more complete material is discovered, the characters and morphometrics presented herein can be used to rule out *A. floridana* during specific assignment of the material.

Specimens in the FM-IP collections unequivocally attributable to *A. floridana* include UF 284000 (the largest documented specimen of this species at 121.5 mm TL and 142.6 mm TW), as well as UF 284001–284003, all collected at the type locality of the species from the Sopchoppy Limestone Member of the Torreya Formation, Sopchoppy River, Wakulla County, Florida (FM locality WA013). Additional material of *A. floridana* are also in the collections of the California Academy of Sciences (CASG 91729–46), and were used for assessment of morphometrics presented herein.

ABERTELLA CARLSONI n. sp.

(Figs. 101, 106, 110–119)

Diagnosis.—*Abertella* of small size, less than 50 mm TL; gonopores already present in specimens approximately 25 mm TL; anal notch deeper, more strongly developed than in comparably sized specimens of other species.

Description.—Test small, largest specimen less than 50 mm TL. Test not widened or alate, TW averaging 104.25% TL (112.5% in holotype). Aboral surface slightly domed, oral surface flat, nearly planar and without significant sculpting or radial depressions. Highest point of test just anterior to apical system. Strongly defined posterior notch, well developed even in small specimens (Figs. 106, 110–111), notch widening near ambitus. Marginal indentations well developed where perradial suture meets ambitus in posterior paired ambulacra, much shallower in anterior paired ambulacra.

Apical system monobasal, star-shaped, approximately half of TL from ocular III to anterior edge of test, numerous hydropores scattered over madreporic plate. Four gonopores, one in each of paired interambulacra and located at suture between madreporic plate and first adapical plates of interambulacral column. Gonopores first appear in small specimens, still not formed in specimens less than 20 mm TL.

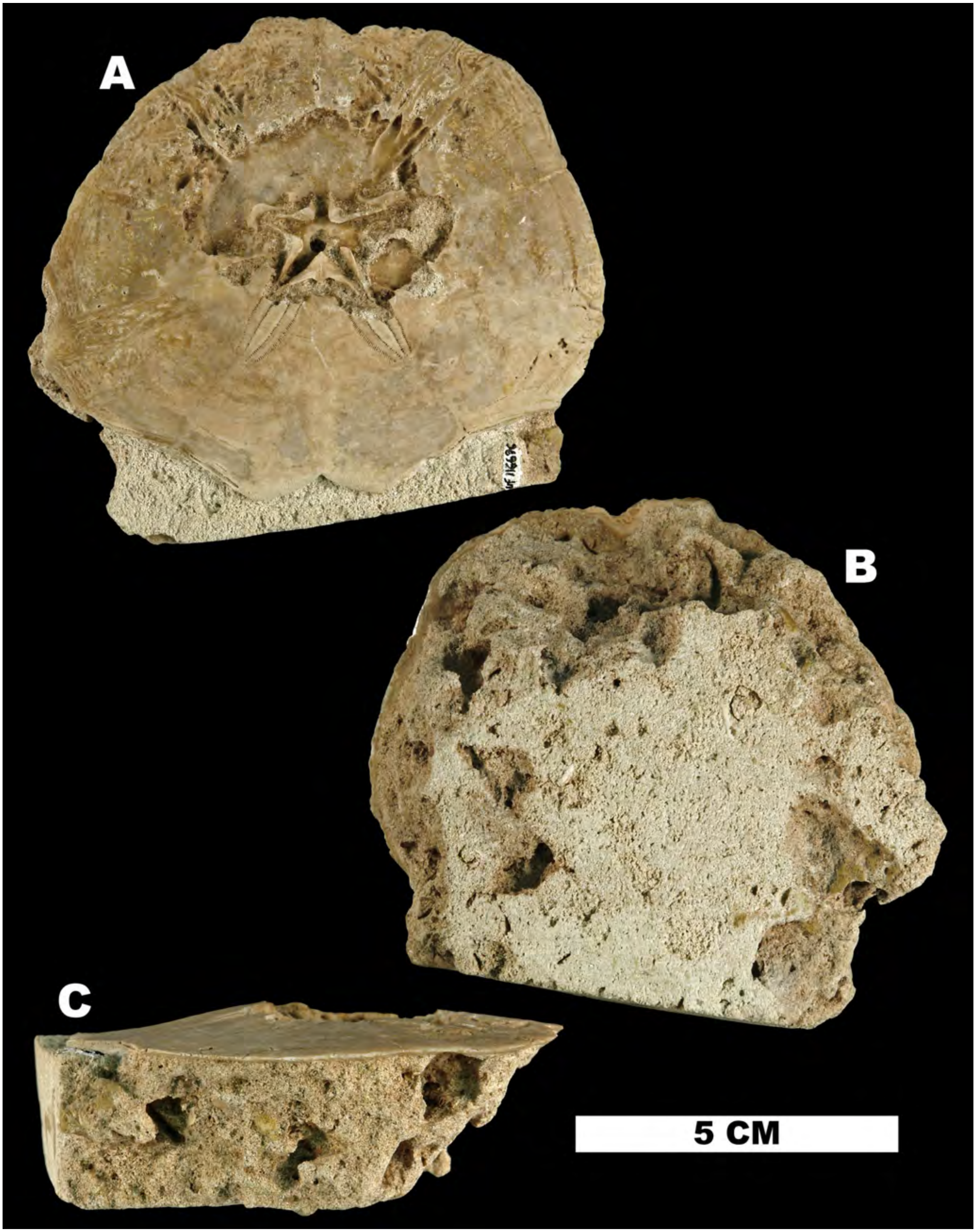


Figure 108. *Abertella* aff. *floridana* (UF 116696), Chipola Formation (FM locality CA067). A. aboral view, B. oral view, C. right lateral view.

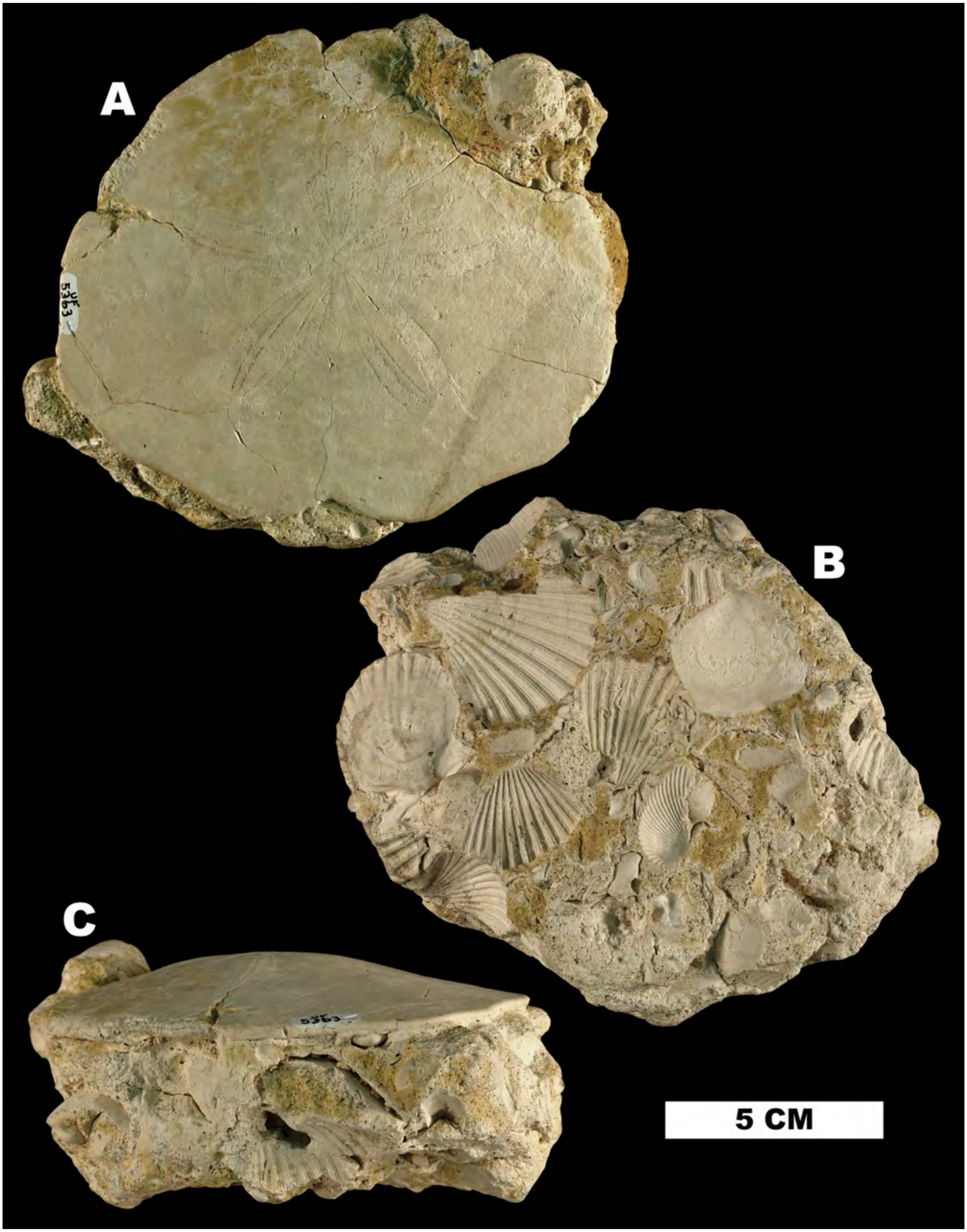


Figure 109. *Abertella* aff. *floridana* (UF 5363), upper Arcadia Formation (FM locality PO002). A. aboral view, B. oral view, C. lateral view.

Ambulacra petaloid adapically, lanceolate but not distally attenuated or pointed. Posterior paired petals (I and V) longest, but only slightly so, averaging about 28% TL, anterior paired petals 25% TL, anterior petal just less than 25% TL. Petals almost closed distally, with two or three trailing tube feet pores at distal end of each column of respiratory tube feet pores, petal III slightly more open than others, distal width of interporiferous zone in petal III averaging 3.9 % TL, that of paired petals averaging 2.3% TL. Respiratory tube foot pore pairs strongly conjugated, inner pore slightly elongate or almost circular, outer pore extremely elongated, comprising about two thirds length of pore pair. Four or five occluded plates present at tips of petals. At ambitus, ambulacra greatly widened, forming strip-like ambital plates, curving strongly adapically to form test wall along each side of posterior notch. Ambulacra all in agreement with Lovén's Rule (sensu David et al. 1995). Ambulacral basicoronal plates all similar, narrow and straight with almost parallel radial sutures on each side (Figs. 112–113).

Interambulacra narrow and straight on oral surface, narrowing towards ambitus, but containing paired, zig-zag plates right up to madreporic plate. On oral surface, four postbasicoronal plates in each half-interambulacrum in interambulacrum 5, five or six in interambulacra 1 and 4, and four or five interambulacra 2 and 3 (Figs. 112–113). Widest point of each interambulacrum at first or second postbasicoronals, about one third of way to ambitus, narrowing only imperceptibly distally, but more strongly to about one third that width in the posterior interambulacrum. In each paired interambulacrum, first postbasicoronal slightly elongated, about two to three times as long as wide in paired interambulacra, about twice as long as wide in posterior interambulacrum. All interambulacral columns discontinuous, basicoronal separated from first postbasicoronals by adjacent ambulacral first postbasicoronals, very widely so in interambulacrum 5, but by far less than 1/4 length of a corresponding basicoronal in paired interambulacra (Figs. 112–113).

Peristome circular, relatively large for genus, about 5.8% TL in holotype, with distinct perradial process in each ambulacrum extending into peristome beyond slight bulge containing sphaeridium. Periproct relatively large for genus, about 4.5% TL in holotype, situated 91.7% TL from anterior edge of test in holotype, between second and third pairs of postbasicoronals.

Aboral tuberculation homogeneous, oral tuberculation nearly so, without discernible enlargement of tubercles in oral interambulacral regions. Tube foot pores generally not visible in food grooves due to preservation.

Food grooves well developed, restricted to oral surface, with primary bifurcation near adapical ends of ambulacral basicoronal plates. After this branch point, food grooves continuously diverging as they approach ambitus. Secondary branching faint or non-existent, likely due to preservation. No significant depressions along perradial sutures on oral surface, no evidence of pressure drainage channels.

Zoobank Nomenclatural Act.—8D18D178-E4BF-4872-9C60-FA319B5EE196.

Material.—The species is known from the holotype, UF 284011, and paratypes UF 284004–284010, UF 28401–284017, and CASG 91717-27, plus additional non-type material housed at both institutions.

Occurrence.—Type locality, lower Miocene Tampa Member of the Arcadia Formation, St. Joseph Sound, Pinellas County, Florida (FM locality PI025). It has not been documented outside of the type locality.

Discussion.—*Abertella carlsoni* n. sp. is both the earliest and smallest of the four species of North American *Abertella*. It has not been documented outside of the lower Miocene Tampa Member of the Arcadia Formation, where it occurs in material dredged during the deepening of the boating channel in St. Joseph Sound, west of Dunedin, in Pinellas County, Florida. At the type locality, this species is abundant, though seldom complete, and occurs in a horizon where *A. carlsoni* n. sp., is the dominant megafossil, and the only echinoderm present. The sand dollars are usually preserved so that only the aboral or oral surface is exposed, seldom with both surfaces showing.

The small size of individuals in this popula-

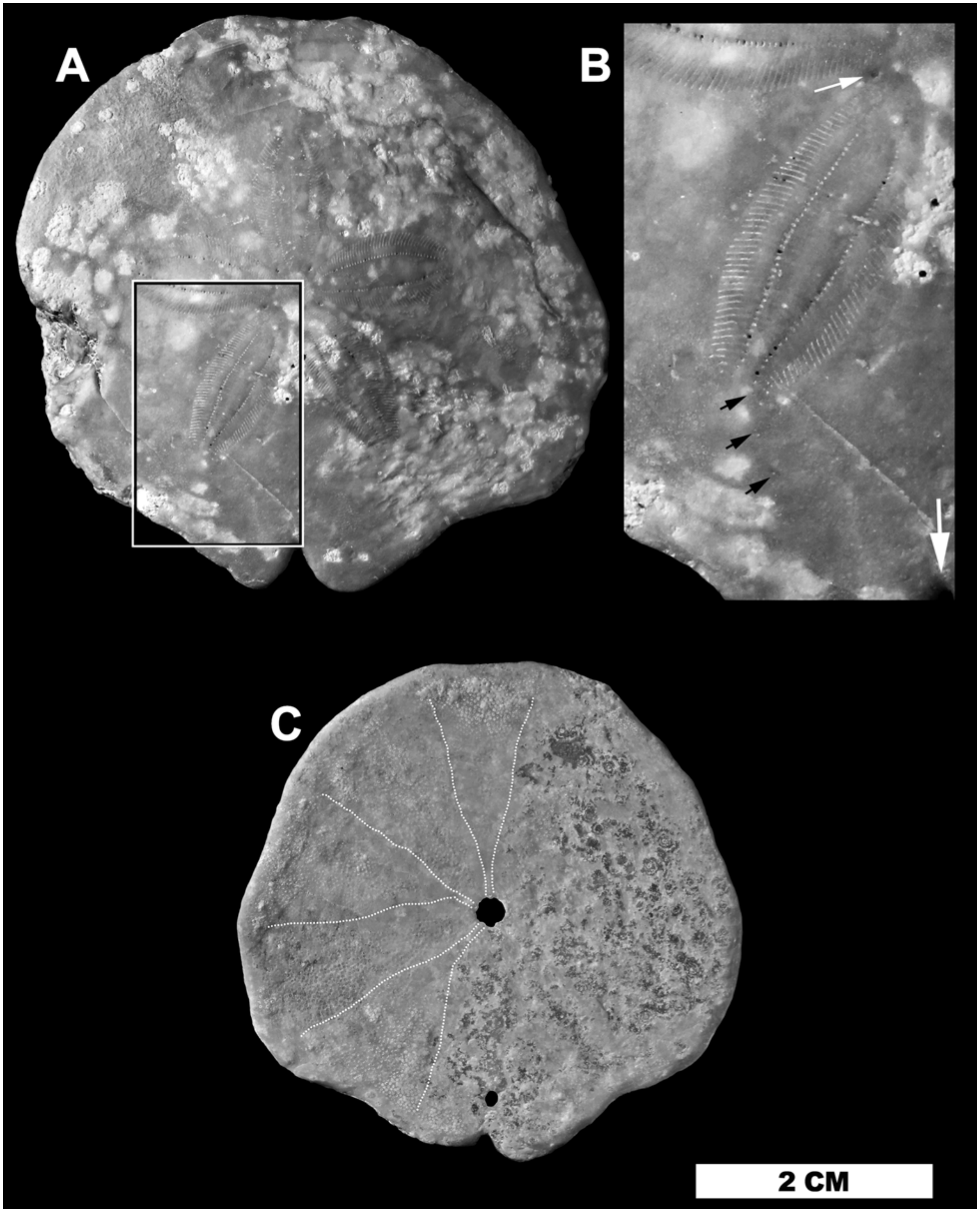


Figure 110. Details of morphology of *Abertella carlsoni* n. sp. A, aboral view of CASG 91726, boxed area shown in B. B, magnified view of boxed area in A showing entire petal in ambulacrum V, trailing tube feet (small black arrows), gonopore (small white arrow), and proximal end of anal notch (large white arrow). C, oral view of UF 284010 showing peristome and periproct (solid black), and path of main branches of food grooves in ambulacra I, II, and III (dotted white lines). Anterior towards top of page.

Figure 111. Photographs of the aboral surfaces of specimens of *Abertella carlsoni* n. sp. (UF 284013), *A. aberti* (USNM 438162) and second *A. aberti* (uncataloged RMAA04) at similar sizes. Anterior is towards the top of the page. Gonopores indicated by arrows.

tion of *Abertella* provides the impression that these are juveniles of a species that could attain a larger size. However, the present data indicate that this is not the case. Our data come from specimens ranging from 12.0 to 49.8 mm TL. Gonopores have not yet appeared in a specimen 17.2 mm TL, and are first detected in a specimen 23.3 mm TL. In contrast, in *A. aberti*, gonopores are first detected in a specimen 45.4 mm TL, but have not yet appeared in a specimen as large as 37.4 mm TL, about twice the size of a specimen of *A. carlsoni* n. sp. at time of gonopore appearance (Figs. 110–111). If gonopore appearance can be used as a marker for ontogenetic trajectory (though not necessarily for time of maturity, as gonadal development is unknown for fossils), then these data strongly support our assertion that *A. carlsoni* n. sp. likely reaches reproductive maturity at smaller sizes than its North American, if not all other, congeners.

In addition, even small specimens of *A. carlsoni* n. sp. illustrate characteristics of adults of other species. For example, the distinctive anal notch of *A. carlsoni* n. sp. is well developed at smaller sizes than in other species (Fig. 106), as is the degree of disjunction of the oral interambulacra.

The test of *A. carlsoni* n. sp. is easily distinguished from the proportionately wider tests of *A. floridana* and *A. dengleri*, whose width to length ratios at their largest sizes are much higher than those for the largest *A. carlsoni* n. sp. The onset of the increase in TW of species such as *A. dengleri* occurs at about the time that *A. carlsoni* n. sp. reaches its maximum size (Fig. 101). *Abertella carlsoni* n. sp. maintains similar, if not slightly

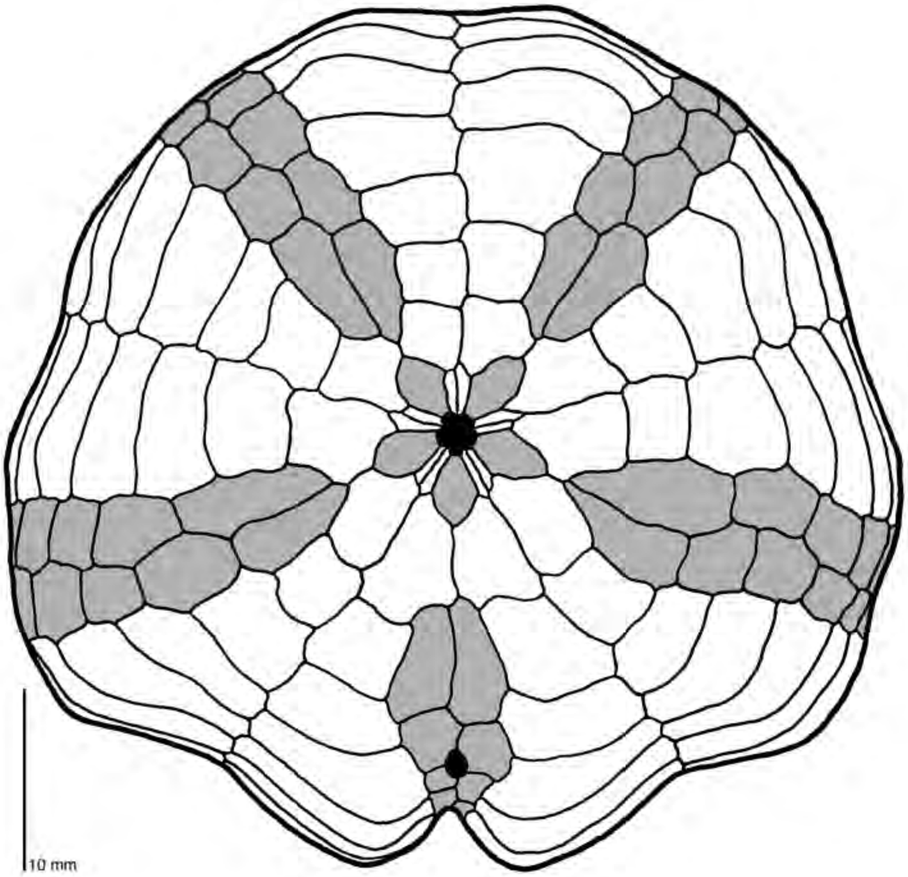


Figure 112. Oral plate architecture of the holotype of *A. carlsoni* n. sp. (UF 284011). Anterior is towards top of page, peristome and periproct are in solid black, interambulacral plates are shaded.

wider, test proportions to those of *A. aberti* (Fig. 101), but as noted above, is differentiated by the much larger maximum size of the latter, and the much lower degree of disjunction in the oral interambulacral columns (Fig. 113).

When compared to other species in the genus, it would appear that *A. carlsoni* n. sp. represents a paedomorphic form of *Abertella*. Some of the features that distinguish *A. carlsoni* n. sp. from its congeners, such as the degree of disjunction of the oral interambulacra, or the increase in the TW to TL ratio, begin to accentuate in the larger species at about the time that *A. carlsoni* seems to attain sexual maturity. Verification of these patterns will depend on the discovery of additional material not only of *A. carlsoni* n. sp., possibly from other localities, but of small specimens of abertellids such as *A. dengleri*, *A. aberti*, and *A. floridana* to further our knowledge of abertellid ontogenetic patterns.

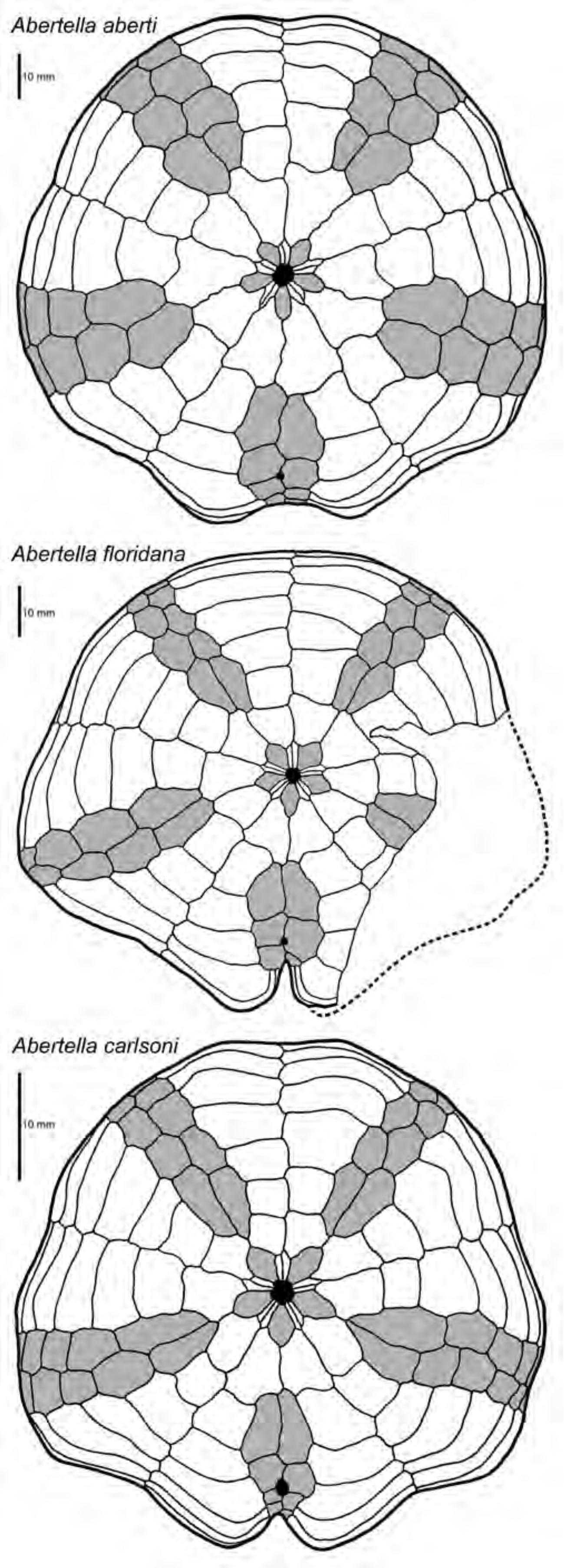
Etymology.—This species is named in honor of Robert Carlson of St. Petersburg, Florida, in recognition of his significant efforts in collecting and preparing impressive collections of specimens of this species. His efforts resulted in material that represents the most complete size range available for an original description of any known *Abertella* species**.**

ABERTELLA sp.

Figures 108–109

Occurrence.—Fragments of abertellid tests that are unidentifiable to species are represented in the FM-IP collections from eight Miocene units: the Arcadia (upper portion), Chipola, Coosawhatchie, Marks Head, Parachula, Statenville, Shoal River, and Torreya Formations (Figs. 1–2).

Discussion.—A review of the extensive



←

Figure 113. Comparison of oral plate architecture for *Abertella aberti* (CASG 91747), *A. floridana* (CASG 91729), and *A. carlsoni* (UF 284011). Anterior is towards top of page, peristome and periproct are in solid black, interambulacral plates are shaded. Outline of left side of test reconstructed with dotted line for *A. floridana*.

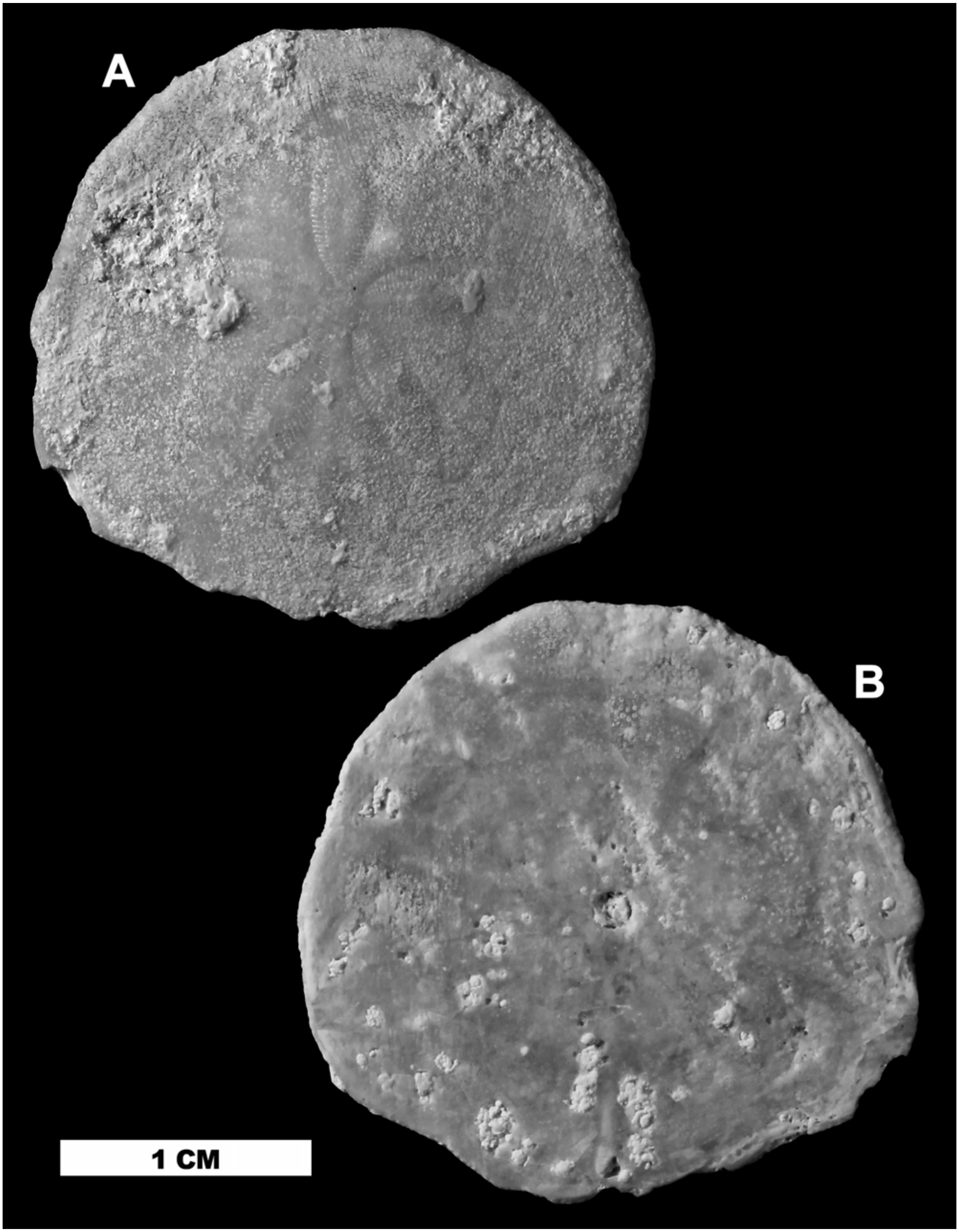


Figure 114. Aboral (left) and oral (right) views of young specimen of *Abertella carlsoni* n. sp. (UF 284006) the smallest specimen with gonopores, Tampa Member (FM locality PI025).

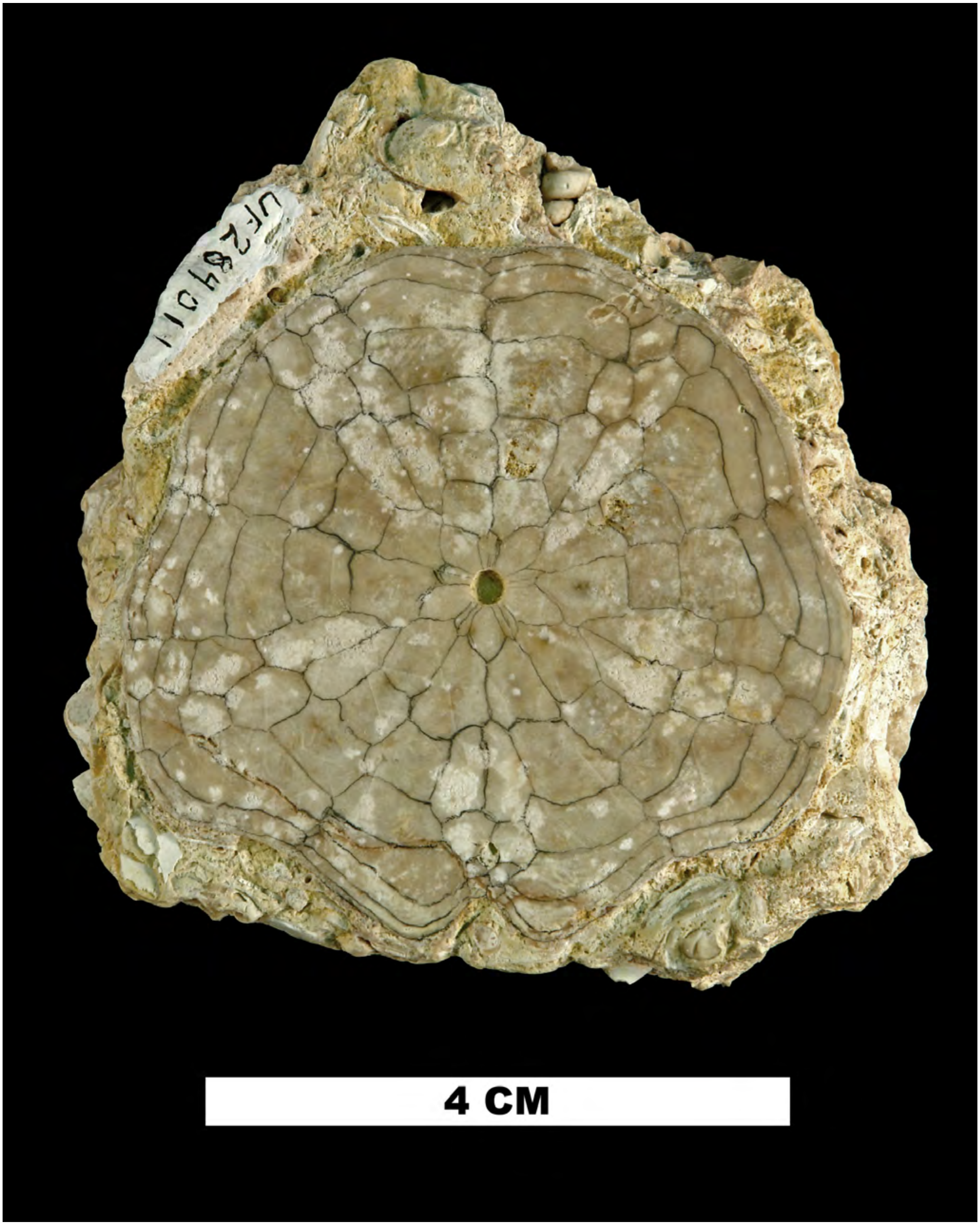


Figure 115. *Abertella carlsoni* n. sp., holotype (UF 284011), Tampa Member (FM locality PI025).

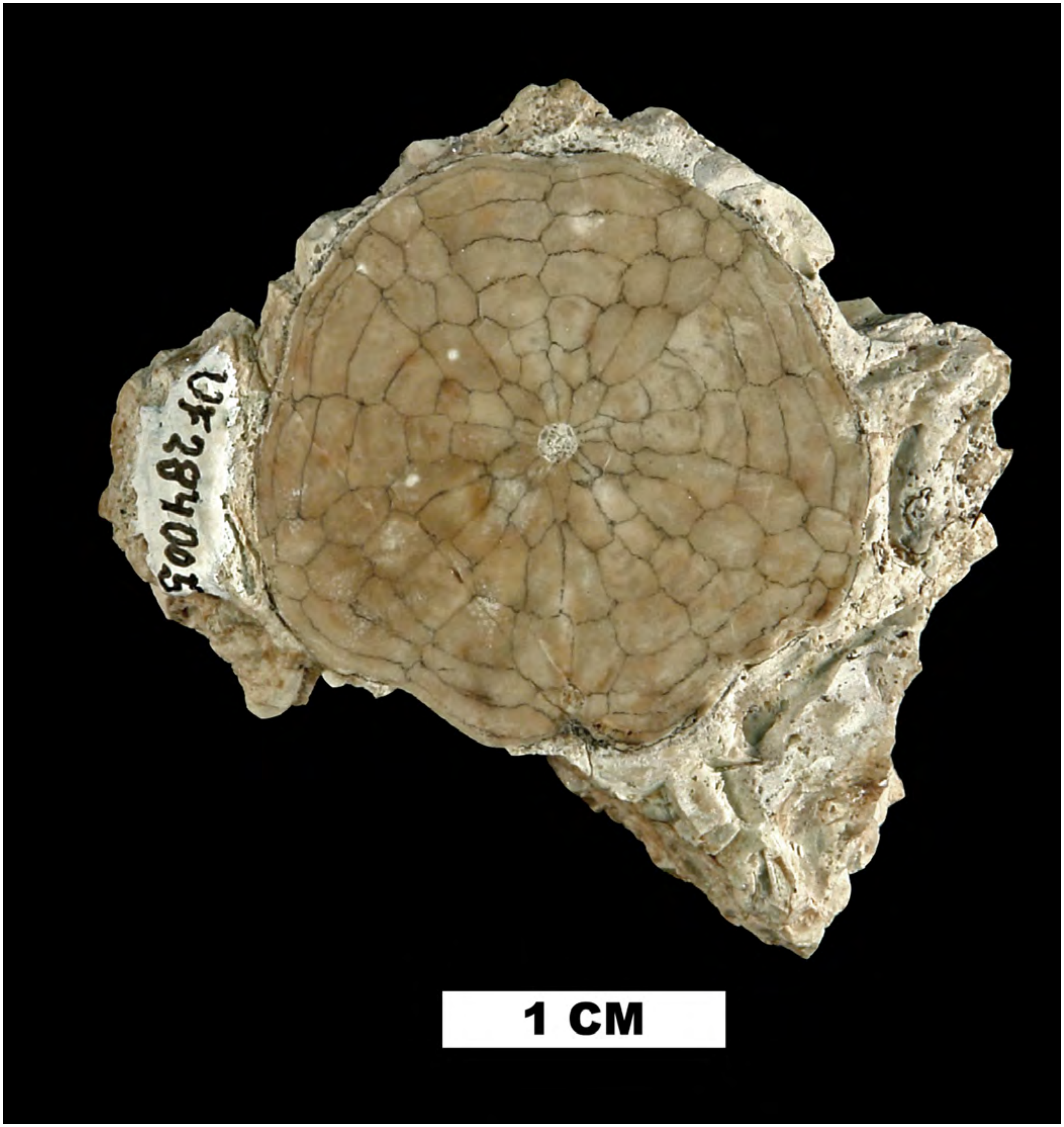


Figure 116. *Abertella carlsoni* n. sp., paratype (UF 284005), Tampa Member (FM locality PI025).

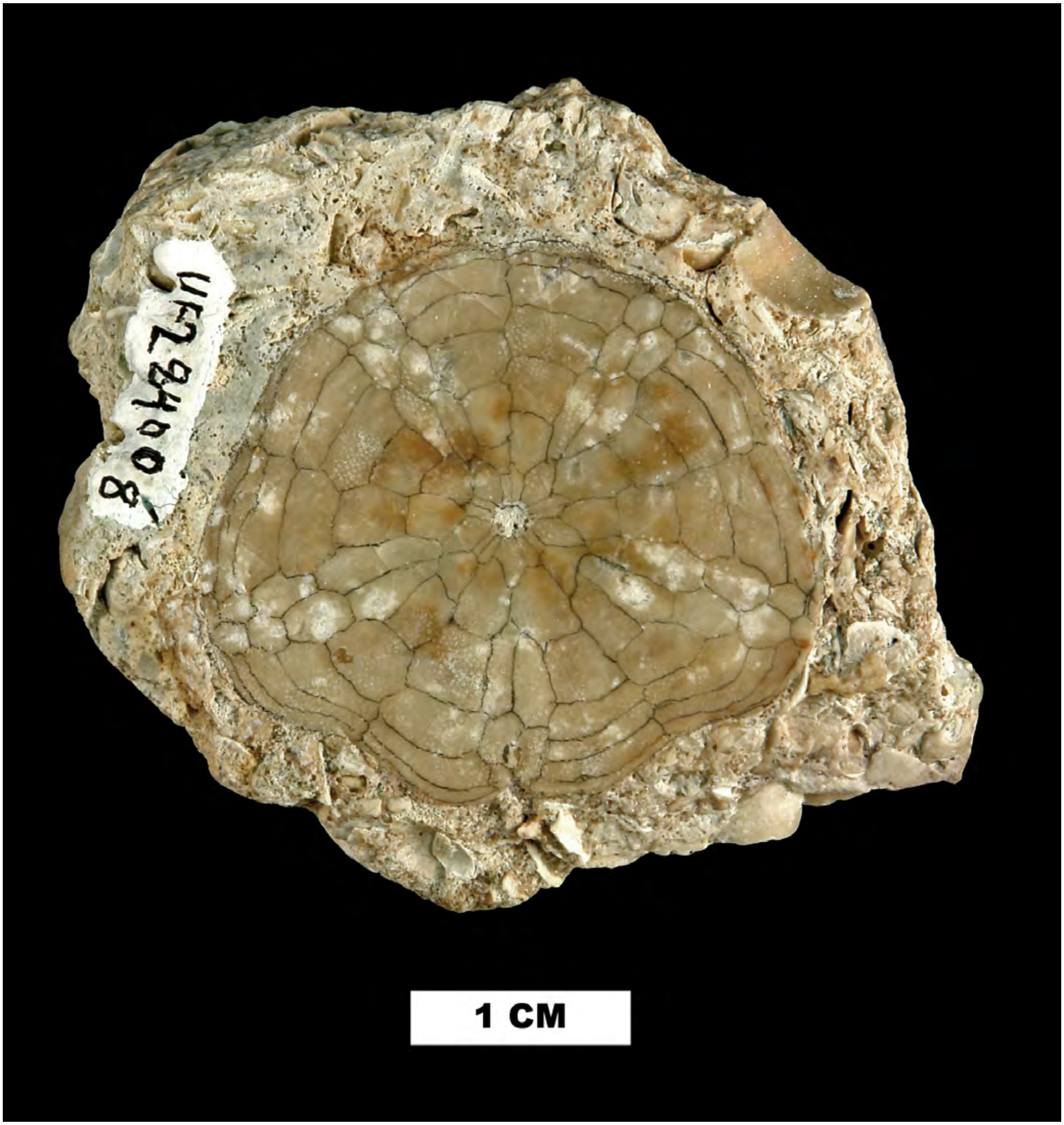


Figure 117. *Abertella carlsoni* n. sp., paratype (UF 284008), Tampa Member (FM locality PI025).

Figure 118. *Abertella carlsoni* n. sp., paratype (UF 284015), Tampa Member (FM locality PI025).

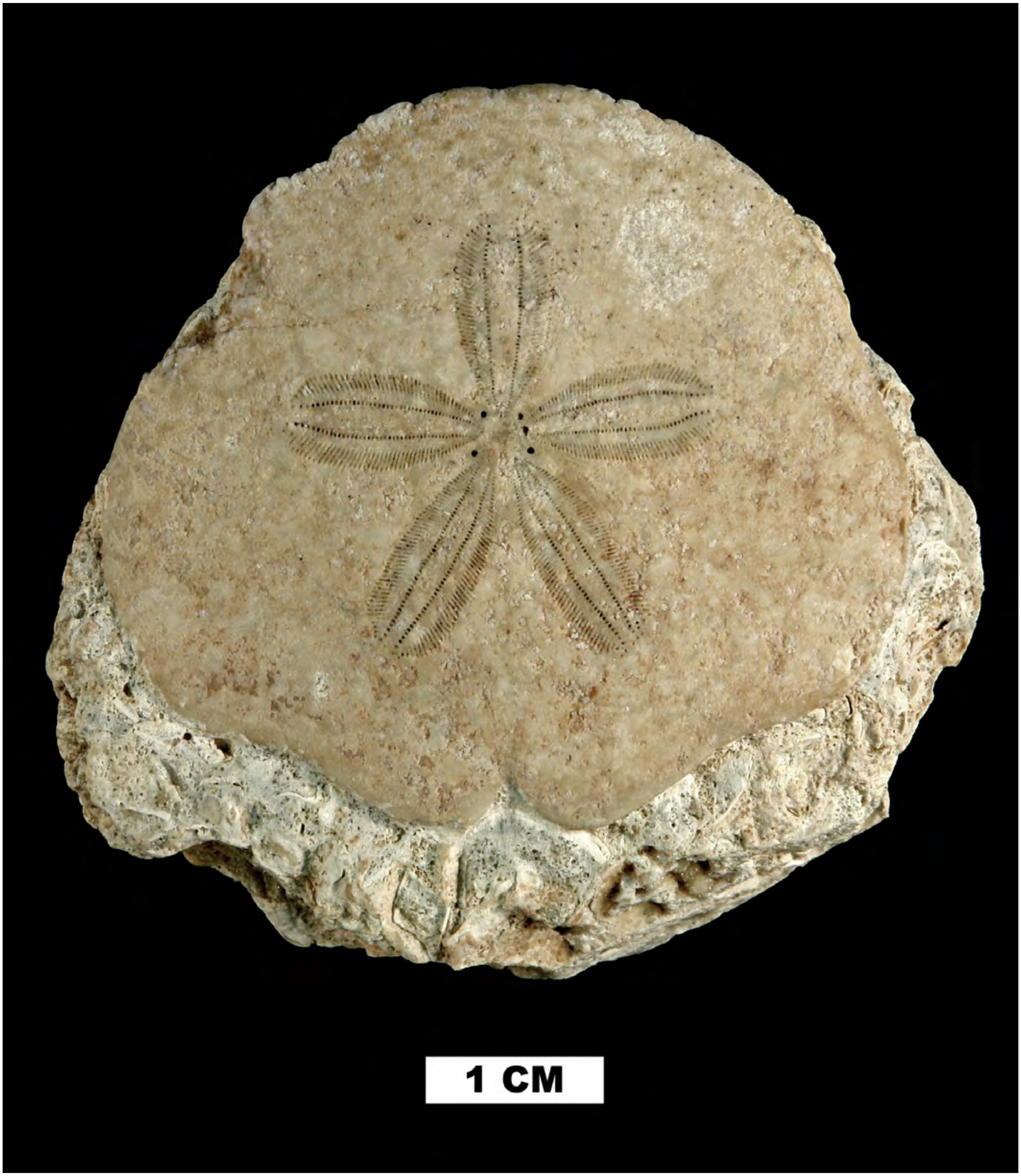


Figure 119. *Abertella carlsoni* n. sp., (UF 289210), Tampa Member (FM locality PI025).

FM-IP collections reveals that fragments of sand dollars attributable to the genus *Abertella* are likely the most widely represented echinoid fossils throughout the Florida Miocene. Specimens referable to the genus, but lacking material complete enough for specific determination, are represented in the collections from eight Miocene units: (Figs. 1–2). Historically, these fragments have been attributable to *A. aberti* (e.g., McKinney, 1985). However, with our recognition of *A. floridana* (middle Miocene Florida panhandle) as a distinct species, designation of *A. dengleri* for the elongate late Miocene specimens from Hardee County, and recognition of *A. carlsoni* n. sp. from the lower Miocene Tampa Member of the Arcadia Formation in Pinellas County, fragmentary material attributable to the genus can no longer be attributed to *A. aberti* by default. We are unaware of any fossils of *Abertella* from Florida that can be unequivocally attributed to *A. aberti*.

Two populations of *Abertella* with material insufficient to identify with confidence to species are discussed in the remarks for *A. floridana*. Specimens of *Abertella* from the Chipola Formation collected in the Apalachicola River (FM locality CA067), Calhoun County, (best represented by UF 116696; Fig. 108), are smaller than any known specimens of *A. floridana* and do not have completely preserved ambulacra. Specimen UF 116696 has maximum available measurements of 88.7 mm TW and 74.2 mm TL, although neither margin is entirely complete. These specimens are wider than *A. aberti*, yet not nearly as wide as *A. dengleri*. Additionally, the specimens display a much shallower anal notch than either *A. dengleri* or *A. floridana*; however, this could be attributed to their smaller size. Specimens of this size of *A. floridana* from the type locality are not available for comparison, thus these specimens are best referable to *Abertella* cf. *floridana*.

In addition, specimens in the FM-IP collections from the lower Miocene portion of the Arcadia Formation of Polk County Florida (best represented in the collections by UF 104448 and UF 5363) have poorly preserved surface detail, yet their overall shape is wider than typical for *A. aberti*, and more similar to *A. floridana*. UF 104448 does not have a well-preserved anal notch. UF 5363 (Fig. 109) displays a much shallower anal notch that is more reminiscent of *A. aberti* than either *A. floridana* or *A. dengleri*. However, this specimen is wider than typical for *A. aberti* (112.9 mm TL, 128.5 mm TW, 19.8 mm TH) with a TW 113% of TL. These specimens are here referred to as *A.* cf. *floridana*, pending collection of additional, better preserved, and more complete material (Fig. 2).

A juvenile *Abertella* just 11 mm in diameter (UF 112150) was obtained from strata Paul Huddlestun (personal communication with RWP) referred to the Torreya Formation, in the Langston Quarry, Liberty County (FM locality LI005). The specimen is too small to attribute it with confidence to any known species of *Abertella*. Additional collections of incomplete abertellid material from the Miocene strata of the state are herein referred to as *Abertella* sp.

Order **SPATANGOIDA** L. Agassiz, 1840
Family **BRISSIDAE** Gray, 1855
Genus ***BRISSUS*** Gray, 1825
BRISSUS GLENNI Cooke, 1959
Figure 120

Brissus glenni Cooke, 1959, p. 82, pl. 36. figs. 5, 6.
Brissus glenni (Cooke). Lewis et al., 2006, pp. 130–131, fig. 1.
Brissus glenni? (Cooke). Lewis et al., 2006, pp. 131, 133, fig. 2.
Brissus sp. indet., Lewis et al., 2006, pp. 133–134, fig. 3.
Brissus glenni (Cooke). Ciampaglio et al., 2009, fig. 2.
Brissus glenni (Cooke). Ciampaglio and Osborn, 2011, fig. 2.
Brissus cf. *glenni* (Cooke). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Upper Pliocene Tamiami Formation: Quality Materials Quarry, Charlotte County (FM locality CH080). This species also occurs in the lower Pleistocene Waccamaw Formation of North and South Carolina, as well the upper Pliocene upper Goose Creek Limestone of South Carolina (type locality of the species).

Discussion.—This robust species of *Brissus* was initially described by Cooke (1959) from upper Pliocene-lower Pleistocene spoil material along the Intracoastal Waterway in Horry County, South Carolina.

Brissus glenni is now known to have a much broader range than the type locality. It is a rare fossil in the lower Waccamaw Formation in southeastern North Carolina, where Lewis et al. (2006) documented it near Shallotte, Brunswick County. Ciampaglio and Osborn (2011) documented *B. glenni* in the Tamiami Formation of southwestern Florida.

Lewis et al. (2006:fig. 1) provided an illustration of the holotype of *B. glenni* with the peripetalous fasciole emphasized, providing an enhanced view of the "deeply reentrant" fasciole that Cooke used as one of the features differentiating *B. glenni* from *B. unicolor* Leske, 1778. The other distin-

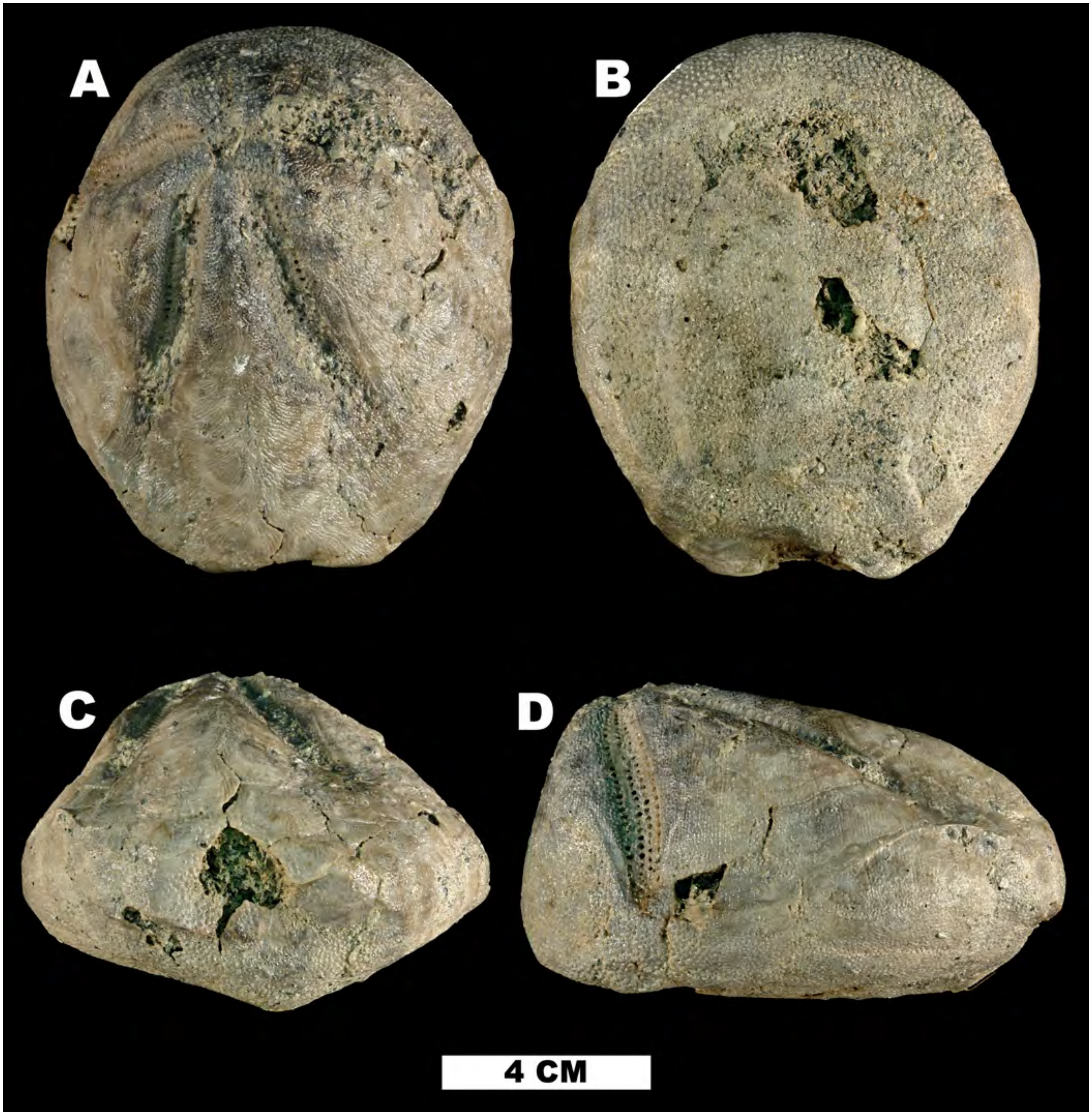


Figure 120. *Brissus glenni* (UF 171498), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. posterior view, D. lateral view.

guishing feature provided by Cooke (1959) was the larger size of *B. glenni*. The largest specimen of *B. glenni* we have examined (UF 171498) from the Tamiami Formation measures 109 mm TL, 94 mm TW, 63 mm TH (Fig. 120).

Specimens of *B. glenni* collected within the sand facies of the Tamiami Formation in the Quality Materials Quarry, Charlotte County (FM locality CH080), were often found retaining spination. This coating of short, coarse spines is very similar to the spination of the modern *Brissus unicolor* and the two species likely had similar life habits.

Genus **PLAGIOBRISSUS** Pomel, 1883

PLAGIOBRISSUS SARAE Ciampaglio, Osborn, and Weaver, 2009

Figures 121–122

Not *Meoma ventricosus* (Lamarck). Donovan and Clements, 2002, pp. 169–176, (the figured and discussed specimen is *P. sarae*).

Plagiobrissus sarae Ciampaglio, Osborn and Weaver, 2009. pp. 205–209, figs. 2, 4, 5.

Plagiobrissus sarae (Ciampaglio et al.). Osborn and Ciampaglio, 2010b, p. 83.

Plagiobrissus sarae (Ciampaglio et al.). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—In Florida, *P. sarae* has been documented in the upper Pliocene Tamiami and Intracoastal Formations: Tamiami Formation (sand facies *sensu* Missimer, 1992), Quality Materials Quarry, Charlotte County (FM locality CH080); Horse Creek, Polk County. Intracoastal Formation: Langston Quarry, Liberty County (FM locality LI005). The species also occurs in the upper Pliocene upper Goose Creek Limestone in Horry County, South Carolina (type locality).

Discussion.—Like its modern congener, *Plagiobrissus grandis* Gmelin, 1791, *P. sarae* is an echinoid of superlatives. When Ciampaglio et al. (2009) documented the species, the largest known specimen was 179 mm TL, making it the largest spatangoid, if not the largest of all echinoids in the Cenozoic deposits of the region. The species is now known to reach dimensions of 189 mm TL and 158 mm TW; undoubtedly the largest species of spatangoid in the fossil record of the Americas. This is not surprising considering that it closely related to *P. grandis*, which attains 230 mm TL (Mortensen, 1951), making it the largest heart urchin in the modern fauna.

When Ciampaglio et al. (2009) described *P. sarae*, it was not known to occur outside of the upper Pliocene, upper Goose Creek Limestone (sensu Campbell and Campbell, 1995) in Horry County, South Carolina. As discussed in Ciampaglio et al. (2009), Oyen and Portell (2001) documented the genus *Plagiobrissus* in the Tamiami Formation of south Florida, and Oyen (2001) illustrated incomplete material representing the genus. He tentatively referred this to *P. grandis*, but admitted to uncertainty due to the incompleteness of the fossils. Subsequent discovery of complete specimens allowed Osborn and Ciampaglio (2010b) and Ciampaglio and Osborn (2011) to document with confidence the occurrence of *P. sarae* in the Tamiami Formation of southwestern Florida, as well as the Intracoastal Formation of Liberty County, in the Florida panhandle.

The largest specimen of *P. sarae* we have examined from the Intracoastal Formation, Liberty County (FM locality LI005), is 134 mm TL and 113 mm TW. Although specimens in the Tamiami Formation are often smaller than those found in the upper Goose Creek Limestone of South Carolina, a specimen (UF 171497) from the Quality Materials Quarry, Charlotte County (FM locality CH080), is 153 mm TL, 128 mm TW (Fig. 121).

Plagiobrissus sarae is morphologically close to the modern *P. grandis* (Fig. 122; Ciampaglio et al., 2009). It is differentiated from *P. grandis* by its much sparser tuberculation, with large primary tubercles on the aboral surface largely limited to interambulacra 1 and 4 in *P. sarae*. These large primary tubercles are also prevalent in interambulacra 2 and 3 of *P. grandis*. Furthermore, large *P. sarae* are often more rotund and less elongated than *P. grandis*, which is also characterized by a flat aboral surface in contrast to the more inflated anterior part of the aboral surface in *P. sarae*, which gently slopes posteriorly from the apical area to the posterior margin of the test. Finally, petals II and IV are proportionately longer on *P. sarae* than *P. grandis*.

The FM-IP collections contain an exceptional specimen of *P. sarae* (UF 171495) from the Tamiami Formation in the Quality Materials Quarry, Charlotte County (FM locality CH080)

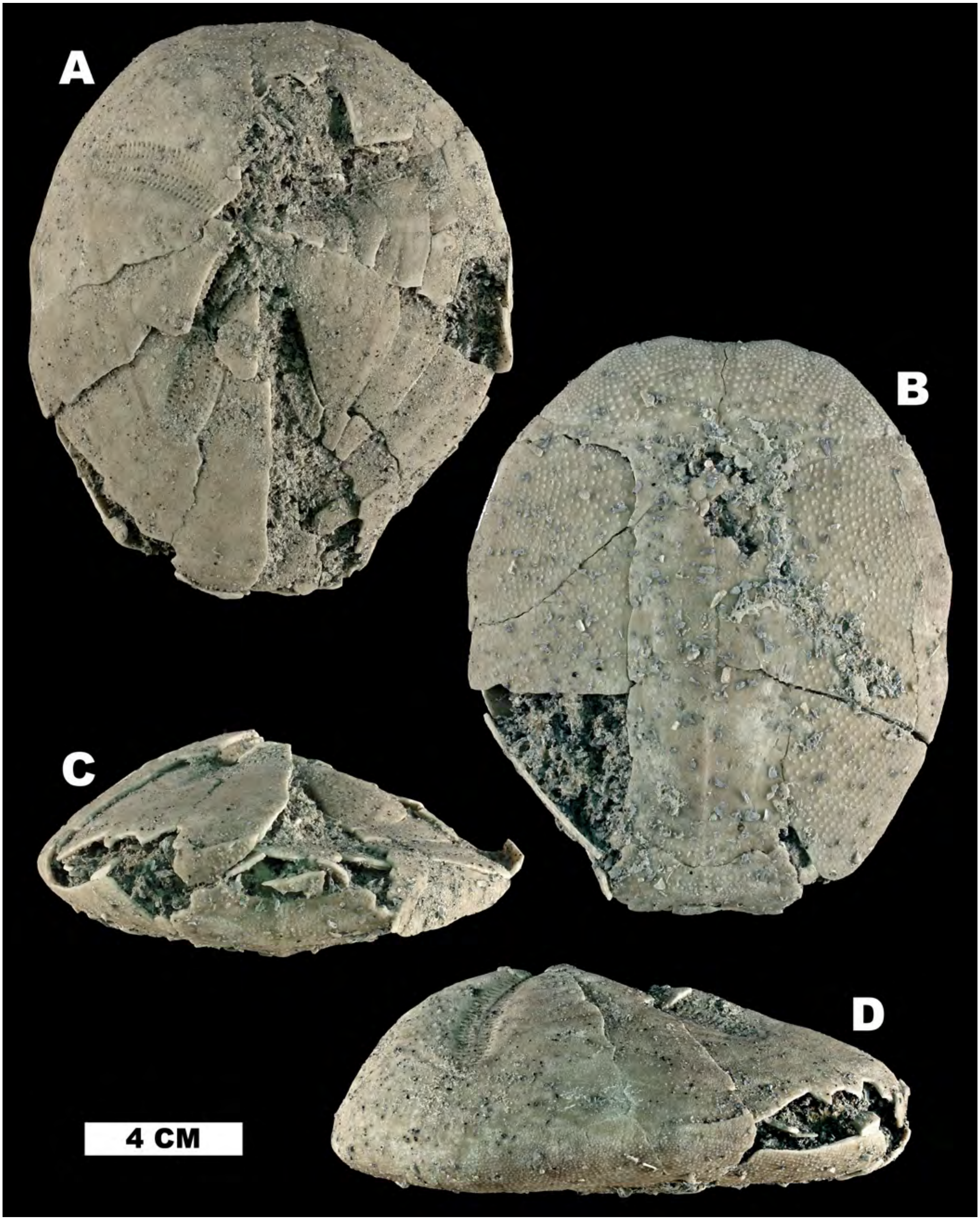


Figure 121. *Plagiobrissus sarae* (UF 171497), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. posterior view, D. lateral view.

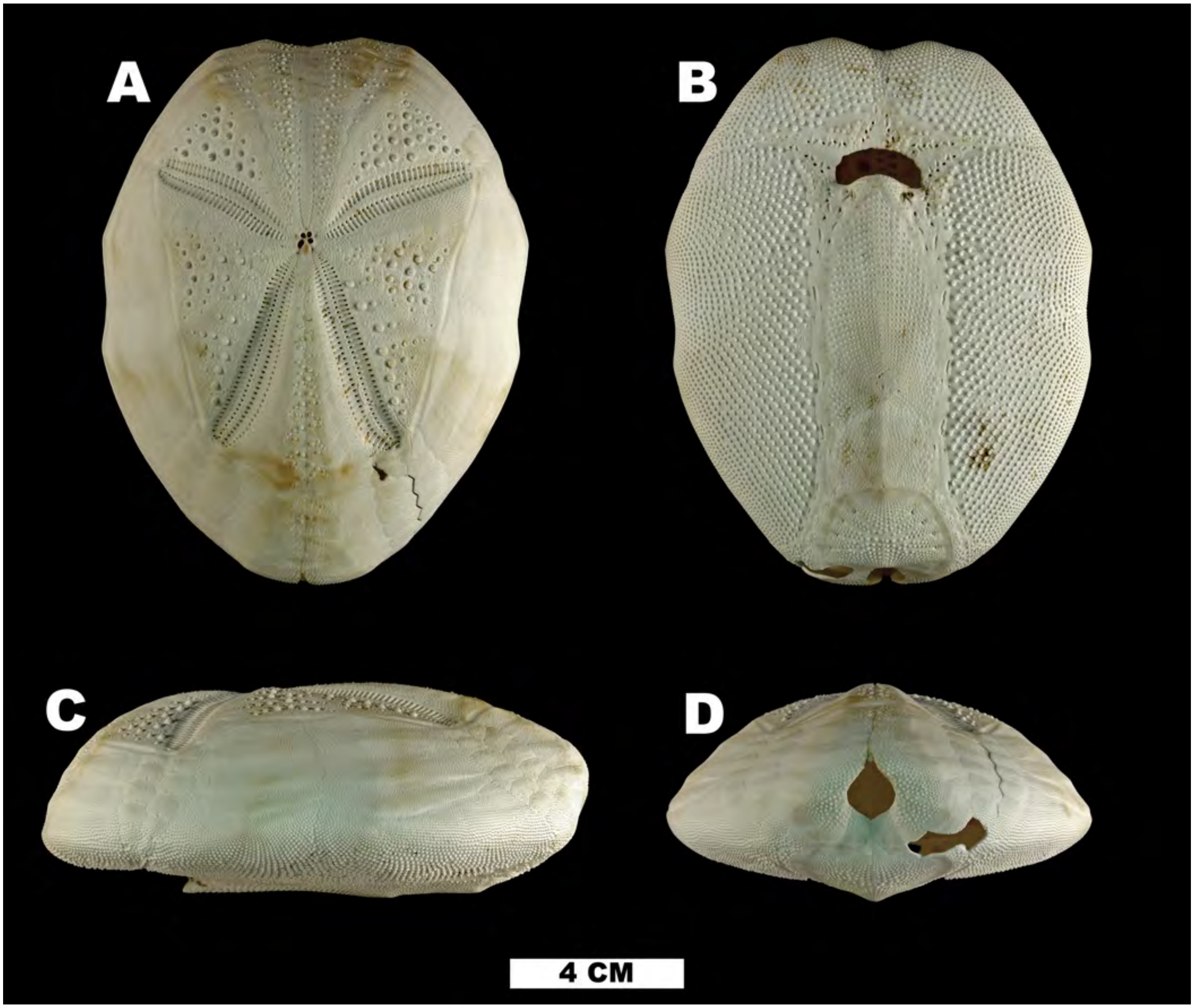


Figure 122. *Plagiobrissus grandis* (UF-IZ 11150), modern specimen for comparison (Gulf of Mexico, south of St. Petersburg at 40 foot depth, Pinellas County, Florida, USA). A. aboral view, B. oral view, C. lateral view, D. posterior view.

that retains nearly complete spination (Fig. 123). The specimen is 120 mm TL, 102 mm TW, and 48 mm TH, and lacks the aboral, enlarged "guard" spines, but the secondary spination consists of a nearly complete canopy very similar to that of the modern *P. grandis*.

Genus ***BRISSOPSIS*** L. Agassiz, 1840
BRISSOPSIS HOFFMANI n. sp.
Figures 125–129

Brissopsis sp., Osborn and Ciampaglio, 2010, p. 207.

Diagnosis.—*Brissopsis* of large size (to 110 mm TL), with a wide test (average TW = 87.5% TL); apical system 48.9% TL from posterior margin; anterior petals (II and IV) typically divergent at ~120°, length averages ~41% TL; length of petals I and V averages 30% TL, depressed in groove, nearly confluent adapically, arched towards margin distally, divergent by ~75° distally.

Description.—Description based on the holotype (UF 283991; Fig. 125), and two other largely complete, but partially corroded paratypes (e.g., UF 178003; Fig 126), as well as two additional, less complete paratypes (UF 283990 and UF

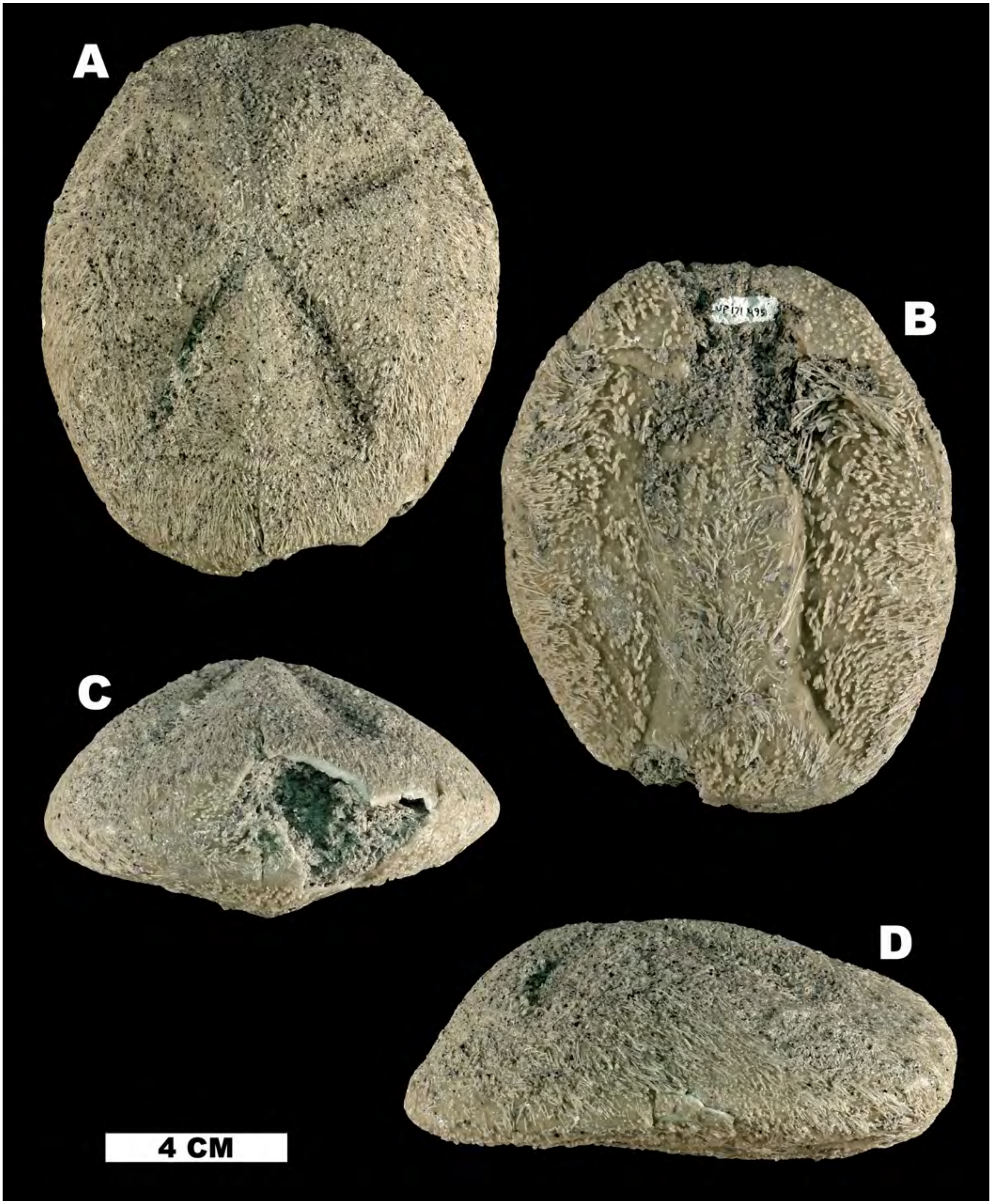


Figure 123. *Plagiobrissus sarae* with spines (UF 171495), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. posterior view, D. lateral view.

253755; Figs. 127–128) and fragmentary non-type specimens (e.g., UF 283992; Fig 129) from the Peace River Formation, Peace River above Zolfo Springs, Florida. Test large, 79–110 mm TL, 68–98 mm TW, TW 81.5–91% of TL (average 87.5%); holotype is 92 mm TL, 75 mm TW (TW = 81.5% TL); ovate, greatest width at or slightly anterior of apical system; depressed, height 38.8–42.1% TL (average 40.9% TL), greatest TH anterior of apical system. Tuberculation poorly preserved on most specimens. UF 253755 consists of an external mold providing RTV casts revealing traces of primary tubercles in anterior interambulacrum on aboral surface. Oral surface densely covered with coarse tubercles outside of plastron, plastron partially preserved in only two specimens, not sufficient for measurements. Apical system ethmolytic, four gonopores, center of apical system on holotype located ~45 mm (= 48.9% TL) from posterior margin, depressed in trough with petals. Anterior ambulacrum III not petaloid, depressed in shallow groove that deepens in larger specimens, forms notch at anterior margin; pores minute. Anterior petals (II and IV) depressed in groove, arched, narrow, typically divergent at ~120°, length averages ~41% TL, point of greatest width averages 9.7% TL, located 35–40% length of ambulacrum from apical system; pore pair series not completely preserved in any specimen. Posterior petals (I and V), depressed in groove, nearly confluent apically, arched towards margin distally, divergent by ~75° distally; shorter than ambs II and IV, length averaging 30% TL, point of greatest width averages 9.5% TL, located 55–60% length of ambulacrum from apical system; pore pair series not completely preserved in any specimen. Peristome anterior, located on average 23% TL from anterior margin to anterior edge of peristome, opening wider than high, complete measurements not available on any specimen, labrum short. Periproct subcircular, located high on vertical posterior truncation, higher than wide, 6.6 mm (= 8.3% TL) wide and 7.5 mm high (= 9.4% TL) on specimen 79 mm TL, 68 mm TW. Fascioles poorly preserved, subanal fasciole present, bilobed, traces too indistinct or damaged to permit measurements on any specimen, anal branches, if present, too poorly preserved to discern. Peripetalous fasciole presumably present, but not preserved.

Zoobank Nomenclatural Act.—7D3B7ED3-0862-41E7-ACC3-BABB420D823C.

Occurrence.—*Brissopsis hoffmani* n. sp. has not been documented outside of the late Miocene (Tortonian), lower portion of the Peace River Formation, within the bed of the Peace River, upriver from Zolfo Springs, Hardee County, Florida (FM locality HR013).

Discussion.—*Brissopsis hoffmani* n. sp. shares the type locality of *A. dengleri* in the bed and banks of the Peace River above Zolfo Springs, Hardee County (FM locality HR013), and is rare in a zone of abundant, largely fragmentary *A. dengleri*, with rare *Rhyncholampas chipolanus* and common spines and rare test fragments of *Prionocidaris cookei*.

The occurrence of this large *Brissopsis* was first documented in Osborn and Ciampaglio (2010). They noted the largest specimen collected at that time was 90 mm TL (Osborn and Ciampaglio, 2010:207). The FM-IP collection contains a partial specimen that although not complete, is a fragment 110 mm TL by 98 mm TW (UF 303930). This is the largest species of *Brissopsis* documented from the fossil record of North America. The additional material allows for a better understanding of this large echinoid, permitting its description as a new species.

The tests of *B. hoffmani* n. sp., like the other echinoids of the fauna with which it occurs, are often silicified casts that typically do not retain finer details of test architecture such as ambulacral pores or the apical system. The fascioles of the species are only partially known, but overall test morphology readily identifies the species as a *Brissopsis*. The holotype UF 283991 (Fig. 125) retains of most of the ambulacra, which are corroded in most specimens. However, the margin, periproct, and entire oral surface are not preserved. The specimen is 92 mm TL, 75 mm TW, and though the margin is not completely preserved, these measurements seem to represent the maximum dimensions of the original test.

A smaller specimen, UF 283990, retains a

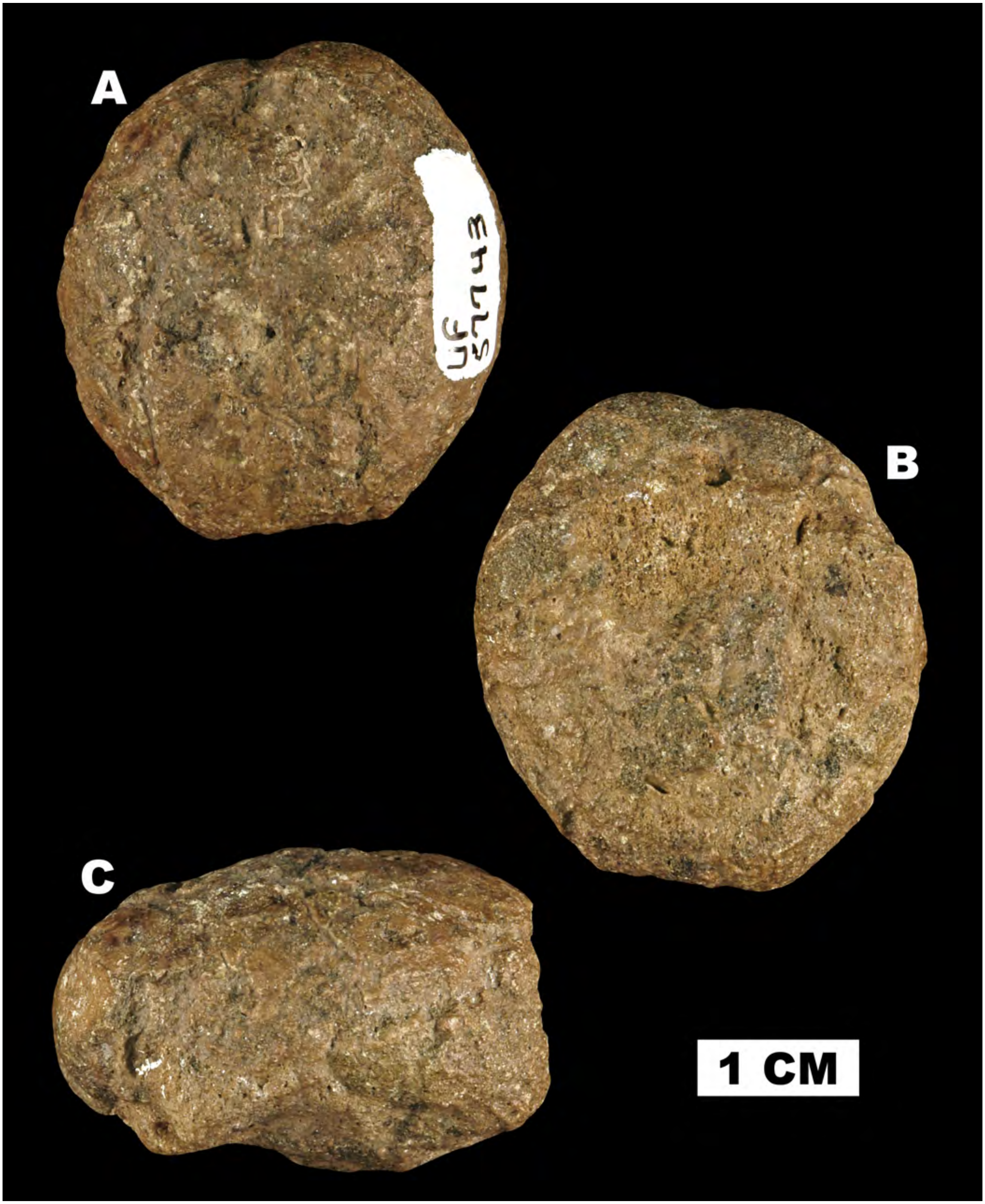


Figure 124. Brissidae gen. et sp. indet. (UF 57743), formation unknown (FM locality 3811). A. aboral view, B. oral view, C. lateral view.

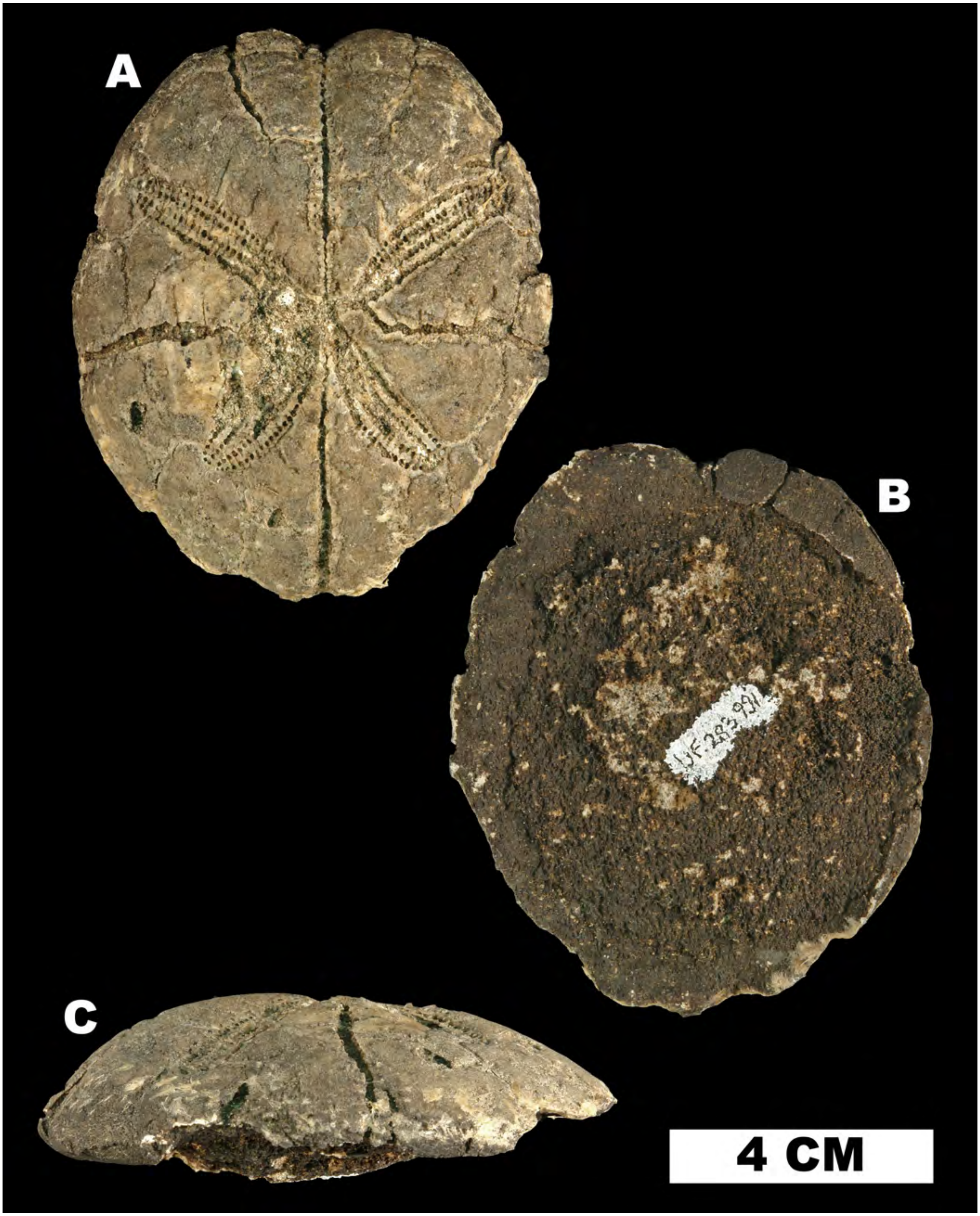


Figure 125. *Brissopsis hoffmani* n. sp., holotype (UF 283991), Peace River Formation (FM locality HR013). A. aboral view, B. oral view, C. lateral view.

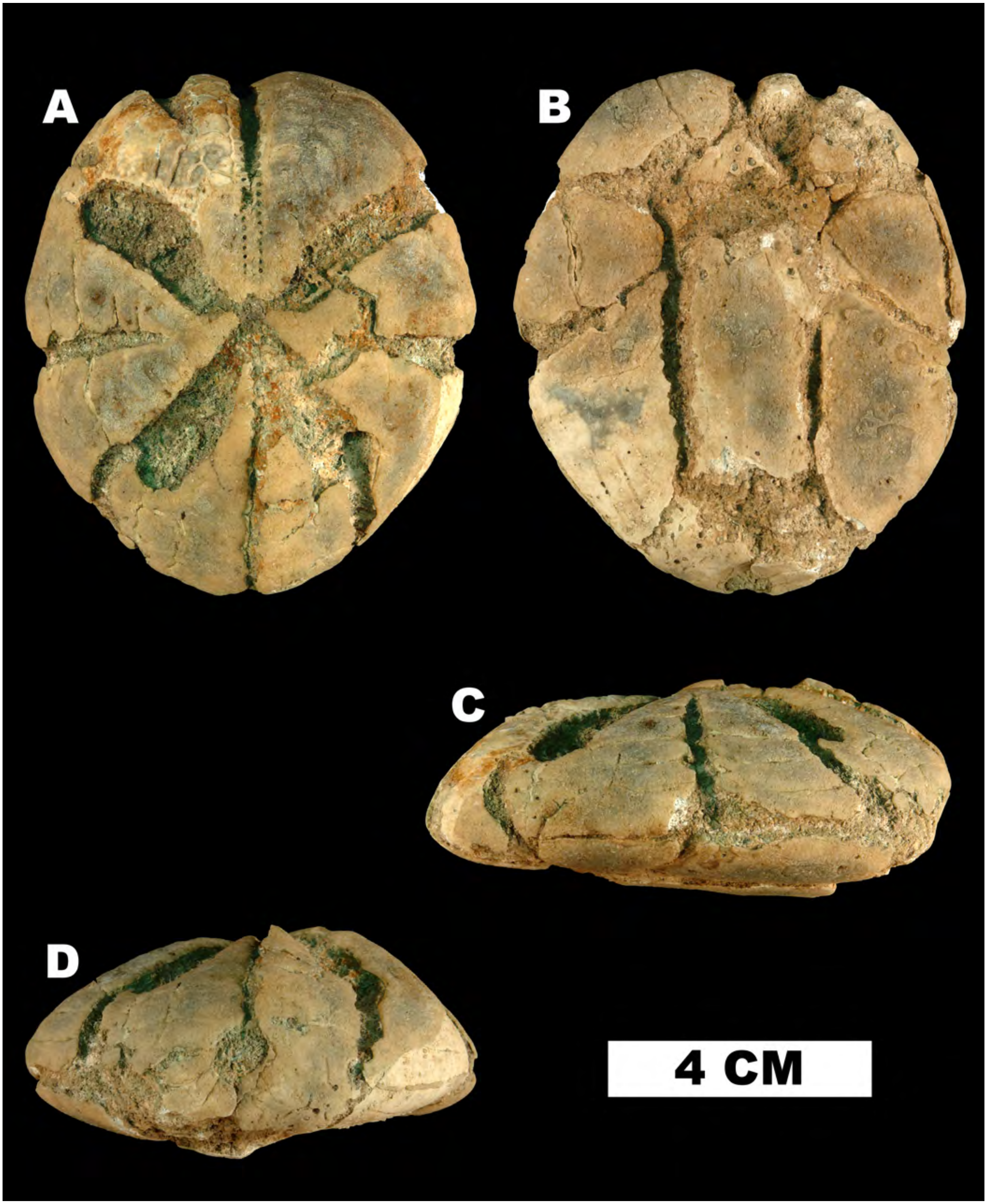


Figure 126. *Brissopsis hoffmani* n. sp., paratype (UF 178003), Peace River Formation (FM locality HR006). A. aboral view, B. oral view, C. lateral view, D. posterior view.

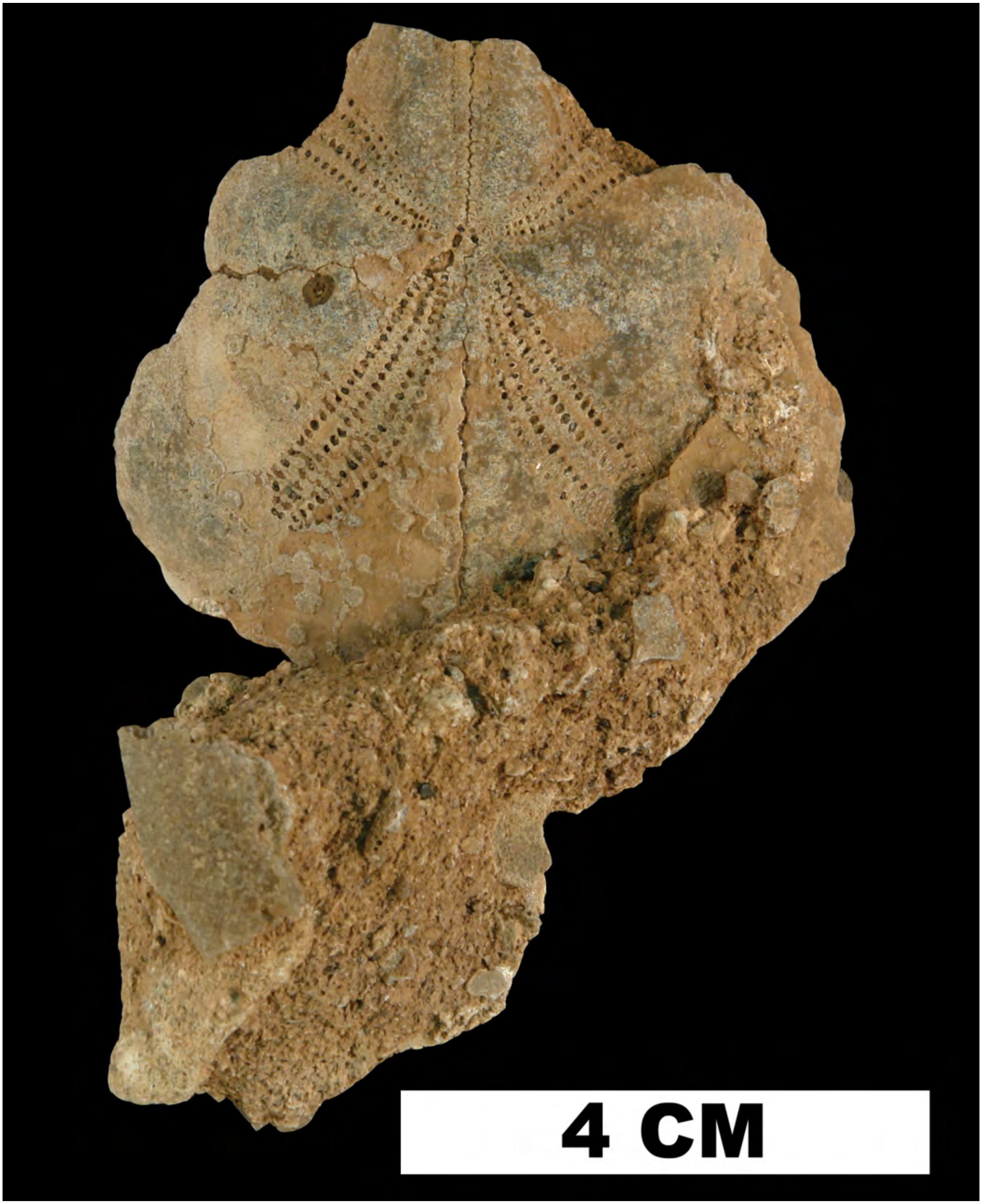


Figure 127. *Brissopsis hoffmani* n. sp., paratype (UF 283990), specimen with best preserved apical system, Peace River Formation (FM locality HR013).

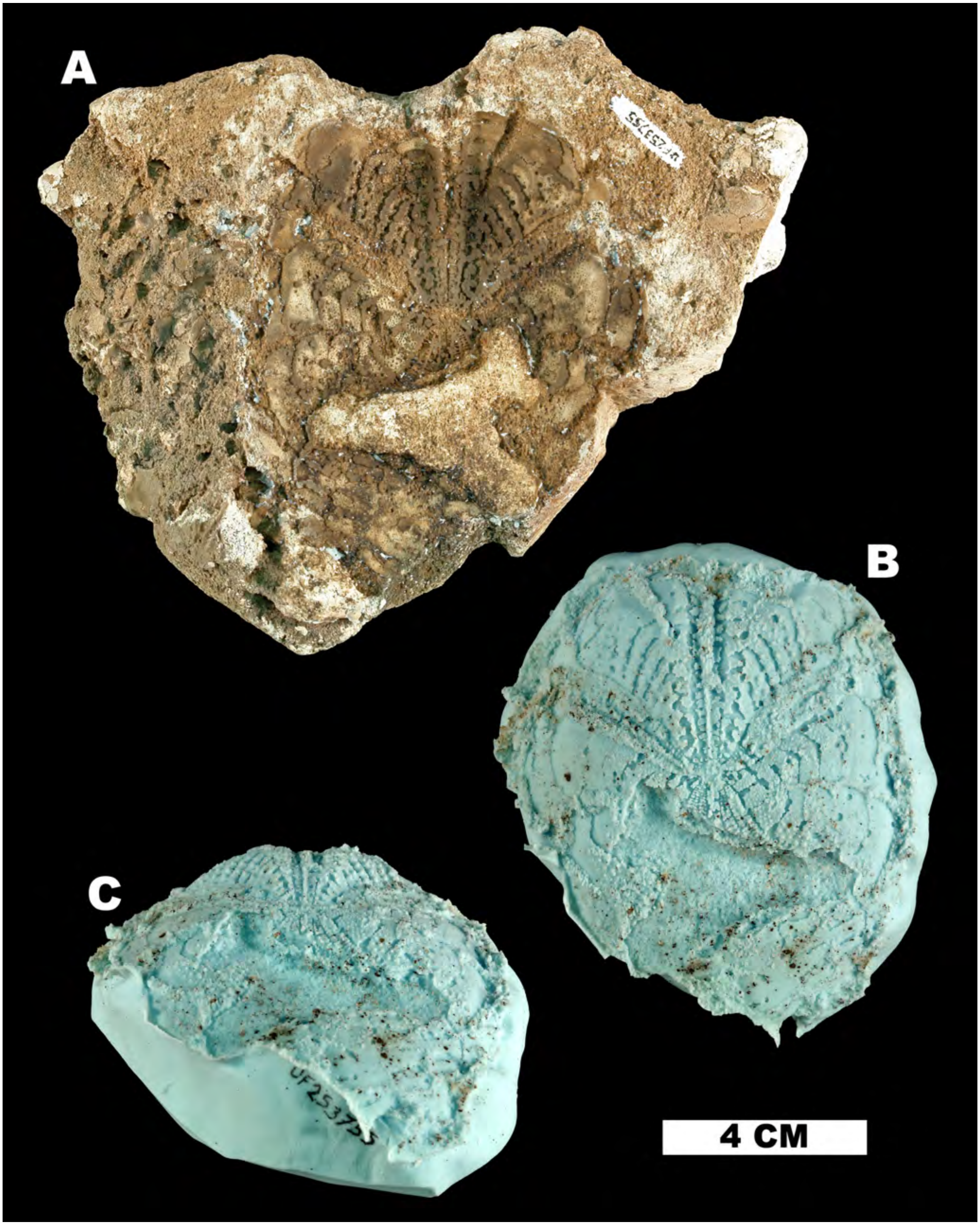


Figure 128. *Brissopsis hoffmani* n. sp., paratype (UF 253755), Peace River Formation (FM locality HR013). A. external mold, B, C. RTV silicone rubber peel.

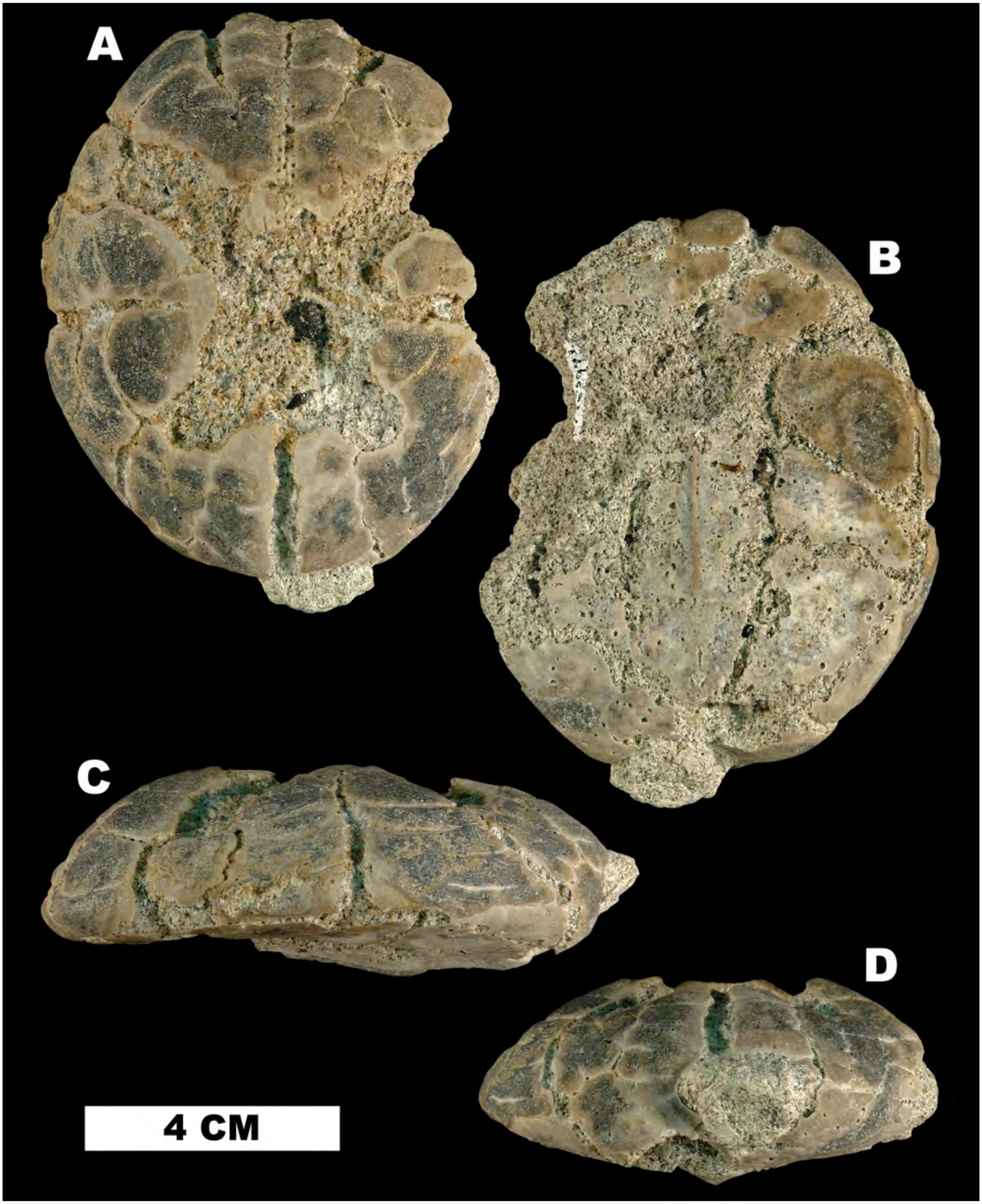


Figure 129. *Brissopsis hoffmani* n. sp., (UF 283992), Peace River Formation (FM locality HR013). A. aboral view, B. oral view, C. lateral view, D. posterior view.

well-preserved apical system (Fig. 127) and majority of the petals, but is missing the entire test margin. A partial external mold of the aboral surface of another specimen (UF 253755) was sufficiently preserved to allow an RTV silicone rubber cast, partially revealing the primary tubercles on the aboral surface, which are otherwise not preserved on most specimens (Fig. 128). The details preserved on the specimens at hand are now sufficient to differentiate this large and robust species from its congeners and describe it as the first Miocene species of the genus documented from the eastern United States.

Preservation of *B. hoffmani* n. sp. is insufficient to ascertain oral surface plating. However, Coppard (2008) stated that the character of the subanal fasciole distinguishes *Brissopsis* (typically bilobed without radiating furrows) from *Metalia* (typically shield-shaped with radiating furrows). In all specimens of *B. hoffmani* n. sp. in which the subanal fasciole is preserved, the traces indicate a bilobed subanal fasciole, strongly suggesting placement in *Brissopsis*.

Kier (1984) recognized two species of *Brissopsis* from the Cuban faunas, both of which occur in Miocene strata: *B. aguayoi* Sánchez-Roig, 1952, and *B. jimenoi* Cotteau, 1875. *Brissopsis hoffmani* n. sp. is readily differentiated from these two species by its more divergent anterior and posterior paired petals and wider test. The same characteristics serve to differentiate *B. hoffmani* n. sp. from the much smaller species *B. antillarum* Cotteau, 1875 from the Miocene of Anguilla.

Kier (1984) neglected to include *Metalia batheri* Lambert, 1922 from the Miocene of Anguilla in his review of echinoids from that region. *Brissopsis hoffmani* n. sp. is superficially similar to *M. batheri*. However, *M. batheri* is a small species that is proportionately narrower (TW = 78% TL), has more divergent, nearly straight anterior paired petals, and posterior petals that are convergent, and less widely divergent posteriorly than *B. hoffmani* n. sp. Given the criteria of Coppard (2008), *Metalia batheri* should be placed in the genus *Brissopsis*, as its subanal fasciole is bilobed and lacks radiating furrows.

The larger test with more widely divergent petals readily differentiate *B. hoffmani* n. sp. from the other Cenozoic species of the genus from the region: *Brissopsis blanpiedi* Grant and Hertlein, 1938 from the Oligocene of the Gulf Coast and *Brissopsis steinhatchee* Cooke, 1942 from the upper Eocene Ocala Limestone of Florida.

Etymology.—Named in honor of Dave Hoffman, collector of one of the paratypes that was crucial to the description of this new species.

Material and Occurrence.—The species is known from the holotype, UF 283991, and less complete paratypes, UF 178003, UF 283878, UF 202640, UF 283989, UF 283990, and UF 253755 collected from the upper Miocene Peace River Formation in the bed and banks of the Peace River, Hardee County, Florida (FM localities HR001, HR005, HR013).

Genus ***FERNANDEZASTER*** Sánchez-Roig, 1952

FERNANDEZASTER WHISLERI n. sp.

Figure 130

Diagnosis.—*Fernandezaster* with TW equal to 89.4% TL; posterior petals 28% TL, diverge at roughly 110°.

Description.—Description based on the holotype UF 114520, the only known specimen. Test large, 152 mm TL, 136 mm TW, 48 mm TH; TW = 89.4% TL, greatest width anterior of apical system; depressed, TH = 31.5% TL, flat on top, highest point anterior of apical system; ambital outline cordate, truncated posteriorly, notched anteriorly. Aboral surface covered with small secondary tubercles, larger primary tubercles absent. Oral surface covered with dense coating of coarse secondary tubercles outside of ambulacra and labrum. Apical system anterior, center located 46% TL of distance from anterior margin (distal end of furrow of ambulacrum III). Anterior ambulacrum III in deep groove, not petaloid, pores greatly reduced. Anterior petals (II and IV) sunken, nearly straight, long, length 19% TL; narrow, width at widest point 5% TL, divergent at approximately 100°, pores large, inner pore of pair round, outer elongated. Posterior petals (V and I) sunken, length approximately 28% TL, parallel or confluent for 28% length of ambulacrum, then turn away sharply distally, diverging at approximately 110°; pores of inner poriferous zone round, smaller than outer pores, which are more elongate. Peristome anterior, distance of posterior edge of opening to posterior of test 80% TL, width 22 mm, 14.4% TL; labrum short. Periproct marginal, opening very large, damaged, located on slightly overhanging, truncated posterior margin. Peripetalous fasciole narrow, width at widest point 1% TL, follows contour of petals, deeply indented in interambulacra, crosses ambulacrum III at a point 31% TL anterior of apical system. Subanal fasciole bilobed, very large: 57 mm wide (37.5% TL), 19 mm high (= 12.5% TL), lacks radiating furrows.

Zoobank Nomenclatural Act.—7D76EBAB-2DD2-470C-8B3A-99E7DAC15AFF.

Discussion.—*Fernandezaster* was erected by Sánchez-Roig (1952) to contain *F. mortenseni* Sánchez-Roig, 1952, which is represented only by the holotype from the Oligocene-Miocene of Cuba (Kier, 1984). The genus is similar to the other brissid genera *Brissopsis* and *Metalia* in having its posterior petals confluent proximally and diverging greatly distally. However, it differs from *Brissopsis* in having an extremely wide test and from *Metalia* in having a broader area enclosed by the subanal fasciole (Kier, 1984), and a very differently shaped subanal fasciole.

At the time of Kier's (1984) review of the spatangoid fauna of Cuba, the genus *Fernandezaster* was represented by the sole holotype of *F. mortenseni*. However, a year after Kier's (1984) review, *Fernandezaster durhami* Fischer, 1985 was documented from the Miocene of Costa Rica. Durham (1961) had previously recognized this specimen as *Brissopsis* sp. nov. Fischer (1985) documented the existence of two specimens of *F. durhami* that were over 90% complete, as well as two fragments. Alvarado et al. (2006) recorded and figured an additional specimen they referred to as *F. durhami* from the Miocene of Costa Rica.

Coppard (2008) did not follow Kier's (1984) assertion that *Fernandezaster* differs from *Brissopsis* in having an extremely wide test, and from *Metalia* in having a broader area enclosed by the subanal fasciole. He chose different features to distinguish between *Brissopsis* and *Metalia*. Coppard (2008) stated that the subanal fasciole of *Brissopsis* is typically bilobed, without radiating furrows, whereas in *Metalia*, it is typically shield-shaped with radiating furrows. The subanal fasciole of *F. whisleri* n. sp. is bilobed and lacks radiating furrows, aligning *Fernandezaster* with *Brissopsis*, although its wide test distinguishes it from members of that genus. Following Kier (1984), we recognize *F. mortenseni* as distinct from *Brissopsis* due to its wide test.

We consider *F. whisleri* n. sp. to be closely related to *F. mortenseni*, the type species of the genus *Fernandezaster*, and consider it best to place *F. whisleri* n. sp. within the genus in recognition of its proportionately wide test, and large, bilobed subanal fasciole. Future considerations on the status of *Fernandezaster*, and the characters that differentiate *Brissopsis* and *Metalia*, could prompt reassignment of *F. whisleri* n. sp. to the genus *Brissopsis*, as *F. whisleri* n. sp. is more similar to the genus *Brissopsis* than it is to *Metalia*, using the criteria of Coppard (2008).

Fernandezaster whisleri n. sp. is readily distinguished from *F. mortenseni* by its proportionately narrower test, 89.4% TL versus 104% TL in *F. mortenseni,* proportionately shorter posterior petals, 28% TL versus 38% TL in *F. mortenseni*, and by the posterior paired petals of *F. whisleri* n. sp. diverging at roughly 110°, versus nearly 150° in *F. mortenseni*.

Fernandezaster whisleri n. sp. is easily distinguished from *F. durhami* by its more cordate outline, with *F. durhami* having a very shallow indentation where ambulacrum III crosses the margin. Also, the test of *F. durhami* is proportionately narrower and has more divergent posterior petals.

The genus *Fernandezaster* is therefore known only from four largely complete specimens: the holotype of *F. mortenseni* and three specimens *F. durhami*. This underscores the importance of *F. whisleri* n. sp. not only as a new member of the regional faunas, but in adding an important, well-preserved specimen (UF 114520) to the list of known specimens.

Fernandezaster whisleri n. sp. has not been documented outside of the upper Pliocene Intra-

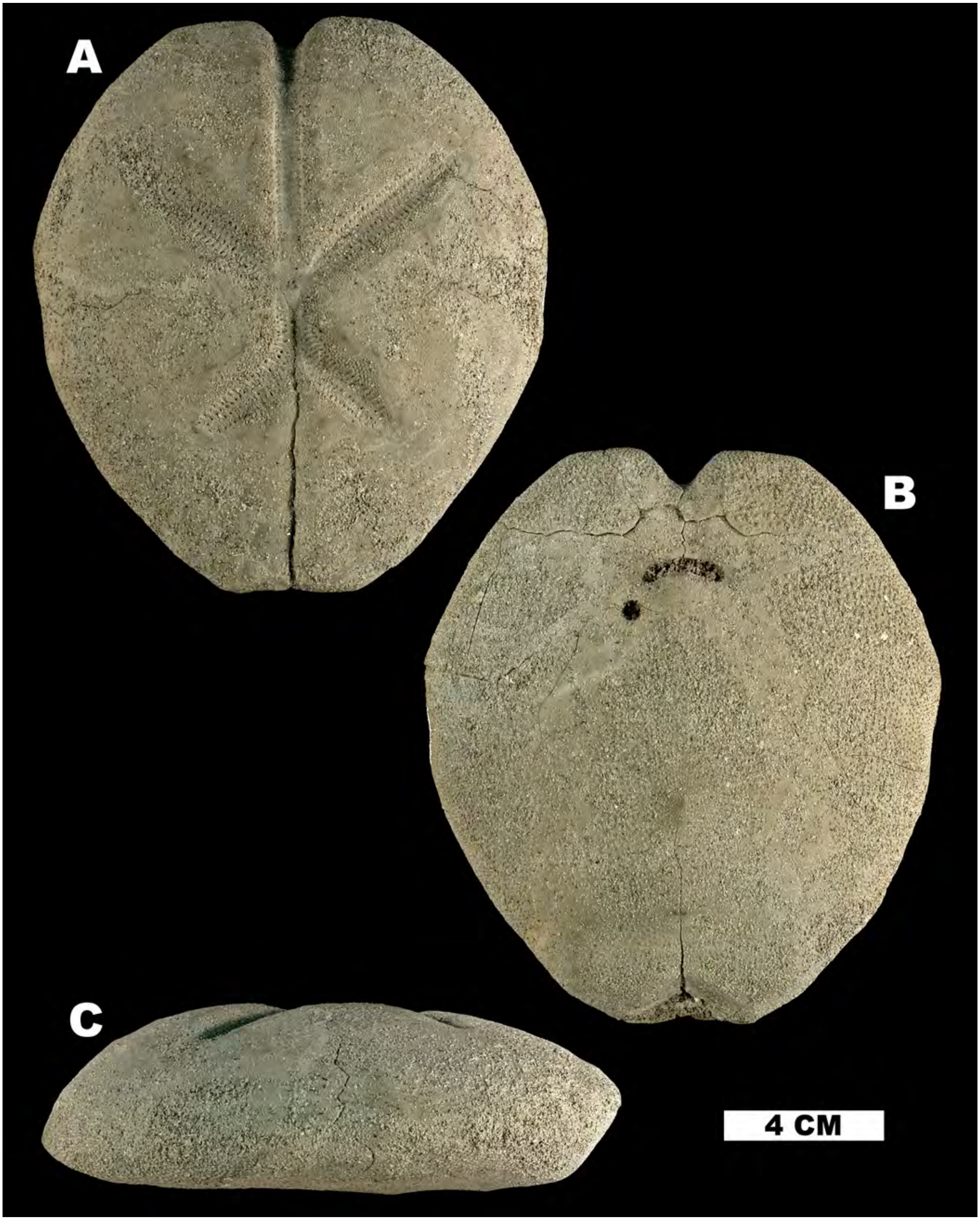


Figure 130. *Fernandezaster whisleri* n. sp., holotype (UF 114520), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

coastal Formation in the Langston Quarry, Liberty County, Florida (FM locality LI005). It is an exceptionally rare occurrence in the quarry, being represented only by the holotype.

Etymology.—This species is named in honor of Phil Whisler, Gainesville, Florida, collector of the holotype and longtime friend and volunteer of the Florida Museum.

Material and Occurrence.—The species is known only from the holotype UF 114520, collected from the upper Pliocene Intracoastal Formation, in the Langston Quarry, Liberty County, Florida (FM locality LI005).

BRISSIDAE gen. et sp. indet. (Oyen et al., 2000)
Figure 124

Brissid, gen et sp. indet., Oyen et al., 2000, pp. 235–241, figs. 7–8.

Occurrence.—Pliocene-Pleistocene? Formation unknown, dredged in a depth of 511 m in the Gulf of Mexico (FM locality 3811).

Discussion.—Oyen et al. (2000) documented a single internal mold of echinoid that is not readily identifiable to family, though it is clearly a spatangoid. They referred the specimen (UF 57743) to the family Brissidae. However, we feel that even that assignment is problematic.

The specimen is 33.5 mm TL, 30.8 mm TW, and 21.1 mm TH, and displays few details permitting identification. The anterior ambitus appears to have a very slight sulcus. However, detail of the petals or other test features, other than overall shape, is lacking. Given the uncertainty of the age designation, or taxonomic assignment of the specimen, we felt it unwarranted to include it in the stratigraphic distributions (Figs. 2–4).

Family **LOVENIIDAE** Lambert, 1905
Genus ***LOVENIA*** Desor in L. Agassiz and Desor, 1847
LOVENIA CLARKI (Lambert in Lambert and Thiéry, 1924)
Figure 131

Echinocardium depressum Clark, 1915, p. 214, pl. 98, figs. 3a–c. (not *Amphidetus depressus* Agassiz, 1847).

Amphidetus clarki Lambert in Lambert and Thiéry, 1924, p. 470, (for *Echinocardium depressum* Clark).

Lovenia clarki (Lambert). Cooke, 1942, p. 60.

Lovenia clarki (Lambert). Cooke, 1959, pp. 77, 78, pl. 33, fig. 6.

Lovenia clarki (Lambert). Oyen and Portell, 2001, pl. I, fig. 11.

Occurrence.—*Lovenia clarki* has not been found outside the lower Miocene Chattahoochee Formation: Chattahoochee, Gadsden County (USGS locality 2565, type locality of the species); road cuts on either side of Jim Woodruff Dam, below Lake Seminole, especially on the western side of the dam in Jackson County, Florida (FM locality JA003).

Discussion.—Cooke (1959) stated that the genus assignment of this species is somewhat uncertain. Many of its features are indeterminate due to the moldic nature of the specimens. Cooke (1959) referred it to *Lovenia* because it is much flatter than *Echinocardium* and had large tubercles.

Examination of dozens of specimens from the Jim Woodruff Dam locality, Jackson County, Florida (FM locality JA003), supports Cooke's (1959) placement within the genus *Lovenia*. At the Jim Woodruff Dam, *L. clarki* is common in a lens of concentration in which preservation consists of molds and casts. Most specimens lack surface detail as the soft limestone weathers quickly upon exposure. However, some characters can be observed, largely from the external molds that tend to preserve traces of the test architecture.

The species is not documented outside of the type locality where it is associated with very rare *Arbia aldrichi*, a single internal mold of a spatangoid we herein refer to as *Schizaster* sp., and an unrecognizable, small regular urchin.

LOVENIA KERNERI n. sp.
(Figs. 132–134)

Diagnosis.—*Lovenia* of large size (largest specimen 73 mm TL) with an elongate, narrow (TW on average 84% TL), high (TH on average 36.9% TL) test; large periproct (width on average 30% TL, height on average 17% TL) located in deep funnel that occupies much of truncate, slightly overhung posterior margin; periproct not completely visible from an oral viewpoint; anterior paired petals 35% TL, posterior petals on average 41% TL.

Description.—Description based on the

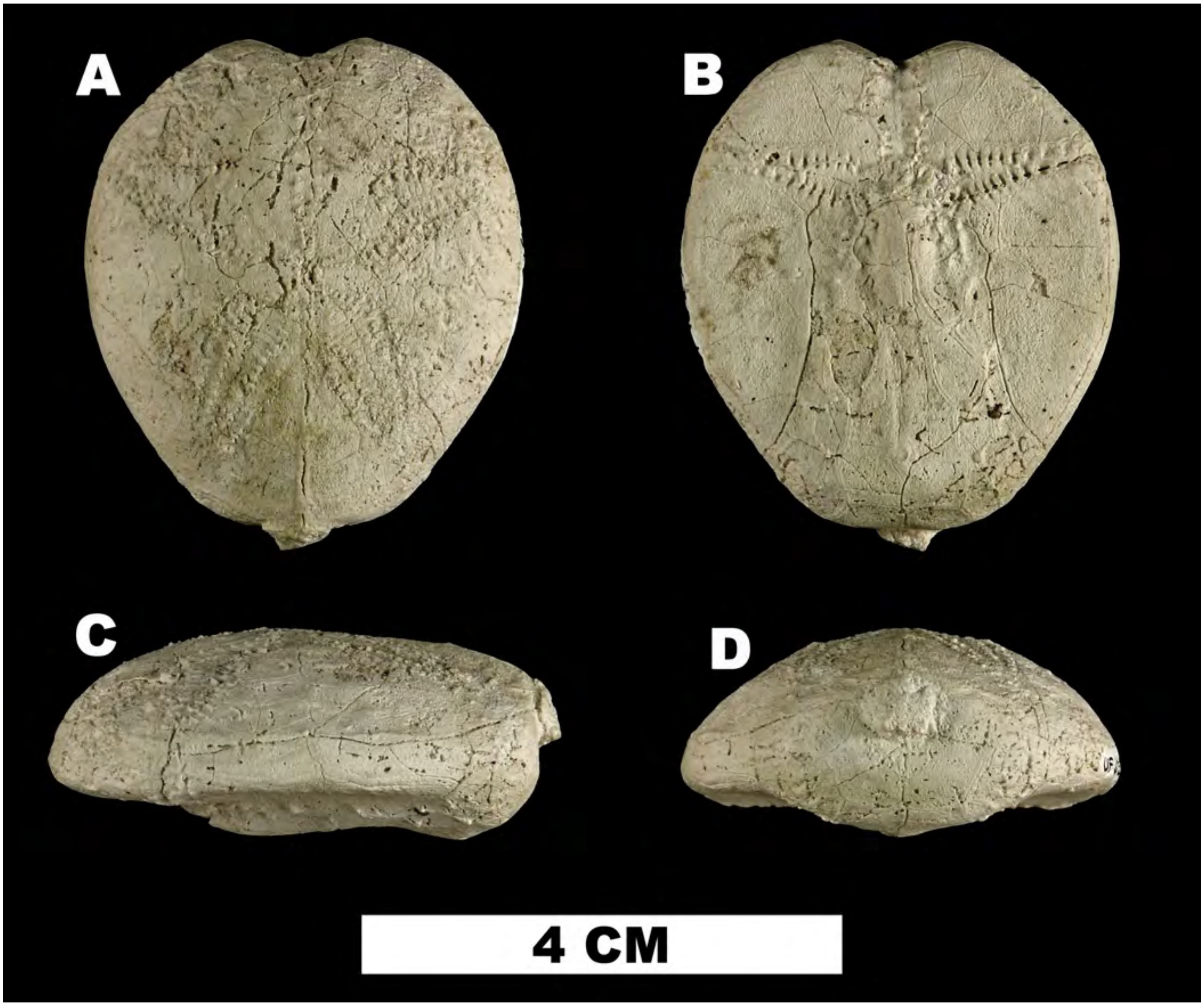


Figure 131. *Lovenia clarki* (UF 102322), Chattahoochee Formation (FM locality JA003). A. aboral view, B. oral view, C. lateral view, D. posterior view.

holotype UF 113412 (Fig. 132) and two less complete paratypes (UF 113796–113797; Figs. 133–134) from the upper Pliocene Tamiami Formation, southwest of Arcadia, DeSoto County (FM locality DE021). Test large, only specimen with complete margin is UF 113412, 73 mm TL, 62 mm TW, 27 mm TH, width 84.0% TL; widest point at apical system, elongate, depressed, highest point at apical system; TH = 36.9% TL. Anterior ambitus well rounded, indented by broad, shallow notch containing the non-petaloid ambulacrum III. Posterior margin tapered from widest point of test towards posterior ambitus, posterior truncated. Oral surface flattened, aboral surface shallowly vaulted towards anterior-posterior axis. Apical system anterior, anterior edge 38% TL from posterior margin; presumably ethmolytic with four gonopores, though not sufficiently preserved to ascertain. Internal fasciole not preserved on holotype, visible on UF 113797, extends posterior of apical system before tapering to a point in posterior interambulacrum; extends anteriorly parallel to ambulacrum III to where it abruptly crosses ambulacrum III, a fainter second branch crosses ambulacrum III more anteriorly. Subanal fasciole bilobed, heavily tuberulated in the lobes. Peristome crescentric, 11 mm wide, 7 mm high in holotype, anteriorly placed, anterior edge of peristome located 26% TL from anterior margin. Periproct very large, 19 mm wide (30% TL), 11 mm high (17% TL) on holotype, located in deep funnel that occupies much of truncate, slightly overhung posterior margin; periproct not completely visible from oral viewpoint. Ambulacrum III shallowly depressed, forming moderate anterior notch crossing ambitus; perforated with minute, conjugate pore-pairs; dense miliary and secondary tubercles both within the internal fasciole and anteriorly, tubercles increase in size medially. Paired ambulacra flush, not depressed, poriferous zones nearly closed distally, do not cross internal fasciole, pore-pairs ovate, depressed, separated from adjacent pores by a keel-like ridge, pores of anterior poriferous zones reduced in size. Petals nearly confluent towards apical area. Anterior paired petals diverging at an angle of approximately 130°, length on average 35% TL, extending to ambitus. Posterior petals diverging at angle of approximately 40°, on average 41% TL, extending to a point approximately 8% TL from ambitus. Lateral interambulacra on aboral surface with prominent fields of non-crenulate primary tubercles set in deeply sunken scrobicules, primarily confined to anterior half of test (extending posteriorly on average 55% TL from anterior margin), primary tubercles lacking within internal fasciole. Remainder of test with fine, dense secondary and miliary tubercles. Interambulacrum 5 raised into a moderate median ridge. Oral surface with amphisternous plastron, widest at posterior margin, tapering anteriorly, raised into weak median ridge, dense secondary tubercles on posterior portion. Labrum long, narrow. Coarse secondary tubercles within lobes of subanal fasciole. Oral ambulacra naked except for scattered miliary tubercles. Lateral and anterior interambulacra on oral surface with coarse secondary tubercles near ambitus, replaced by deeply sunken primary tubercles in from margin. Ambulacral plates adjoining peristome bearing sphaeridiae often enclosed by raised walls forming a cyst-like structure; ambulacra I and V bearing ten sphaeridial pits, ambulacra II and IV each bearing six pits, only two in ambulacrum III.

Zoobank Nomenclatural Act.—4DC03E52-5B43-45B6-875E-04BC62AB4E08.

Discussion.—*Lovenia kerneri* n. sp. is the first *Lovenia* documented from the Pliocene of the eastern United States and is the youngest *Lovenia* in the fossil record of the eastern Americas and the Caribbean region. There are three specimens in the FM-IP collections, all from the upper Pliocene Tamiami Formation in the bed of the Peace River, DeSoto County (FM locality DE021). Fragmentary remains attributable to *L. kerneri* n. sp. are also found in the Tamiami Formation in the bed of Joshua Creek, near Nocatee, DeSoto County.

The holotype, UF 113412 (Fig. 132), consists of a complete specimen that has been chemically hardened in the lab due to its exceptional fragility, but is much worn with only the most persistent surface elements preserved. The two paratypes consists of UF 113796 that is about 40% complete, and retains some glassy spines in matrix on the oral surface (Fig. 133), and UF 113797, which is nearly complete but distorted lengthwise, preventing measurement of TL and TW. However, exceptional surface detail is preserved on this specimen (Fig.134).

At 73 mm TL, *L. kerneri* n. sp. is the largest *Lovenia* in the faunas of the eastern United States. It is rivaled in size in the North American fauna by *Lovenia hemphilli* Israelsky, 1923, from the Pliocene of California. Israelsky (1923) documented one of the cotypes of *L. hemphilli* as 79.5 mm TL. However, *L. kerneri* n. sp. is readily distinguished from *L. hemphilli* by its higher test, which is 36.9% TL, versus the two cotypes of *L. hemphilli* that have TH 26.5% and 25.7% of TL. The periproct of *L. kerneri* n. sp. is also not as visible from an oral viewpoint (compare with Israelsky, 1923:pl. 74, fig. 1b).

Like *L. hemphilli*, the periproct of *L. kerneri* n. sp. is placed in a funnel, which as stated by Henderson (1975:30) is a feature not otherwise present in the species of *Lovenia* from the east coast faunas. This feature alone readily distinguishes *L. ker-*

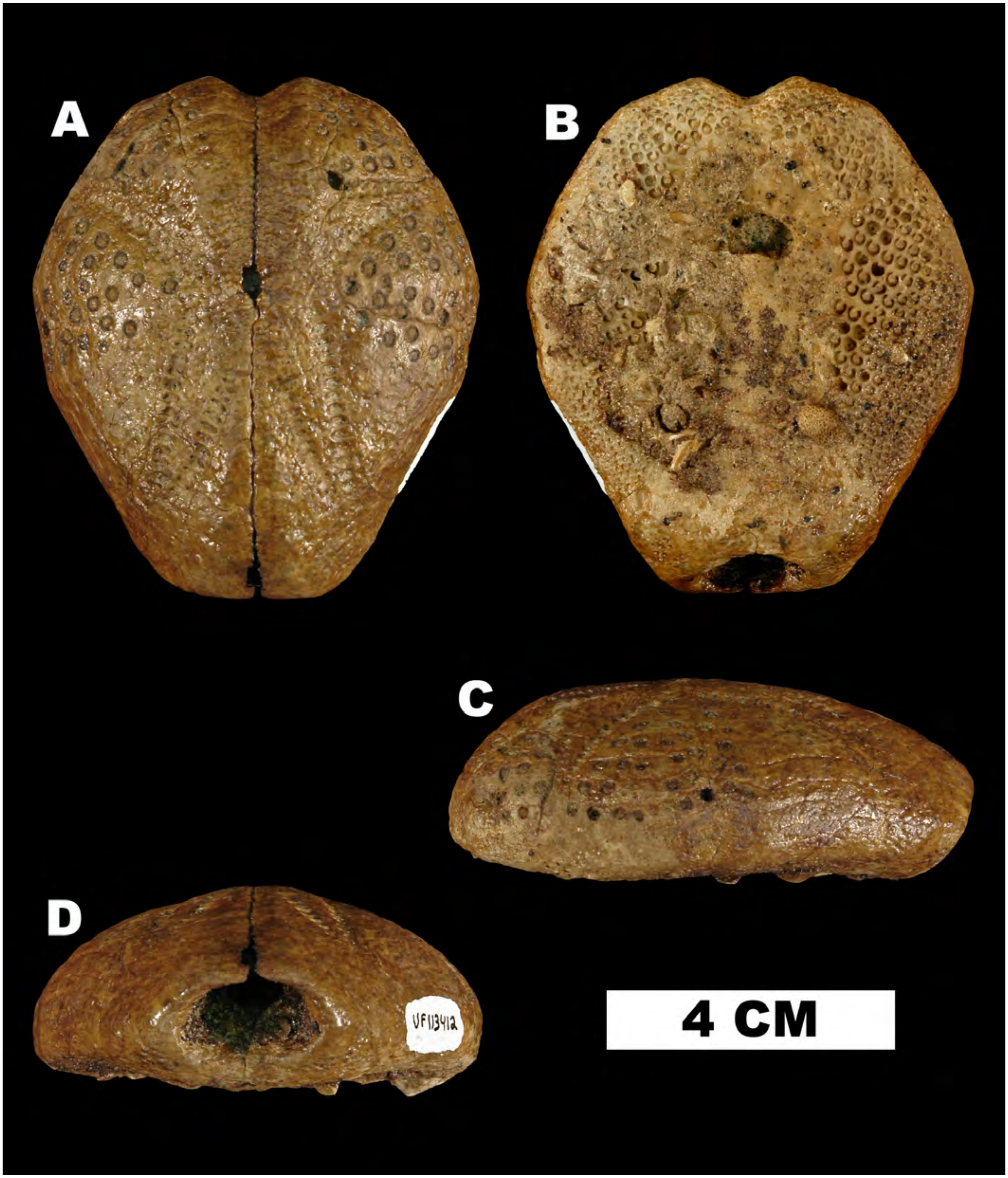


Figure 132. *Lovenia kerneri* n. sp., holotype (UF 113412), Tamiami Formation (FM locality DE021). A. aboral view, B. oral view, C. lateral view, D. posterior view.

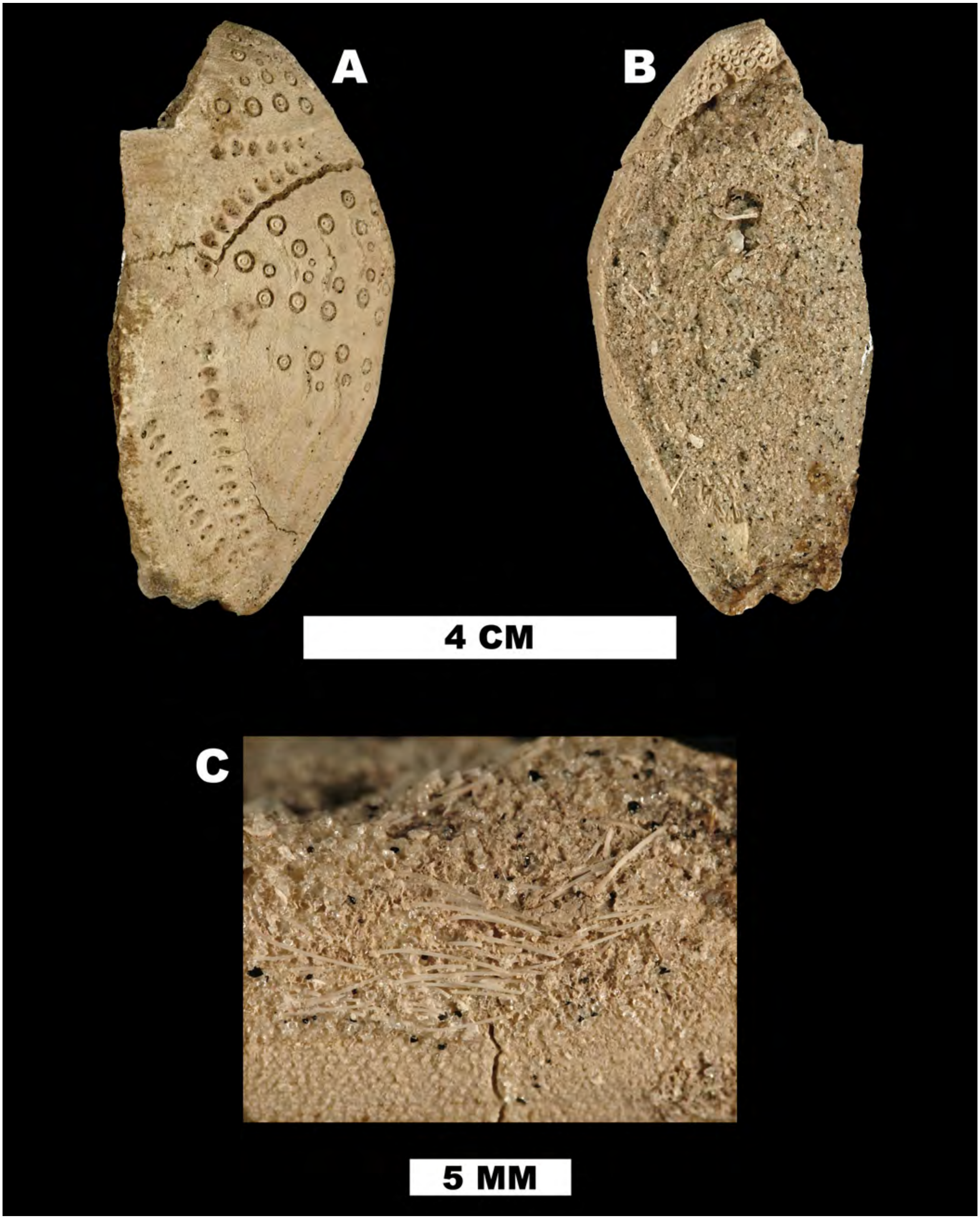


Figure 133. *Lovenia kerneri* n. sp., paratype with some spine retention (UF 113796), Tamiami Formation (FM locality DE021). A. aboral view, B. oral view, C. close up of spines.

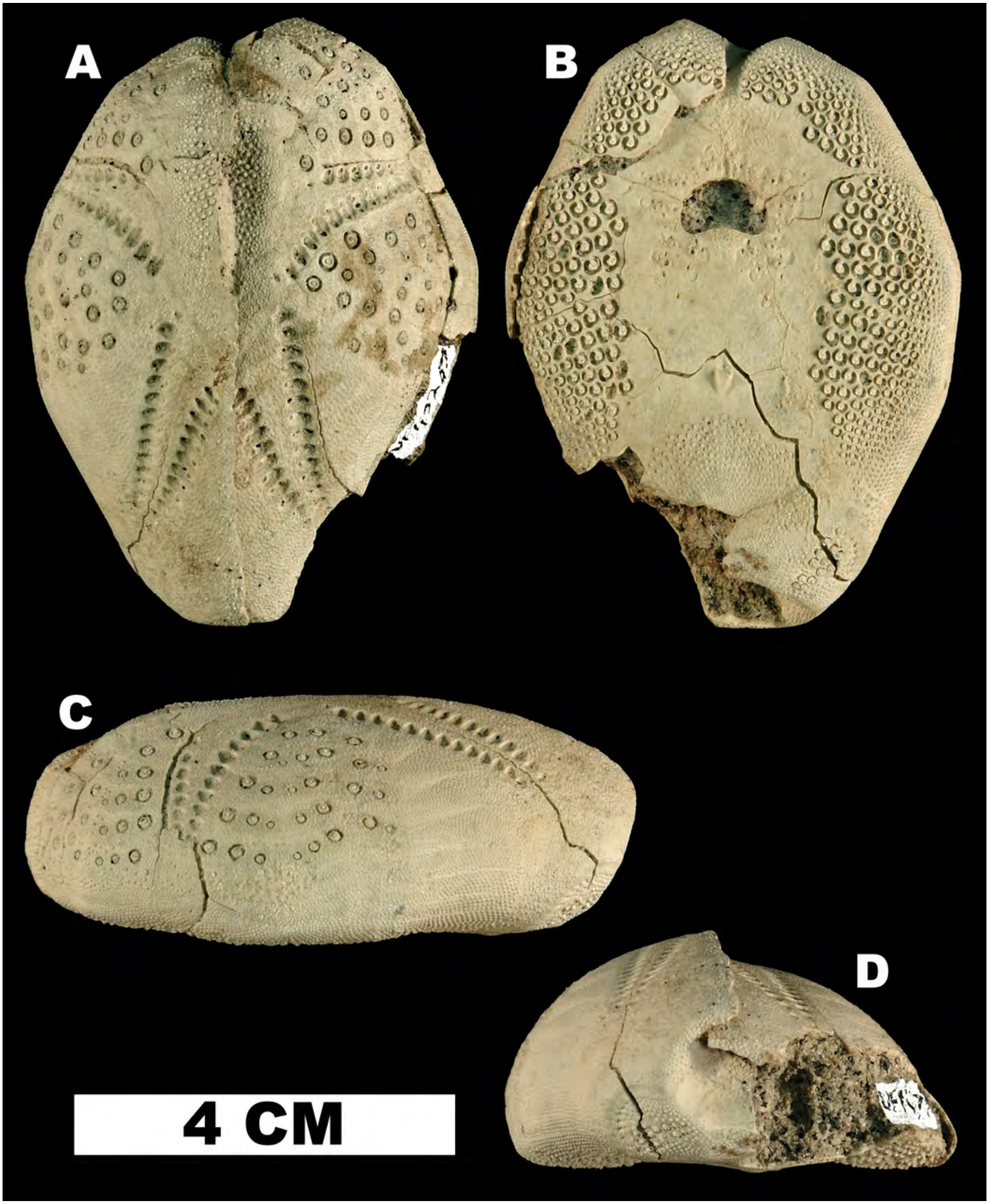


Figure 134. *Lovenia kerneri* n. sp., paratype (UF 113797), Tamiami Formation (FM locality DE021). A. aboral view, B. oral view, C. lateral view, D. posterior view.

neri n. sp. from *L. clarki*, from the Miocene Chattahoochee Formation of northern Florida, and *L. alabamensis* Cooke, 1959, from the upper Oligocene Chickasawhay Limestone of Alabama, Anahuac Formation of Texas, and Long Bay Member of the Antigua Formation of Antigua.

Lovenia dumblei Kew, 1917 was described in Dickerson and Kew (1917) from the Tertiary of northeastern Mexico. However, *L. dumblei* also lacks a funnel-shapped periproctal region. In addition, *L. kerneri* n. sp. is proportionately narrower and longer than *L. dumblei*, which has TW nearly identical to TL. Cooke (1961) documented *L.* cf. *dumblei* from the Miocene of Venezuela. *Lovenia mexicana* Jackson, 1937, from the Miocene Meson Formation of Veracruz, Mexico, is wider and lower than *L. kerneri* n. sp. The holotype of *L. mexicana* is 49 mm TL, 45 mm TW, and 15 mm TH (Jackson, 1937).

Linkimer and Aguilar (2000) recorded *Lovenia* sp. indet. from the Miocene Turrucares Formation of Costa Rica. The specimen is figured in Alvarado et al. (2006:fig. 4E), and is not identifiable to species as only the posterior portion of the aboral surface is preserved, casting doubt even as to its genus.

Lambert (1922) described *L. gregoryi* from the Miocene of Anguilla. Kier (1984:8) neglected to include this species in his review of the fossil spatangoids of Anguilla. This little species, which is represented only by one damaged specimen 28 mm TL, has received little attention from subsequent authors. *Lovenia kerneri* n. sp. is readily distinguished from *L. gregoryi* by its straighter posterior petals, and primary tubercles that do not extend as far posteriorly on the aboral surface as in *L. gregoryi*. Due to the incompleteness of the only known specimen of *L. gregoryi*, additional comparison of the two species is not possible.

Maury (1934a) described *Lovenia baixadoleitensis* from the Cretaceous of northeastern Brazil from a cast of the peristomial region of an echinoid that is clearly a cassiduloid. Maury (1934b) recognized this and erected the genus *Lovenilampas* to contain the specimen. Kier (1962) stated the specimen is unrecognizable but has phyllodes similar to those found in *Pygorhynchus*.

Other than the above discussed species, the genus *Lovenia* is not represented elsewhere in the fossil faunas of the Caribbean region. *Lovenia kerneri* n. sp. is perhaps most similar to the extant *Lovenia elongata* Gray, 1845, which lives in shallow-water sands and gravels in the Indo-Pacific region. We have included images of a specimen of *L. elongata* (FM-IZ 18910) for comparison (Fig. 135). Both species share very similar morphologies, although the test of *L. kerneri* n. sp. is proportionately higher than in typical *L. elongata*. Mortensen (1951) stated the petals of *L. elongata* are about equal in length, whereas the anterior petals of *L. kerneri* n. sp. are 35% TL, and the posterior ones are 41% TL. One of the three available specimens of *L. kerneri* n. sp. has a second branch of the internal fasciole on the anterior end, as often displayed in *L. elongata* (Mortensen, 1951). Cyst-like structures on the sphaeridial pits are also similar to the extant species. However, the periproct of *L. elongata* is proportionately narrower, and is more visible from an oral viewpoint, than for *L. kerneri* n. sp.

This species has not been documented outside of the upper Pliocene Tamiami Formation in the vicinity of Arcadia, DeSoto County where it is associated with *Rhyncholampas evergladensis, Lytechinus variegatus, Agassizia porifera* and other, rarer species.

It is interesting to note that although the genus *Lovenia* is widespread today, it is absent along the Atlantic Coast of the Americas and the West Indies. It is also present throughout the Indo-Pacific, and west coast of the Americas (Mortensen, 1951). The occurrence of *L. kerneri* n. sp. in the late Pliocene therefore represents the youngest documented occurrence of the genus in the eastern Americas and West Indies.

Etymology.—This species is named in honor of Andreas Kerner, collector of the type material.

Material and Occurrence.—The species is known from the holotype UF 113412 and less complete paratypes UF 113796 and UF 113797 collected from the upper Pliocene Tamiami Formation, in the bed of the Peace River, DeSoto County, Flor-

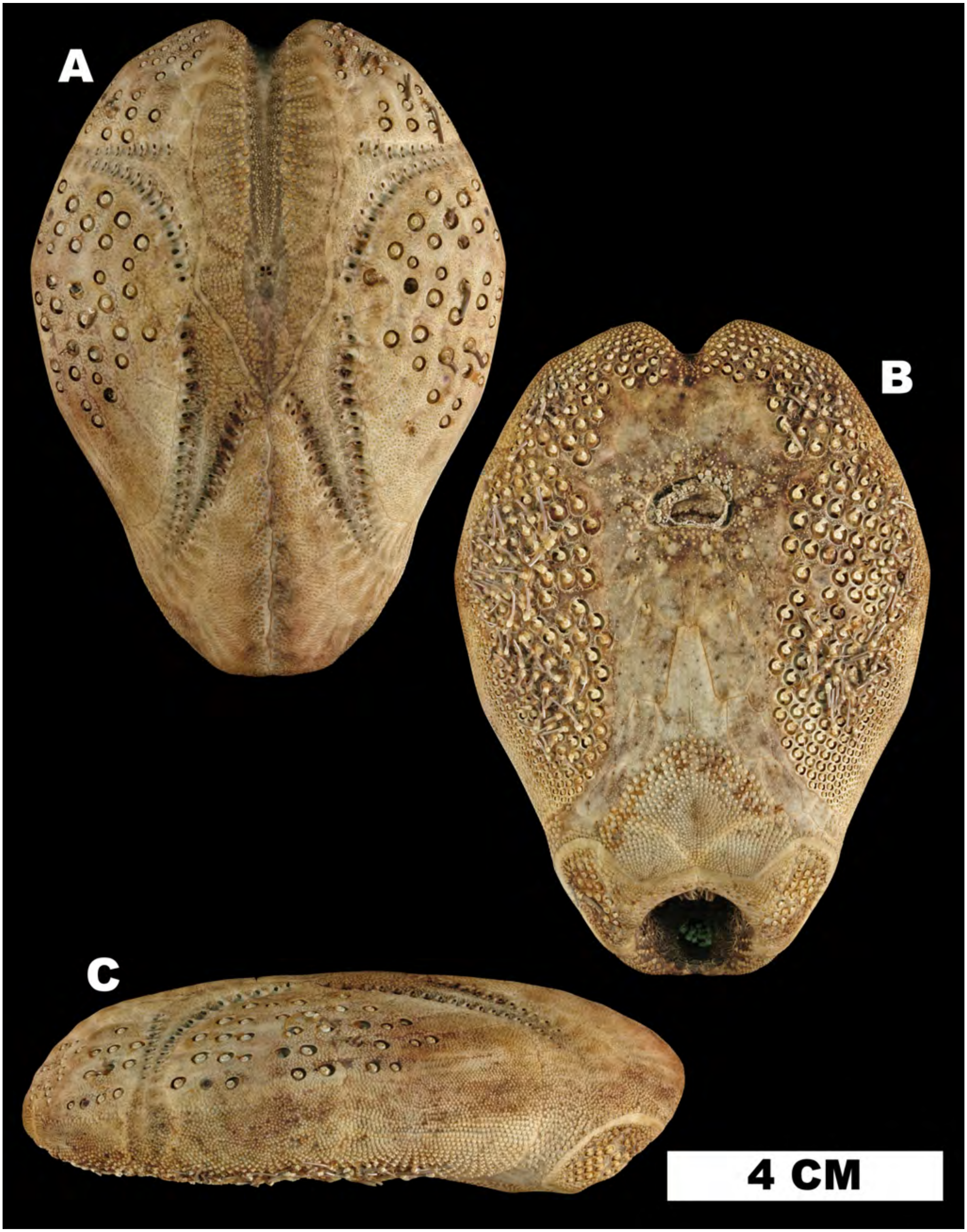


Figure 135. *Lovenia elongata* (UF-IZ 18910), modern specimen for comparison (Balicasag Island at 5 m depth, Bohol, Philippines). A. aboral view, B. oral view, C. lateral view.

ida (FM locality DE021). Fragmentary remains of this species also occur in the bed of Joshua Creek, near Nocatee, DeSoto County, Florida.

Genus **ECHINOCARDIUM** Gray, 1825

ECHINOCARDIUM ORTHONOTUM Conrad, 1843

Figures 136–139

Spatangus orthonotus Conrad, 1843b, p. 327.
Amphidetus virginianus Forbes in Lyell, 1845, p. 425, fig. 1.
Amphidetus orthonotus (Conrad). Conrad, 1846, p. 220.
Amphidetus gothicus Ravenel, 1848, p. 4, figs. 1, 2.
Amphidetus orthonotus (Conrad). Tuomey and Holmes, 1855, pl. 2, figs. 1–1c.
Amphidetus ampliflorus McCrady in Toumey and Holmes, 1855, p. 6, pl. 3, figs. 2, 2a.
Echinocardium virginianum (Forbes). Desor, 1858, p. 408.
Amphidetus virginianus Forbes. Emmons, 1858, p. 310, figs. 245a–c.
Amphidetus ampliforus (McCrady). Meek, 1864, p. 2.
Amphidetus gothicus (Ravenel). Meek, 1864, p. 2.
Amphidetus orthonotus (Conrad). Meek, 1864, p. 2.
Echinocardium orthonotum (Conrad). Clark, 1904, p. 430. (not pl. 119, figs. 1a–c. which is *E. marylandiense*).
Echinocardium orthonotum (Conrad). Grabau and Shimer, 1910, p. 603. (not fig. 1937e, f and Maryland references which are *E. marylandiense*).
Echinocardium gothicus (Ravenel). Clark and Twitchell, 1915, p. 214.
Echinocardium orthonotum (Conrad). Clark and Twitchell, 1915, p. 213, pl. 97, figs. 2a–c, (not pl. 98, figs. 2a–c which is *E. marylandiense*).
Amphidetus gothicus (Ravenel). Lambert and Thiéry, 1924, p. 470.
Echinocardium gothicum (Ravenel). Cooke, 1942, p. 60.
Echinocardium orthonotum (Conrad). Cooke, 1942, p. 60.
Echinocardium gothicum (Ravenel). Cooke, 1959, p. 79, pl. 33. figs. 7–10.
Echinocardium orthonotum (Conrad). Cooke, 1959, pp. 78, 79, (not pl. 33. fig. 1–5 which is *E. marylandiense*).
Echinocardium gothicum (Ravenel). Kier, 1963, p. 56, pl. 11, fig. 4.
Echinocardium orthonotum (Conrad). Kier, 1972, pp. 12–16, fig. 5. pl. 8, figs. 3–7. pl. 9.
Echinocardium orthonotum (Conrad). Ciampaglio et al., 2009, fig. 2.
Echinocardium orthonotum (Conrad). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—*Echinocardium orthonotum* is a common spatangoid of the upper Pliocene strata of Florida and is documented in the Jackson Bluff, Intracoastal, and Tamiami Formations: Jackson Bluff Formation, below the dam on the Ochlockonee River, Leon County (FM locality LN004); Intracoastal Formation, Langston Quarry, Liberty County (FM locality LI005) (Ciampaglio and Osborn, 2011); Tamiami Formation (sand facies *sensu* Missimer, 1992), Quality Materials Quarry, Charlotte County (FM locality CH080); float from spoil banks of canals and north bank of north fork of Alligator Creek west of US Route 41, Sea Lanes Subdivision, Punta Gorda (USGS locality 22454); float from east side of Sam Knight canal crossing with U.S. Route 41, 3.9 km west of Murdock Station (Port Charlotte) Charlotte County (USGS locality 22916) (Kier, 1963).

Echinocardium is also documented in the Nashua Formation, at the East Coast Aggregates Quarry in St. Johns County (FM locality SJ007). However, the specimens available (UF 84281) consist of fragmentary material that is attributable to *Echinocardium* and, lacking other alternatives, most likely *E. orthonotum*. This occurrence was first documented by Oyen (2001) as *E.* cf. *orthonotum*; however, being unable to pinpoint the bed from which Oyen's (2001) *E.* cf. *orthonotum* originated, we are unable to ascertain if the material came from the Pliocene or Pleistocene portion of the Nashua Formation, so we tentatively include the species in the Nashua fauna (Fig. 4). However, it is more likely the specimens originated in the late Pliocene portion exposed at the site, as *E. orthonotum* is not otherwise documented from the Pleistocene.

This species also occurs in the late Pliocene upper Goose Creek Limestone of South Carolina and the middle Pliocene Yorktown Formation of Virginia.

Discussion.—Kier (1963) recorded the occurrence of fragmentary *Echinocardium* in the barnacle-echinoid facies of DuBar (1958, 1962) (sand facies *sensu* Missimer, 1992) of the Tamiami Formation in Charlotte County, Florida. He tentatively attributed the material to *E. gothicum*, but due to the incompleteness of the material, he could not support the identification. Kier (1972) subsequently designated *E. gothicum* as a subjective junior synonym of *E. orthonotum*, an assertion with which we concur. This material is therefore attributable to *E. orthonotum* and this occurrence greatly expands southward the known distribution.

Kier (1972) stated that the specimen Cooke (1959) referred to *E. orthonotum* from the upper

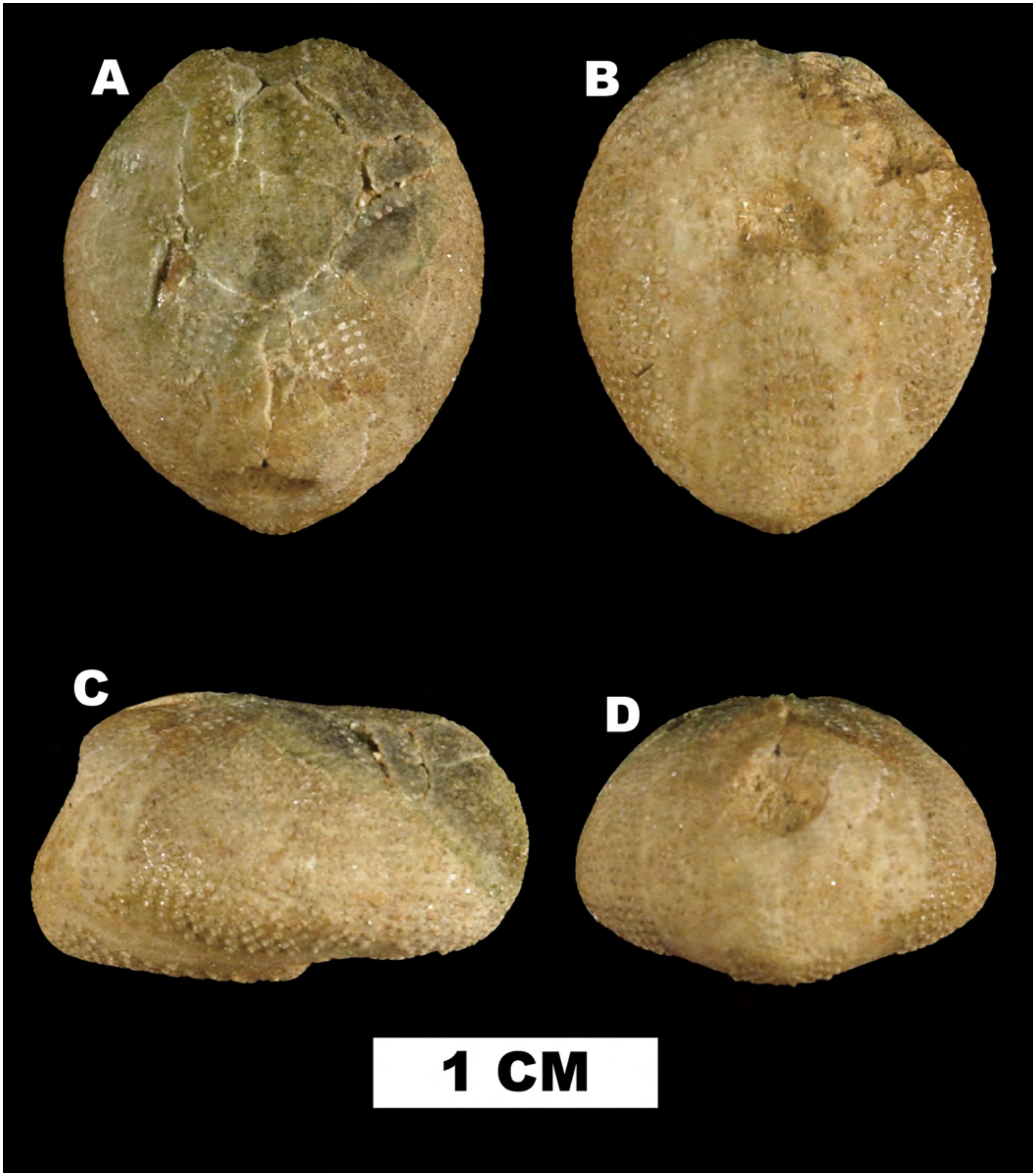


Figure 136. *Echinocardium orthonotum* (UF 300114), Jackson Bluff Formation (FM locality LN008). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

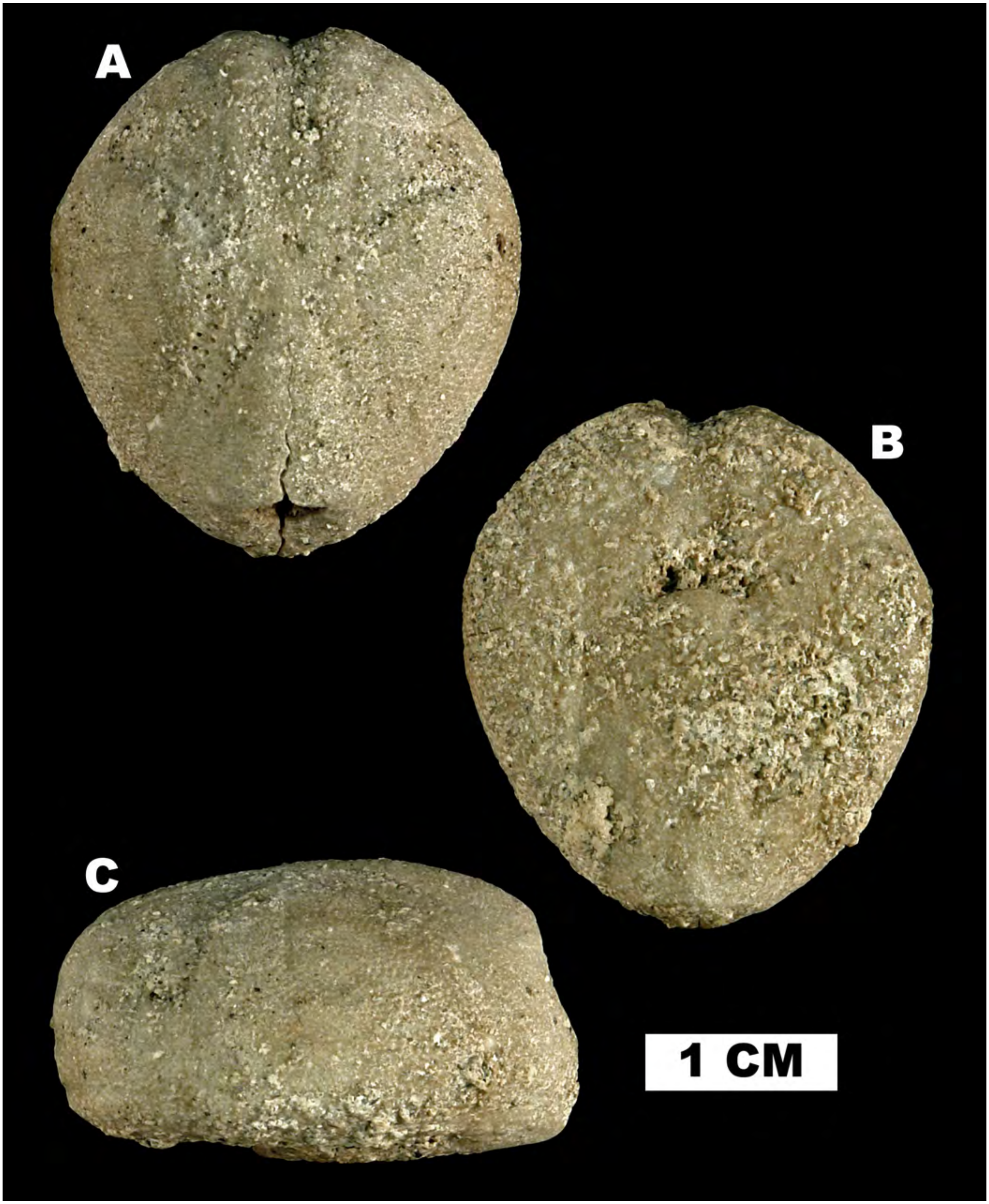


Figure 137. *Echinocardium orthonotum* (UF 289229), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. lateral view.

Pliocene Jackson Bluff Formation at Jackson Bluff (FM locality LN004) is too poorly preserved to attribute to the species. Additional material from this locality (UF 300114) is attributable to *E. orthonotum* (Fig. 136). In addition, Ciampaglio and Osborn (2011) documented the occurrence of *E. orthonotum* in the upper Pliocene Intracoastal Formation of Liberty County in the Florida panhandle (UF 289229; Fig. 137).

Specimens of *E. orthonotum* have been collected in the upper Pliocene Tamiami Formation in the Quality Materials Quarry in Charlotte County (FM locality CH080) that retain their complete spination (UF 289218; Fig. 138). An additional specimen from the Tamiami Formation in DeSoto County (UF 114430; Fig. 139) retains spination largely on the oral surface. The spination is very similar to that of Recent *Echinocardium cordatum* (Pennant, 1777) and *Echinocardium leopolitanum* Radwański and Wysocka, 2001 from the Ukrainian

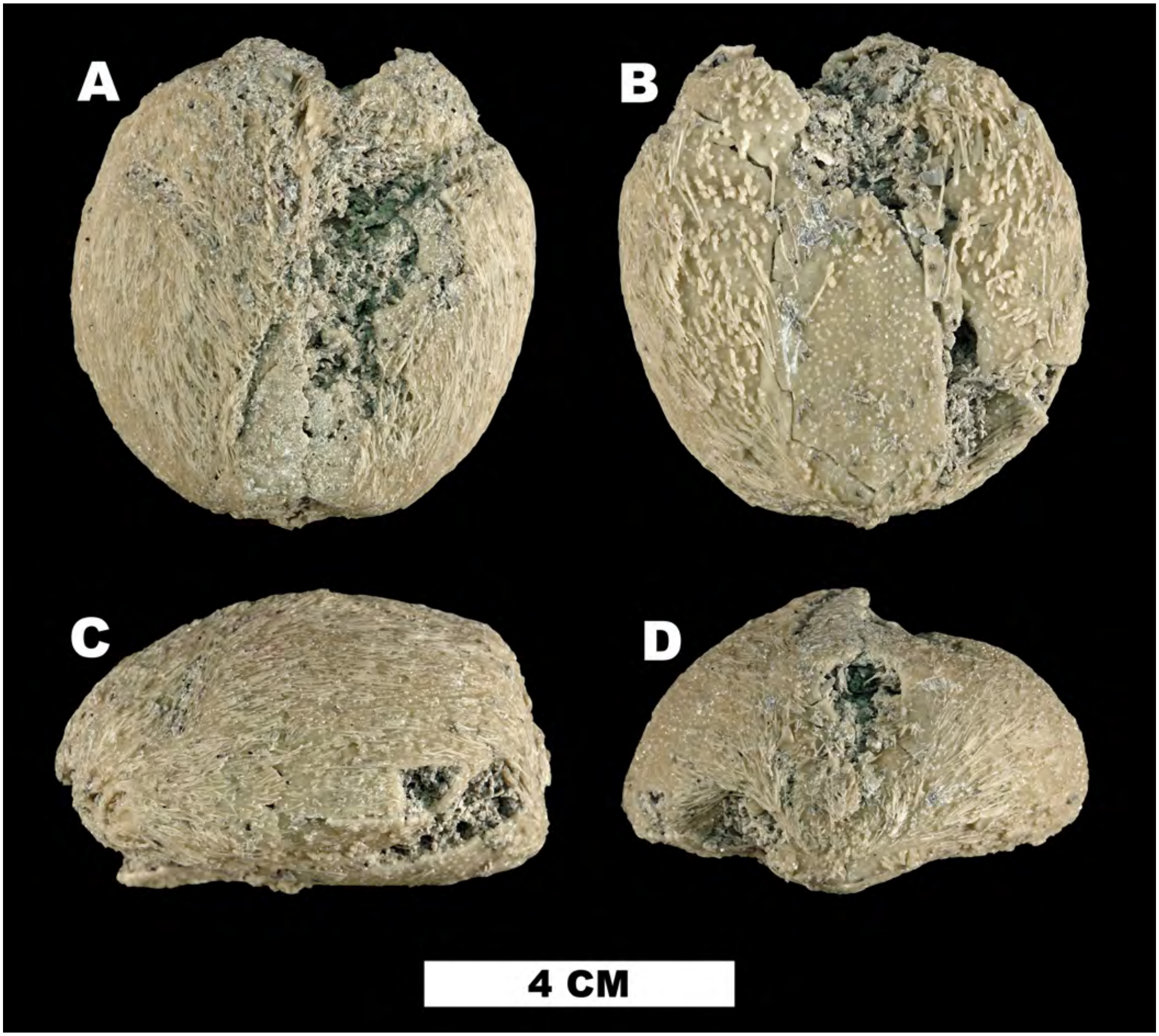


Figure 138. *Echinocardium orthonotum* with spines (UF 289218), Tamiami Formation (FM locality CH080). A. aboral view, B. oral view, C. lateral view, D. posterior view.

Miocene documented by Radwański and Wysocka (2001) and Radwański et al. (2014), with no discernible differences.

Family **SCHIZASTERIDAE** Lambert, 1905
Genus ***MOIRA*** A. Agassiz, 1872
MOIRA ATROPOS (Lamarck, 1816)
Figures 140–141

Spatangus atropos Lamarck, 1816, p. 32.
Echinocardium atropos (Lamarck). Gray, 1825, p. 430.
Schizaster atropos (Lamarck). Agassiz, 1836, p. 185.
Schizaster atropos (Lamarck). Ravenel, 1848, p. 4.
Schizaster atropos (Lamarck). Holmes, 1860, p. 5, pl. 2, fig. 3.
Moira atropos (Lamarck). A. Agassiz, 1874, p. 365, pl. 23.
Moira atropos (Lamarck). Cooke, 1942, p. 43.
Moira atropos (Lamarck). Mortensen, 1951, p. 329, pl. 19, figs. 15, 20. pl. 55, figs. 11, 16, 19–23 (includes significant additional synonymy).

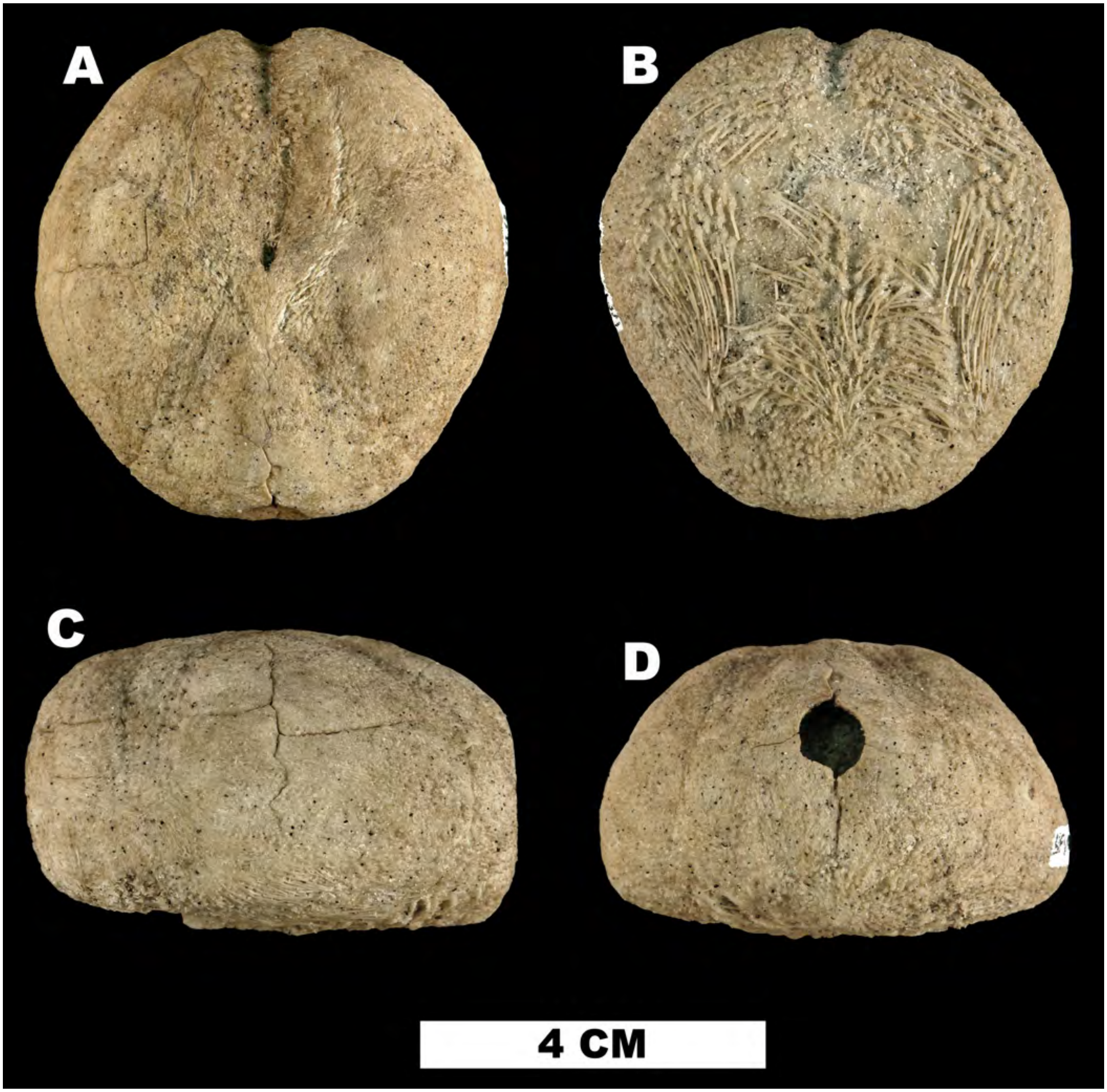


Figure 139. *Echinocardium orthonotum* with spination on oral surface (UF 114430), Tamiami Formation (FM locality DE021). A. aboral view, B. oral view, C. lateral view, D. posterior view.

Moira atropos (Lamarck). Cooke, 1959, pp. 73, 74, pl. 30, figs. 1–4.
Moira atropos (Lamarck). Cooke, 1961, pp. 22, 23, pl. 6, figs. 1–4.
Moira atropos (Lamarck). Chesher, 1963, pp. 549–573.
Moira atropos (Lamarck). Fischer, 1966, p. U576, figs. 456, 3a–3e.
Moira atropos (Lamarck). Moore and Lopez, 1966, pp. 648–667.
Moira atropos (Lamarck). Weisbord, 1969, pp. 325–329, pl. 53, figs. 4–10 (includes extensive additional references).
Moira atropos (Lamarck). Kier, 1975, pp. 15, 16, pl. 8.6–8.10.
Moira atropos (Lamarck). Serafy, 1979, pp. 91–93, fig. 39.
Moira atropos (Lamarck). Kier, 1992, p. 20, pl. 7, figs. 3, 4.
Moira atropos (Lamarck). Hendler et al., 1995. pp. 238, 239, figs.127, 135C.
Moira atropos (Lamarck). Oyen, 2001, p. 226, figs. 3–39 A–H.
Moira atropos (Lamarck). Pomory, 2003, pp. 37–39, fig.16.
Moira atropos (Lamarck). Mihaljevic et al., 2010, pp. 10–12, fig. 8.

Occurrence.—*Moira atropos* is documented in the Florida fossil record from the middle Pleistocene Bermont Formation in the Longan Lakes Quarry, Collier County (FM locality CR015), and temporary exposures near Cooper City, Broward County (FM locality BD004). Fragmentary material (UF 105553) that is definitely schizasterid, and potentially referable to *M. atropos*, was obtained from the Nashua Formation in Putnam County (FM locality PU004). However, this material is insufficient to unequivocally identify even to genus and is therefore not included in Fig. 4.

The species is also tentatively documented from the Pleistocene of South Carolina (Cooke, 1959) and the fossil record of the Caribbean Region: Dominican Republic (Pliocene [Kier, 1992]); Venezuela (Pliocene-Pleistocene [Cooke, 1961; Weisbord, 1969; Mihaljevic et al., 2010]).

Discussion.—*Moira atropos* occurs today from Cape Hatteras, North Carolina and Bermuda, southward through the Greater and Lesser Antilles and along the coasts of the Gulf of Mexico and Central and South America to Sao Paulo Brazil (Serafy, 1979).

This fragile little species cannot be confused with any other echinoid in the region. Its very deeply sunken frontal ambulacrum is unique. Chesher (1963) completed a detailed review of the morphology and function of this anterior ambulacrum and stated that is the most deeply sunken ambulacrum to be found in any echinoid. The great depth of the frontal ambulacrum permits *Moira* to have many large tube feet in a small area. This increase in size and number of aboral tube feet gives *Moira* a greater burrowing range, and provides for the transport of nutrient-rich surface debris to the peristome. Chesher found that this highly specialized ambulacrum functions well in almost any substrate ranging from the finest silt to heavy coral gravel. However, *M. atropos* lives primarily in soft mud where food is more abundant (Chesher, 1963).

Oyen (2001) provided the first documentation of *M. atropos* in the Pleistocene of Florida when he figured and discussed a specimen from the Bermont Formation of south Florida. A search of the University of Florida collections reveals additional specimens, largely fragmentary, that are referable to this species from the Bermont Formation and potentially from the Nashua Formation (UF 105553), as discussed above in the occurrence overview for the species; proving the species has greater presence in the fossil record of the region than previously known.

The best-preserved representative from the fossil record of Florida is UF 100180 from the Bermont Formation, Broward County (FM locality BD004; Fig. 140). A modern representative of the species from Marco Island is shown in Figure 141.

Genus ***SCHIZASTER*** L. Agassiz, 1836

SCHIZASTER KIERI Osborn, 2011

Figure 142

Schizaster kieri Osborn in Ciampaglio and Osborn, 2011, pp. 95–102, pl. 1, figs. a–e.

Occurrence.—*Schizaster kieri* has not been documented outside of its type locality in the Langston Quarry, Liberty County (FM locality LI005), where it rarely occurs in the upper Pliocene Intracoastal Formation.

Discussion.—When Ciampaglio and Osborn (2011) documented the presence of *S. kieri* in the Intracoastal Formation, it was the first documented occurrence of the genus *Schizaster* in the Pliocene of the east coast of North America. It is readily differentiated from its stratigraphically nearest eastern North American congener, the Oligocene *S. americanus*, by its much more elongate test, more wedge-shaped profile, and more posterior apical

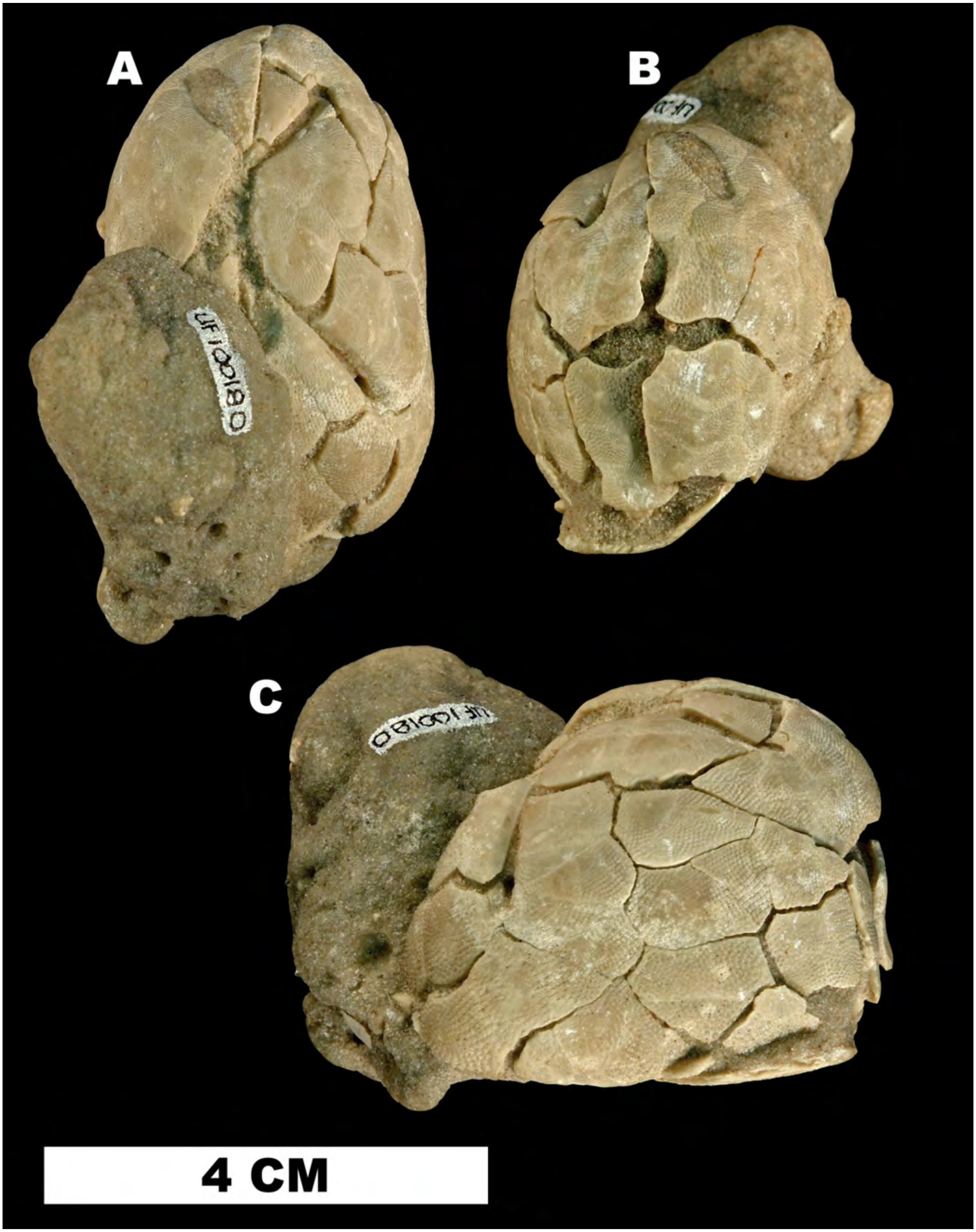


Figure 140. *Moira atropos* (UF 100180), Bermont Formation (FM locality BD004). A. aboral view, B. posterior view, C. right lateral view.

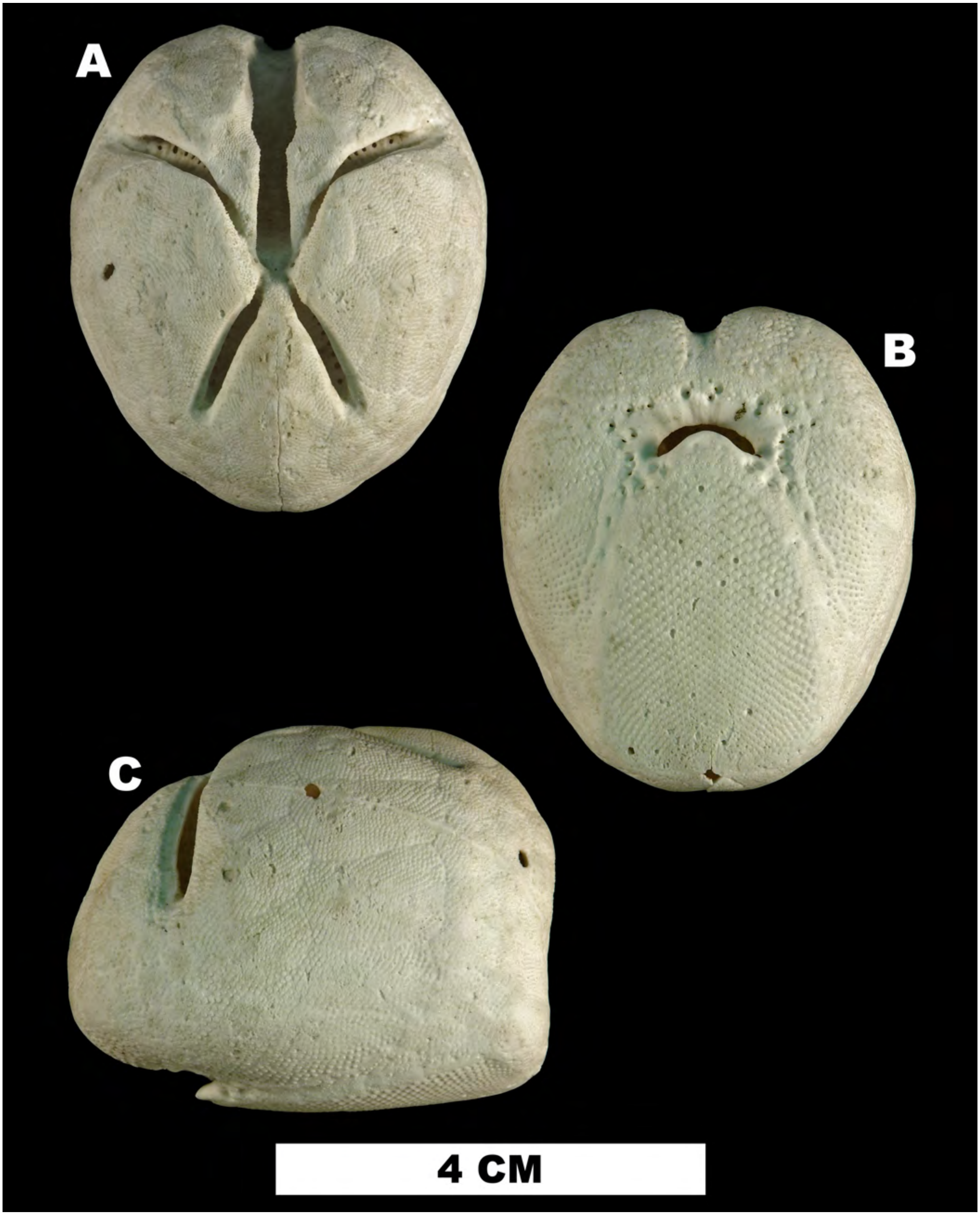


Figure 141. *Moira atropos* (UF-IZ 18911), modern specimen for comparison (off Marco Island, Collier County, Florida, USA). A. aboral view, B. oral view, C. lateral view.

system (Fig. 142).

Schizaster kieri has not been documented outside of the upper Pliocene Intracoastal Formation, in the Langston Quarry, Liberty County (FM locality LI005), where it is rare, but is part of a diverse assemblage of echinoids, including *Arbacia improcera, Clypeaster sunnilandensis, Encope aberrans, Genocidaris oyeni* n. sp., and a spatangoid fauna dominated by *Echinocardium orthonotum* with limited occurrences of *Plagiobrissus sarae* and *Fernandezaster whisleri* n. sp., and other, rarer species.

SCHIZASTER sp.

Figure 143

Occurrence.—Lower Miocene Chattahoochee Formation, Jim Woodruff Dam (FM locality JA003), Gadsden County, Florida.

Discussion.—This specimen (UF 229789) is significant as the only documented occurrence of *Schizaster* in the Miocene of the region. The specimen consists of an internal mold that measures 58 mm TL, 55.8 mm TW, and roughly 30 mm TH (precise height is obscured by matrix). This is one of only three echinoid taxa documented in the Chattahoochee Formation, joining rare *Arbia aldrichi* in a fauna dominated by *Lovenia clarki*. The only known specimen is a weathered internal mold that preserves very little detail other than the overall shape of the test (Fig. 143). The test is inflated, wedge-shaped (in typical *Schizaster* fashion), with furrows on the aboral surface that are likely the traces of very depressed ambulacra. The anterior ambulacrum cuts the anterior ambitus with a frontal sinus, the depth of which is slightly obscured with matrix. In all aspects, the specimen is a *Schizaster*, but additional material will be required to allow better characterization.

Family **PERICOSMIDAE** Lambert, 1905

Genus ***PERICOSMUS*** L. Agassiz in L. Agassiz and Desor, 1847

PERICOSMUS sp.

Figures 144–145

Pericosmus sp. Oyen et al., 2000, pp. 235–241, figs 7–8.

Occurrence.—Pliocene-Pleistocene? formation unknown, dredged in 510–520 m of water depth in the Gulf of Mexico (FM localities 3784 and 3810).

Discussion.—Oyen et al. (2000) documented the occurrence of internal molds of a species of echinoid they referred to the genus *Pericosmus*. Although we find that condition of the specimens precludes unequivocal identification, we here follow Oyen et al. (2000) in suggesting it is a member of *Pericosmus*. The two specimens (UF 101885 [Fig. 144] and UF 66566 [Fig. 145]) suggest a large, heart-shaped, depressed spatangoid, with the larger of the two measuring 97.8 mm TL and 93 mm TW.

The anterior is notched where ambulacrum III crosses the ambitus, creating a moderately deep sulcus. However, details of the ambulacral (other than the distal ends of two petals on one specimen) or other test features besides overall shape, are lacking. Given the uncertainty of the age assignment and only tentative taxonomic assignment of this material, it was not included in the stratigraphic distribution in Figures 2–4.

Family **PRENASTERIDAE** Lambert, 1905

Genus ***AGASSIZIA*** Valenciennes, 1846

AGASSIZIA PORIFERA Ravenel, 1848

Figures 146–147

Brissopsis poriferus Ravenel, 1848, p. 4, figs. 5, 6.
?*Brissopsis rimulatus* Ravenel, 1848, p. 4, figs. 3, 4.
Agassizia porifera (Ravenel). McCrady in Tuomey and Holmes, 1855, p. 5, pl. 1, figs. 5–5b; pl. 2, figs. 4, 4a.
?*Agassizia rimulata* (Ravenel). McCrady in Tuomey and Holmes, 1855, p. 5.
Agassizia porifera (Ravenel). A. Agassiz, 1872, p. 88.
Agassizia porifera (Ravenel). A. Agassiz, 1874, p. 751.
Agassizia porifera (Ravenel). Clark and Twitchell, 1915, p. 212, pl. 97, figs. 1a–d.
?*Brissopsis rimulatus* Ravenel. Clark and Twitchell, 1915, p. 154.
Agassizia porifera (Ravenel). Cooke, 1942, p. 45.
?*Agassizia rimulata* (Ravenel). Cooke, 1942, p. 45.
Agassizia porifera (Ravenel). Cooke, 1959, pp. 74, 75, pl. 31. figs. 1–8.
Agassizia porifera (Ravenel). Kier, 1963, pp. 52–56, pl.16, figs. 1–2; pl. 18, figs. 1–5; text figs. 51–58.
not *Agassizia scrobiculata* (Valenciennes). Weaver et al., 2006, p. 80, fig. 6.1–6.4 (specimen is not *A. scrobiculata*).
Agassizia porifera (Ravenel). Ciampaglio et al., 2009, fig. 2.
Agassizia porifera (Ravenel). Ciampaglio and Osborn, 2011, fig. 2.

Occurrence.—Within Florida, this rotund species has been documented in both the upper

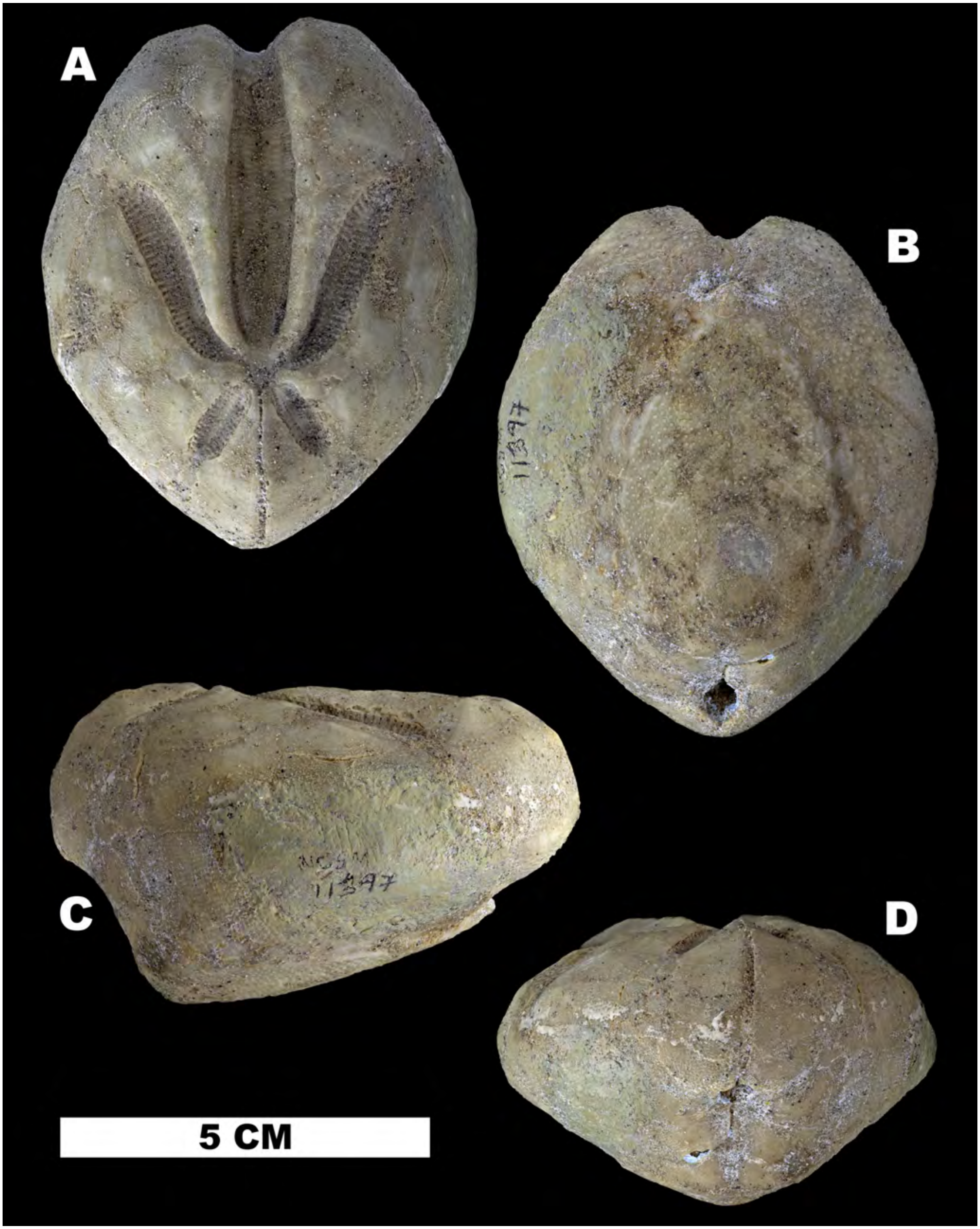


Figure 142. *Schizaster kieri* holotype (NCSM 11397), Intracoastal Formation (FM locality LI005). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

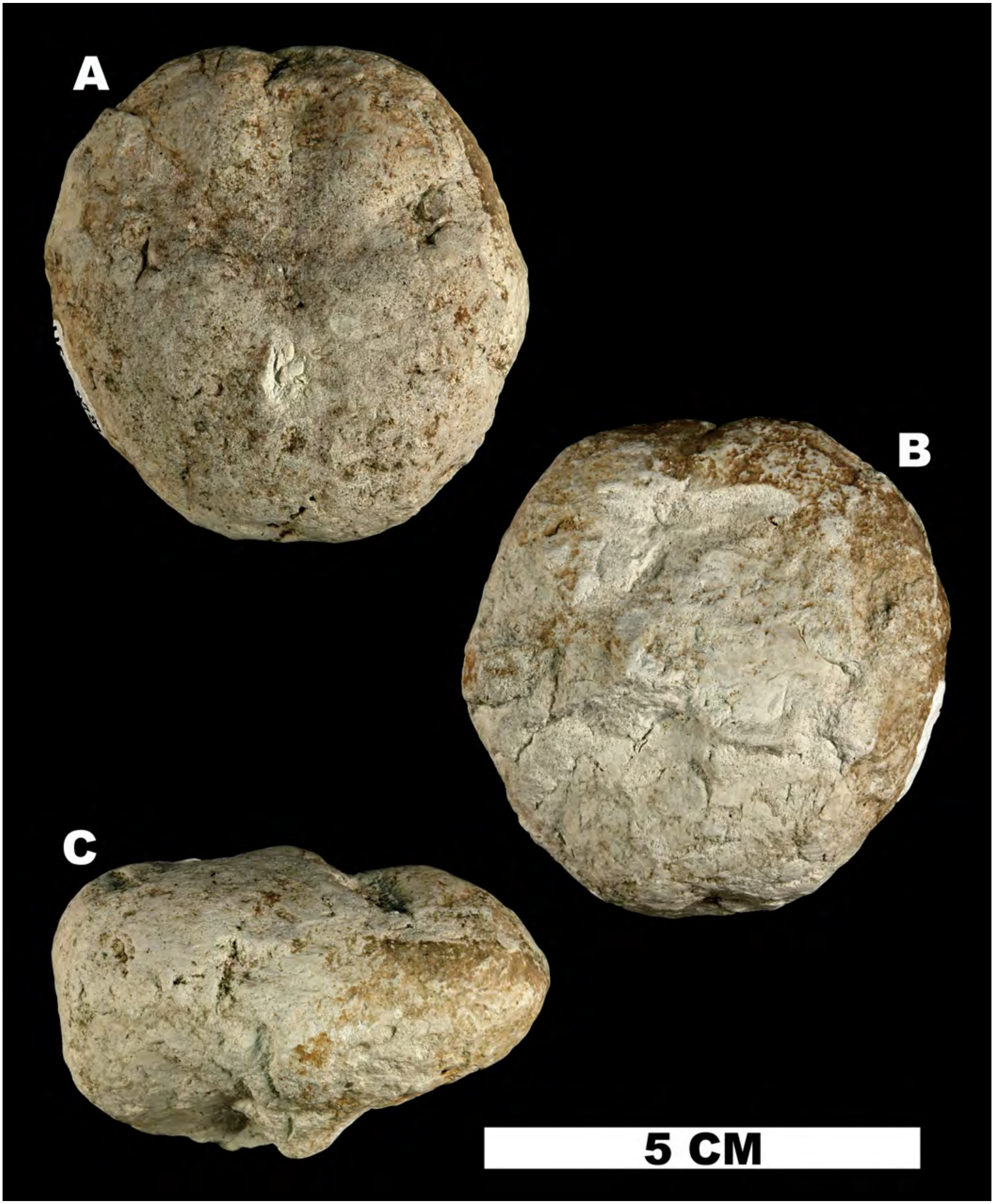


Figure 143. *Schizaster* sp. (UF 229789), Chattahoochee Formation (FM locality GD005). A. aboral view, B. oral view, C. right lateral view.

Figure 144. *Pericosmus*(?) sp. (UF 101885), formation unknown (FM locality 3784). A. aboral view, B. oral view, C. lateral view.

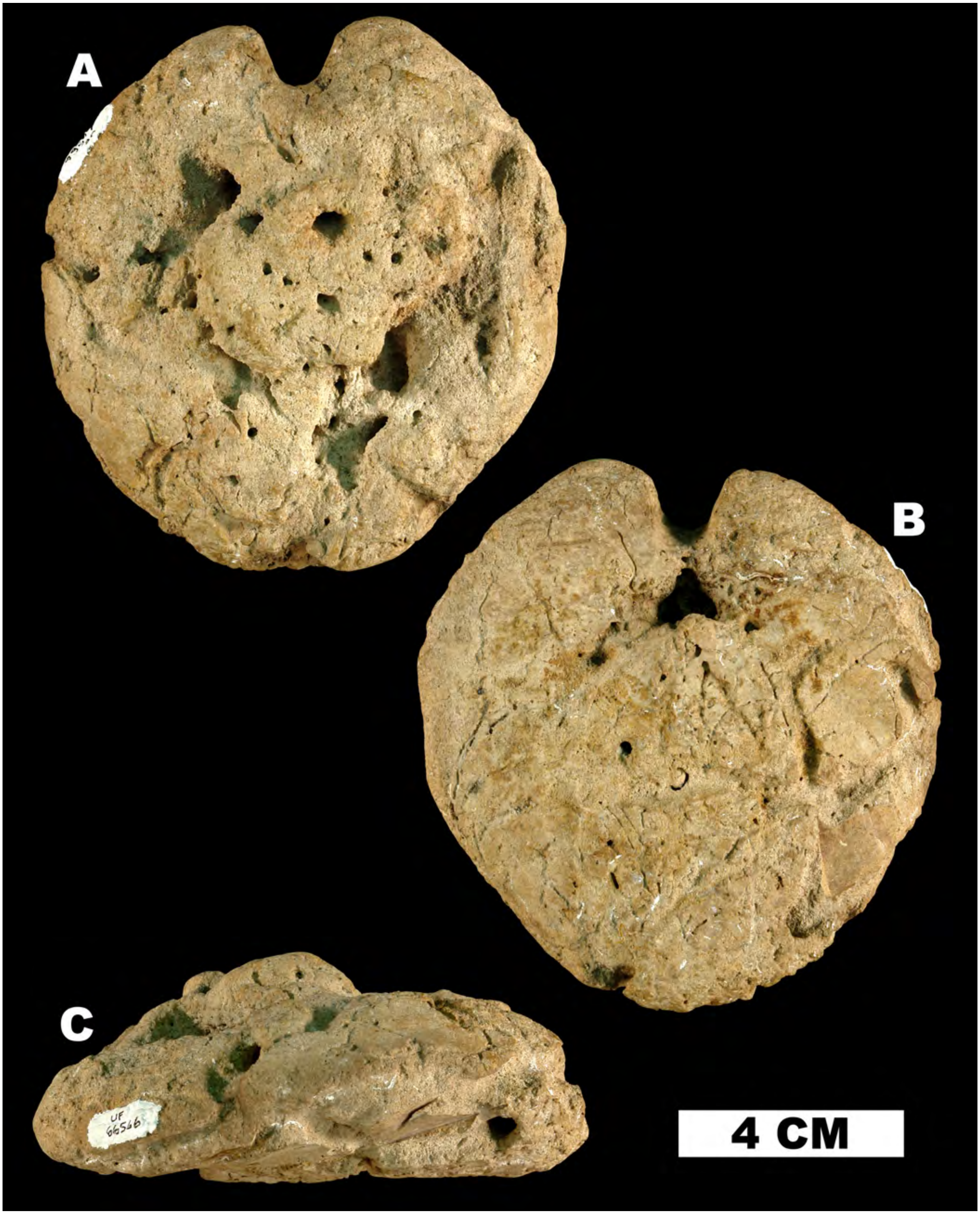


Figure 145. *Pericosmus*(?) sp. (UF 66566), formation unknown (FM locality 3810). A. aboral view, B. oral view, C. lateral view.

Pliocene Tamiami and lower Pleistocene Caloosahatchee Formations. Tamiami Formation: Quality Materials Quarry, Charlotte County (FM locality CH080); Caloosahatchee Formation (Bee Branch Member sensu DuBar, 1958): float from the north bank of the Caloosahatchee River and from road metal ("LaBelle") pits on the north bank of the Caloosahatchee River in SE¼ sec. 12, T, 43 S., R. 28. E., Sears Quadrangle, Hendry County (USGS locality 23082); float in Denaud pits, in NW¼ sec. 14, T. 43 S., R. 28 E., Sears Quadrangle, Hendry County (USGS locality 22373) (Kier, 1963); and Cochran Shell Pit, Hendry County (FM locality HN004).

Agassizia porifera also occurs in the lower Pleistocene James City and Waccamaw Formations of North Carolina, and the upper Pliocene Goose Creek Limestone and lower Pleistocene Waccamaw Formation of South Carolina.

Discussion.—Cooke (1959) attributed *A. porifera* to the late Miocene of South Carolina. However, current understanding of the strata at the type locality, the plantation of Dr. Ravenel, known as "The Grove" along the Cooper River, near Charleston, places it in the upper Pliocene, Goose Creek Limestone (sensu Campbell and Campbell, 1995).

Kier (1963) subsequently documented the occurrence of *A. porifera* in the lower Pleistocene Caloosahatchee Formation near LaBelle, Florida. Ciampaglio et al. (2009:fig. 2) then documented it in the upper Pliocene Goose Creek Limestone of South Carolina as well as the lower Pleistocene Waccamaw Formation of the Carolinas. Ciampaglio and Osborn (2011) provided the first documented occurrence of *A. porifera* in the upper Pliocene Tamiami Formation of Florida.

Concerning the population from the Caloosahatchee Formation, Kier (1963) stated that the Florida specimens are clearly conspecific with those described and illustrated by Cooke (1959:74, pl. 31, figs. 1–8) from South Carolina. Kier (1963) noted that on first impression they do not appear to be conspecific with Ravenel's holotype as figured by McCrady (in Tuomey and Holmes, 1855:1, figs. 5–5b) because most of the Florida specimens he had available for examination were larger and more inflated. However, Kier noted that one specimen is approximately the same size as the holotype and cannot be identified to species.

The largest specimens of *A. porifera* in the FM-IP collections are from the Caloosahatchee Formation in the Cochran Shell Pit, Hendry County (FM locality HN004). These specimens range from 64 to 74.9 mm TL, 58 to 70.3 mm TW, 48 to 56 mm TH, and are significantly larger and more swollen in appearance than *A. porifera* from the upper Pliocene Tamiami Formation of southwestern Florida (Fig. 146). The largest specimen Kier (1963) had available for study measured 79 mm TL, 76 mm TW, and 64 mm TH, and was also from the Caloosahatchee Formation. We herein figure specimens from both units. The largest specimen available from the Tamiami Formation (UF 117110) measures 60 mm TL, 57 mm TW, 46 mm TH (Fig. 147), rivaling the Caloosahatchee specimens in size.

In the Bee Branch Member (sensu DuBar, 1958) of the lower Pleistocene Caloosahatchee Formation of Hendry County Florida, *A. porifera* occurs with *Clypeaster subdepressus, Clypeaster rosaceus, Encope michelini, Rhyncholampas ayersi*, and other, rarer species. In the underlying upper Pliocene Tamiami Formation, *A. porifera* is rare, but most commonly found in the sand facies of Missimer (1992), especially in the Quality Materials Quarry, Charlotte County (FM locality CH080), where it occurs with an extensive suite of echinoids, including *Encope tamiamensis, Lytechinus variegatus, Rhyncholampas evergladensis,* and many other, rarer species.

AGASSIZIA sp. 1
Figure 148

Occurrence.—A single specimen of this genus, UF 28401, was collected in the lower Miocene portion of the Arcadia Formation at Deans Trucking Pit in Sarasota County (FM locality SO006).

Discussion.—The only known specimen of this taxon (Fig: 148) consists of an internal mold with petaloid structure and general morphology indistinguishable from the genus *Agassizia*. The specimen measures 13.2 mm TL, 13.9 mm TW, and

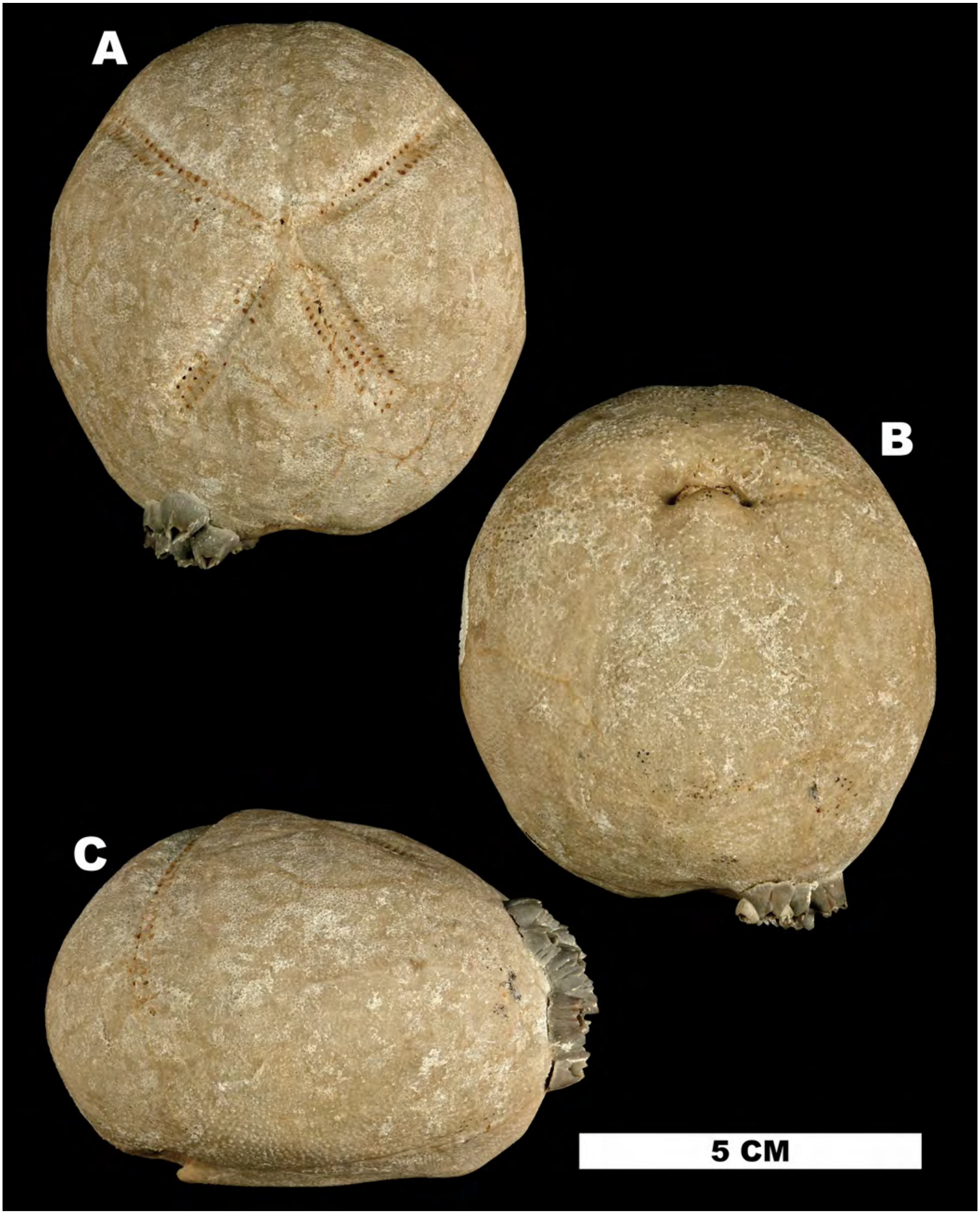


Figure 146. *Agassizia porifera* (UF 12894), Caloosahatchee Formation (FM locality HN004). A. aboral view, B. oral view, C. lateral view.

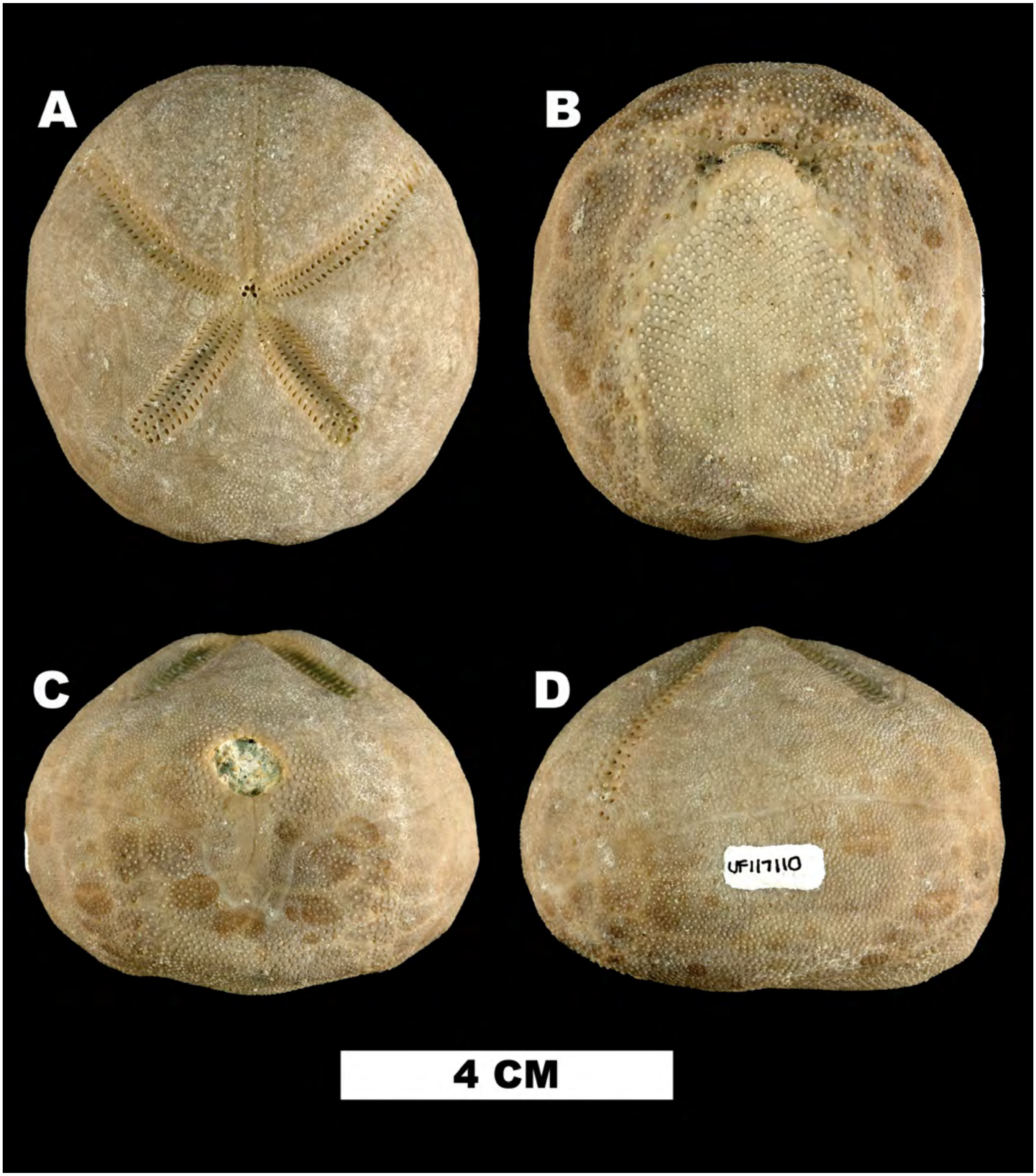


Figure 147. *Agassizia porifera* (UF 117110), Tamiami Formation (FM locality 3241). A. aboral view, B. oral view, C. posterior view, D. lateral view.

9.3 mm TH. However, the specimen is compressed, incomplete, and lacks sufficient details to determine if it is an existing or new species. Other than an additional internal mold of an *Agassizia* from the upper Arcadia Formation (discussed below), the genus *Agassizia* is not documented in the Miocene strata of the eastern United States. This specimen has a much more anterior apical system than UF 237249. Additional material, preferably non-moldic, will be required to ascertain variation within the species, and assessment of relevant characteristics that might warrant its description as new to science.

AGASSIZIA sp. 2

Figure 149

Occurrence.—A specimen of an undetermined *Agassizia* (UF 237249) was collected in the lower Miocene portion of the Arcadia Formation at Fort Meade in Polk County (FM locality PO035).

Discussion.—The only known specimen of this taxon (Fig. 149) consists of an internal mold with petaloid structure and general morphology indistinguishable from the genus *Agassizia*, with a more posterior apical system, than seen in UF 28401. However, as for specimen UF 28401 (also from the upper portion of the Arcadia Formation), discussed above, the mold lacks details sufficient to be attributed into an existing species. Other than UF 28401, *Agassizia* is not documented in the Miocene strata of the eastern United States.

This specimen measures 37 mm TL, 30 mm TW, 29 mm TH, and appears to have an apical system located much further posteriorly than in *Agassizia porifera*, its stratigraphically nearest congener, or UF 28401 (Fig. 148). However, additional material, preferably non-moldic, will be required to ascertain variation within the species, and assessment of relevant characteristics that might warrant its description as a new species. We include it herein to draw attention to the Miocene form of the region, pending discovery of additional material.

CONCLUSIONS

This work includes all occurrences of echinoids currently known to the authors within Florida's

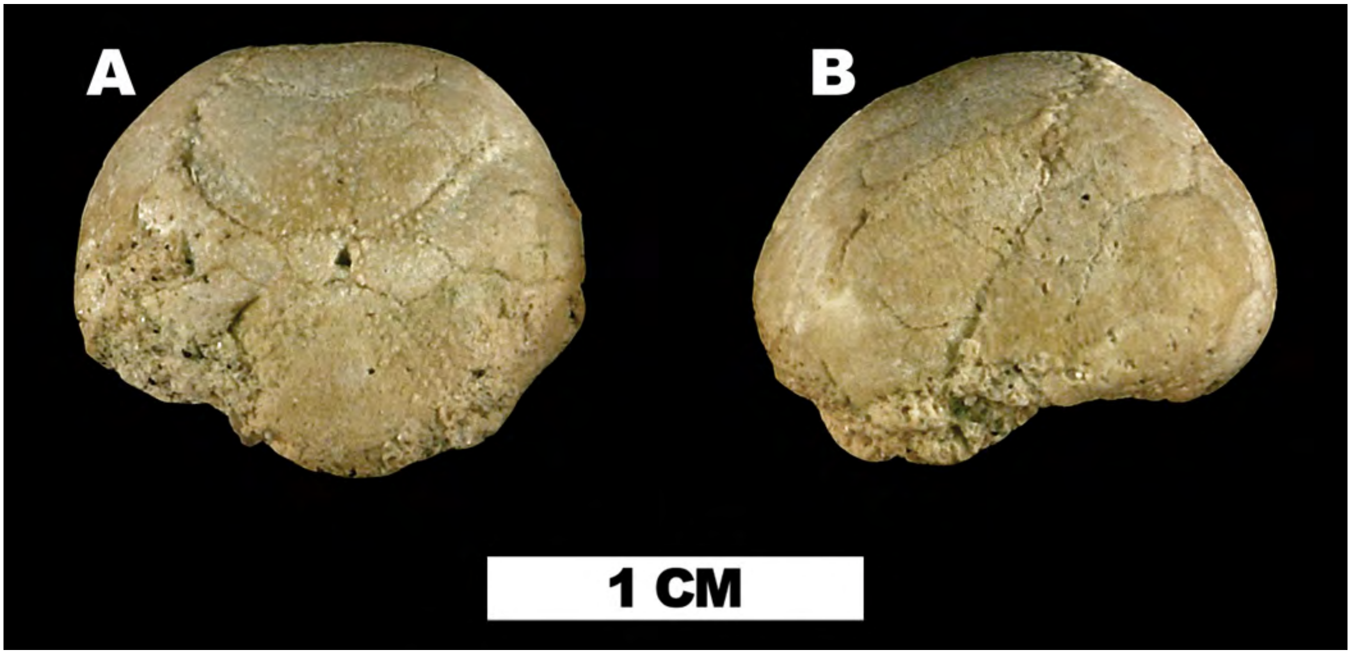


Figure 148. *Agassizia* sp. 1 (UF 28401), upper Arcadia Formation (FM locality SO006). A. aboral view, B. lateral view.

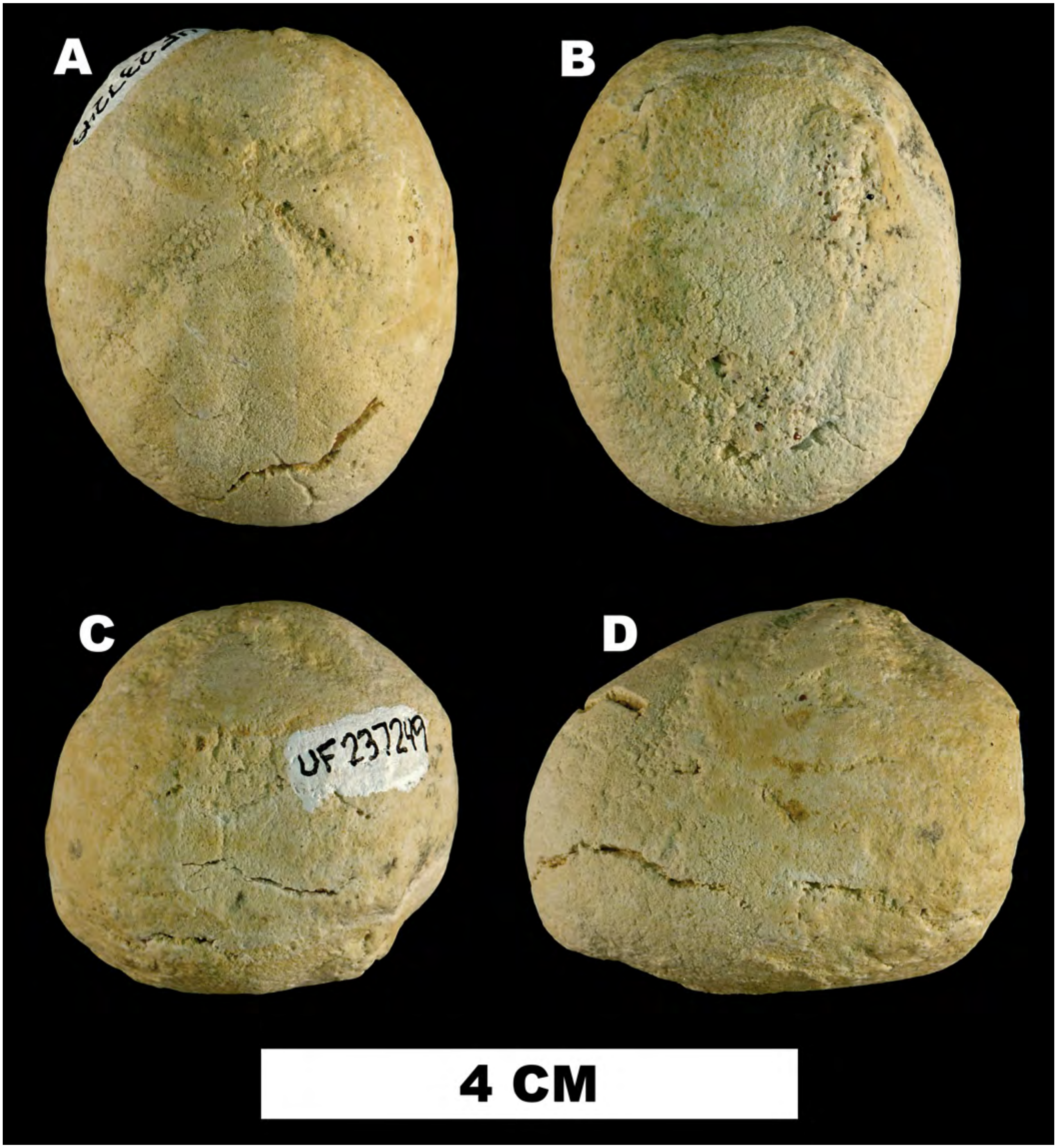


Figure 149. *Agassizia* sp. 2 (UF 237249), upper Arcadia Formation (FM locality PO035). A. aboral view, B. oral view, C. right lateral view, D. posterior view.

Neogene strata. It is based on decades of extensive collecting, thorough examination of the FM-IP collections, the collections of regional institutions, and the collections of numerous avocational collectors whose diligence and willingness to share important specimens is unrivaled and worthy of recognition. In spite of their extensive and valued efforts, there undoubtedly remain large numbers of undocumented species. It is hoped that a monographic treatment such as the one presented here will spark further interest in the echinoids of this important and crucial time interval on the part of both avocational paleontologists and professional scientists. In this way, new data can be developed concerning the evolution of echinoid faunas in the region, and bring to light additional material of described species as well as of species new to science.

The Neogene strata of Florida are heavily collected, but often by eyes more eager to seek out the world-famous vertebrates and molluscs contained within its layers, and not so much the echinoids that co-occur. Additional examination by sediment screening will be particularly helpful in uncovering new specimens, as small echinoids that might otherwise be overlooked can greatly add to our understanding of echinoid distributions within the Florida Neogene. The present work is not intended to be the final word, but another benchmark in a historically rich path to more completely understand the diversity of echinoids within the sedimentary sequences of Florida.

ACKNOWLEDGMENTS

We thank the following individuals for significant contributions that led directly to the completion of this work, either through specimen donations, time spent collecting specimens in the field, or discussions about echinoids that led to improvements of the manuscript: John Beerensson, the late Billy Bell, the late Evelyn and Ernest Bradley, Jon Bryan, David and Billy Cale, Rob Carlson, David Cass, Janessa Cobb, Wendy Conway, Ed Derouin, the late Jules DuBar, Joseph Dumont, Kendell Fountain, George Hecht, Fred Hendershot, Joan Herrera, Dave Hoffman, the late Muriel Hunter, Sue and Steve Hutchens, Douglas Jones, Eric Kendrew, Andreas Kerner, Alex Kittle, Curtis Klug, Gunther Lobisch, Fred Mazza, Guy H. Means, Gary Morgan, Jim Morris, Andy Murray, the late Craig Oyen, James Pendergraft, Michelle Penkrot, Carol and Bernie Peterson, Greta Polites, Pam Plummer, John Sacha, Craig and Lori Samuel, Gary Schmelz, Kevin Schindler, Thomas Scott, Steve, Chris, and Michael Sharpe, Byron Shumaker, the late Malcolm Telford, David Tharpe, Joseph Valentine, John Waldrop, Joseph and Shirley Welch, and Phillip Whisler. Additionally, we are indebted to the land owners and quarry operators who allowed access to their property and excavations: Stephen Addington, Joe Alex, W.F. Barton, D.E. Bleakley, Herb Bowman, Sonny Cochran, Walter Crabtree, William Casey, Jon Courtney, Joe Duke, Glenn Freemont, Anna Handgen, Terry Hall, Mitchell Hancock, Burke and Burt Hayes, Larry Heimer, Eugene Henshaw, Jr., James Ivey, Tom Jones, Pete Karashay, Howard Kirk, Elaine Klein, Mark Kneehouse, Gene Langston, Robert Larson, Todd Lybrand, Pete Miniear, Aleta Mitchell-Tapping, Dave Myers, Jimmy and Pat Philman, Nancy Plank, Bryan Register, Cecil Sexton, Glenn Simpson, Andrew Slagle, Tom Street, Steven Strombaugh, David Tatum, Kelly Tribble, Chaidi and Jim Vaccaro, Archie and Vicki Whittington, C.T. Williams, Susan and Haynes Williams, Don Wilson, Gary Wilson, and Rob Wolfe. Financial support to RWP for fieldwork provided, in part, by Barbara Toomey and her son, James Toomey. Sean Roberts (Florida Museum) assisted with digital photography. David Pawson and Cynthia Ahern (United States National Museum of Natural History) and Bushra Hussaini (American Museum of Natural History) permitted RWP to study collections under their care. Tobias Grun and Louis Zachos provided thoughtful reviews of this manuscript, though any errors or omissions are solely the responsibility of the authors. Some specimens utilized in this project were available for study due to field collections funded under grants by the National Science Foundation to Carrie Tyler and Michał Kowalewski (EAR SGP-1630475 and EAR SGP-1630276). This is University of Florida Contribution to Paleobiology 839.

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APPENDIX 1.

FM-IP FLORIDA LOCALITIES

2601. Collier Co., Sunniland, Century Industries Quarry east of SR29. Pliocene Tamiami Formation.

2879. Hendry Co., in and around LaBelle. Lower Pleistocene Caloosahatchee Formation.

3241. Collier Co., Sunniland. Pliocene Tamiami Formation.

3784. Gulf of Mexico, approximately 250 km west-southwest of Tampa (27.0166°, -84.9333° no datum given). Plio-Pleistocene.

3810. Gulf of Mexico, approximately 250 km west-southwest of Tampa (26.9381°, -84.9291° no datum given). Plio-Pleistocene.

3811. Gulf of Mexico, approximately 250 km west-southwest of Tampa (27.0833°, -84.95° no datum given). Plio-Pleistocene.

5706. Wakulla Co., dredge from the St. Marks River. Lower Miocene St. Marks Formation.

6022. Glades Co., approximately 7 miles east of LaBelle, small pit one mile west of road to Ortona Lock on the north side of SR80. Lower Pleistocene Caloosahatchee Formation.

BD004 (National Car Rental Center). Broward Co., west-southwest of Sunrise (26.1522°, -80.3222° NAD27). Pleistocene.

BD005 (Cooper City 01). Broward Co., quarry spoil southwest of Cooper City. T51S, R40E, sec.15 NE1/4, SE1/4, Cooper City Quadrangle USGS 7.5' series (1983). Upper Pleistocene Fort Thompson Formation.

BR008 (Brevard Beaches 01). Brevard Co., south of Patrick Air Force Base along beach near Pineda Causeway (SR404) south to Melbourne Beach. T26-28S, R37/38E, Tropic/Melbourne East Quadrangles USGS 7.5' series (1988/1980). Upper Pleistocene Anastasia Formation.

CA001 (Chipola 01 – McClelland's Farm). Calhoun Co., Chipola River, 0.5 mile downstream from mouth of Tenmile Creek (30.4812°, -85.1647° WGS84). Lower Miocene Chipola Formation.

CA011 (Tenmile Creek – General). Calhoun Co., along banks of Tenmile Creek. Lower Miocene Chipola Formation.

CA020 (Tenmile Creek 04). Calhoun Co., Tenmile Creek, approximately 1.5 miles west-northwest of creek mouth along south bank (30.4954°, -85.1881° WGS84). Lower Miocene Chipola Formation.

CA025 (Cooter Bluff). Calhoun Co., Chipola River, approximately 2500 feet upstream from mouth of Fourmile Creek (30.4541°, -85.1651° WGS84). Lower Miocene Chipola Formation.

CA036 (Chipola 22). Calhoun Co., Chipola River, approximately 1.3 miles downstream from mouth of Tenmile Creek on east bank (30°.4714, -85.1574° NAD27). Lower Miocene Chipola Formation

CA067 (Apalachicola 02). Calhoun and Liberty Counties, on bottom of Apalachicola River (30.4172°, -85.0332° NAD27). Lower Miocene Chipola Formation.

CH003 (Lomax-King Pit). Charlotte Co., 0.75 mile southeast of Acline (26.8787°, -82.0187° WGS84). Upper Pliocene portion of the Tamiami Formation.

CH026 (Casa de Meadows 02). Charlotte Co., 0.75 mile east of Grove City (26.9128°. -82.3091° WGS84). Upper Pliocene portion of the Tamiami Formation.

CH046 (Quality Materials Quarry 01). Charlotte Co. Approximately 4 miles northeast of Placida (26.8667°, -82.1994° WGS84). Upper Pliocene portion of the Tamiami Formation.

CH080 (Quality Materials – General). Charlotte Co., Approximately 4 miles northeast of Placida (26.8657°, -82.2044° WGS84). Upper Pliocene portion of the Tamiami Formation.

CR006 (Golden Gate). Collier Co., Big Corkscrew Island. Sec.14/23, T48S, R27E, Corkscrew SE Quadrangle USGS 7.5' series (1973). Lower Pleistocene Caloosahatchee Formation.

CR009 (Sunniland 03). Collier Co., Sunniland, three pits, one across from Humble office, one north of the office, and one 1.5 miles south on SR29. Sec.17/20, T48S, R30E, Sunniland Quadrangle USGS 7.5' series (1982). Pliocene Tamiami Formation.

CR015 (Longan Lakes 01). Collier Co., approximately 13 miles southwest of Immokalee, Longan Lakes Quarries (26.3589°, -81.5655° WGS84). Lower Pleistocene Caloosahatchee Formation.

CR017 (Longan Lakes 01B). Collier Co., approximately 13 miles southwest of Immokalee, Longan Lakes Quarries (26.3585°, -81.5657° WGS84). Middle Pleistocene Bermont Formation.

CR041 (Copeland Pit 01). Collier Co., west side of Copeland (25.9536°, -81.3627° WGS84). Pliocene Tamiami Formation.

DA008 (Rinker Brothers CSR Pit 01A). Miami-Dade Co., approximately 3 miles northwest of (25.7943°, -80.4302° WGS84). Upper Pleistocene Miami Limestone.

DA012 (Glenwood Heights 01). Miami-Dade Co., Backhoe excavation at northeast corner of northwest 27th Avenue and northwest 62nd Street in Miami (25.8318°, -80.2401° NAD27). Upper Pleistocene Fort Thompson Formation.

DE021 (Peace River 01). DeSoto Co., approximately 1 mile west of Nocatee in Peace River (27.1557°, -81.9505° NAD27). Pliocene Tamiami Formation.

GD005 (Chattahoochee 02). Gadsden Co., Chattahoochee, bluff above Jim Woodruff Dam (30.7038°, -84.8544° WGS84). Lower Miocene Chattahoochee Formation.

GL007 (Lake Hicpochee 01). Glades Co., 1.5 miles west of Lake Hicpochee (26.7869°, -81.187° WGS84). Pleistocene.

HA001 (White Springs). Hamilton Co., at or near SR136 bridge in White Springs along Suwannee River (30.3279°, -82.7597° NAD27). Lower Miocene Parachucla Formation,

HN004 (Cochran Shell Pit). Hendry Co., approximately 6.5 km southwest of LaBelle (26.7339°, -81.483° WGS84). Lower Pleistocene Caloosahatchee Formation.

HN017 (Clewiston). Hendry Co., Clewiston (26.75389°, -80.9338° WGS84). Lower Pleistocene Caloosahatchee Formation.

HR005 (Zolfo Springs 01). Hardee Co., north of Zolfo Springs on Peace River (27.5068°, -81.7971° NAD27). Upper Miocene Peace River Formation.

HR006 (Zolfo Springs 02). Hardee Co., north of Zolfo Springs on Peace River (27.5094°, -81.7961° WGS84). Upper Miocene Peace River Formation.

HR013 (Peace River 05). Hardee Co., north of Zolfo Springs on Peace River (27.5134°, -81.7926° WGS84). Upper Miocene Peace River Formation.

IR003 (Vero Beach Landfill 01). Indian River Formation, 6.5 miles west of Oslo (27.5751°, -80.4908° WGS84). Late Pleistocene.

JA003 (Jim Woodruff Dam). Jackson Co., approximately 1.5 miles northwest of Chattahoochee (30.7041°, -84.8704° WGS84). Lower Miocene Chattahoochee Formation.

JA041 (Apalachicola 06). Jackson Co., 4.39 miles southwest of Chattahoochee in Apalachicola River (30.657°, -84.8914° NAD27). Lower Miocene Chattahoochee Formation.

LE009 (Burnt Store Road Pit 01). Lee Co., northwest side of Cape Coral (26.7068°, -82.0439° NAD27). Pliocene Tamiami Formation.

LE020 (Cape Coral 01). Lee Co., canal 0.25 mile north of intersection of Knott Road and Trafalgar Parkway in Cape Coral (26.6259°, -82.0161° NAD27). Pleistocene-Holocene.

LI001 (Alum Bluff 01 – General). Liberty Co., 2 miles north northwest of Bristol on Apalachicola River (30.4642°, -84.9871° WGS84). Lower Miocene Chipola Formation and upper Pliocene Jackson Bluff Formation.

LI003 (Alum Bluff 01B). Liberty Co., 2 miles north northwest of Bristol on Apalachicola River (30.464°, -84.9871° WGS84). Lower Miocene Chipola Formation.

LI005 (Langston Quarry 01). Liberty Co., north of Carrabelle (30.01°, -84.61° WGS84). Pliocene Intracoastal Formation.

LN004 (Jackson Bluff – General). Leon Co., bluff on Ochlockonee River (30.3876°, -84.6454° WGS84). Upper Pliocene Jackson Bluff Formation.

LN008 (Jackson Bluff 04). Leon Co., Jackson Bluff Dam on Lake Talquin (30.3869°, -84.6468° NAD27). Upper Pliocene Jackson Bluff Formation.

MA004 (West Manatee 01). Manatee Co., approximately 1 mile south of Bradenton (27.4472°, -82.6041° no datum). Upper Pleistocene.

NA002 (Rose's Bluff). Nassau Co., approximately 3.25 miles northwest of Chester (30.7063°, -81.5848 WGS84°). Upper Pleistocene Satilla Formation.

OB013 (101 Ranch Pit 02B). Okeechobee Co., approximately 9.3 miles west of Fort Drum (27.5253°, -80.9686° WGS84). Lower to middle Pleistocene Caloosahatchee and Bermont Formations.

OR002 (F & W Mine). Orange Co., 9 miles south of Christmas (28.3981°, -80.9332° WGS84). Lower Pleistocene portion of the Nashua Formation.

PB001 (Belle Glade 01). Palm Beach Co., approximately 1 mile south of Belle Glade in rock pit (26.6595°, -80.6764° WGS84). Middle Pleistocene Bermont Formation.

PB007 (South Bay 04). Palm Beach Co., 14.8 miles southeast of South Bay (26.6089°, -80.6089° WGS84). Middle Pleistocene Bermont Formation.

PB014 (Star Ranch 01). Palm Beach Co., 11.5 miles south of South Bay (26.5005°, -80.6802° WGS84). Lower Pleistocene Caloosahatchee Formation.

PI025 (St. Joseph Sound 01). Pinellas Co., 0.97 mile southwest of Ward Island (28.0421°, -82.8001° WGS84). Lower Miocene Tampa Member of the Arcadia Formation.

PO002 (Ft. Green 13 Dragline 01). Polk Co., 4.0 miles south of Bradley Junction (27.7318°, -81.9771° WGS84). Lower Miocene portion of the Arcadia Formation.

PO035 (Fort Meade 01). Polk Co., 13.8 miles west southwest of Fort Meade (27.7227°, -82.0261° WGS84). Lower Miocene portion of the Arcadia Formation.

PU004 (Cracker Swamp Ranch 01). Putnam Co., 2.5 miles northwest of Orange Mills (29.6972°, -81.5346° WGS84). Lower Pleistocene portion of the Nashua Formation.

SJ004 (East Coast Aggregates 02). St. Johns Co., approximately 2.6 miles south southwest of Hastings (29.68°, -81.52° WGS84). Upper Pliocene portion of the Nashua Formation.

SJ008 (East Coast Aggregates 03). St. Johns Co., approximately 2.4 miles southwest of Hastings (29.68°, -81.51° WGS84). Upper Pliocene portion of the Nashua Formation.

SL003 (Dickerson Pit 01). St. Lucie Co., approximately 7 miles west of Indrio (27.5379°, -80.4703° WGS84). Upper Pleistocene Anastasia Formation.

SL004 (Dickerson Pit 02). St. Lucie Co., approximately 7 miles west of Indrio (27.5256°, -80.467° WGS84). Upper Pleistocene Anastasia Formation.

SO006 (Deans Trucking Pit). Sarasota Co., approximately 4 miles northeast of Laurel (27.1589°, -82.3904° NAD27). Lower Miocene portion of the Arcadia Formation.

WA001 (Crawfordville 01. Wakulla Co., 2.3 miles southwest of Crawfordville at Taft Pit (30.1503°, -84.389° WGS84). Lower Miocene Torreya Formation.

WA011 (Woodville 02). Wakulla Co., approximately 1.4 miles southeast of Woodville (30.3034°, -84.2273° WGS84). Lower Miocene St. Marks Formation.

WA013 (Sopchoppy 01). Wakulla Co., west side of Sopchoppy on river (30.0634°, -84.5004° WGS84). Lower Miocene Sopchoppy Member of the Torreya Formation.

FM-IP SOUTH CAROLINA LOCALITIES

ZS041 (Waccamaw Construction Company Pit 01). Horry Co., 3.23 miles northeast of North Myrtle Beach (33.8644, -78.6413 NAD27). Lower Pleistocene Waccamaw Formation.