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Cover image: *Eupatagus antillarum* holotype (left) and *Eupatagus mooreanus* (right); see caption for figure 99 within text.

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Paleogene Echinoids of Florida

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Sixty-five species and nine indeterminate taxa of Florida Paleogene echinoids are discussed, and their geographic and stratigraphic distributions provided. These include 49 species documented from the Eocene and 16 from the Oligocene. Ten new species are described: *Prionocidaris robertsi* n. sp., *Rhyncholampas mariannaensis* n. sp., *Rhyncholampas bao* n. sp., *Weisbordella inglisensis* n. sp., *Weisbordella libum* n. sp., *Durhamella tetrapora* n. sp., and *Brissus jonesi* n. sp. from the Eocene; and *Plagiobrissus cassadyi* n. sp., *Eupatagus dumonti* n. sp., and *Schizaster carlsoni* n. sp. from the Oligocene. We reconsidered subjective junior synonyms of all species and resurrect *Neolaganum archerensis, Echinocyamus macneili,* and *Eupatagus mooreanus*. Furthermore, we updated the taxonomy for all included species and their known distributions and provide emended diagnoses for the genera and species of Florida Neolaganidae. In addition, we herein report the occurrence of *Porpitella micra* in Cretaceous strata of the subsurface of Florida. This remarkable finding makes *P. micra* the earliest known of all the scutelloids. Echinoids within the Ocala Limestone are placed in five echinoid biozones, which are defined within, these include the *Oligopygus phelani, Oligopygus haldemani, Oligopygus wetherbyi, Wythella eldridgei*, and *Haimea brooksi* Zones. This document complements the Neogene (including the Quaternary) fossil echinoid fauna of Florida we published in 2020 and represents a compilation of the known Florida Paleogene echinoid record. The region is currently known to have the most speciose and diverse assemblage of Paleogene echinoids in the United States.

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INTRODUCTION

The importance of echinoids in modern ecosystems underscores the need to understand how their diversity has changed through time. 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 and comprehensive accounting to date of the diversity of the Florida Paleogene echinoid fauna. In the process, it demonstrates that the state has the most speciose and diverse assemblage of Paleogene echinoids in the eastern United States.

An updated taxonomy for all known Paleogene echinoid species of Florida and document of their distributions is long overdue. The fauna includes 49 species from the Eocene and 16 from the Oligocene, as well as nine additional taxa left in open nomenclature at or below genus level. We describe ten new species: ***Prionocidaris robertsi*** n. sp., ***Rhyncholampas mariannaensis*** n. sp., ***Rhyncholampas bao*** n. sp., ***Weisbordella inglisensis*** n. sp., ***Weisbordella libum*** n. sp., ***Durhamella tetrapora*** n. sp., and ***Brissus jonesi*** n. sp. from the Eocene; and ***Plagiobrissus cassadyi*** n. sp., ***Eupatagus dumonti*** n. sp., and ***Schizaster carlsoni*** n. sp. from the Oligocene.

With the abundance of material now available, we reconsidered subjective junior synonyms for all species, and resurrect *Neolaganum archerensis* (Twitchell in Clark and Twitchell, 1915); *Echinocyamus macneili* Cooke, 1959; and *Eupatagus mooreanus* Pilsbry, 1914. A review of the distinguishing characteristics of regional genera and species of neolaganids was required to inform taxonomic assignment of three new species; emended diagnoses are included for these taxa. In addition, we recognize *Rhyncholampas lyelli* (Conrad, 1850) as a subjective junior synonym of *R. conradi* (Conrad, 1850), and *R. globosus* (Fischer, 1951) to be synonymous with *R. georgiensis* (Twitchell in Clark and Twitchell, 1915). We examined hundreds of specimens of Oligocene species of *Clypeaster* and recognize three distinct forms that do not fall within the variation of any documented taxa. We were unwilling to name new species of this already overly split genus, and identify them as *Clypeaster* sp. A, B, and C. We also document what is likely the first occurrence of *Prenaster* in North American strata. In addition, we herein record the occurrence of *Porpitella micra* H. L. Clark, 1937, in Cretaceous strata of the subsurface of Florida. This remarkable find makes *P. micra* the earliest known of all the scutelloids. Echinoids within the Ocala Limestone are placed in five echinoid biozones, which are defined within, these include the *Oligopygus phelani, Oligopygus haldemani, Oligopygus wetherbyi, Wythella eldridgei*, and *Haimea brooksi* Zones. Lastly, this paper serves as the companion to Osborn et al. (2020) which discussed the occurrences of 43 species of echinoids from the Florida Neogene (including the Quaternary) and included a historical summary of the echinoid research in the state.

MATERIALS AND METHODS

The extensive collections in the Florida Museum of Natural History, Invertebrate Paleontology (FM-IP) Collection at the University of Florida (UF) 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 unique catalog number. We also indicate Florida Museum localities by ”FM-IP”. Other institutions to whose localities or material we refer include the United States Geological Survey (USGS), California Academy of Sciences’ Geology collections (CASG), and University of California Museum of Paleontology (UCMP). We also examined specimens from the Smithsonian Institution’s National Museum of Natural History (USNM). 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, Florida.

Standard caliper measurements in millimeters include test length (TL), test width (TW), test height (TH), and test diameter (TD). Room Temperature Vulcanizing (abbreviated as ”RTV”) silicone rubber was used to make casts of some moldic specimens, as noted.

THE EOCENE

With 49 species and 54 distinct taxa (Table 1), Eocene strata of Florida (Fig. 1) contain the highest diversity of Cenozoic echinoids in the eastern United States (Osborn et al., 2016). The greatest diversity occurs in the Upper Eocene Ocala Limestone (OLS), which contains 44 documented species and 49 taxa (Table 1). This is an increase of 12 taxa since the OLS echinoid fauna was last detailed by Osborn et al. (2016). This Upper Eocene peak of echinoid diversity in the region follows a global trend of an Eocene maximum bounded by much lower diversities in the Paleocene and Oligocene (McKinney et al., 1992), and aligns with the conclusion of Carter (1987a), who stated that the Upper Eocene (Jacksonian-Priabonian) strata of the southeast contain the most diverse echinoid fauna of the region.

Influence Of The Gulf Trough On Echinoid Distribution In The Upper Eocene

The boundary between the Gulf Coast and Florida provinces of Carter (1987a) coincides with an area of southern Georgia and the eastern panhandle of Florida known as the Gulf Trough. The Gulf Trough is a subsurface geological feature that was scoured by a strong marine current from the Late Cretaceous through the Oligocene (Fig. 2). The Gulf Trough is often referred to as the Suwannee Strait, or Suwannee Channel (e. g. Cheetham, 1963), but Huddlestun (1993) makes a distinction. The Suwannee Channel is a very broad feature, functional from the Late Cretaceous through Middle Eocene. The Gulf Trough was a much narrower channel (occupying essentially the same area), and functional from the Middle Eocene to Middle Miocene, at which time the feature became sediment filled. The current that flowed through either Suwannee Channel or Gulf Trough is properly called the Suwannee Current. The Suwannee Strait is technically a descriptive, geographic term referring to the Cretaceous to Miocene marine passage that separated the continental mainland from the shallow, carbonate producing Florida Bank. The Gulf Trough itself is a well-documented, subsurface, stratigraphic feature that has, at times, been implicated in influencing echinoid distribution in the region. Most Upper Eocene echinoid species are typically restricted to one side or the other (Carter, 1987a). As discussed below, perhaps no taxon better represents this pattern than the oligopygids.

Carter (1987a) suggested that the Suwannee Strait did not operate as a physical barrier to echinoid migration during Jacksonian times. He used the modern example of the Florida Strait, which is a deeper and wider barrier than the Suwannee Strait, and therefore presumably had a stronger current. He correctly noted that the Florida Strait do not serve as a barrier in echinoid distributions. Carter (1987a) and Carter and McKinney (1992) suggested these differences can, in part, be explained by stratigraphic mismatching, in which biozones in Florida are not stratigraphically preserved in the strata of Georgia, north of the strait. Therefore, no barrier is necessary to explain the faunal disparities.

Carter (1987a) suggested that the most likely cause of the faunal differences between the Late Eocene of the Florida platform and remainder of the Gulf Coast is an environmental distinction, with depth disparities between the depositional environments of these two regions at least in part accounting for the contrasting echinoid faunas. Carter (1987a) noted that of those species which occur on both sides of the strait, most do not occur far from it, and in fact many species tend to cluster near the strait [*Macropneustes mortoni* (Conrad, 1850) and *Weisbordella johnsoni* (Twitchell in Clark and Twitchell, 1915) for example], suggesting that some environmental gradient straddled the strait. Carter (1987a) concluded that even if better collections of late Jacksonian age strata of Georgia were to reveal species currently restricted to the Florida platform, the differences in the relative abundance of the species between the two regions would remain.

Table 1: Distribution of Eocene echinoids of Florida. *The stratigraphic occurrence of taxa known only from deep wells is discussed in the remarks for each species herein.

	Avon Park Fm.	**OLS *O. phelani* Zone**	**OLS *Haimea brooksi* Zone**	**OLS *O. haldemani* Zone panhandle**	**OLS *O. haldemani* Zone peninsula**	**OLS *O. wetherbyi* Zone**	**OLS *Spirulaea/ Wythella* Zone**	***From deep Wells**
Phyllacanthus mortoni (Conrad, 1850)			■	■	■	■	■	
Prionocidaris robertsi n. sp.		■	■					
Euechinoidea gen. et sp. indet.			■					
Acanthechinus dixie (Cooke, 1941)				■		■	■	
Brochopleurus pretiosus (Clark, 1915)				■		■		
Lytechinus floralanus (Cooke, 1941)				■		■		
unidentified aulodont							■	
Amblypygus americanus Michelin, 1856				■		■		
Haimea brooksi Osborn et al., 2016			■					
Oligopygus haldemani (Conrad, 1850)			■	■	■			
Oligopygus phelani Kier, 1967		■						
Oligopygus rotundus Cooke, 1942			■					
Oligopygus wetherbyi de Loriol, 1887						■		
Eurhodia patelliformis (Bouvé, 1851)				■	■	■		
Rhyncholampas conradi (Conrad, 1850)				■	■	■		
Rhyncholampas ericsoni (Fischer, 1951)		■						
Rhyncholampas fontis (Cooke, 1942)								■
Rhyncholampas georgiensis (Twitchell, 1915)		■	■	■				
Rhyncholampas mariannaensis n. sp.			■					
Rhyncholampas trojanus (Cooke, 1942)							■	
Rhyncholampas bao n. sp.			■					
Echinolampas tanypetalis Harper and Shaak, 1974						■		
Echinocyamus macneili Cooke, 1959								■
Fibularia vaughani (Twitchell, 1915)		■			■	■		
Durhamella floridana (Twitchell, 1915)		■			■			
Durhamella ocalana (Cooke, 1942)		■			■			
Durhamella tetrapora n. sp.		■						
Neolaganum archerensis (Twitchell, 1915)	■							
Neolaganum dalli (Twitchell, 1915)	■							
Neolaganum durhami Cooke, 1959		■						
Weisbordella cubae (Weisbord, 1934)		■			■	■	■	
Weisbordella inglisensis n. sp.		■						
Weisbordella johnsoni (Twitchell, 1915)			■	■				
Weisbordella libum n. sp.						?	?	
Wythella eldridgei (Twitchell, 1915)							■	
Periarchus floridanus Fischer, 1951		■						
Periarchus quinquefarius (Say, 1825)						?	?	
Protoscutella pentagonium Cooke, 1942								■
Gillechinus alabamensis (Cooke, 1942)				■				
Ova beckeri (Cooke, 1942)						■	■	
Ova ocalanus (Cooke, 1942)						■		
Schizaster armiger Clark, 1915					■	■	■	
Agassizia clevei Cotteau, 1875		■	■	■	■	■		
aff. *Prenaster* sp.			■					
Brissopsis steinhatchee Cooke, 1942		■				■	■	
aff. *Brissopsis* sp.							■	
Brissus jonesi n. sp.			■					
Plagiobrissus curvus (Cooke, 1942)		■	■	■	■	■	■	
Plagiobrissus dixie (Cooke, 1942)					■	■	■	
Macropneustes mortoni (Conrad, 1850)				■				
Eupatagus clevei (Cotteau, 1875)		■				■		
Eupatagus mooreanus Pilsbry, 1914		■						
Eupatagus ocalanus Cooke, 1942						■	■	
Eupatagus sp. A			■					
Total = 49 species and 54 taxa	2	18	15	14	12	20	13	3

Figure 1: Generalized Florida geologic map depicting occurrences of Eocene and Oligocene sediments exposed in outcrop and shallow subcrop (sediments slightly more than 6 m depth). Modified from Scott et al. (2001). Note: in some areas where Eocene sediments only are shown both Eocene and Oligocene sediments may co-occur.

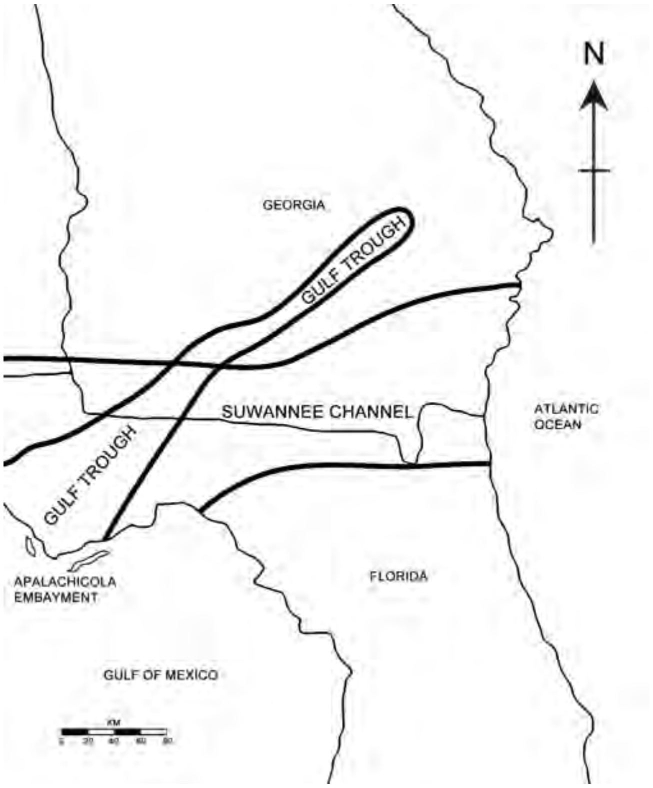


Figure 2: Approximate placement of the Late Cretaceous to Middle Eocene Suwannee Channel and the Middle Eocene through Middle Miocene Gulf Trough. These are the former areas through which the Suwannee Current flowed. Modified from Bryan et al. (2008).

Carter and McKinney (1992) noted that lithologic differences between early Jacksonian strata of Florida and southern Georgia may partially explain the disparity of the faunas. Clastic rocks make up much of the earliest Jacksonian strata of Georgia, these contrasting with the carbonates of Florida. The middle Jacksonian strata of Georgia contain higher proportions of carbonate mud than the more calcareous limestones of the correlative OLS of central Florida. As noted by Carter (1989), most spatangoids prefer, or at least tolerate, significant carbonate mud in the substrate.

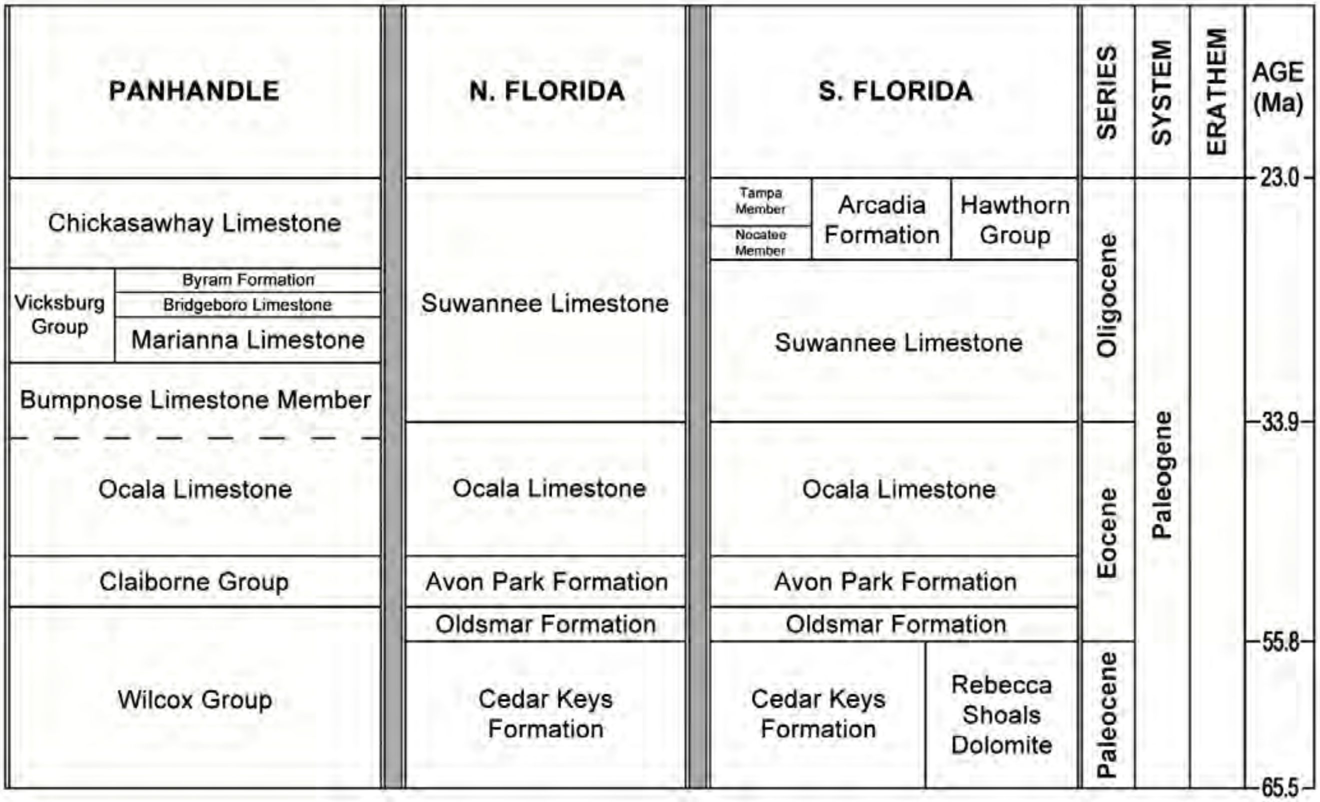
As an example, the Muckalee Member of the OLS (member of the Williston Limestone per Huddlestun, 1981), well exposed near Albany, Georgia, has a higher percentage of carbonate mud than the equivalent *Oligopygus haldemani* Zone of the OLS of Florida (Carter and Hammack, 1989). Therefore, this mud contains a rich diversity of spatangoids, with only very rare occurrences of neolaganids or oligopygids that characterize the zone in central Florida. Comparison to habitats of laganids and cassiduloids, forms respectively similar to the taxa noted above, indicate that their tolerance of fine substrates is much less than that of spatangoids.

The substrate preferences of Jacksonian echinoids of the eastern Gulf Coast are discussed by Carter et al. (1989), and the echinoid faunas are further reviewed by McKinney and Zachos (1986), Carter (1987a, 1989, 1990), Carter and Hammack (1989), and Carter and McKinney (1992).

Avon Park Formation

The Middle Eocene Avon Park Formation is a largely subsurface unit underlying the OLS in central Florida (Table 2). *Neolaganum dalli* (Twitchell in Clark and Twitchell, 1915) is the only identifiable echinoid documented from surface exposures of this unit and could be collected in abundance in the now inactive Gulf Hammock Quarry (FM-IP LV004, FM-IP LV039), Levy County. However, well cores often bring a profusion of specimens of *N.*

Table 2: Correlation of Florida Paleogene stratigraphic units referenced herein, modified from Scott et al. (2001).



PANHANDLE		N. FLORIDA	S. FLORIDA			SERIES	SYSTEM	ERATHEM	AGE (Ma)
									23.0
Chickasawhay Limestone		Suwannee Limestone	Tampa Member Nocatee Member	Arcadia Formation	Hawthorn Group	Oligocene	Paleogene		
Vicksburg Group	Byram Formation Bridgeboro Limestone Marianna Limestone		Suwannee Limestone						
Bumpnose Limestone Member									
									33.9
Ocala Limestone		Ocala Limestone	Ocala Limestone			Eocene			
Claiborne Group		Avon Park Formation	Avon Park Formation						
Wilcox Group		Oldsmar Formation	Oldsmar Formation						
									55.8
		Cedar Keys Formation	Cedar Keys Formation	Rebecca Shoals Dolomite		Paleocene			
									65.5

dalli to the surface (Cole and Ponton, 1932; Vernon, 1951), along with rarer specimens of *Neolaganum archerensis* (Twitchell in Clark and Twitchell, 1915). The holotypes of *N. archerensis* and *N. dalli* were collected by William Healey Dall in cuttings from a deep well near Archer early in the 20th century. Carter (1987a) noted that the depositional environment of the shallow water carbonates of the Avon Park Formation would dictate low diversity and contain species able to tolerate ecological conditions not found in other regions, which likely explains the abundance of *N. dalli*, but the overall sparse fauna.

The Avon Park Formation has limited surface exposures, largely restricted to two large, irregular shaped outcrops in central and southeastern Levy County, the latter extending into Citrus County along the Withlacoochee River (Vernon, 1951). Small, irregular outcrops are present along the Withlacoochee River at the Florida Power Corporation dam where the contact of the Avon Park and overlying dolomites of the OLS (portion formerly referred to the Inglis Formation) can be seen. Vernon (1951) described the unconformable contact here evidenced by a rubble and pebble bed at the base of the OLS formed across eroded dolomite beds of the Avon Park Formation.

Ivany et al. (1990) documented the occurrence of six poorly preserved (moldic) regular urchin specimens on Avon Park Formation seagrass blades from the Dolime Quarry (FM-IP CI009). Unfortunately, none can be assigned with confidence even to family level.

OCALA LIMESTONE (OLS)

The term Ocala Limestone (hereafter referred to as the OLS) was proposed by Dall (1892) for limestone exposures near Ocala, Florida. Cooke (1916) defined it as Jacksonian in age (Upper Eocene) and that it underlies the Marianna Limestone (Table 2). Cooke and Mossom (1929) lumped all exposed Eocene sediments of Florida into the OLS and, for the first time, discussed its fauna at numerous localities throughout the state, affirming the presence of 12 species of echinoid in the unit which were first described by Twitchell in Clark and Twitchell (1915) (Cooke and Mossom, 1929:50).

Applin and Applin (1944) subdivided the OLS into lower and upper members. Vernon (1951) proposed extending the Moodys Branch Formation from the Gulf Coastal Plain into Florida because of a continuity of biozones from the type locality near Jackson, Mississippi, and the gradual lateral change in facies from clastic to carbonate. For what he stated was Applin and Applin's (1944) lower member of the OLS, Vernon (1951: 111) proposed the name Inglis Member and Williston Member for the overlying strata. Vernon (1951) therefore proposed restricting the designation of the OLS to only the upper-most portion of the OLS of Applin and Applin (1944). However, as discussed below, others have interpreted Applin and Applin's lower member to include strata in both Vernon's Inglis and Williston Members.

Puri (1957) attempted to shed some light on this and provided the most complete foraminiferal zonation of the unit to date, asserted the OLS is distinct from the Moodys Branch Formation, raised the OLS to group status, and recognized three formations within it, from lowest to highest: the Inglis Formation, the Williston Formation, and a proposed Crystal River Formation (which was initially recognized in Puri [1953: 130]) for the upper beds of the unit. Puri (1957) also recognized eight foramaniferal faunal zones within the Ocala Group of Florida.

Randazzo (1976) pointed out that the splitting and lumping of the OLS discussed above was done before the inception of the Code of Stratigraphic Nomenclature in 1961, which is published by the American Commission on Stratigraphic Nomenclature. Randazzo noted that geologists studying the OLS must identify biostratigraphic horizons rather than lithologic changes to distinguish between the Crystal River, Williston, and Inglis Formations and if the microfossils utilized in Puri's (1957) zonation are missing or poorly preserved, users cannot appropriately identify these formations. He then asserted that splitting the OLS into three formations is not useful and misleading to all but a micropaleontologist. Therefore, Randazzo (1976) proposed adopting the United States Geological Survey's definition of the OLS, which divides the OLS into two members: a lower member (the Inglis and Williston Formations) and an upper member (the Crystal River Formation). He acknowledged that the lithologic distinctions between the two members is subtle but proposed the Williston and Inglis Formations be treated as a micritic-skeletal limestone, lower member of the OLS, and the coarser-grained, skeletal-micritic limestone above these beds (Crystal River Formation) be considered the upper member of the OLS.

Miller (1986) reiterated the points made by Randazzo and said Puri's three formations cannot be recognized lithologically, even at their type sections, nor can they be differentiated in subsurface deposits. Subsequently, Scott (1991) stated the Florida Geological Survey no longer recognized the formational designations of Puri (1957) and reduced the Ocala Group to formational status. The OLS, at this time, is therefore treated as a single lithostratigraphic unit (Table 2) but is informally divided into lower and upper divisions: the lower OLS, which includes strata formerly included in the Inglis and Williston Formations and the upper OLS, which includes strata formerly referred to the Crystal River Formation.

Scott (1991) stated that the lower subdivision consists of a more granular limestone not present everywhere that may be partially to completely dolomitized in some regions. The upper subdivision is composed of variably muddy (carbonate), granular limestone that is often very soft and friable with numerous large foraminifera. Scott (1991) also included the very late Eocene to early Oligocene Bumpnose Limestone within the upper OLS due to its lithological similarities to that unit. This was followed by Ellwood et al (2019) and we concur. For clarity, the Bumpnose Limestone, which is limited in outcrop to Jackson County, is discussed separately from the OLS in the Oligocene section below.

However, as discussed by Randazzo (1976) and Miller (1986), differentiating the lithologies of the lower and upper divisions of the OLS remains difficult. Nevertheless, "finding one's place" in the unit can be made easier by using index taxa. For instance, the lowermost portion of the OLS in Citrus and Levy Counties is a dolomitic horizon, the lower portion of what was referred to as the Inglis Formation, and it contains characteristic internal and external molds of *Eupatagus clevei* Cotteau, 1875, and *Periarchus floridanus* Fischer, 1951. Immediately above this is a series of limestones with *E. mooreanus* and the much less common *Oligopygus phelani* Kier, 1967, of the *Oligopygus* zonation discussed below. This is the upper portion of what used to be called the Inglis Formation, and because of its echinoid fauna, this zone is also distinctive.

Therefore, considering the difficulties differentiating the lithologies of the lower and upper divisions of the OLS, we will discuss the stratigraphic distribution of the echinoids within the OLS using *Oligopygus* zonations.

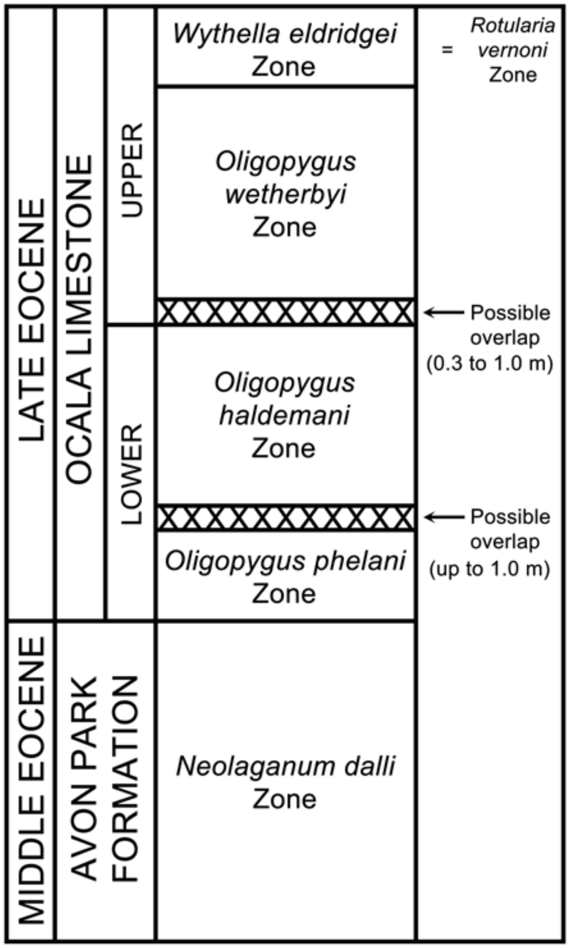
OLIGOPYGUS ZONATION IN THE OCALA LIMESTONE

Oligopygus de Loriol, 1887 is arguably the most stratigraphically important echinoid genus of the Florida Eocene (Carter, 1990; Croft and Shaak, 1985; McKinney and Jones, 1983; McKinney and Zachos, 1986). The type species is *Oligopygus wetherbyi* de Loriol, 1887. *Oligopygus* is known from the southeastern United States and throughout the Middle to Upper Eocene of the Caribbean region as far south as Venezuela (Cooke, 1941b and 1961; Kier, 1967). In his review of the oligopygoids, Kier (1967) recognized 13 species of *Oligopygus*: *O. nancei* Cooke, 1941b; *O. zyndeli* Jeannet, 1928; *O. jamaicensis* Arnold and Clark, 1927; *O. rotundus* Cooke, 1942; *O. kugleri* Jeannet, 1928; *O. wetherbyi*; *O. pinguis* Palmer in Sánchez-Roig, 1949; *O. sanchezi* Lambert, 1932; *O. costuliformis* Jeannet, 1928; *O. haldemani* (Conrad, 1850); *O. putnami* Israelsky, 1933; *O. curasavica* Mollengraaff, 1929, and the aforementioned *O. phelani*. He considered an additional six species (largely from Cuba) to be too inadequately described or figured, and for which he could not locate holotypes.

Cooke (1959) and Kier (1967) recognized four species of *Oligopygus* in the region: *O. rotundus* (Middle to Upper Eocene), as well as *O. haldemani, O. phelani,* and *O. wetherbyi* (Upper Eocene). Regional occurrences of the genus are largely confined to the OLS of Florida where it is a ubiquitous presence at most exposures and is only very rarely represented elsewhere in the region: *O. rotundus* also occurs in southeastern Alabama and southwestern Georgia, and *O. haldemani* occasionally occurs in Georgia.

Species of *Oligopygus* are well-documented index taxa for correlation within the OLS of Florida and Georgia (Table 3). Their suitability as index taxa is due to many factors that include: durability of the test, which lends itself to excellent preservation; ease in differentiating the species; abundance of the species within their respective horizons; and constrained zonation of most of the species. The biozonation is well documented in Carter (1990), Croft and Shaak (1985), McKinney and Jones (1983), McKinney and Zachos (1986), Zachos and Shaak (1978), and others.

Table 3: Echinoid zonation in the Ocala Limestone of the Florida peninsula.



LATE EOCENE	OCALA LIMESTONE	UPPER	*Wythella eldridgei* Zone	= *Rotularia vernoni* Zone
			Oligopygus wetherbyi Zone	
			XXXXXXXXXXX	← Possible overlap (0.3 to 1.0 m)
		LOWER	*Oligopygus haldemani* Zone	
			XXXXXXXXXXX	← Possible overlap (up to 1.0 m)
			Oligopygus phelani Zone	
MIDDLE EOCENE	AVON PARK FORMATION		*Neolaganum dalli* Zone	

A summary of the zonation discussed in these works is as follows: *O. wetherbyi* is the youngest species and occurs in the upper portion of the upper OLS (the Crystal River Formation of Puri [1957]); *O. haldemani* largely occurs in the upper portion of the lower OLS (the Williston Formation of Puri [1957]), though it may extend into the lower portion of the upper OLS [McKinney and Jones, 1983], it does not overlap the range of *O. wetherbyi*; and *O. phelani* occurs in the underlying lower OLS (Inglis Formation of Puri [1957]), though not in the lower dolomitic portion of the unit, which contains *Eupatagus clevei* and *Periarchus floridanus* in Citrus and Levy Counties (Table 3).

Oligopygus rotundus has the most complex stratigraphic distribution of the four regional species of the genus, occurring in the Middle Eocene of Geneva County, Alabama (type locality), Middle Eocene Lisbon Formation of Early County, Georgia (Toulmin, 1977), as well as with *O. haldemani* in the lower portion of the upper OLS in Jackson County, Florida (Osborn et al., 2016). Due to the lack of continuity in stratigraphic distribution of this species, *O. rotundus* is not suitable as an index taxon.

McKinney and Jones (1983) stated that the overlap of the *Oligopygus* biozones is minimal and rarely, if ever, exceeds 1 m in thickness. We have not found *O. haldemani* and the younger *O. wetherbyi* occurring *in situ* in the same horizon, nor have we encountered *O. haldemani* and the older *O. phelani* occurring *in situ* together. Although it is feasible that there may be overlap with these two species, other than in mixed spoil in quarries on the Florida peninsula, we have not encountered them together *in situ*, despite intensive work throughout the region. The only definitive *in situ* sympatric occurrence of species within the genus occurs in Jackson County where *O. rotundus* and *O. haldemani* occur together, with *Haimea brooksi* Osborn et al., 2016, in the lowest bed currently quarried in the Brooks Quarry (FM-IP JA039), near Marianna (Fig. 3).

Features differentiating *O. phelani, O. wetherbyi,* and *O. haldemani* have very little overlap. The species are easily separated by periproct placement and peristome roundness when in bivariate plots (McKinney and Jones, 1983). McKinney and Jones (1983) did not include *O. rotundus* in their study. However, it is differentiated from the other three species (see remarks for *O. rotundus* herein). McKinney and Jones (1983) also demonstrated that there was not a long-term evolutionary trend of these traits in these species. In other words, in Florida populations specifically, the species transitions are abrupt, with virtually no signs of overlap.

The only area of difficulty for *Oligopygus* zonation appears to be at the upper and lower boundaries of the unit itself. The issue with *O. phelani*, as an indicator of the lowermost stratum of the OLS, formerly included in the Inglis Formation, is that it

Figure 3: Brooks Quarry (FM-IP JA020), Jackson County, Florida. Arrows indicate top and bottom of Bumpnose Limestone (Eocene/Oligocene boundary is within this unit). Overlying stratum is the Lower Oligocene Marianna Limestone and underlying stratum is the Upper Eocene Ocala Limestone.

isn't very common. However, *Eupatagus mooreanus* and *Periarchus floridanus* are ubiquitous (often as test fragments) at nearly every outcrop of the basal limestone of the OLS. Beneath this is a bed of dolomite that forms the base of the unit in Citrus and Levy Counties, with *E. clevei* and *P. floridanus*. So, *E. mooreanus* and *P. floridanus* serve well as an indicator of the lower portion of the OLS, that is, the Inglis Formation of Puri (1957).

At the top of the OLS in northern Peninsular Florida (excluding Jackson County) (Fig. 1) is a soft limestone that lies immediately above the *O. wetherbyi* Zone and directly below overlying Oligocene strata. This horizon is, at least in part, the *Spirolaea* (now *Rotularia*) *vernoni* Zone of Puri (1957). Given the absence of *Oligopygus* in this bed, we herein use a different echinoid and recognize this as the *Wythella eldridgei* Zone (Table 3).

Hunter (1976) noted that Cheetham (1963), intentionally or not, raised the *Spirolaea vernoni* Zone of the OLS, at least in part, to an equivalent of the *Lepidocyclina chaperi* Zone of Jackson County, which is the Bumpnose Limestone (Fig. 3). Effectively, Cheetham (1963) considered the Bumpnose Limestone to be correlative of Puri's (1957) *Spirolaea vernoni* Zone, without naming it.

Cheetham's (1963) correlation likely led to Hunter's (1972, 1976, 1981) recognition of the Bumpnose Limestone (Puri's *Spirolaea vernoni* Zone) in peninsular Florida where it is lithologically dissimilar to the type Bumpnose Limestone. However, the *Rotularia vernoni* Zone is clearly Upper Eocene, as evidenced by its correlation to the *Asterocyclina* Zone when Puri (1957) erected his zonation, and reaffirmed by Nicol et al. (1976, 1984, 1989), Jones and Nicol (1989), and others. Bryan (1993) stated that the usage of the term Bumpnose Limestone in peninsular Florida, advocated by Hunter (1972, 1976, 1981), should be discontinued. Therefore, within Florida, we recognize the Bumpnose Limestone only in its type area near Marianna (the unit does extend into southern Alabama), and recognize the *Wythella eldridgei* Zone as the uppermost bed of the OLS in northern peninsular Florida.

The *Wythella eldridgei* Zone is characteristic throughout the northern peninsula, especially in Taylor, Lafayette (Fig. 4), Suwannee (Fig. 5), and Dixie Counties, and typically contains an abundance of *Wythella eldridgei* (Twitchell in Clark and Twitchell, 1915), a diversity of spatangoids including *Schizaster armiger* Clark in Clark and Twitchell, 1915; *Brissopsis steinhatchee* Cooke, 1942; *Ova beckeri* (Cooke, 1942); *Eupatagus ocalanus* Cooke, 1942; *Plagiobrissus dixie* (Cooke, 1942); *Plagiobrissus curvus* (Cooke, 1942), and other, rarer species. Lacking *Oligopygus* in this horizon, *W. eldridgei* serves as an ideal index taxon as it has not been documented outside of this horizon. Above this zone are Oligocene strata. A classic exposure of this horizon is found along the west bank of the Suwannee River west of Dowling Park, as documented by Bryan (1993).

Thus, other than the lack (or extreme rarity) of *Oligopygus* at the base and top of the OLS in peninsular Florida, the *Oligopygus* zonation discussed above works well for correlating strata in the OLS of peninsular Florida. However, near Marianna, in the Florida panhandle, north of the Suwannee Strait (a feature discussed above), this zonation has drawbacks when compared to the foraminifera zonation of Puri (1957). *Oligopygus haldemani* occurs throughout the upper OLS in Jackson County, with the morphotype attributed by Miller et al. (2014) to *O. colsoni* Lambert, 1932 occurring up to the top of the OLS in Jackson County without the occurrence of *O. wetherbyi* between it and the overlying Lower Oligocene portion of the Bumpnose Limestone.

However, this occurrence is within the *Asterocyclina* Zone, which Puri (1957) considered to reside at the top of the OLS. This should be the *O. wetherbyi* Zone according to *Oligopygus* zonation. It is important to note that the *Asterocyclina* Zone is not present in peninsular Florida (Puri, 1957) where *Asterocyclina* is very rare. Contrarily, *O. wetherbyi* is virtually absent north of the Suwannee Strait, being reported merely as rare specimens from residual float in southwestern Georgia documented by Carter (1989: 190). As noted by Hunter (1976), the *Asterocyclina* Zone of the Florida panhandle has no recognized peninsular equivalent.

Figure 4: Dell Limerock Mine (FM-IP LF001), Lafayette County, Florida. Exposed rocks are the *Oligopygus haldemani* and *Oligopygus wetherbyi* Zones of the Upper Eocene Ocala Limestone.

This situation implies several possibilities. It could be that Puri's assertion that the *Asterocyclina* Zone is the uppermost zone of the OLS is incorrect, with the *Asterocyclina* Zone marking the uppermost horizon of OLS that is present only in Jackson County, Florida (horizons above it implied to be absent). This is a possibility, as Puri (1957: 55) stated that the top of the *Asterocyclina* Zone is marked by an unconformity between it and the overlying latest Eocene to lowermost Oligocene strata (*Lepidocyclina chaperi* Zone, which resides within the Bumpnose Limestone near Marianna).

Another possibility is that *O. haldemani*, while occurring stratigraphically below *O. wetherbyi* in the Florida peninsula, appears either coeval to it, with *O. wetherbyi* absent in Jackson County, or above it north of the Suwannee Strait. This seems unlikely.

Yet another prospect was discussed by Miller et al. (2014) when they asserted that populations of *O. haldemani* in Jackson County are *O. colsoni* (they proposed reinstating Lambert's [1932] taxonomic assignment for these specimens). This assertion removes the stratigraphic ambiguity discussed above, as *O. colsoni* would then occur above the *Oligopygus wetherbyi* Zone, removing the conflict between the *Oligopygus* zonation and the foraminiferal zonation of Puri (1957).

Miller et al. (2014) revised the *Oligopygus* zonation to proceed as follows, from earliest to latest: *O. phelani, O. haldemani, O. wetherbyi* and finally *O. colsoni*. This would be tenable if *O. haldemani* and *O. colsoni* could be consistently distinguished, which Cooke (1942, 1959) and Kier (1980) asserted was not possible. This issue is treated in detail below in the entry for *O. haldemani*.

It could be that the zonation (*sensu* Carter, 1990; Croft and Shaak, 1985; McKinney and Jones, 1983; McKinney and Zachos, 1986) is best applied only south of the Suwannee Strait, where it has only been traditionally useful anyway, given the dearth of documented occurrences of *O. wetherbyi* and *O. phelani* north of the Suwannee Strait. Recognition of *O. colsoni* as a distinct species would only be useful

Figure 5: Denali Quarry (FM-IP SU003), Suwannee County, Florida. Exposed rocks are the *Oligopygus wetherbyi* and *Wythella eldridgei* Zones of the Upper Eocene Ocala Limestone.

if it is readily distinguishable from *O. haldemani*, though even Miller et al. (2014) admitted that it is not. If *O. colsoni* is indeed a distinct but cryptic species, it could serve as an indicator for Miller et al.'s (2014) zonation scheme, although other explanations for the stratigraphic placement of *O. haldemani* are plausible, as discussed above (also, see Table 3).

An alternative solution is to consider that the *Oligopygus* zonation used south of the Suwannee Strait cannot be applied in northern Florida. This is comparable to the foraminiferal zones of Puri (1957), which are not repeatable in their entirety south of the Suwannee Strait where *Asterocyclina* is no longer a dominant species of large foraminfera (Puri, 1957; Hunter, 1976). This would imply that Puri was incorrect in replicating the northern foraminiferal zonations to peninsular Florida without differentiating between the two regions. Indeed, a zone of *Asterocyclina* does not form the uppermost bed of the OLS in peninsular Florida, where the soft pale limestone containing *W. eldridgei*, discussed above, occupies the uppermost portion of the unit.

McKinney (1984) and Rice (1997) discussed the ontogeny and heterochrony of *O. phelani, O. haldemani,* and *O. wetherbyi*. McKinney (1984) studied this apparent lineage and considered it an excellent opportunity to examine the relationships between heterochrony and environmental change. Each species is similar to, but larger than, the preceding one. He asserted that the morphological differences among these species may not have resulted from selection directed at those traits but were simply a secondary result of size increase or of changes that occurred to permit the size increase. McKinney's assertion that each species is larger than the preceding one does not hold true when *O. rotundus* is added to the argument, since the latter is not smaller than *O. haldemani*.

McKinney (1984) determined that characteristic test shape, peristome shape, and periproct position of the larger species are generally either simple extensions of preexisting ontogenetic trajectories related to size increase or result from other heterochronic processes that change the trajectory in such a way as to permit the larger size. Rice (1997) asserted that many of these changes occurred because of changes in development, not just at the rate which the development proceeded. How a change in rate is not a change in development is not abundantly clear, and in this light, Rice (1997) points to issues with the term heterochrony itself. Given that heterochrony is also defined in terms of ancestors and descendants, it is curious that no one has recognized the logical step of trying to discover phylogenetic relationships among species of *Oligopygus*. However, neither Rice nor the authors whose work he discusses (notably McKinney, 1984) tried to perform phylogenetic analyses on the echinoids in question. Therefore, the value of heterochronic studies involving *Oligopygus* has yet to be assessed on either side of the argument. What is clear, however, is that the species used to differentiate the *Oligopygus* zones have distinct identities and stratigraphy.

Thus, herein, echinoid distribution of the OLS will be indicated based on the *Oligopygus* zonation discussed above: *Oligopygus phelani* Zone (lowermost OLS/Inglis Formation; perhaps best indicated by presence of *E. mooreanus*); *Oligopygus haldemani* Zone (upper portion of the lower OLS/Williston Formation, lowermost Crystal River Formation); *Oligopygus wetherbyi* Zone (upper OLS/Crystal River Formation); and *Wythella eldridgei* Zone (top of OLS in peninsular Florida) (Table 3). This applies to peninsular Florida.

The upper OLS in Jackson County, from the upper contact with the overlying Bumpnose Limestone, down to the *Haimea brooksi* Zone dredged up to 33 m below the top of the unit in the Brooks Quarry (FM-IP JA039) (Fig. 6), will be discussed distinctly as either residing in the *Haimea brooksi* Zone (the most characteristic element of the lowermost strata quarried in Jackson County), or the overlying limestone better characterized by the presence of *O. haldemani*, all of which contains an abundance of *Asterocyclina*. The base of the *Haimea* Zone was not reached during quarrying in the Brooks Quarry, nor is it visible in Jackson Blue Spring, so the lower boundary of the unit is unknown. Care will be taken to be precise with the stratigraphic placement of species in Jackson County, given the number of new taxa, and its disparity from the echinoid fauna of peninsular Florida.

ECHINOID DISTRIBUTION IN THE OCALA LIMESTONE

Although the OLS extends beyond Florida, into southwestern Georgia (Huddlestun and Hetrick, 1986) and southeastern Alabama (Toulmin, 1977), the greatest diversity of echinoids within the OLS is undoubtedly in Florida. Osborn et al. (2016: Table 2) documented 36 species of echinoid in the OLS of Florida, and herein we document 49 species and 54 distinct taxa in the unit (Table 1). The OLS is nearly always richly fossiliferous, and along with the characteristic foraminifera (Puri, 1957, discussed above) echinoids are also exceptionally important to the zonation of the unit within Florida (Table 3). Echinoid distribution in the Oligocene portion of the Bumpnose Limestone Member of the OLS is discussed below in the remarks for the Bumpnose Limestone.

As shown, the uppermost portion of the OLS in peninsular Florida consists of a soft limestone, above the *Oligopygus wetherbyi* Zone, that is characterized by the presence of *W. eldridgei*, as well as *Rhyncholampas trojana* (Cooke, 1942) (which also appears to be restricted to this horizon), and a diversity of spatangoids including *S. armiger*; *B. steinhatchee, O. beckeri*, *E. ocalanus, P. dixie, P. curvus,* other, rarer species (Table 1). This zone is well exposed in Lafayette and Dixie Counties, as far west as Taylor County (Martin Marietta Perry Quarry), and as far south as Sumter County where the horizon is intermittently exposed in quarrying in the Cemex Quarry at Center Hill (FM-IP SM010). As noted above, this horizon is herein recognized as the *Wythella eldridgei* Zone (Table 3) and is overlain by Oligocene age strata wherever it occurs.

Underlying the *Wythella eldridgei* Zone in peninsular Florida is the *Oligopygus wetherbyi* Zone, which is well exposed at many localities throughout the Ocala Arch region of central Florida (see occurrences in the discussion for *O. wetherbyi*). *Oligopygus wetherbyi, Weisbordella cubae* (Weisbord, 1934)*, R. conradi, Amblypygus americanus* Michelin, 1856, *Ova ocalana* (Cooke, 1942), and the rarer *Echinolampas tanypetalis* Harper and Shaak, 1974 (which appears to be restricted to this horizon), best characterize the unit, although additional species are present (Table 1). Within peninsular Florida, *A. americanus* appears to be restricted to the *O. wetherbyi* Zone, although in Jackson County it occurs in the uppermost OLS and Eocene portion

Figure 6: Brooks Quarry (FM-IP JA039), Jackson County, Florida. Exposed rocks are the *Haimea brooksi* Zone of the Upper Eocene Ocala Limestone, quarried by dragline below water level at a depth of up to 24 m, which is 29-30 m below the top of the Eocene exposures within the quarry.

of the overlying Bumpnose Limestone, exposed in the Brooks Quarry (FM-IP JA039) (Fig. 3).

The *Oligopygus haldemani* Zone, which underlies the *Oligopygus wetherbyi* Zone in peninsular Florida, often contains an abundance of *Durhamella ocalana* (Cooke, 1942), *Durhamella floridana* (Twitchell in Clark and Twitchell, 1915), *W. cubae*; *Agassizia clevei* Cotteau, 1875, *Eurhodia patelliformis* (Bouvé, 1851), *R. conradi*, and *Phyllacanthus mortoni* (Conrad, 1850), which is often represented by an abundance of spines and test fragments, in addition to many rarer species (Table 1). Other than *O. haldemani*, *E. patelliformis* appears to be the only echinoid restricted to this horizon in Florida. However, it occurs in Alabama and Georgia where it is not associated with *O. haldemani*, but *Oligopygus* is either absent or exceedingly rare in those exposures, so the Florida *Oligopygus* zonation does not apply. This zone is well exposed in many quarries in Florida, including the expansive Haile quarry complex in Alachua County (FM-IP AL004) (Fig. 7).

The *Oligopygus phelani* Zone underlies the *Oligopygus haldemani* Zone and occupies the sequence of limestone in the upper portion of what was formerly recognized as the Inglis Formation (Puri, 1957), largely exposed in Citrus and Levy Counties. Limestone exposures in this area are often richly fossiliferous. As discussed above, although *O. phelani* is typically rare, *E. mooreanus* (formerly

Figure 7: Limestone Products Quarries (FM-IP AL004), part of the Haile Quarries Complex, Alachua County, Florida. Exposed rocks are from the Upper Eocene Ocala Limestone.

referred to *Eupatagus antillarum* Cotteau, 1875) is abundant at most exposures.

The echinoid fauna of this unit was reviewed by Fischer (1951). although at the time this limestone was considered to belong to the Moodys Branch Formation. Fischer (1951) stated that some of the best-preserved echinoids in Florida were collected from this stratum, and while echinoids are often the most distinctive elements of the fauna and very well preserved, they are no better preserved than those of the upper OLS. Fischer (1951) documented 15 taxa in the Inglis Member (= *Oligopygus phelani* Zone), with most from the Withlacoochee River area. He named three new taxa: *Periarchus lyelli floridanus* (= *P. floridanus*), *Cassidulus ericsoni* [= *R. ericsoni* (Fischer, 1951), and *Cassidulus globosus* (= *R. georgiensis*). We herein document 18 taxa within this stratum (Table 1).

This unit, formerly recognized as the Inglis Formation, consists of two distinct facies, an upper limestone (*Oligopygus phelani* Zone) and lower dolomitic facies, which, as discussed above, contains *E. clevei* and *P. floridanus*. The upper limestone is well-exposed along the Cross Florida Barge Canal south of Inglis (FM-IP CI003, CI012, CI015, CI020-CI022, CI038), especially west of HWY 19/98, the Withlacoochee River west of Inglis (FM-IP CI052, FM-IP LV021, FM-IP LV101, FM-IP LV104, FM-IP LV106), spoil islands offshore at the mouth of the Withlacoochee River (FM-IP CI004, FM-IP CI024, FM-IP LV035), and numerous small quarries in Levy County. *Eupatagus mooreanus* and *P. floridanus* are ever-present within the limestone horizon, with some lenses composed largely of fragmented tests of *P.*

floridanus. This is the *Oligopygus phelani* Zone and a search of fine sediment and gravels often reveals an abundance of smaller species, especially *O. phelani*, *Fibularia vaughani* Twitchell in Clark and Twitchell, 1915, *Weisbordella inglisensis* n. sp., *Durhamella tetrapora* n. sp., *D. floridana*, and *D. ocalana*. The later two *Durhamella* have tests typically smaller than examples in the overlying *Oligopygus haldemani* Zone of the upper OLS.

The lower dolomitic zone of the lower OLS is well-exposed along the Cross Florida Barge Canal south of Inglis, as well as the CEMEX and Red Level quarries (FM-IP CI014) south of Inglis. This zone typically contains internal and external molds of echinoid tests, but includes sporadic concentrations of the large spatangoid *E. clevei* and lesser numbers of *P. floridanus*, and *Rhyncholampas* sp. It is interesting that when Fischer (1951) completed his detailed review of the echinoid fauna of the Inglis Member, he noted that a single specimen of *E. clevei* was collected. This specimen, which he figured, is beautifully preserved, retains its calcitic test, and was obtained from the limestone horizon along the Withlacoochee River. It appears that Fischer likely did not examine the dolomitic horizon, otherwise he would have noted the abundant fossils of this species which, although moldic, are nonetheless recognizable as *E. clevei*.

The stratigraphy of the Inglis Formation was discussed by Puri (1957), Vernon (1951), Puri and Vernon (1964), and especially Puri (1970). The molluscan fauna was reviewed by Richards and Palmer (1953), the ostracods by Swain (1946), and the foraminifera by Puri (1957).

The echinoid zonation reviewed above applies to peninsular Florida (south of the Suwannee Strait) (Table 3). However, north of the Suwannee Strait, in Jackson County, the OLS has a distinctly different fauna than that of peninsular Florida and contains species more commonly found in the muddier facies of the OLS of Georgia, as well as some elements of peninsular Florida. In the mining operation of Leon Brooks (FM-IP JA0009, (FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039), northwest of Marianna in Jackson County (Fig. 3), the OLS is overlain by the Bumpnose Limestone (which transitions across the Eocene and Oligocene boundary and is further discussed in the Oligocene section herein) and nearly 30.5 m of the OLS are quarried, with *O. haldemani* and the distinctive, large, star-shaped foraminiferan, *Asterocyclina*, occurring throughout the entire OLS sequence.

The geology of Jackson County was reviewed by Moore (1955) and further discussed by Bryan et al. (2008) and Herbert (2012). Herbert (2012: 11) examined the uppermost bed of the OLS in the Brooks Quarry, and Bryan et al. (2008: 90) figured the OLS/Bumpnose contact (Fig. 3), as well as the overlying Bumpnose/Marianna contact. Diagnostic Upper Eocene echinoid species, such as *Amblypygus americanus* and *Rhyncholampas conradi,* occur in the lower (Upper Eocene) portion of the Bumpnose Limestone that were obtained *in situ* above the OLS/Bumpnose contact.

Macropneustes mortoni, P. curvus, R. conradi, Weisbordella johnsoni (Twitchell in Clark and Twitchell, 1915)*, O. haldemani, A. clevei*, and other, rarer species are common in the upper 3 m of OLS in the Brooks Quarry. Below this horizon is a less fossiliferous zone that extends for at least 10 m and contains little except *O. haldemani* and *W. johnsoni*.

In the northwestern most excavations within the Brooks Quarry complex (FM-IP JA039), the limestone brought up from the greatest depth with a dragline (~29-30.5 m below the OLS/Bumpnose contact, Fig. 6) contains an interesting fauna that includes *H. brooksi*; *O. rotundus*, *O. haldemani*, *R. georgiensis*, *W. johnsoni*, the herein described *Rhyncholampas mariannaensis* n. sp., *Rhyncholampas bao* n. sp., *Brissus jonesi* n. sp., and numerous rarer taxa (Osborn et al., 2016) (Table 1). This fauna not only includes numerous taxa seldom documented elsewhere, such as *H. brooksi* and the herein described *B. jonesi* n. sp., *R. mariannaensis* n. sp., and *R. bao* n. sp., but an exceptionally diverse echinoid fauna that is perhaps best characterized by the presence of *H. brooksi*. The presence of the latter species distinguishes it from the overlying strata that also contains *O. haldemani*, but none of the new taxa listed above, all of which appear to be restricted to the *Haimea brooksi* Zone.

This horizon, with *H. brooksi*, is also exposed

Table 4: Distribution of Oligocene echinoids documented from Florida.

Taxon	**Bumpnose Limestone**	**Marianna Limestone**	**Suwannee Limestone**	**Bridgeboro Limestone**
Phyllacanthus mortoni (Conrad, 1850)		■	■	■
Phymotaxis mansfieldi Cooke, 1941			■	
Gagaria mossomi (Cooke, 1941)			■	
Lytechinus floralanus (Cooke, 1941)				■
Clypeaster cotteaui Egozcue, 1897				■
Clypeaster marinanus Jackson, 1937	■		■	
Clypeaster oxybaphon Jackson, 1922				■
Clypeaster rogersi (Morton, 1834)		■		
Clypeaster sp. A			■	
Clypeaster sp. B			■	
Clypeaster sp. C			■	
Rhyncholampas gouldii (Bouvé, 1846)			■	
Echinolampas aldrichi Twitchell, 1915		■		
Schizaster americanus Clark, 1915		■	■	■
Schizaster carlsoni n. sp.			■	
Agassizia mossomi Cooke, 1942		■	■	■
Brissus bridgeboroensis Carter, 1987			■	
Plagiobrissus cassadyi n. sp.		■		
Eupatagus dumonti n. sp.			■	■
Eupatagus sp. B			■	
Total Species= 16; total taxa= 20	1	6	14	7

deep within the underground cavern system at Jackson Blue Spring, east of Marianna, Jackson County (FM-IP JA033). Here, at over 33 m depth, certified cave divers collected *H. brooksi, R. georgiensis, W. johnsoni*, the herein described *B. jonesi* n. sp., *Prionocidaris robertsi* n. sp. (abundant spines of this species are present), and rarer taxa, including *O. beckeri*. Neither excavation in the Brooks Quarry or exposures in Jackson Blue Springs expose the base of the *Haimea brooksi* Zone, so the echinoid fauna of this portion of the OLS, as well as correlation of the *Haimea brooksi* Zone and the *Oligopygus phelani* Zone of peninsular Florida, is unknown. However, within Jackson County, the *Haimea brooksi* Zone is the lowest exposed portion of the OLS, residing beneath the zone of abundance of *Oligopygus haldemani*.

THE OLIGOCENE

The regional echinoid fauna experienced a dramatic drop in diversity at the start of the Oligocene (Table 4), which was likely the result of a global-scale deterioration of the physical environment at the Eocene/Oligocene boundary. The ultimate cause of this deterioration is inferred to be climatic cooling in the Early Oligocene that was perhaps associated with the isolation of Antarctica (McKinney et al., 1992). This deterioration was most evident in the Early Oligocene, but likely continued through most of the epoch (see Prothero et al., 2003).

Whereas the Middle to Upper Eocene strata of the region saw the extensive evolution of the protoscutellids (which includes many of the most important Claibornian and Jacksonian Stages index taxa within the region), the Early Oligocene saw the disappearance of such forms, and the proliferation of the clypeasteroids and other scutelloids in the region throughout the Oligocene.

The greatest diversity of Florida Oligocene echinoids occurs in the Suwannee Limestone, which contains 14 taxa (Table 4). The most widespread unit in the southeastern United States is the Marianna Limestone, which comprises a thick sequence of soft limestone that extends from the Mississippi River southeastward to its type area in Jackson County (FM-IP JA084) in northern Florida. The Marianna Limestone contains the characteristic species *Clypeaster rogersi* (Morton, 1834) in most exposures throughout the region, and within Florida, the Marianna Limestone contains six taxa (Table 4).

McKinney et al. (1992) stated that Lower Oligocene strata of the region contained only *Cyclaster drewryensis* Cooke, 1942 from the Red Bluff Formation of southwestern Alabama. However, the Early Oligocene fauna is now considered to be more diverse, though only slightly, than previously understood (Table 4). Two basal Oligocene units contain echinoid faunas within the region: the Red Bluff Formation of southeastern Mississippi and southwestern Alabama, and the Bumpnose Limestone of southeastern Alabama and northern Florida, especially Jackson County.

The Bridgeboro Limestone crops out in southwestern Georgia, northern Florida, and southeastern Alabama, and is currently known to contain at least seven echinoid species within Florida (Table 4). This fauna is further discussed below.

Additional Oligocene units occur in the region but do not contain documented echinoids or have very sparse assemblages. The Oligocene portions of the Arcadia Formation of southern Florida do not contain any documented echinoids, although the Miocene portions of the unit does [see Osborn et al. (2020)].

Bumpnose Limestone

The Bumpnose Limestone is best exposed near its type area in Jackson County, where it is exposed in its entirety in the Brooks Quarries, northwest of Marianna (FM-IP JA021, FM-IP JA025, FM-IP JA030) (Fig. 3). When Moore (1955) named the Bumpnose Limestone, he believed it to be uppermost Jacksonian in age, but it is now considered to straddle the Eocene and Oligocene Boundary (Ellwood et al., 2019) (Table 2). At the Brooks Quarry, the unit is approximately 3.5 m thick (Herbert, 2012: 11).

MacNeil (1944), Moore (1955), Huddlestun and Toulmin (1965), Miller (1986), and others noted that the Bumpnose Limestone correlates with the basal Oligocene Red Bluff Clay in Alabama (which also contains *Clypeaster marinanus* Jackson, 1937). Miller (1986) stated that gulfward, the Bumpnose Limestone merges with a thick sequence of unnamed limestone and finely crystalline dolomite. The unit pinches out southwestward in western Bay County. Without a doubt, the best exposures of the typically glauconitic *Lepidocyclina chaperi*-packstone of the Bumpnose Limestone are found near the type area in Jackson County.

As noted above, Cheetham's (1963) correlation likely led to Hunter's (1972, 1976, 1981) recognition of the Bumpnose Limestone (for Puri's *Spirolaea vernoni* Zone) in peninsular Florida. However, the *vernoni* Zone is considered Upper Eocene, as evidenced with its correlation to the *Asterocyclina* Zone when Puri (1957) erected his zonation, and reaffirmed by Nicol et al. (1976, 1984, 1989), Jones and Nicol (1989) and others. Bryan (1993) stated the usage of the term Bumpnose Limestone in peninsular Florida should be discontinued. However, the Bumpnose in Jackson County does straddle the Eocene/Oligocene boundary, so perhaps the equivalency is merely in the Eocene portion. The echinoids of the *Rotularia vernoni* Zone (*Wythella eldridgei* Zone) are Eocene in age, as discussed in the OLS section above.

Therefore, within Florida, we recognize the Bumpnose Limestone only in its type area near Marianna (the unit does extend into southern Alabama). The geology of Jackson County is reviewed by Moore (1955) and further discussed by Bryan et al. (2008), Ellwood et al. (2019), and Herbert (2012).

Scott (1991) stated the Florida Geological Survey no longer recognized the Bumpnose Limestone as a distinct formation, and due to its lithological similarities treated it as the uppermost bed of the OLS (effectively extending the OLS into the Oligocene). Ellwood et al. (2019) recognized the Bumpnose Limestone as the upper member of the Ocala Limestone.

Huddlestun (1993) stated the Bumpnose is "Ocala-like" but glauconitic and clarified that there are no known deposits of Bumpnose Limestone correlative strata outside of the Gulf Trough in Georgia.

Bryan et al. (2008) and Ellwood et al. (2019) figured the contact with the Bumpnose Limestone and underlying OLS in the Brooks Quarries (FM-

IP JA018-JA021), as well as the contact with the overlying Marianna Limestone. Both contacts are sharp, and form indurated ledges that are visible as thick white bands in the quarry face. The Bumpnose Limestone therefore occurs between these two pale ledges. The Bumpnose Limestone does not appear to exceed 5 m in thickness in Jackson County (Moore, 1955).

The Bumpnose Limestone is characterized by the large foraminiferan, *Lepidocyclina chaperi* Lemoine and Douville, 1904, and within Jackson County, the underlying OLS and lowermost Bumpnose Limestone are characterized by the large star-patterned foraminiferan, *Asterocyclina*. The upper indurated bed of the Bumpnose Limestone is glauconitic, which is also characteristic of the unit in Jackson County.

Just above the pale indurated ledge at the OLS/Bumpnose contact, the Bumpnose Limestone in the Brooks Quarry complex contains an often nodular, semi-indurated limestone with *Amusium ocalanum* Dall, 1898, and the characteristic Eocene echinoids *Amblypygus americanus*, and *Rhyncholampas conradi*, this being the Eocene portion of the Bumpnose Limestone.

The remainder of the overlying lowermost Oligocene-portion of the Bumpnose Limestone consists of *Lepidocyclina* packstone with *L. chaperi, Aturia alabamensis* (Morton, 1834), *Spondylus dumosus*, and other mollusks, as well *Clypeaster marinanus*, which is the only known echinoid in the Oligocene portion of the Bumpnose Limestone (Table 4). The overlying Marianna Limestone contains *Clypeaster rogersi*.

Moore (1955: 38) stated that he asked C. Wythe Cooke to examine specimens of *Clypeaster* from the Bumpnose Limestone, and that Cooke determined they represent a new species closely allied to *C. rogersi*. However, Cooke (1959) did not describe the taxon. Huddlestun (1993) also noted the Bumpnose Limestone contains an undescribed species of *Clypeaster* he assumed was likely ancestral to *C. rogersi*. We recognize this form with typically shorter petals and a thinner margin than *C. rogersi* as Jackson's (1937) *C. marinanus*. Moore (1955) also stated the Bumpnose contains a new species of *Anisopetalus* (= *Rhyncholampas*). However, we have been unable to verify this occurrence (it is possible he was referring to large specimens of *R. conradi*, which occur in the Eocene portion of the lower Bumpnose Limestone). Herbert (2012) stated that the Bumpnose Limestone in the Brooks Quarries (FM-IP JA021, FM-IP JA025, FM-IP JA030) contains *C. rogersi*, which is likely a misidentification of *C. marinanus*, as we have only found *C. rogersi* in the overlying Marianna Limestone in this quarry.

Marianna Limestone

The Marianna Limestone was named by Matson and Clapp (1909) from exposures at Marianna in Jackson County (FM-IP JA084), which he defined as a soft, porous, light gray to white limestone characterized by an abundance of *Orbitoides mantelli* Morton, 1833 (= *Lepidocyclina mantelli*). Cooke and Mossom (1929) clarified that Matson and Clapp's (1909) Marianna Limestone included strata then recognized within the OLS and refined understanding of the unit as the "white limestone or chimney rock" that overlies the OLS at Marianna and containing *L. mantelli* and *Pecten poulsoni* Morton, 1834. The subsequent recognition of the Bumpnose Limestone by Moore (1955) modified Cooke and Mossom's definition slightly and the Marianna Limestone of northern Florida is now recognized as residing above the Upper Eocene-Lower Oligocene Bumpnose Limestone and below the Chattahoochee Formation in Jackson County, and Bridgeboro Limestone in Washington County at Duncan Church (FM-IP WG002).

The Marianna Limestone is now considered to be Early Oligocene (Rupelian) and extends northeastward from the type area to Pulaski County, Georgia (Huddlestun, 1993), and northwestward across southern Alabama and Mississippi to the Mississippi River, where the unit thins substantially (Dockery, 1982). The lithology of the Marianna in Georgia, northern Florida, Alabama, and eastern Mississippi is the typical, soft white limestone described by Matson and Clapp (1909), with *C. rogersi* being the characteristic echinoid of the unit (Dockery, 1980; 1982). In Jackson County, *Schizaster americanus* Clark in Clark and Twitchell, 1915 is also found with persistent collecting.

South of Marianna, in southern Jackson County, quarries (e.g., FM-IP JA014) and natural exposures (e.g., FM-IP JA010), provide glimpses of a dolomitic limestone with a diverse echinoid fauna indicative of the Marianna Limestone, but the lithology is decidedly not like the soft pale limestone of the Marianna Limestone several kilometers northward at its type locality. A collectable exposure of this horizon is seen during low water levels along the banks of Dry Creek (FM-IP JA010) southwest of Marianna. Here, the tan to brown dolomitic limestone is variably indurated and contains an abundance of *Lepidocyclina* sp. and a diverse echinoid fauna preserved as internal and external molds, including abundant specimens of the characteristic Marianna Limestone species, *Clypeaster rogersi* and *Schizaster americanus,* as well as *Plagiobrissus cassadyi* n. sp., rarer *Agassizia mossomi* Cooke, 1942, and *Phyllacanthus* cf. *P. mortoni*. A quarry north of Altha (FM-IP JA014) provided extensive exposures of this dolomitic horizon, with an abundance of *C. rogersi, Echinolampas aldrichi* Twitchell in Clark and Twitchell, 1915 (the first documented occurrence of this species in Florida), and *S. americanus*.

Moore (1955) mapped the Suwannee Limestone in this area of Jackson County and described the unit here as tan to bluff colored limestone and dolomitic limestones residing above the Marianna Limestone and below the Tampa Limestone (now considered Chattahoochee Formation). This stratum is therefore certainly that which Moore (1955) referred to the Suwannee Limestone. However, the lithology is decidedly not synonymous with the current understanding of the Suwannee Limestone (Huddlestun, 1993). Spencer and Loyd (1999: 10) also erroneously stated that the dolomitic limestone south of Marianna is Suwannee Limestone.

Green et al. (2002) and Rupert and Means (2009) noted that the unit mapped as Suwannee Limestone in this area of Florida is likely either Bridgeboro Limestone or undifferentiated Marianna/Bridgeboro Limestone in cross sections. Bryan et al. (2008: 92) stated that south of Marianna the Marianna Limestone is a dolostone, as exposed in the quarries north of Altha. Clearly there is no consensus, but we include the Dry Creek echinoid assemblage in the Marianna Limestone in Table 4 with the understanding that the lithology is decidedly distinct from either the typical Marianna or Suwannee Limestones.

SUWANNEE LIMESTONE

The Suwannee Limestone is the dominant Oligocene unit of peninsular Florida. The name Suwannee Limestone was proposed by Cooke and Mossom (1929) for yellowish limestone exposed along the Suwannee River from Ellaville nearly to White Springs in northern Florida. This stratum had previously been referred to as the Hawthorn Formation (Matson and Clapp, 1909) and Tampa Limestone (Cooke and Mossom, 1929). Huddlestun (1993) made a persuasive argument for including the unit entirely within the Early Oligocene (Rupelian), which was validated by Brewster-Wingard et al. (1997) and Scott (2001). In peninsular Florida, the Suwannee Limestone crops out on the northwestern, northeastern, and southwestern flanks of the Ocala Platform and is absent on the eastern coast, either due to erosion, non-deposition, or both (Scott, 2001). Although Huddlestun (1993) recognized a dolostone directly below the typical Suwannee Limestone near Ellaville as a distinct unit, the Suwannee Limestone does have dolomitized and silicified beds throughout its distribution.

Huddlestun (1993) refined the Suwannee Limestone by removing a few distinct mappable lithologies, several of which contain echinoids and are discussed below, especially near Ellaville, in northern Florida. This clarified the unit, and by including only the uppermost limestone beds along the Suwannee River at Ellaville within the Suwannee Limestone, Huddlestun (1993) revised the concept of the unit to be compatible with much of the limestone of west central and northern Florida that has traditionally been included within the Suwannee Limestone. In the type area of the Suwannee Limestone, and throughout its extent from southern Georgia to west central Florida, the unit can be described as a very pale orange, massive-bedded and structureless to poorly but thickly stratified, coarse-grained, variably soft and hard limestone that is sporadically richly macrofossiliferous (Huddlestun, 1993).

Huddlestun (1993) erected the Ellaville Limestone for Lower Oligocene limestone that crops out along the Suwannee and (lower only) Withlacoochee River in Madison, Hamilton, and Suwannee Counties, and is present in the subsurface of southwestern Georgia. At the type locality of the unit, along the Suwannee River near Ellaville in Hamilton County, Florida, the Ellaville Limestone is a lithologically nondistinctive, sparsely but variably macrofossiliferous, relatively pure, moderately indurated limestone with minor components of dolomite and dolostone. Intraformational breccia (with mud rip-up clasts) occur in the Ellaville, indicating peritidal conditions.

Cooke and Mossom (1929: 72, 73) referred these beds at the type locality of the Ellaville Limestone to the Glendon Limestone. Cooke (1945) included this stratum in the Byram Limestone, and Hunter (1972) referred this unit to the Bumpnose Limestone.

The Ellaville Limestone overlies the Upper Eocene OLS and is overlain by the Lower Oligocene Suwannacoochee Dolostone (of Huddlestun, 1993) which gradationally and conformably overlies the Ellaville Limestone at Ellaville, Florida. Huddlestun (1993) erected the Suwannacoochee Dolostone for lithologically distinctive dolostone around the (lower only) Suwannee and Withlacoochee Rivers in Madison, Hamilton, and Suwannee Counties, Florida, as well as in the subsurface of southern Georgia. The type locality is along the Suwannee River at Ellaville, Florida where it immediately overlies the stratotype Ellaville Limestone. This dolostone has traditionally been included within the Suwannee Limestone. However, Huddlestun (1993) proposed excluding it from that unit due to its distinctive, mappable, dolostone lithology.

Scott (2001) stated that the Ellaville Limestone and Suwannacoochee Dolostone are not differentiated on the geological map of Florida (Scott et al. 2001) and are instead included within the Suwannee Limestone due to the limited data on the areal distribution of the two units. The Ellaville Limestone and Suwannacoochee Dolostone are not included in Table 4 merely to simplify the table, as both units are known to contain only *Rhyncholampas gouldii* (Bouvé, 1846). However, *Clypeaster* cf. *C. marinanus* occurs in dolomitic facies of the Suwannee Limestone exposed in the Cabbage Grove Quarry west of Perry (FM-IP TA001). This form has a much thinner test and shorter ambulacra than *C. rogersi* and has not hitherto been identified in the Suwannee Limestone of peninsular Florida.

Rhyncholampas gouldii is the ubiquitous echinoid of the Suwannee Limestone. However, other species are present, though less abundant (Table 4). In the Brooksville Rock Quarry (now Vulcan Quarry), northwest of Brooksville in Hernando County (FM-IP HE007, FM-IP HE012, FM-IP HE026, FM-IP HE028, FM-IP HE034), the regular echinoids *Gagaria mossomi* (Cooke, 1941a) and *Phymotaxis mansfieldi* Cooke, 1941a occur throughout the majority of the Suwannee Limestone, but their presence is greatly overshadowed by the abundant *R. gouldii*. A mollusk-mold and foraminifera-rich limestone is intermittently exposed in the lowest beds within this quarry that contains an echinoid fauna that is very distinct from the remainder of the unit (Fig. 8). This horizon contains an abundance of *Clypeaster* sp. B, which characterizes the fauna, as well as large specimens of *R. gouldii*, and rarer *Agassizia mossomi, Phyllacanthus* cf. *P. mortoni*, and the herein described *Schizaster carlsoni* n. sp., and *Eupatagus dumonti* n. sp. This is the only documented occurrence of this echinoid faunal assemblage within the Suwannee Limestone, and as they have not excavated below this horizon in the Cargil Vulcan Quarry, it is not possible to determine how deep in the Suwannee Limestone this horizon occurs, though it is certainly quite low in the unit.

Southwestward in the Sunwest Mine, near Aripeka, *R. gouldii* occurs with *Phymotaxis mansfieldi, Gagaria mossomi,* and the much rarer *Brissus bridgeboroensis* Carter, 1987b.

Bridgeboro Limestone

The Bridgeboro Limestone, a rhodolithic limestone that occurs in southwestern Georgia, southeastern Alabama, and northern Florida, was introduced by Huddlestun (1981), adopted by Manker and

Figure 8: Vulcan Brooksville Quarry (FM-IP HE038) Hernando County, Florida. Exposed rocks are the Lower Oligocene Suwannee Limestone. Limestone in foreground (excavated beneath typical floor of quarry) is the lowermost bed containing *Clypeaster* sp. B., *Eupatagus dumonti* n. sp., and *Schizaster carlsoni* n. sp.

Carter (1987), and formally named by Huddlestun (1993).

The type locality of the unit is the southernmost pit of the Bridgeboro Lime and Stone Company quarry, almost 10.5 km southwest of Bridgeboro in Mitchell County, Georgia, where Huddlestun (1993) documented *R. gouldii, Clypeaster cotteaui* Egozcue in Cotteau, 1897 (which is the characteristic echinoid of the unit throughout its extent), and, questionably, *C. rogersi*. Manker and Carter (1987: table 2) also documented an undescribed *Brissus* and an undescribed *Prionocidaris*(?) (= *Phyllacanthus* cf. *P. mortoni*?) from the rhodolith facies of the Bridgeboro Limestone.

Huddlestun (1993) designated the Duncan Church Quarry (FM-IP WG002) (Fig. 9), in Washington County, Florida, as a reference section for the lower boundary of the unit where it gradationally overlies the Marianna Limestone.

Huddlestun (1993) erected the Florala Limestone Member of the Bridgeboro Limestone for a fossiliferous, *Lepidocyclina*-rich, non-rhodolithic facies of the Bridgeboro Limestone. The type locality for this member is the Stovall Quarry, located about 11 km east of Florala, southern Covington County, Alabama (FM-IP ZA023), very near the Alabama/Florida border (Huddlestun, 1993). The Florala Limestone Member appears to be an offshore, likely deeper, quieter water facies of the typical Bridgeboro Limestone. It contains a more diverse echinoid fauna than the typical unit.

Huddlestun (1993) documented *C. cotteaui*; *C. rogersi*; *B. bridgeboroensis*, *Lytechinus floralanus* (Cooke, 1941a), and *Macropneustes mortoni* from the Florala Limestone Member at its type locality. See the remarks for *M. mortoni* for discussion on this occurrence in the Florala Member.

At the Duncan Church Quarry (FM-IP WG002) (Fig. 9) in the northern Florida panhandle, the Bridgeboro Limestone conformably over-

Figure 9: Duncan Church Quarry (FM-IP WG002), Washington County, Florida. Exposed rocks are the Lower Oligocene Marianna and Bridgeboro Limestones.

lies the Marianna Limestone (which contains *C. rogersi*) and contains a much greater diversity of echinoids than the typical Bridgeboro Limestone, with an abundance of *C. cotteaui*, as well as additional rarer species, including *A. mossomi, L. floralanus, C. rogersi*, *Phyllacanthus* cf. *P. mortoni*, *S. americanus*, and *E. dumonti* n. sp (Table 4). The Bridgeboro Limestone at Duncan Church contains rare rhodoliths and a greater concentration of *Lepidocyclina* than the typical Bridgeboro Limestone. The fauna and lithology of the Bridgeboro Limestone at Duncan Church is therefore more like that of the Florala Member at its type locality than to that of the typical Bridgeboro Limestone. However, Huddlestun (1993: 55) included the Duncan Church beds in the undivided Bridgeboro Limestone. Bryan (1993) referred to the Bridgeboro Limestone at Duncan Church as the Duncan Church beds.

SYSTEMATIC PALEONTOLOGY

Classification follows Kroh (2020), the World Echinoidea Database (Kroh and Mooi, 2022), and Stokes and Kroh (2022). Species within the genera are listed alphabetically after type species of the genus, if included, and new species are described in alphabetical order at the end of the treatment for the relevant genus. Synonymies of commonly cited species are abbreviated, consisting of unique formulations of names referring to the taxon in question, as well as names occuring in major monographs or most recent works. Descriptions are provided for new species only. Readers interested in descriptions of previously named taxa can reference original descriptions listed in the synonymy for each species and consult our images. Diagnoses contain characters pertinent to recognition of the new taxon to the species level. However, due to the nature of the taxa and the limited knowledge concerning them, these characters are not always autapomorphies, and we must rely on unique combinations of multiple characters. Usage of aff. and cf. in taxonomic designations follows Lucas (1986). Terminology follows that of Mortensen's "Monograph of the Echinoidea" (volumes spanning 1925 to 1952), and Smith and Kroh (2011).

Class **ECHINOIDEA** Schumacher, 1817
Subclass CIDAROIDEA Smith, 1984
Order CIDAROIDA Claus, 1880
Family CIDARIDAE Gray, 1825
Genus *Phyllacanthus* Brandt, 1835

Phyllacanthus mortoni (Conrad, 1850)
(Figs. 10-15)

Cidarites mortoni Conrad, 1850. p. 40. pl. 1, fig. 13.
?Cidaris blandus Gregorio, 1890. p. 253. pl. 44, fig. 5. (Typographical error for *blandis*)
?Cidaris moerens Gregorio, 1890. p. 252. pl. 43, figs. 22, 23.
?Cidaris modestus Gregorio, 1890. p. 253. pl. 43, fig. 26.
?Cidaris ordinatus Gregorio, 1890. p. 252. pl. 44, fig. 1.
?Cidaris perdubius Gregorio, 1890. p. 253. pl. 44, fig. 2.
?Cidaris moereus (Gregorio). Clark and Twitchell, 1915. p. 115. (Typographical error for *moerens*)
?Cidaris modestus (Gregorio). Clark and Twitchell, 1915. p. 115.
?Cidaris ordinatus (Gregorio), Clark and Twitchell, 1915. p. 115.
?Cidaris perdubius (Gregorio). Clark and Twitchell, 1915. p. 116.
?Cidaris blandis (Gregorio). Clark and Twitchell, 1915. p. 116.
Cidaris mortoni (Conrad). Clark and Twitchell, 1915. p. 157. pl. 73, fig. 1.
Cidaris georgiana Clark, in Clark and Twitchell, 1915. p. 158. pl. 73, fig. 4.
Cidaris (*Dorocidaris*) *georgiana* (Clark). Lambert and Thiéry, 1925. p. 560.
Phyllacanthus mortoni (Conrad). Cooke, 1941a. p. 3. pl. 1, figs. 16-18.
Cidaris (*Phyllacanthus*) *mortoni* (Conrad). Fischer, 1951. p. 55.
Phyllacanthus mortoni (Conrad). Cooke, 1959. p. 11. pl. 1, figs. 15-17.
Phyllacanthus mortoni (Conrad). Osborn et al., 2016. tbl. 2.

Occurrence.—*Phyllacanthus mortoni* occurs in Florida throughout the OLS, although it is most abundant in the upper portion of the unit where it is often associated with *O. wetherbyi* in quarries northwest of Mayo, Lafayette County (FM-IP LF001); the Branford 01A Quarry (FM-IP SU003) north of Branford, Suwannee County and west of Dowling Park, Lafayette County (FM-IP LF010), among other many other localities. Persistent searching in the *Oligopygus wetherbyi* Zone will usually reveal at least test fragments or spines of this distinctive species, although complete tests are rare. The species also occurs in the *Oligopygus haldemani* Zone at the Brooks Quarries (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031), northwest of Marianna, Jackson County, and a quarry northwest of Mayo (FM-IP LF001), Lafayette County. This species is occasionally found in the *Oligopygus phelani* Zone, along the Withlacoochee River west of Yankeetown (FM-IP LV024) and the Cross Florida Barge Canal south of Inglis in Citrus and Levy Counties (e.g., FM-IP CI001).

Phyllacanthus mortoni is widely distributed in Upper Eocene strata in Alabama, where it occurs in the OLS and Yazoo Clay, as well as Georgia where it appears in the OLS.

We also document the occurrence of partial tests of a cidarid in Oligocene strata that cannot be differentiated from *P. mortoni* in the Duncan Church beds of the Bridgeboro Limestone at Duncan Church (FM-IP WG002), Washington County and in the dolomitic facies of the Marianna Limestone at Dry Creek (FM-IP JA010) south of Marianna, Jackson County. Fragments also occur in the Marianna Limestone at a limestone quarry southeast of Brooklyn, Alabama (FM-IP ZA147).

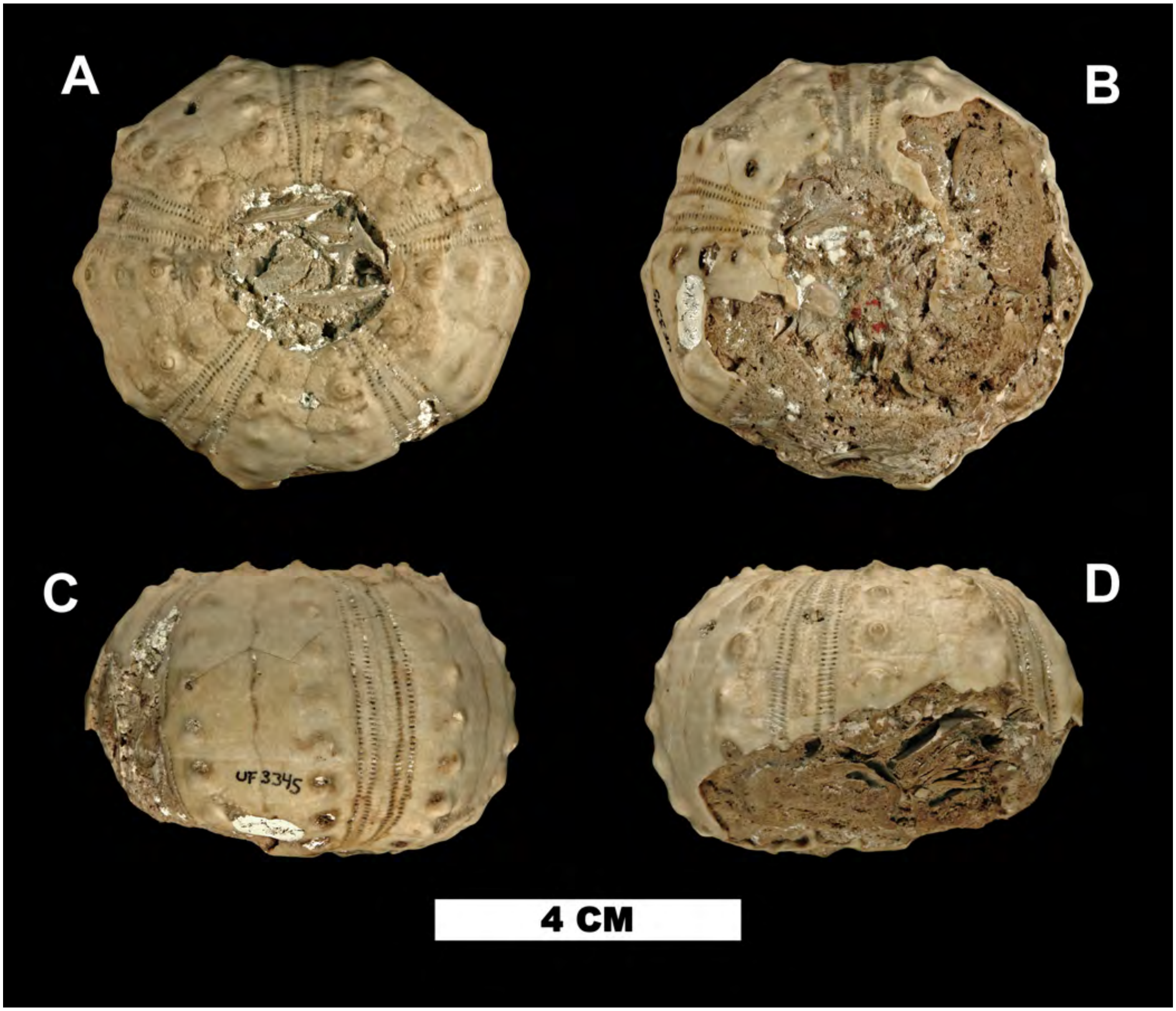


Figure 10: *Phyllacanthus mortoni* (UF 3345), 58 mm TD, 37 mm TH, Upper Eocene, Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A. aboral. B: oral. C, D: lateral.

Cooke (1961) documented *P. mortoni* in his work on the echinoids of Trinidad and Venezuela. However, Cutress (1980) referred that specimen to *Prionocidaris loveni* (Cotteau, 1875).

Discussion.—Conrad (1850) described *Cidarites mortoni* from Eocene strata near New Palmyra, Lee County, Georgia. However, four years earlier, Morton (1846) described *Cidaris alabamensis*, but did not figure it, from the Eocene of Washington County, Alabama. Clark and Twitchell (1915), in asserting that Morton very inadequately described *C. alabamensis*, also stated that no material could be obtained that can be regarded as belonging to that species.

Subsequently, Cooke (1941a) placed *Cidarites mortoni* in *Phyllacanthus* but only questionably placed *C. alabamensis* into synonymy with *P. mortoni*, again stating that it had not been figured or distinguished using Morton's original description. Having done so, though, Cooke implicitly recognized priority of the name *C. alabamensis* Morton, 1846, even after correctly stating that should it prove to be identical with *P. mortoni*, its name would have priority. We do not include Morton's *C. alabamensis* in our synonymy. If *C. alabamaensis* can be shown to be a valid taxon

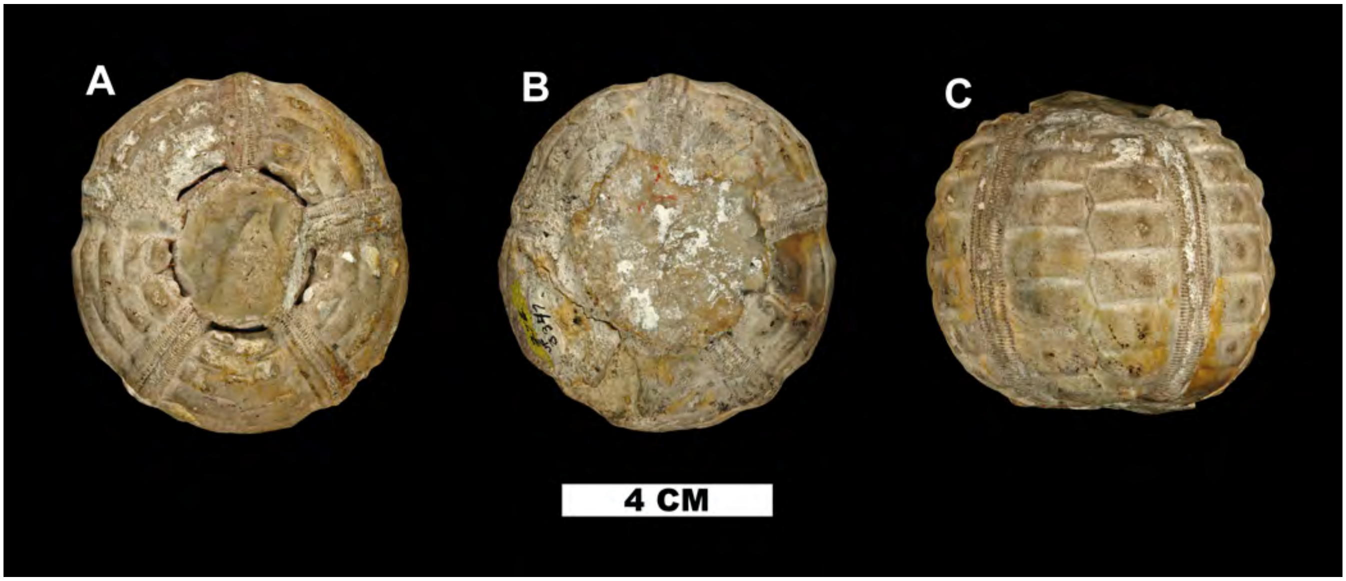


Figure 11: *Phyllacanthus* cf. *P. mortoni* (UF 3347), 69 mm TD, 55 mm TH, Upper Eocene, Ocala Limestone, Alachua County, Florida (FM-IP 2613). A. aboral. B: oral. C: lateral.

identical with *P. mortoni*, the latter would become a subjective junior synonym of *C. alabamensis*. Nevertheless, without types of *C. alabamensis*, and given the meager description and locality information of Morton (1846), we, like Clark and Twitchell (1915) and Cooke (1941a, 1959), cannot presently conceive of a situation where this would be warranted.

Clark in Clark and Twitchell (1915), named *Cidaris georgiana* from Muckafoonee Creek, Georgia, in strata he referred to the Oligocene, which is now considered Late Eocene. Asserting that it comes from beds known to contain *P. morton*i, Cooke (1941a) placed *C. georgiana* into synonymy with *P. mortoni*, an action with which we agree.

Cooke (1959) considered *Phyllacanthus carolinensis* (Emmons, 1858) and *Phyllacanthus mitchellii* (Emmons, 1858) to be subjective junior synonyms of *P. mortoni*. However, Cutress (1980) and Kier (1980) disputed this assertion and treated these species as distinct. We have examined specimens of *P. carolinensis* from the OLS of Georgia and the Castle Hayne Formation of North Carolina and find differentiation of the species not at all troublesome. The broad area of coarse granulation in the interambulacrals and less prominent scrobicular ring of *P. carolinensis* readily differentiate the two species. In addition, *P. carolinensis* has nonconjugate pores, whereas *P. mortoni* has clearly conjugate pores. We follow Kier (1980) and retain *P. carolinensis* as a distinct species. We also concur with Cutress (1980) and Kier (1980) and recognize *P. mitchellii* as a species distinct from *P. mortoni*. As noted by Kier (1980), *P. mitchellii* differs from *P. mortoni* in having its peristome smaller than its apical system, the interambulacral granular zone is wider in *P. mitchellii* and there are 11 to 11.5 ambulacral plates adjacent to each interambulacral plate at the midzone, whereas there are only seven to eight in *P. mortoni*.

In the OLS of Florida, *P. mortoni* is most associated with *O. wetherbyi,* though it is present throughout the unit. This large cidarid could only be confused with *Prionocidaris robertsi* n. sp., which is readily differentiated by the granules of the interambulacral area being arranged in clear, longitudinal rows in *P. mortoni*, but not so in *Pr. robertsi* n. sp. In addition, the spines associated with *Pr. robertsi* n. sp. are heavily thorned and often flare at their apex, whereas spines associated with *P. mortoni* lack these prominent thorns or flared distal end and are relatively smooth or corrugated with rows of fine to coarse granulations. *Phyllacanthus mortoni* cannot be confused with any other echinoid currently documented from the Eocene of Florida.

We figure a very large internal mold of a cidarid (UF 3347) that is likely *P. mortoni*, but

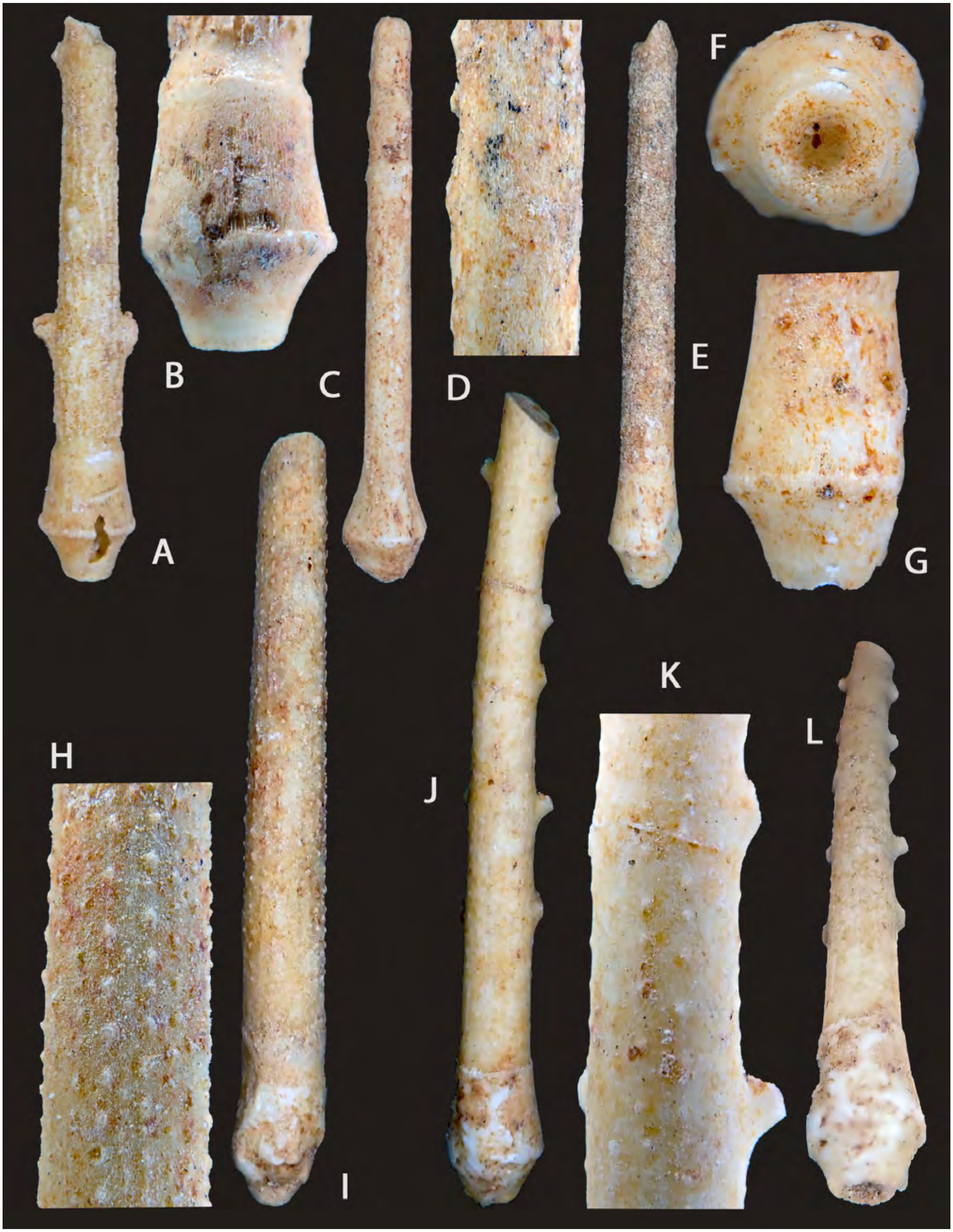


Figure 12: *Phyllacanthus mortoni* spines (UF 338012), none is complete but show variation in ornamentation; *Oligopygus haldemani* Zone of Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA086). A, B: 21.6 x 3.7 mm. C, D: 23.3 x 3.4 mm. E-G: 26.5 x 4.1 mm. H, I: 27.8 x 3.6 mm. J-L: 30.2 x 3.7 mm.

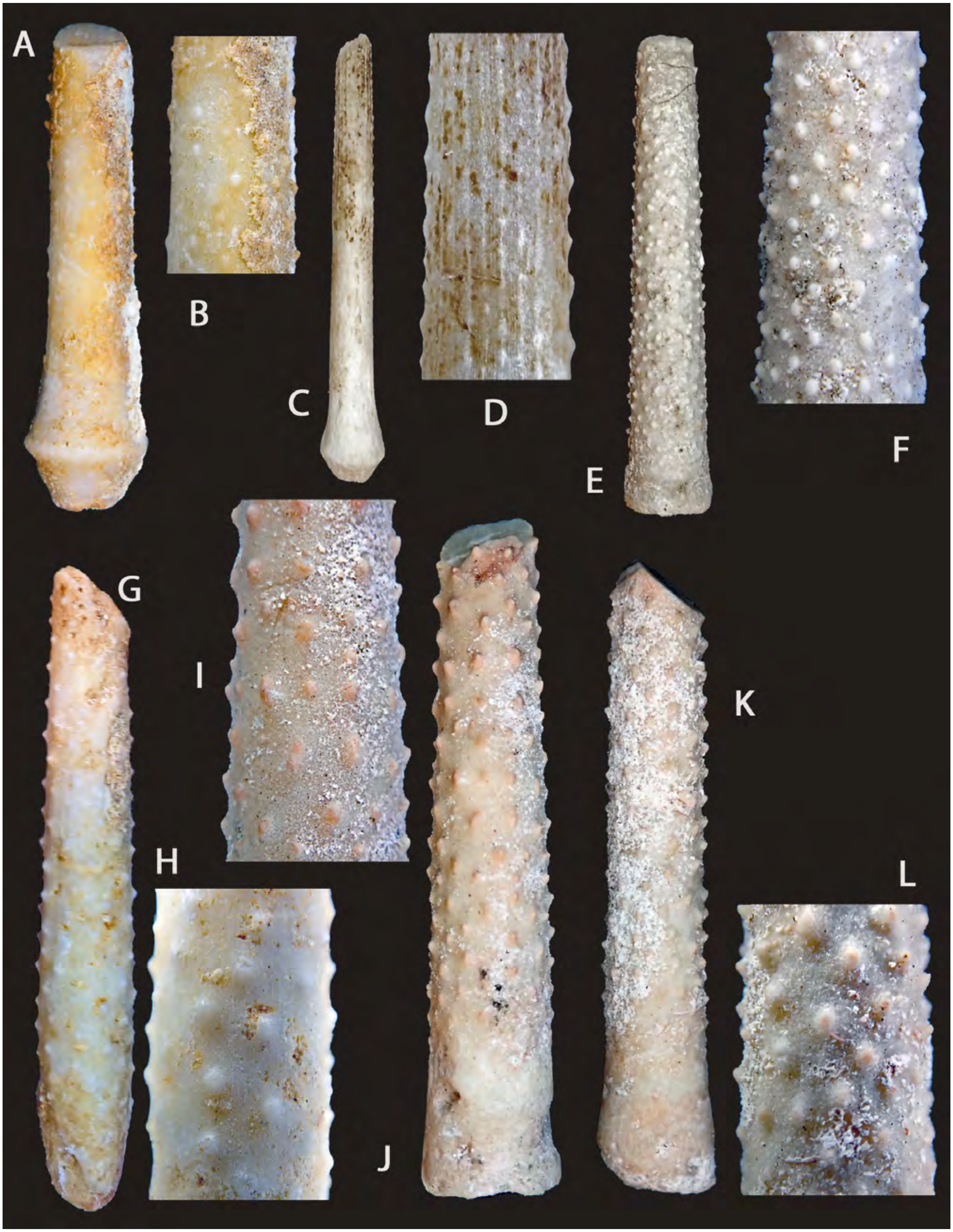


Figure 13: *Phyllacanthus mortoni* spines (UF 338013) none is complete but show variation in ornamentation; *Oligopygus wetherbyi* Zone of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A, B: 21.6 x 5.3 mm. C, D: 26.4 x 3.9 mm. E, F: 29.6 x 5.6 mm. G, H: 30.8 x 4.9 mm. I, J: 31.4 x 6.1 mm. K, L: 32.8 x 5.9 mm.

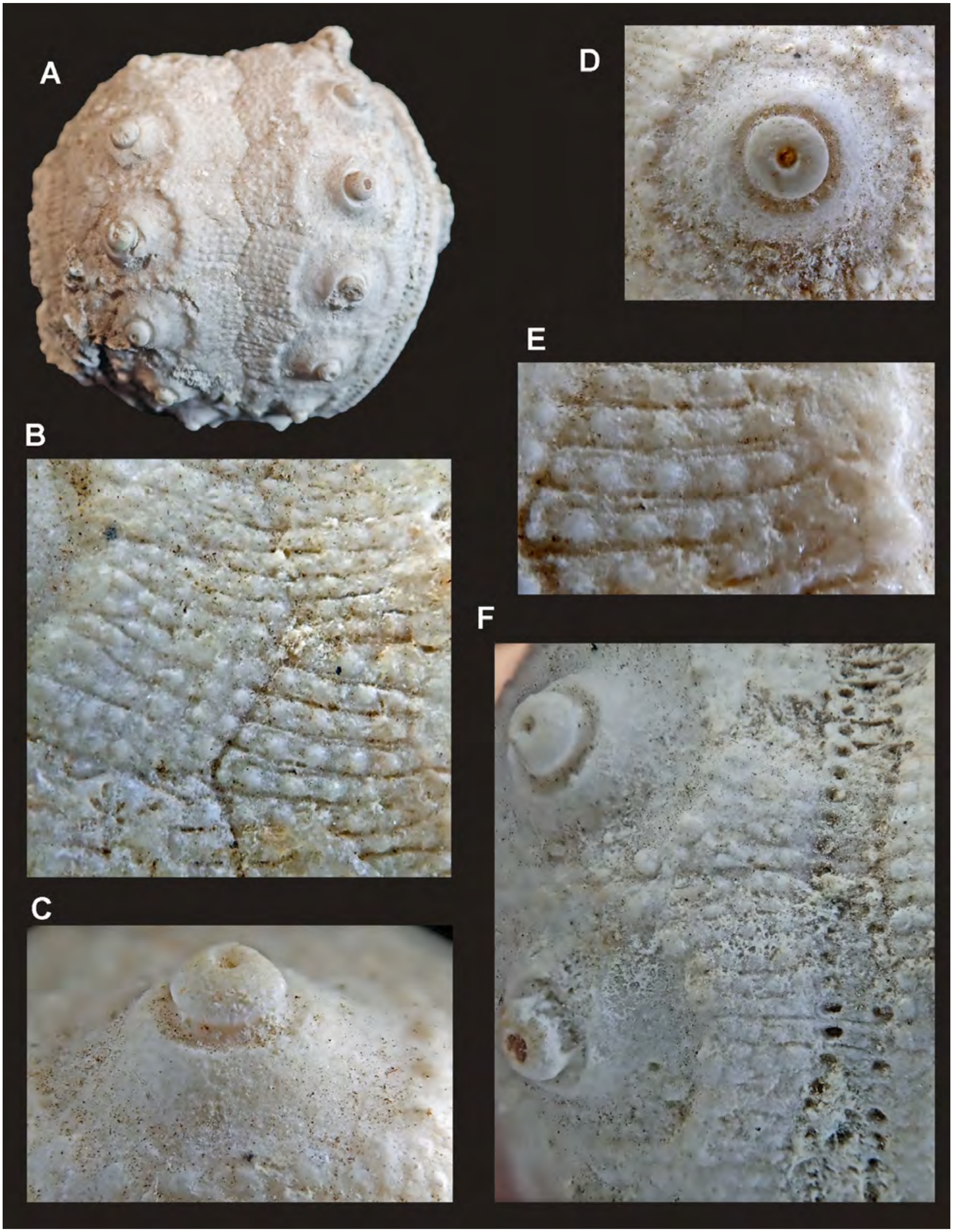


Figure 14: *Phyllacanthus* cf. *P. mortoni* (UF 337994), 36 mm x 35 mm, Oligocene Duncan Church Beds, Bridgeboro Limestone, Washington County, Florida (FM-IP WG002). A: interambulacrum. B, E: medial area showing granular-like tubercles arranged in rows, as in *P. mortoni*. C, D: close-up of non-crenulated, perforate primary tubercle. F: pore-pairs of ambulacrum and oblique view of interambulacral tuberculation.

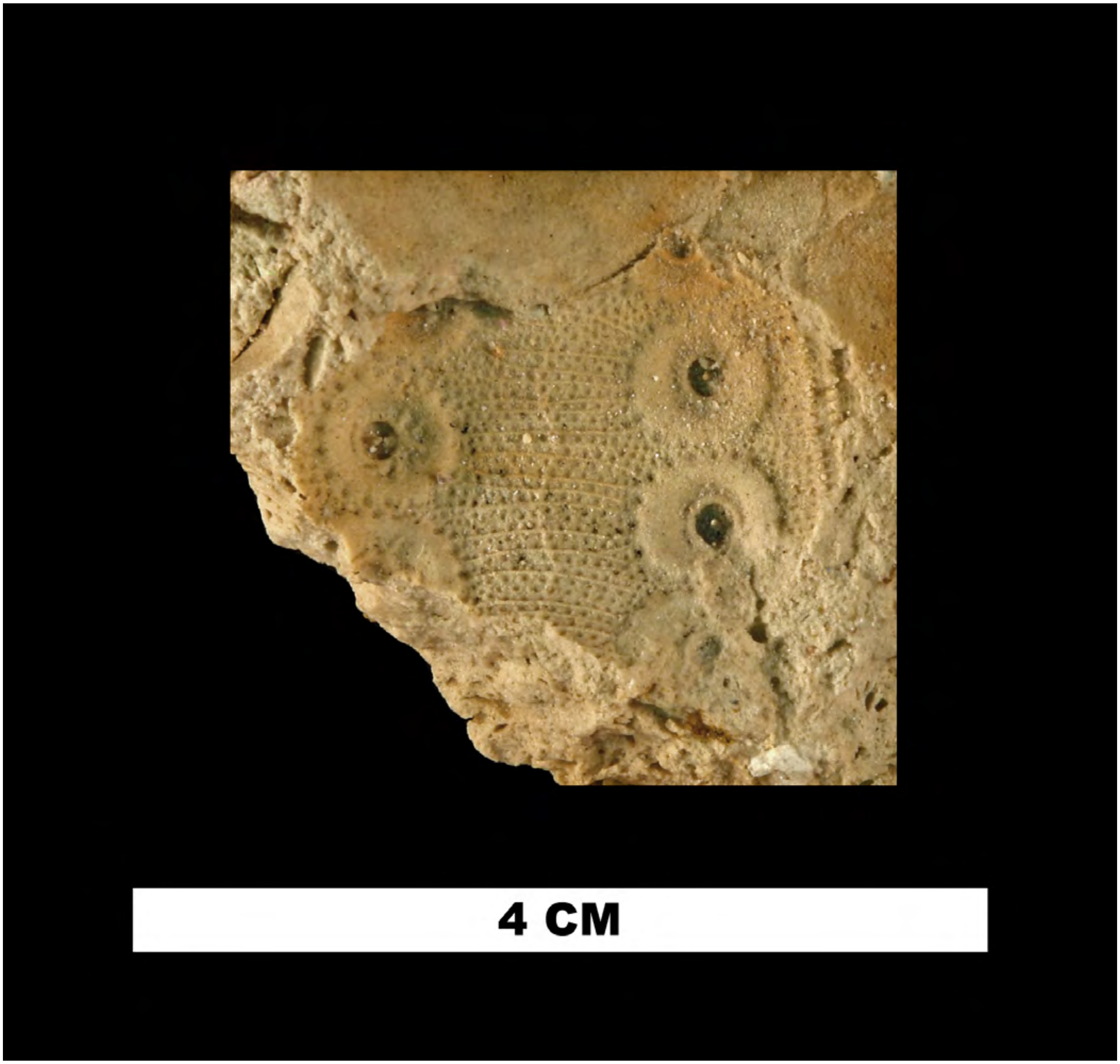


Figure 15: *Phyllacanthus* cf. *P. mortoni* (UF 337991) 21 mm x 28 mm, external mold in matrix from dolomitic portion of lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010).

which lacks surface details that could definitively place it in this species. It measures 69 mm in diameter, and 55.5 mm in height (Fig. 11), and was collected from FM-IP 2613.

As noted in the discussion above, *P. mortoni* has historically been referred to as Oligocene, based on a few subjective junior synonyms. However, these instances are either based on assumptions, or occurrences in strata that have subsequently been referred to the Eocene. Therefore, no definitive occurrences of *Phyllacanthus* species have previously been documented from the Oligocene of the region.

We document incomplete *Phyllacanthus* tests from the Oligocene Duncan Church beds of the Bridgeboro Limestone at the Duncan Church (Fig. 14), south of Chipley, Washington County (UF 337994), and from the dolomitic facies of the Marianna Limestone at Dry Creek (FM-IP JA010) south of Marianna, Jackson County (UF 337991) (Fig.

15). Given the incompleteness of the tests, we exercise caution and only refer to these as *Phyllacanthus* cf. *P. mortoni*. These fossils are not separable from *P. mortoni*, but more complete material would need to be collected from *in situ* Oligocene deposits before we can assert that *P. mortoni* crosses from the Late Eocene into the early Oligocene.

Genus ***Prionocidaris*** A. Agassiz, 1863

Prionocidaris robertsi n. sp.
(Figs. 16-19)

Diagnosis.—*Prionocidaris* with small tubercles in medial areas of interambulacra not aligned in distinct horizontal rows, ambulacra at ambitus only 36% width of interambulacra, and four columns of tubercles in interporiferous area of ambulacra. Associated spines adorned with pronounced thorns that are not verticillate (formed in whorls), with coronate cup-like cluster of thorns at tip; up to nearly twice as long (175%) as greatest diameter of only known complete test.

Description.—Test small, only one known complete test (holotype: UF 147100) 28.3 mm TD, 16.2 mm TH; low: TH 57% TD. Aboral surface flattened; apical system missing, opening 13.7 mm x 13.6 mm. Peristomial plating unknown, opening larger than apical opening which is 11.9 mm x 12.9 mm. Ambulacra almost straight, very slightly sinuous, average of all five ambulacra 4.1 mm wide at ambitus, 1.5 mm at apical plate, 2.6 mm wide at peristomial edge, total number of pore pairs or ambulacral plates indeterminate due to damage; ambulacra on average 36% interambulacral width at ambitus. Poriferous areas slightly depressed, on average 1.6 mm wide at ambitus; pores oval, conjugate, on average 0.4 mm wide at ambitus, on average 57 pore pairs per poriferous area, gap between pore pairs on average 3.7 mm. Interporiferous areas on average 1.4 mm wide at ambitus, 87% width of poriferous areas; with two pairs of distinct columns of small tubercles, each pair of columns separated by narrow naked medial area 40% width of interporiferous area. Interambulacra on average 11.3 mm wide at ambitus, 275% width of ambulacra at ambitus, two columns of primary tubercles per interambulacrum, five to seven tubercles per column; areolas ovate, large, on average 4.1 mm wide and 3.7 mm high at ambitus, 36% width of interambulacra at ambitus; rings of scrobicular tubercles distinct and well-separated at ambitus, intersecting, with rings becoming less distinct orally and aborally, areoles often not separated by distinct scrobicular rings furthest from ambitus. Primary tubercles large, moderately high, platforms smooth, not crenulated, mamelon perforate. Medial areas covered by small tubercles, not aligned in distinct horizontal rows.

Numerous associated spines available (paratype: lot UF 117489: 17 spines); longest complete spine 49.8 mm in length (175% TD of only known complete test), 4.5 mm wide at coronate distal end, 5.0 mm wide at widest thorn; with distinct thorns, not verticillate, thorns perpendicular to spine, becoming inclined distally toward distal end of spine; thorn length up to 55% greatest width of spine, often lacking in medial area of spine, replaced by small thorns or nodules often in vertical ridge-like columns; slightly tapered; coronate at tips, rimmed by large spinules in a cup-like arrangement.

Zoobank Nomenclatural Act.—C7C32F9A-C284-4EF6-B39C-B6B6AE8D060A

Discussion.—While studying the only known complete test of *Prionocidaris robertsi* n. sp. (UF 147100) (Fig. 16) and associated spines (UF 117489) (Fig. 17), it became clear that although this taxon was readily distinguishable as a new species, assigning it to a genus (either *Phyllacanthus* or *Prionocidaris*) is not simple. Modern classification of the Cidaroida is largely based on work by Mortensen (1903; 1928, especially) which was, as was much of Mortensen's work, largely based on the pedicellariae. For this reason, Lambert and Thiéry (1909, 1910) and Gignoux (1933) rejected Mortensen's classification, but as noted by Philip (1963), although Mortensen's system is not perfect, it is preferred over any previously proposed system. However, the fact remains that it is difficult to apply this classification to fossil forms lacking the appendages and less often preserved

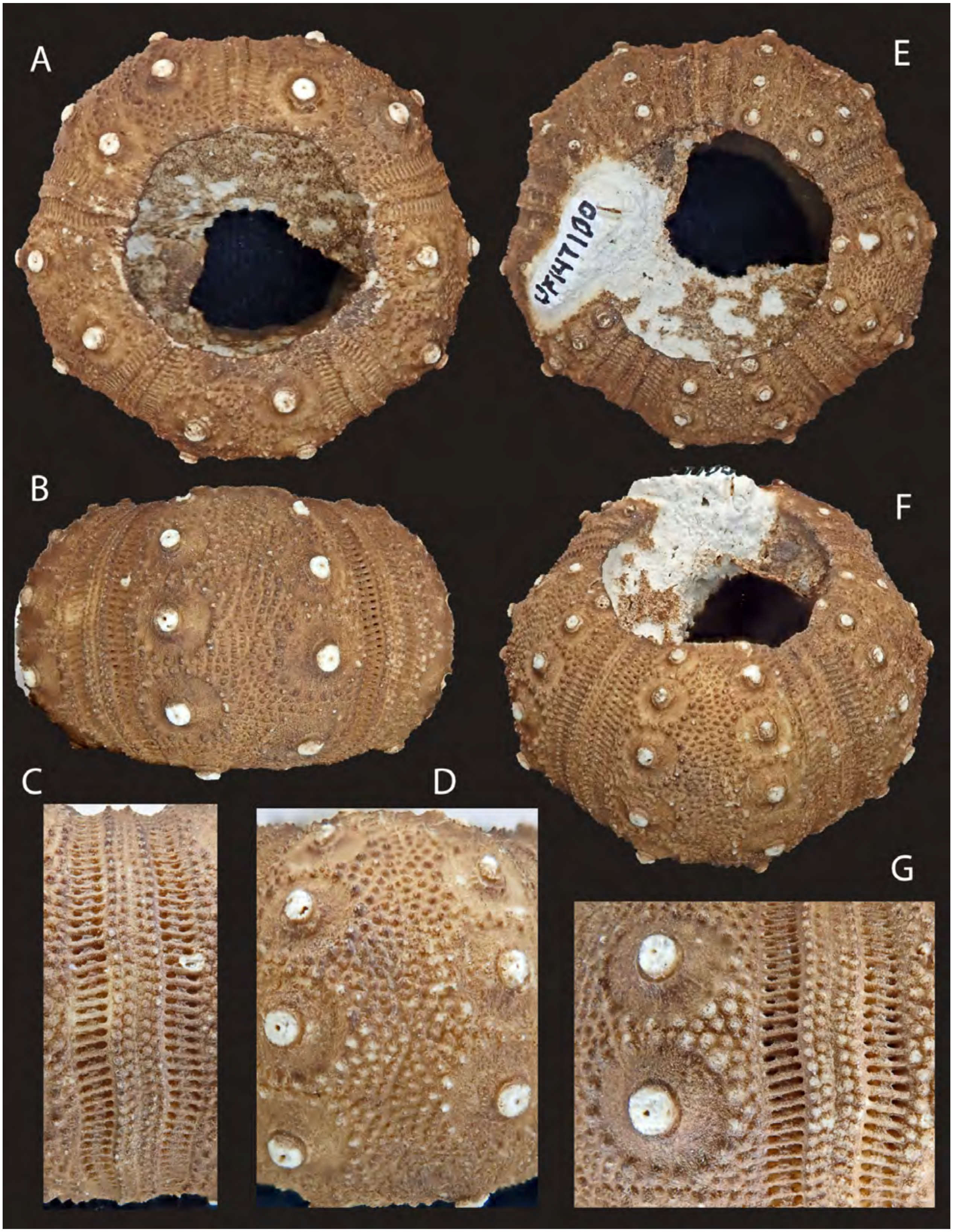


Figure 16: *Prionocidaris robertsi* n. sp., holotype (UF 147100), 28.3 mm TD, 16.2 mm TH, Upper Eocene, Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033). A: aboral. B: lateral, interambulacrum center. C: ambulacrum. D: interambulacrum. E: oral. F: tilted aboral viewpoint, interambulacrum center. G: close-up of primary tubercles (very worn) and ambulacrum near ambitus.

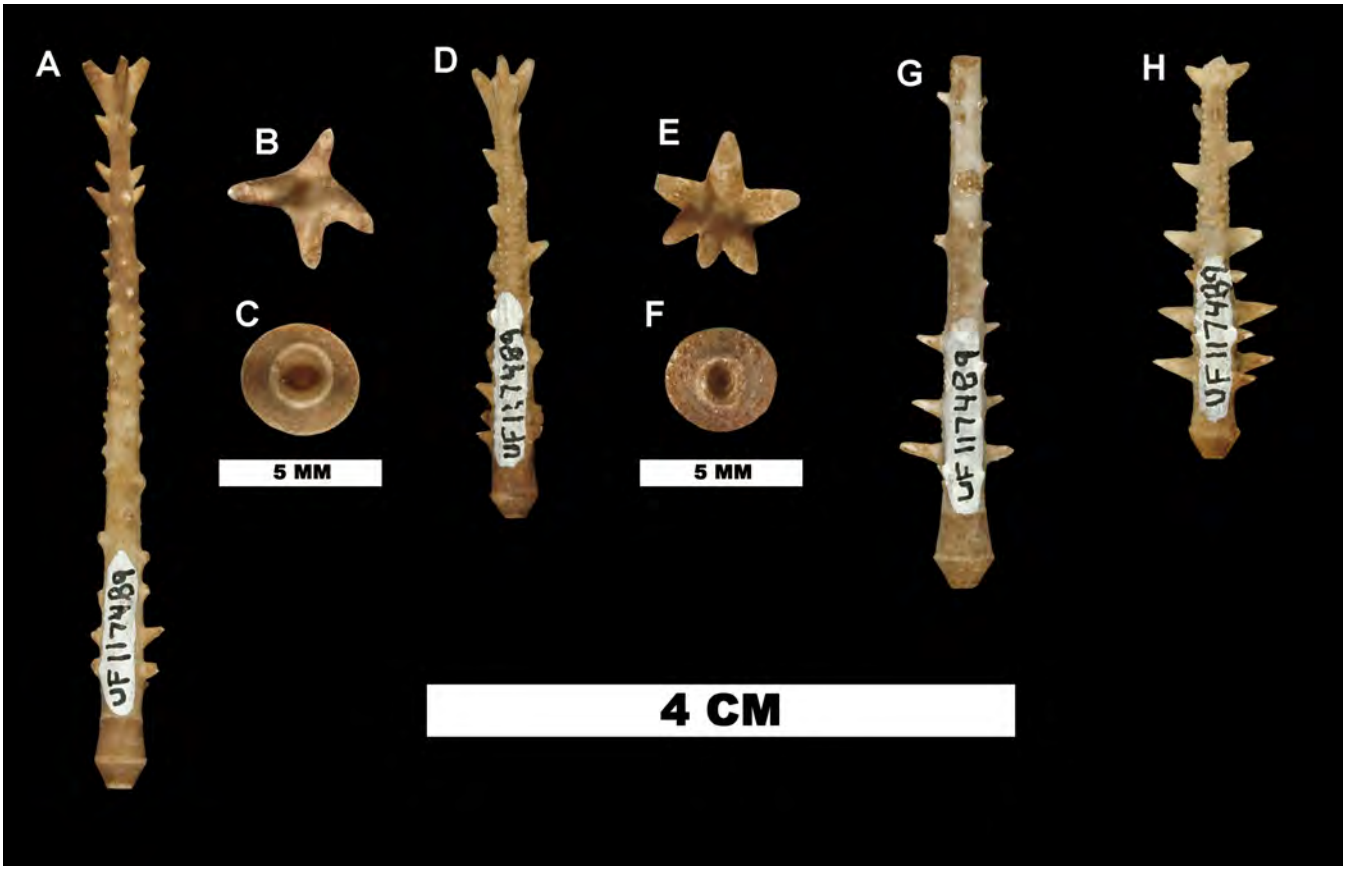


Figure 17: *Prionocidaris robertsi* n. sp., spines (UF 117489), Upper Eocene, Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033).

regions used in Mortensen's classification. Cooke (1946, 1953, 1957, 1959) was an opponent of applying Mortensen's classification to fossil specimens due to the inadequacy of characters seen in many fossils (typically tests and disassociated spines).

Another approach, notably seen in the works of Chapman and Cudmore (1934), Fell (1954, 1966), and Philip (1963) was to attempt to recognize affinities in fossil forms that give an indication of the modern genus to which the echinoid could be assigned. However, as cautioned by Philip (1963), names extracted from the list of living genera should be employed only as "form genera" with their identification based on but a single attribute (spines with cup-shaped terminations = *Goniocidaris*; spines with thorns = *Prionocidaris*; spines with flanges = *Chondrocidaris*, etc.). As Philip (1963) stated, this can lead to unsatisfactory taxonomy, but it is still often possible to ascertain genus affinities of Cenozoic species from a detailed study of living cidarids. Philip (1963) accomplished his review of the Australian fossil cidarids by making comparisons with the modern forms of the Indo-Pacific region. He emphasized that because of the inherent uncertainty of cidarid taxonomy, this method usually leads to a very broad interpretation of some genera. This was noted by Cutress (1980) when she stated that her use of *Cidaris* (for species with nonconjugate pores, noncrenulate tubercles, and simply tapered, ridged spines) is not to be recognized in the strict sense of the Recent genus.

Fell (1966) stated that although the usual keys to the identification of cidaroids are difficult to apply to fossils due to the lack of preserved pedicellariae, if attention is paid to the sum of available characters of the spines and test, most fossils can be classified into taxa that are unlikely to differ substantially from characters used for the living species. Fell (1966) provided diagnoses using spine and test characteristics for all fossil and modern cidarid genera. It is also important to note that in many cases, the problem of higher taxon determination can be greatly reduced

Figure 18: *Prionocidaris robertsi* n. sp., (UF 341763), 18 mm x 14 mm, test fragment with half an interambulacrum and half an ambulacrum, Upper Eocene, Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033).

by using features that clearly eliminate possible genus assignments for the fossil in question.

The test of *Pr. robertsi* n. sp. is very similar to that of *Phyllacanthus*, possessing noncrenulate, perforate, primary tubercles, well-separated areoles, and conjugate pore pairs. However, the test of *Pr. robertsi* n. sp. is readily distinguished from *P. mortoni*, which occurs in overlying strata of the OLS in Jackson County, because the granulations of the interambulacra are not latitudinally arranged. In *P. mortoni* these granules are latitudinally (horizontally) arranged in rows, whereas in *Pr. robertsi* n. sp. they are not aligned in rows.

Fortunately, many spines are associated with *Pr. robertsi* n. sp. and are exceptionally abundant on the floor of Jackson Blue Spring (Fig. 17). These spines are usually adorned with sharp thorns whose length often exceeds the thickness of the shaft, and complete spines are often flared at the distal end (coronate *sensu* Cutress, 1980) with flared thorns protruding in a cup-like shape (Figs. 17, 19). These spines help confirm the genus assignment to *Prionocidaris* for this species and are very similar to those of the modern *Prionocidaris bispinosa* (Lamarck, 1816) of the Indo-Pacific region (see Mortensen, 1928: pl. XLIV, fig. 2). However, in *Pr. bispinosa*, the lowermost thorns on the spine are often verticillate, whereas the thorns in *Pr. robertsi* are not. Fell's (1966: U330) diagnosis for *Prionocidaris* described the spines as: "primary spines long, tapering with coarse thorns in longitudinal series, less commonly cylindrical, smooth or widened distally, or with thorns arranged in whorls."

No evidence of any other cidarid exists in this horizon (the *Haimea brooksi* Zone of the OLS is also exposed in a quarry of Leon Brooks, 8 mi. to the west), so attributing these spines to the single,

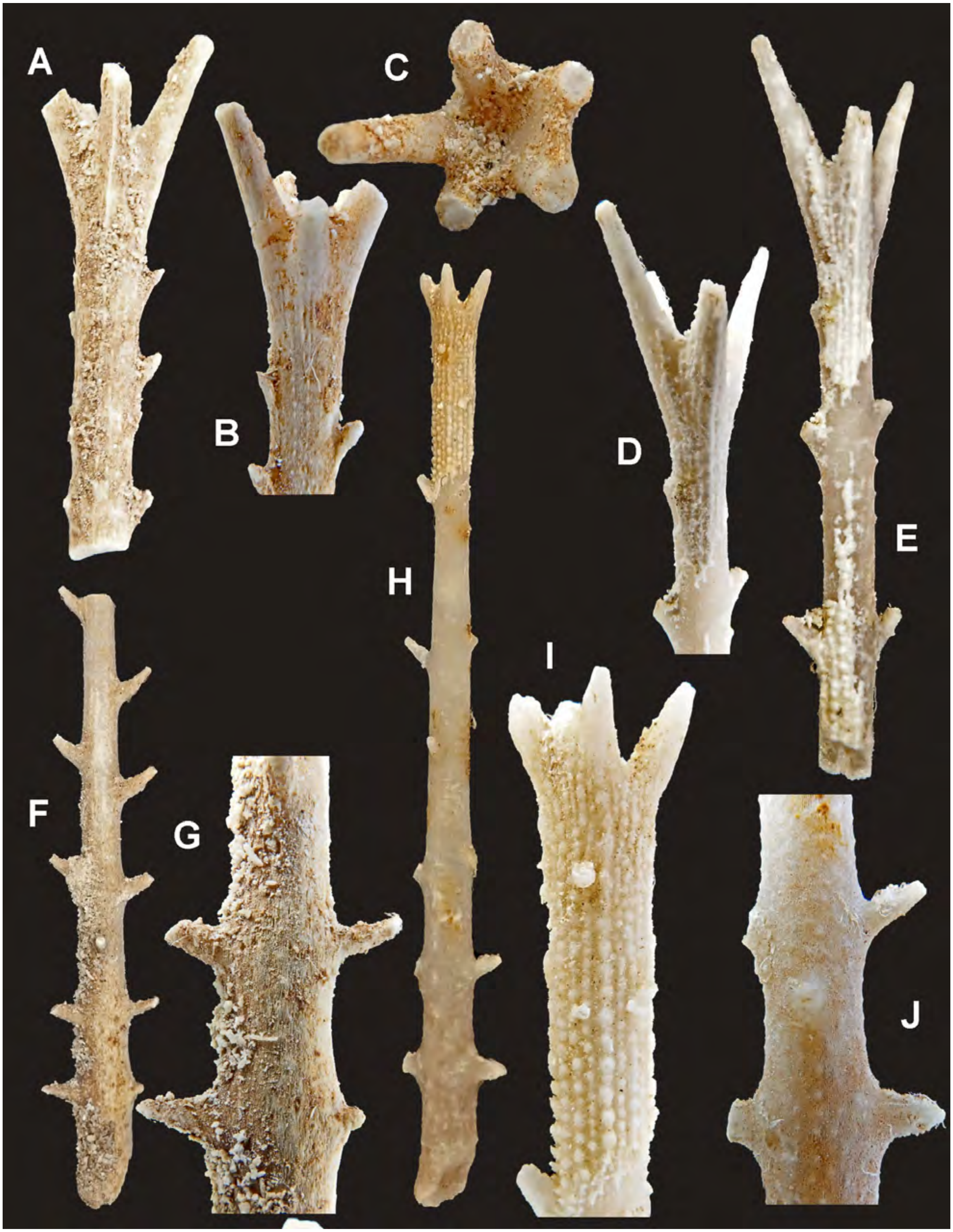


Figure 19: *Prionocidaris robertsi* n. sp., spines, none of which is complete (UF344344-46), Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, Briar Cave (FM-IP MR018), south of Ocala, Marion County, Florida (SL= spine length, SD = widest diameter of spine). A-C: 15.2 mm SL, 5.4 mm SD. D, E: 21.6 mm SL, 5.4 mm SD. F, G: 37.9 mm SL, 3.3 mm SD. H-J: 44.7 mm SL, 2.9 mm SD.

complete, test of this species that was collected amongst them seems justified. Although *P. mortoni* occurs in strata above this horizon in the Brooks Quarry (FM-IP JA039), the spines of *P. mortoni* are typically thick and cylindrical with a shaft covered in fine granules that are typically arranged in longitudinal series. They may develop larger granules that resemble "bumps" but never with prominent thorns and coronate tips as seen in *Pr. robertsi* n. sp. Fell's (1966: U330) diagnosis for *Phyllacanthus* describes the spines as: "primary spines cylindrical, thick, robust, with fine granules arranged in regular longitudinal series on shaft."

However, as cautioned by Cutress (1980), cidarids are highly variable, and though she asserted the spines may in some instances provide better taxonomic characters than the test, they can be highly variable, especially in *Prionocidaris*. Cutress (1980) stated that it was discouraging that the modern species of *Prionocidaris* were among the most variable of the species she studied, particularly *Pr. bispinosa* and *Pr. hawaiiensis* (Agassiz and Clark, 1907). She stated these two species had variation in measurements that ranged as high as 36% and in the less variable species of the genus, the range was still 12 to 18%. Given this variability, Cutress (1980) cautioned against isolating taxa based on discontinuities in her measured data, which she provided in tables.

Variability of the test of *Pr. robertsi* n. sp. cannot be determined until additional specimens are collected. However, spine variability is demonstrated in Figs. 17 and 19. The typical spines of this species are heavily thorned, and when complete, usually show the flared coronate tip. Non-thorned spines are much rarer, as seen in specimens of the modern *Pr. bispinosa* (Mortensen, 1928: pl. XLIV, fig. 2).

Although it is evident this species is not comparable to any other species from Cenozoic strata in North America, many cidarids occur in the Caribbean region that require comparisons. Thankfully, Cutress (1980) compiled all known occurrences of fossil cidarids of the Caribbean area, providing a useful series of figures and an updated taxonomy. She identified six species in *Prionocidaris*: *Pr. cojimarensis* (Lambert and Sánchez-Roig in Sánchez-Roig, 1926), from the Miocene to Pliocene throughout the Caribbean area; *Pr. spinidentatus* (Palmer in Sánchez-Roig, 1949), from the Oligocene to Miocene of Cuba, Antigua, and Puerto Rico; *Pr. katherinae* Cutress, 1980, from the Miocene of Cuba and Puerto Rico; *Pr. clevei* (Cotteau, 1875), from the Miocene of Anguilla; *Pr. cookei* Cutress, 1976, from the Miocene of Florida and Cuba, and *Pr. loveni* (Cotteau, 1875), from the Eocene of St. Bartholomew, Cuba, and Jamaica.

Cutress (1980) noted that the tubercles of *Pr. cojimarensis* are crenulate, whereas they are not in *Pr. robertsi*. Cutress also stated that spines of *Pr. cojimarensis* are exceptionally variable, ranging from evenly spinose to distinctly verticillate, nodulose, or ridged, yet none exhibits thorns as pronounced as those of *Pr. robertsi*, nor are the distal ends flared and coronate.

In fact, the thorny, coronate spines of *Pr. robertsi* n. sp. distinguishes it from all other representatives of the genus in the Caribbean region except for *Pr. spinidentatus*. The spines of these two species are very similar (see Cutress, 1980: pl. 8), though the thorns are less densely arranged on the spines of *Pr. robertsi*. However, the tests of these two species are very dissimilar. The small tubercles in the medial area of the interambulacral of *Pr. spindentatus* are aligned in horizontal rows as opposed to the haphazard arrangement of these small granule-like tubercles in *Pr. robertsi*.

At its type locality, 30 m below the surface of Jackson Blue Spring east of Marianna, Jackson County, Florida (FM-IP JA033), *Pr. robertsi* n. sp. occurs with abundant specimens of *H. brooksi, O. haldemani,* and *R. georgiensis*, as well as *W. johnsoni*, *B. jonesi* n. sp., rare specimens of *O. beckeri*, and an undetermined species of regular urchin discussed herein as Euechinoidea gen. et sp. indet.

Spines of *Pr. robertsi* n. sp. occurs in the *O. phelani* Zone of the lower OLS at Briar Cave (FM-IP MR018), in Marion County. These (UF 344344-UF 343446; Fig. 19) are found with the typical fauna of the *Oligopygus phelani* Zone, including *E. mooreanus, P. floridanus, Durhamella ocalana,* and *Weisbordella inglisensis* n. sp.

Etymology.—This species is named in honor

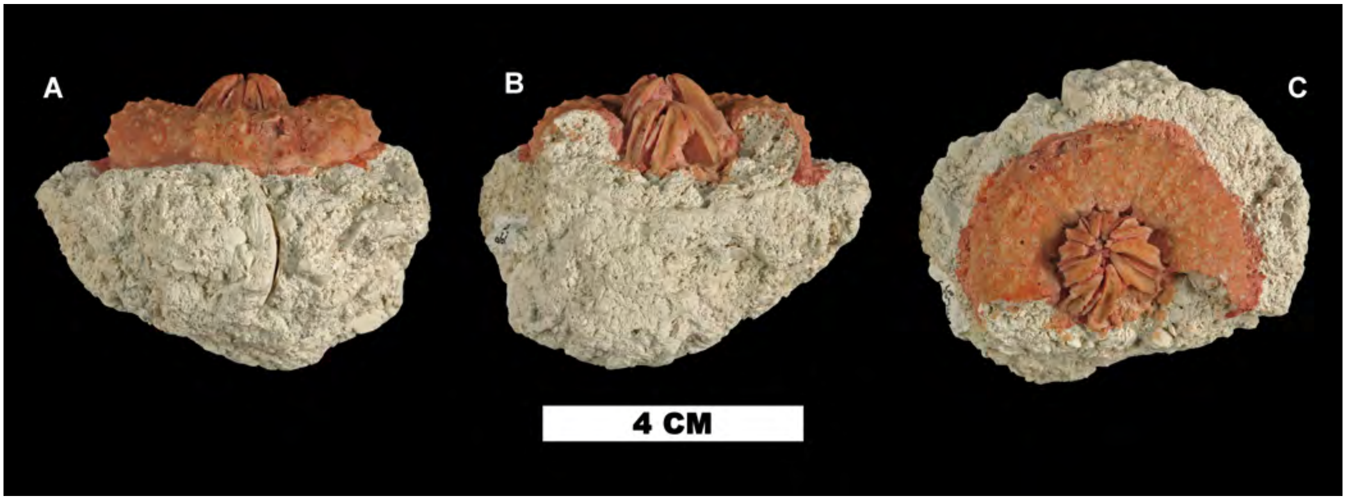


Figure 20: *Acanthechinus dixie* (UF 66559), 45 mm TD, partial specimen with preserved Aristotle's Lantern, Upper Eocene, upper portion of Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A, B: lateral viewpoints. C: oral.

of Sean W. Roberts, who (along with Rebecca Roberts and Melissa Marzahn) collected the Jackson Blue material used in this study through recreational SCUBA diving.

Materials and Occurrence.—Holotype UF 147100 (test) and paratypes (UF 117489), 17 associated spines, from OLS, associated with *H. brooksi* in Jackson Blue Spring (FM-IP JA033), Jackson County, Florida.

Subclass **EUECHINOIDEA** Bronn, 1860
Infraclass **AULODONTA** Jackson, 1912

Aulodonta gen. et sp. indet.

Discussion.—This taxon is represented by a single test (UF 332884), which is complete but broken into two pieces, with preserved Aristotle's lantern and some associated spines. It was collected from the upper portion of the OLS (either *Oligopygus wetherbyi* Zone or overlying *Wythella eldridgei* Zone), in a now-inactive and waterfilled quarry (FM-IP TA004) near Tennille, Taylor County, Florida. The specimen is remarkable for several reasons. It is large (~52 mm TD) with a thin, fragile, test, and remarkable retention of delicate features as indicated above. An extensive search of regional collections, both institutional and of avocational collectors, failed to locate even a fragment of a similar taxon.

The specimen is so unlike any known fossil echinoid from the eastern Americas and Caribbean region (see Table 5), that it requires study that will go beyond the time frame for the present work. Aulodonts are generally so rare in the fossil record of the region, a stand-alone publication will be necessary to place the fossil in the correct taxon and perform a full revision of the group to which it might belong, depending on how this find impacts the systematics of that group. To be as inclusive as possible, yet not delay publication of the present work, we refer to it as an unidentified aulodont.

Infraclass **CARINACEA** Kroh and Smith, 2010
Order **PHYMOSOMATOIDA** Mortensen, 1904
Family **PHYMOSOMATIDAE** Pomel, 1883
Genus ***Acanthechinus*** Duncan and Sladen, 1882

Acanthechinus dixie (Cooke, 1941a)
(Figs. 20, 21)

Phymosoma dixie Cooke, 1941a. p. 17. pl. 2, fig. 15; pl. 4, figs. 1, 2, 9.
Dixieus dixie (Cooke). 1948a. p. 607.
Phymosoma dixie (Cooke). Fell and Pawson in Moore, 1966. p. 396.
Dixieus dixie (Cooke). Mortensen, 1951. p. 558, fig. 281 (after Cooke).

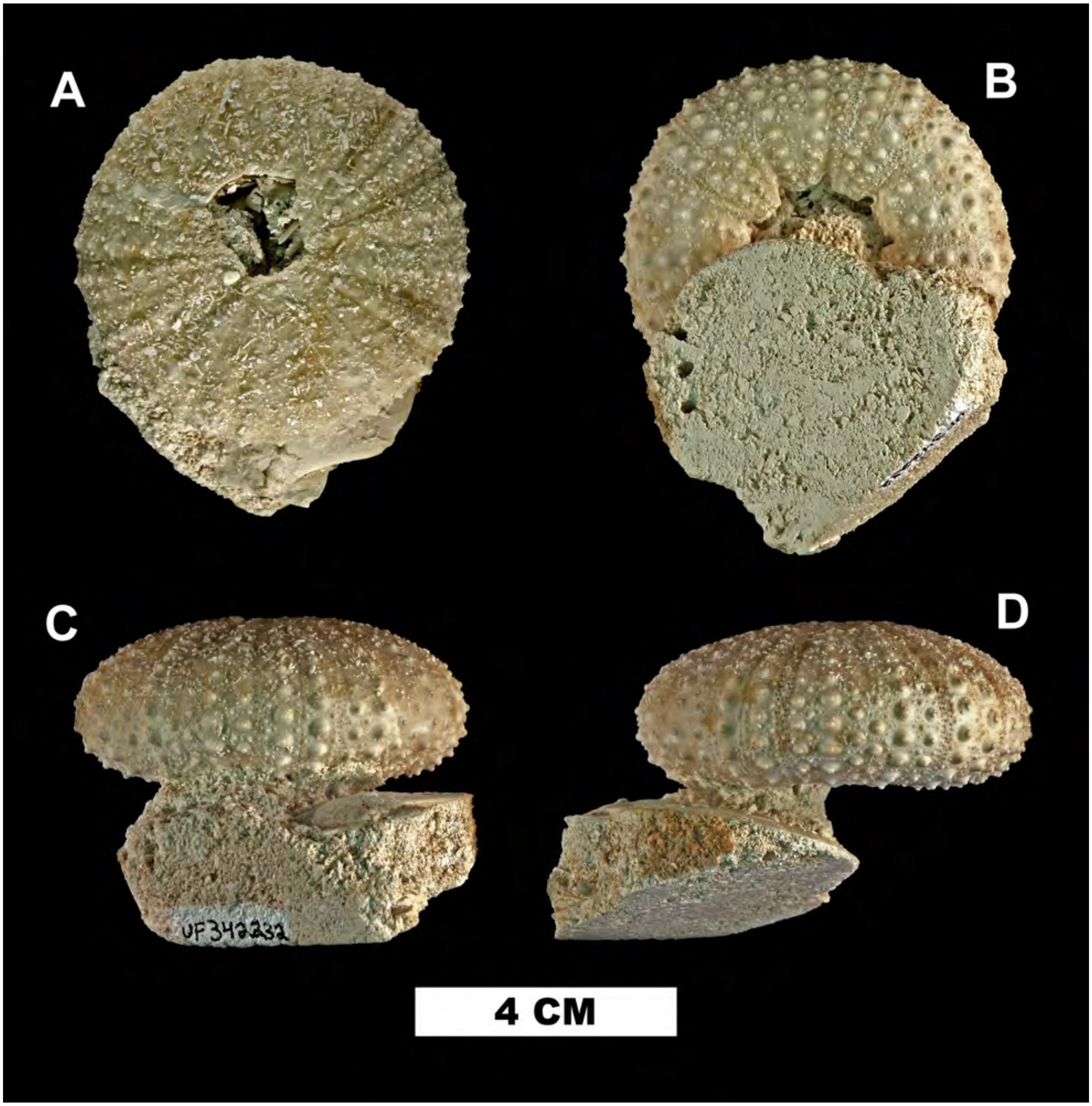


Figure 21: *Acanthechinus dixie* (UF 342232), 61.8 mm TD, 26 mm TH (maximum measurable TH due to matrix), Upper Eocene upper Ocala Limestone, Jackson County, Florida (FM-IP JA018). A. aboral. B: oral. C, D: lateral.

Dixieus dixie (Cooke). Cooke, 1959. p. 24. pl. 5, figs. 8-10.

Dixieus dixie (Cooke). Kier, 1980. p. 21. pl 5, figs. 1-3.

Dixieus cf. *D. dixie* (Cooke). Kier, 1997. p. 3. pl. 1, figs. 1-4.

Dixieus dixie (Cooke). Osborn et al., 2016. tbls. 1, 2.

Acanthechinus dixiei (Cooke). Kroh and Mooi, 2023. p. 1.

Occurrence.—*Acanthechinus dixie* is present, though typically rare, at numerous localities in the Upper Eocene OLS, including quarries northwest of Mayo (FM-IP LF001), Lafayette County; the Branford 01A Quarry (FM-IP SU003) north of Branford, Suwannee County, and south of Tennille (FM-IP DI001), Dixie County, among other localities. Cooke (1959) designated the type locality of *A. dixie* as a quarry east of Steinhatchee River north of U.S. Highway 19 near Clara, in Dixie County, Florida

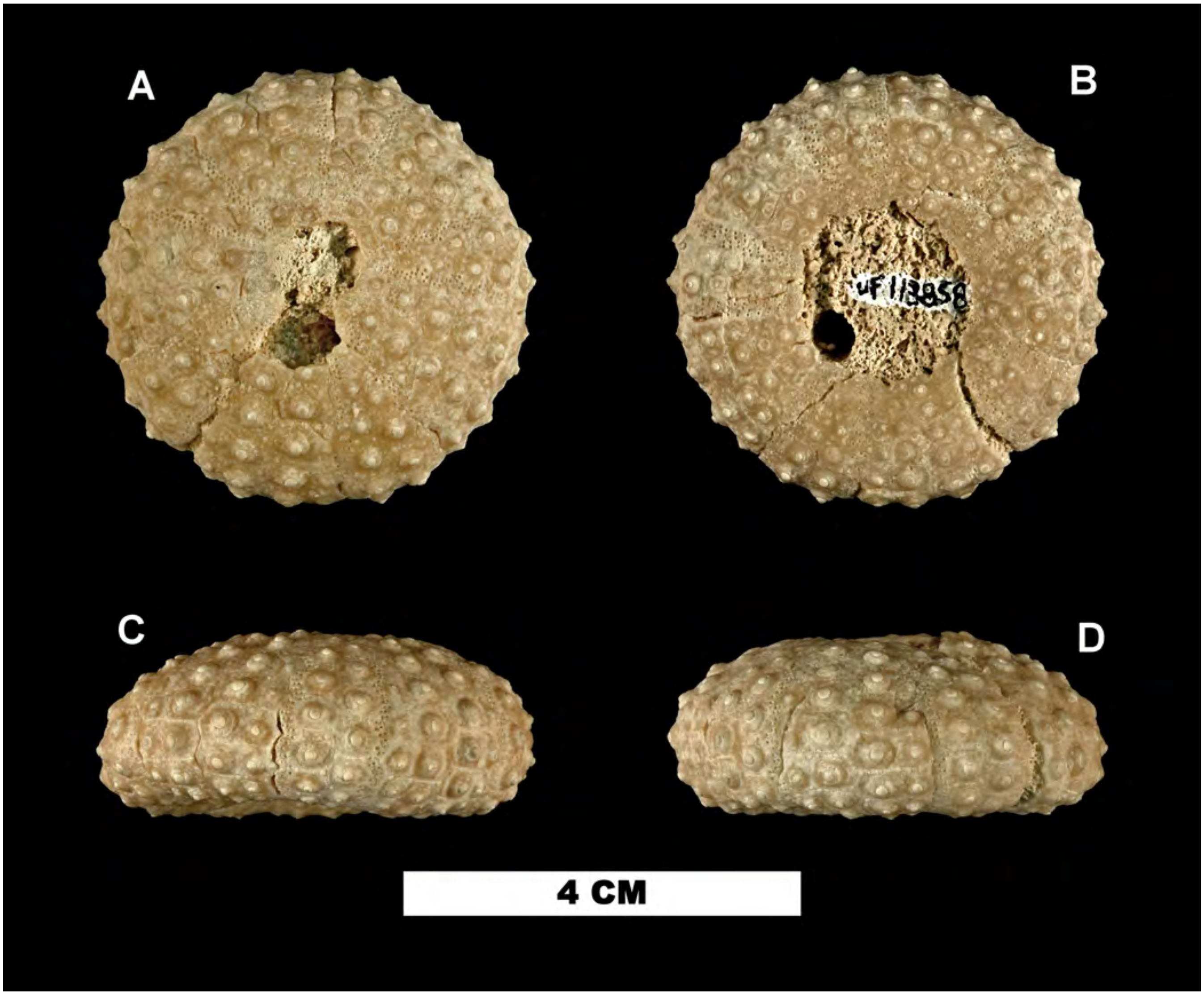


Figure 22: *Phymotaxis mansfieldi* (UF 113858), 43 mm TD, 17 mm TH, Lower Oligocene Suwannee Limestone, Hernando County, Florida (FM-IP HE017). A: aboral. B: oral. C, D: lateral.

(type locality-USGS 12747). It is most frequently encountered in the uppermost OLS where it occurs in the *Wythella eldridgei* Zone.

The species is also documented in the Middle Eocene Clinchfield Sand in southwest Georgia (Carter and Hammack, 1989) and Castle Hayne Limestone of North Carolina (Kier, 1980).

Discussion.—Cooke (1941a) initially described this species as *Phymosoma dixie* but subsequently (Cooke, 1948a) designated it as the type of his new genus *Dixieus* which he stated differs from *Phymosoma koenigi* (Mantell, 1822), the type species of *Phymosoma*, in the greater number of zygopores (twice as many), the biserial part of its poriferous zones, the smaller size and more equilateral shape of its apical system, its more tumid, less discoid shape, its larger, more deeply notched peristome, and its smaller tubercles, which exhibit more even gradation in size.

Fell and Pawson (1966) considered *Dixieus* a subjective junior synonym of *Phymosoma*. However, this assertion has not been followed by most echinoid workers of the region (Kier, 1980; 1997). Smith and Kroh (2011) considered *Dixieus* to be a subjective junior synonym of *Acanthechinus* (Duncan and Sladen, 1882). We agree that no genus-level differences are apparent between *D. dixie* and *Acanthechinus pelorius* (Arnold and Clark, 1927) from

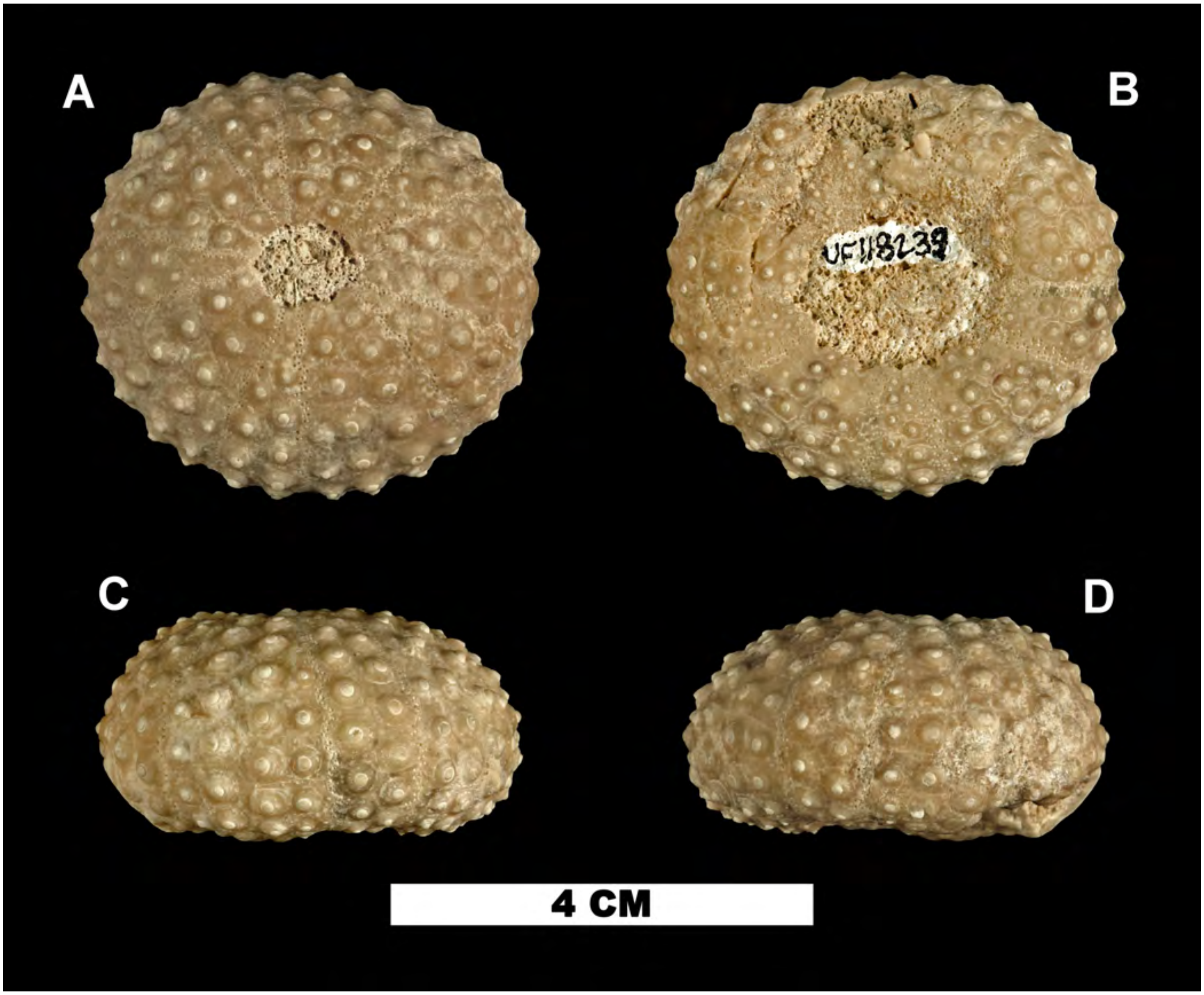


Figure 23: *Phymotaxis mansfieldi* (UF 118239), 44 mm x 41 mm TD, 21 mm TH, Lower Oligocene, Suwannee Limestone, Hernando County, Florida (FM-IP HE007). A: aboral. B: oral. C, D: lateral.

the Eocene of Jamaica, or *Acanthechinus abnormale* (Duncan and Sladen, 1882: 32) from the Late Paleocene-Early Eocene of Pakistan. In the World Echinoidea Database, Kroh and Mooi (2023) refer to this species as *A. dixiei*. We are unable to support this change, since the taxon is named not for a person but for a county, much as for another of Cooke's (1942) species, *Plagiobrissus dixie*.

Acanthechinus dixie is most common in the uppermost horizon of the upper OLS of Florida where it occurs with *W. eldridgei, S. armiger, B. steinhatchee, E. ocalanus, P. dixie,* and other species, above the horizon of *O. wetherbyi* in the *Wythella eldridgei* Zone.

We figure an exceptional specimen (UF 66559) that retains its Aristotle's lantern (Fig. 20).

Order **STOMOPNEUSTOIDA** Kroh and Smith, 2010
Family **STOMOPNEUSTIDAE** Mortensen, 1903
Genus ***Phymotaxis*** Lambert and Thiéry, 1914

Phymotaxis mansfieldi Cooke, 1941a
(Figs. 22, 23)

Phymotaxis mansfieldi Cooke, 1941a. p. 18. pl. 4, figs. 6-8.
Phymotaxis mansfieldi (Cooke). Cooke, 1959. p. 24.

pl. 6, figs. 4-8.

Occurrence.—*Phymotaxis mansfieldi* is not documented outside of the Lower Oligocene, Suwannee Limestone. Cooke (1941a) designated Brooksville, Florida as the type locality of the species, where it can still be collected in numerous quarries west of Brooksville, Hernando County (FM-IP HE019).

Discussion.—*Phymotaxis mansfieldi* occurs with the very abundant *R. gouldii*, as well as *G. mossomi* and other, rarer echinoid species, in the Lower Oligocene Suwannee Limestone. Smaller specimens of *P. mansfieldi* can be confused with *G. mossomi* in the field. However, they can be readily differentiated by the poriferous zones, which are straight in *G. mossomi* and in arcs in *P. mansfieldi*, which gives the poriferous zones in the latter a sinuous appearance.

Order **CAMARODONTA** Jackson, 1912

”**Triplacidiids**” temporary family (Kroh and Mooi, 2022)

Genus ***Gagaria*** Duncan, 1889

Gagaria mossomi (Cooke, 1941a)

(Figs. 24-26)

Thylechinus (*Gagaria*) *mossomi* Cooke, 1941a. p. 13. pl. 2, fig.16; pl. 3, figs. 6-9; pl. 4, figs. 3-5.

Gagaria mossomi (Cooke). Cooke, 1959. p. 17. pl. 3, figs. 10-14.

Gagaria mossomi (Cooke). Fell and Pawson, 1966. pp. U430, U431. figs. 319.1a-c.

Gagaria mossomi (Cooke). Pickering, 1970. pp. 20, 29.

Gagaria mossomi (Cooke). Kier, 1997. p. 5. pl. 2, figs. 1-5.

Gagaria mossomi (Cooke). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 6.

Occurrence.—Within Florida, *G. mossomi* is not documented outside of the Suwannee Limestone, where it is commonly associated with *R. gouldii* near Brooksville (FM-IP HE019), the now defunct Morrell Pit in Pasco County (FM-IP PA002), and Terramar Quarry in Polk County (FM-IP PO017). The species is also documented in the Oligocene of Georgia (Pickering, 1970) and North Carolina (Kier, 1997).

Discussion.—When Cooke (1941a) initially described *G. mossomi*, he designated two syntypes (USNM 372885) but no holotype. The syntypes consist of a fragment and complete test (Cooke, 1941a: pl. 4, figs. 3-5). However, Cooke (1959), in the captions for plate 3, figures 10-14, identified the figured specimens (USNM 498884a-c) as paratypes. Yet, these specimens were not identified as paratypes when Cooke (1941a) erected the species. Paratypes cannot be named as such after the original description, even if they were part of the same suite of specimens used in the description. To further complicate matters, these three specimens are now cataloged in the USNM database as syntypes with distinct catalog numbers: USNM 498884, 648532, 648533.

Cooke appears to have included fragmentary material of what was likely *P. mansfieldi* in his original description (Cooke, 1941a). In that description, Cooke (1941a) described the poriferous zones of *G. mossomi* as nearly straight but confused the issue by noting that each group of three pore pairs slightly curves around a large tubercle, which is often the case in poriferous zones of many camarodonts, among other non-irregular echinoid groups. He corrected his description of *G. mossomi* in his 1959 monograph and removed reference to arc-forming pore pairs.

Specimens of this small species, usually less than 2.5 cm in diameter, can be confused with juvenile specimens of the usually larger *P. mansfieldi*, as both typically occur in the same stratigraphic horizons. As stated by Cooke (1959) and well-illustrated by Kier (1997: pl. 2, fig. 5), closer examination will easily differentiate them as, the poriferous zones of *G. mossomi* are straight, whereas in *P. mansfieldi*, the pore pairs are arranged in arcs that give the poriferous zones a sinuous appearance.

We figure (Fig. 24) a very large specimen (UF 28244) from the Suwannee Limestone of Pasco County (FM-IP PA002) that measures 40.7 mm

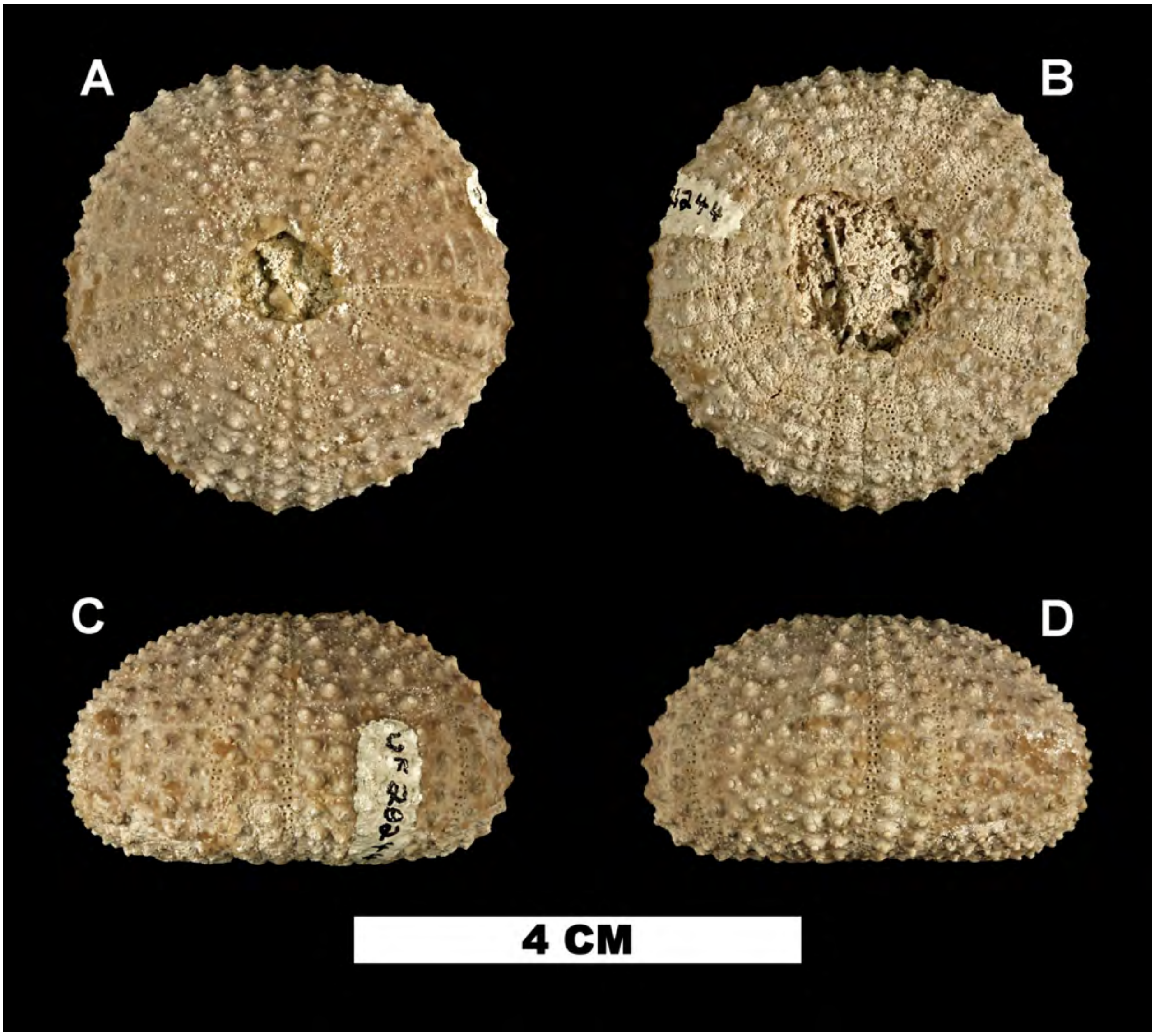


Figure 24: *Gagaria mossomi* (UF 28244), 40 mm TD, 22 mm TH; very large specimen for the species, Lower Oligocene Suwannee Limestone, Pasco County, Florida (FM-IP PA002). A: aboral. B: oral. C, D: lateral. A: aboral. B: oral. C, D: lateral.

maximum TD and 21.2 mm TH.

Family **TRIGONOCIDARIDAE** Mortensen, 1903
Genus ***Brochopleurus*** Fourtau, 1920

Brochopleurus pretiosus (Clark in Clark and Twitchell, 1915)
(Fig. 27)

Orthechinus pretiosus Clark in Clark and Twitchell, 1915. p. 118. pl. 56, figs. 2a-b.
Gagaria americana Clark in Clark and Twitchell, 1915. p. 159. pl. 73, figs. 8a-b.
Thylechinus americanus (Clark). Lambert and Thiéry, 1925. p. 567.
Progonechinus pretiosus (Clark). Cooke, 1941a. p. 15. pl. 2, figs. 4-6.
Pseudodiadema(*?*) *americanum* (Clark). Cooke, 1941a. p. 8.
Brochopleurus pretiosus (Clark). Cooke, 1959. p. 18. pl. 4, figs. 4-6.

Occurrence.—Within Florida, *B. pretiosus* is only known from the Upper Eocene OLS in the Brooks Quarry, near Marianna, Jackson County (FM-IP JA031). *Brochopleurus pretiosus* is more

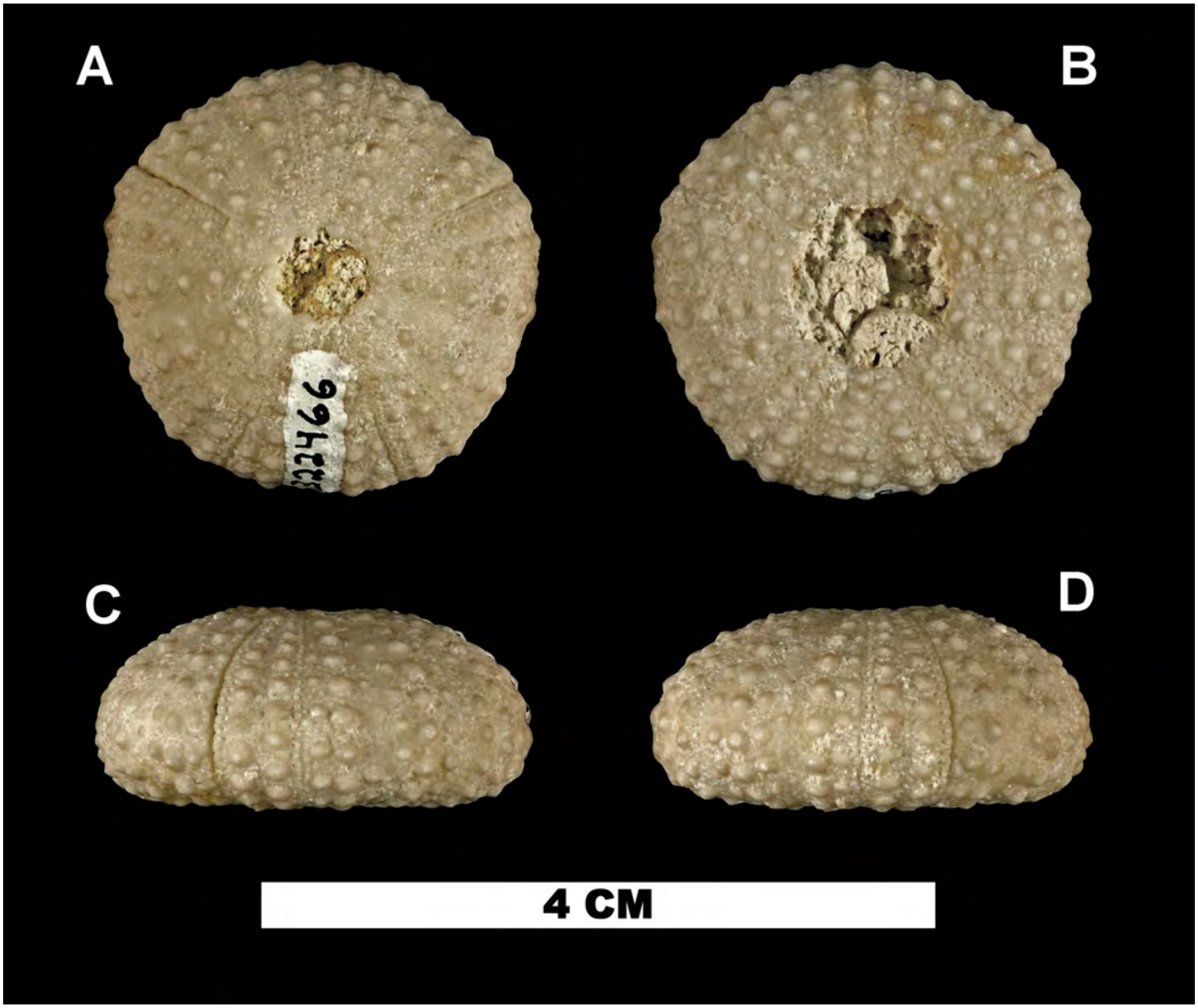


Figure 25: *Gagaria mossomi* (UF 322466), 26 mm TD, 12 mm TH, Lower Oligocene, Suwannee Limestone, Hernando County, Florida (FM-IP 6340). A: aboral. B: oral. C, D: lateral.

widespread in Upper Eocene strata of Alabama and Georgia (Cooke, 1959).

Discussion.—This is the first documentation of *B. pretiosus* from Florida. Its minute tubercles readily differentiate it from other regular urchins in the region. The lone documented Florida specimen of *B. pretiosus* was collected with *M. mortoni*, *R. conradi, O. haldemani,* and other, rarer species in the upper portion of the upper OLS exposed in the Brooks Quarries (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039), northwest of Marianna, Jackson County.

Mortensen (1943) stated that *Brochopleurus* is likely a junior synonym of *Scolechinus* Lambert (in Lambert and Thiéry, 1925), and Nisiyama (1966) stated the genus was very closely related to *Javanechinus* (Jeannet in Lambert and Jeannet, 1935) from the Miocene of Java and Fiji, and may be identical to it. Nisiyama (1966) also remarked on the similarity between *Brochopleurus* and the modern genus *Desmechinus* (H. L. Clark, 1923). However, *Brochopleurus* was considered by Smith and Kroh (2011) and Kroh and Mooi (2022) as a junior synonym of *Ortholophus*. However, Borghi et al. (2022) disagreed and stated *Temnechinus stellatus* Duncan and Sladen, 1886 (the type species of *Brochopleurus*) has smooth, non crenulate, tubercles, differentiating

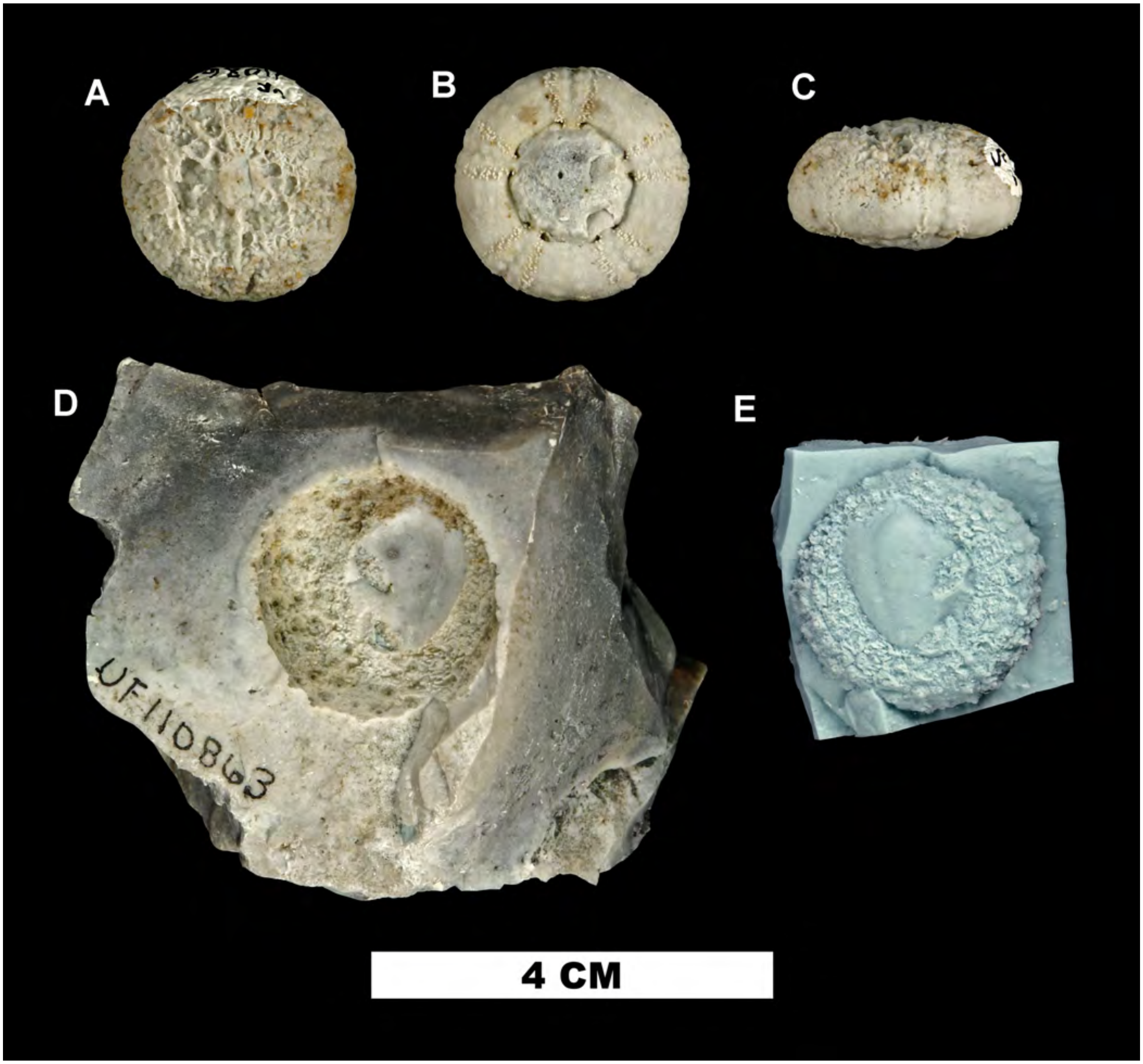


Figure 26: *Gagaria mossomi* (UF 110863), 23 mm TD, 12 mm TH, external mold in silicified limestone with RTV cast, Lower Oligocene Suwanee Limestone, Alachua County, Florida (FM-IP AL030). A: aboral. B: oral. C: lateral. D: external mold. E: RTV cast of external mold.

it from *Scolechinus* and *Ortholophus*. Borghi et al. (2022) therefore maintained *Brochopleurus* as distinct from both *Scolechinus* and *Ortholophus*. In the absence of further data, we maintain *Brochopleurus* for this species.

We figure a specimen (UF 68923) from the Upper Eocene Yazoo Formation near Perdue Hill, Alabama (FM-IP ZA026) that has excellent preservation of plate details to aid identification of this taxon (Fig. 27).

Family **TOXOPNEUSTIDAE** Troschel, 1872
Genus ***Lytechinus*** A. Agassiz, 1863

Lytechinus floralanus (Cooke, 1941a)
(Figs. 28, 29)

Psammechinus floralanus Cooke, 1941a. p.15. pl. 3,

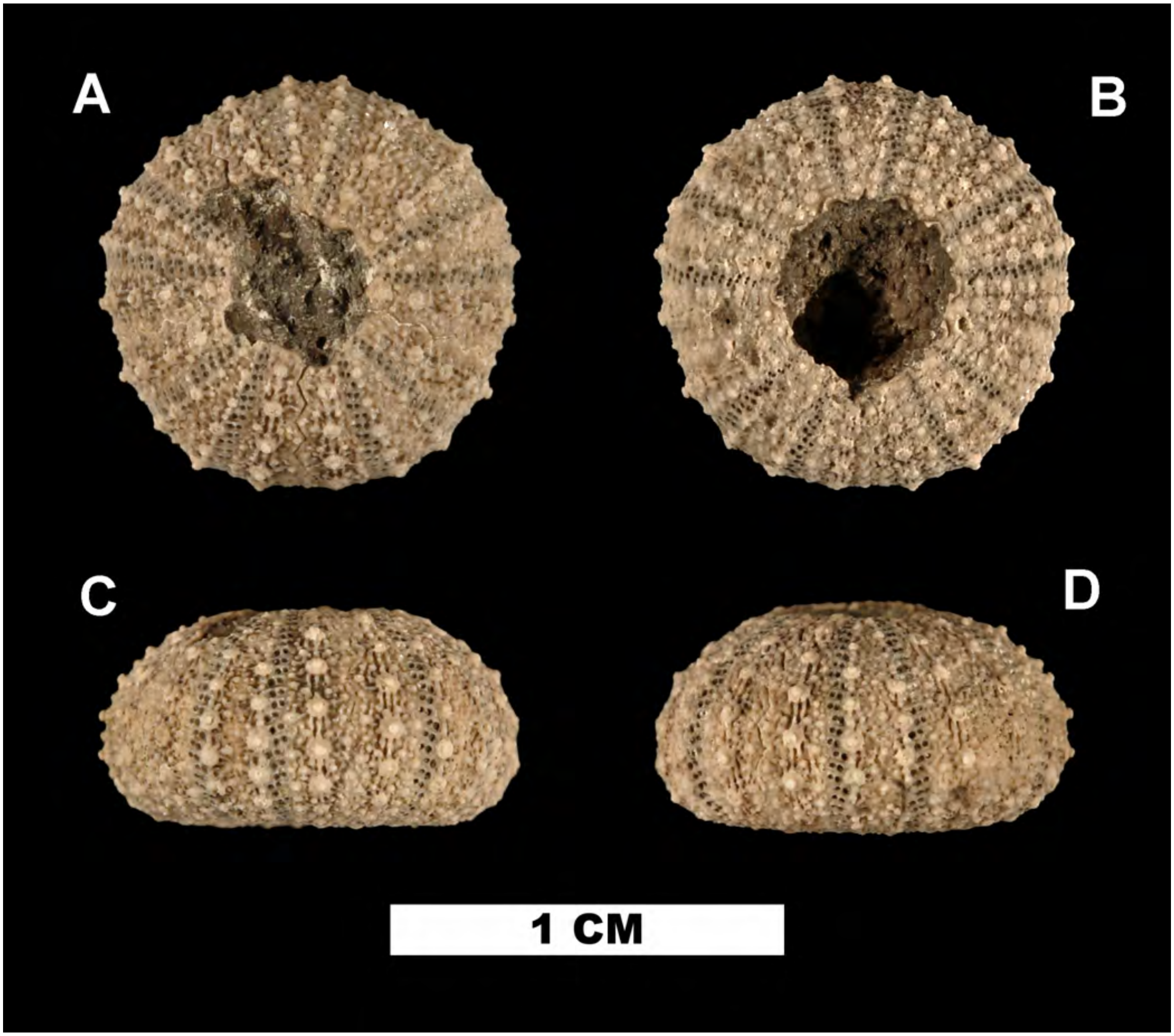


Figure 27: *Brochopleurus pretiosus* (UF 68923), 11 mm TD, 6 mm TH, Upper Eocene Yazoo Formation, Perdue Hill, Monroe County, Alabama (FM-IP ZA026). A: aboral. B: oral. C, D: lateral.

figs. 10, 11.

Psammechinus(*?*) *ocalanus* Cooke. 1941a. p.16. pl. 2, figs. 9-11.

Lytechinus floralanus (Cooke). Cooke. 1959. p. 15. pl. 2, figs. 17-21.

Lytechinus floralanus (Cooke). Kier. 1974. txt. fig. 10A.

Lytechinus floralanus (Cooke). Osborn et al. 2016. tbl. 2.

Occurrence.—*Lytechinus floralanus* is one of the rare species that occurs in both the Upper Eocene and Lower Oligocene strata of the region. Within Florida, it is known from the Upper Eocene, uppermost portion of the OLS in the Brooks Quarries near Marianna, Jackson County (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031) and the Lower Oligocene Bridgeboro Limestone at Duncan Church, Washington County (FM-IP WG002).

This species is commonly found in the Oligocene Marianna and Bridgeboro Limestones of Alabama, especially at its type locality in the Florala Limestone Member of the Bridgeboro Limestone, Florida Lime Products Quarry, east of Florala, Cov-

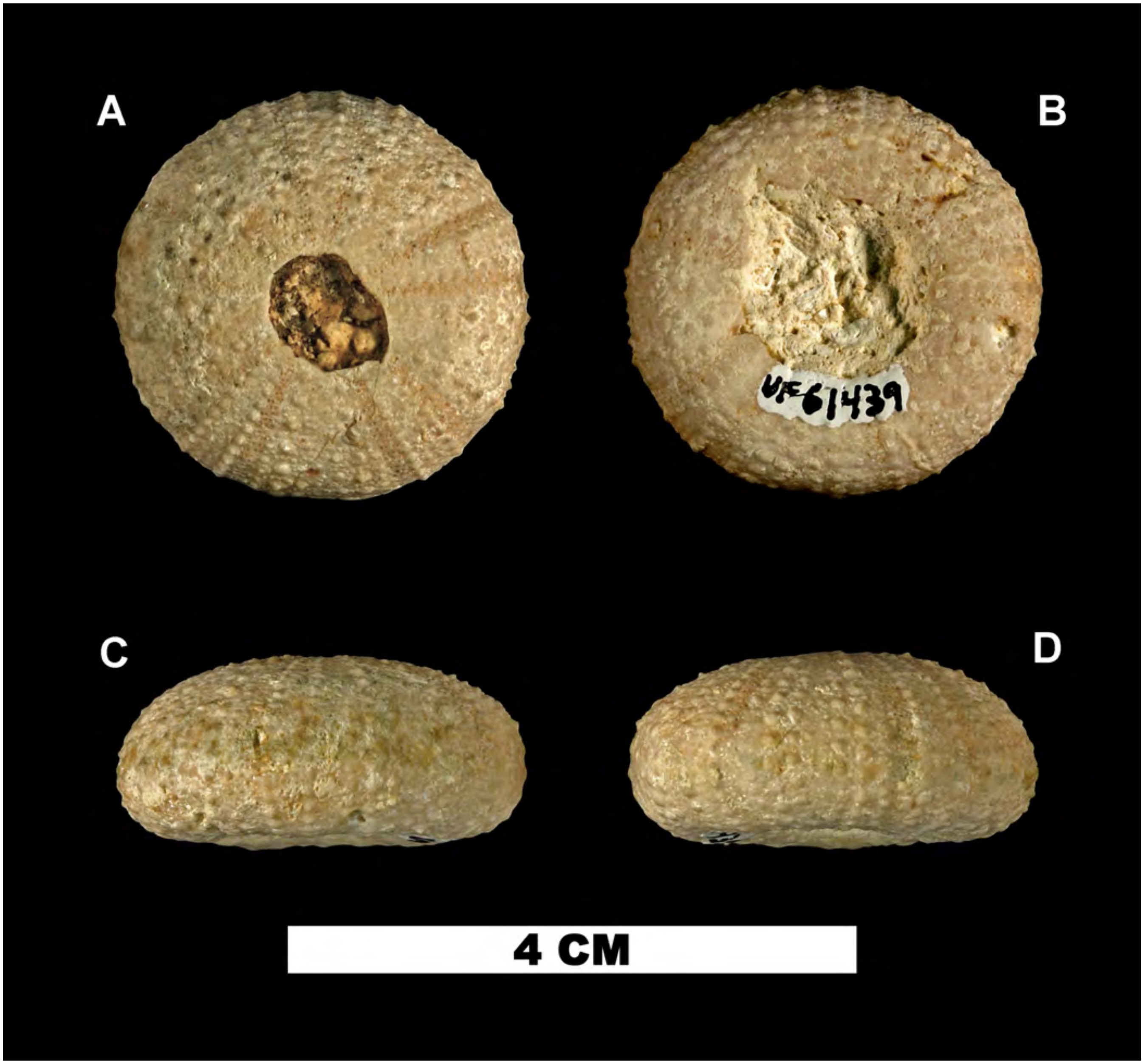


Figure 28: *Lytechinus floralanus* (UF 61439), 28 mm TD, 12 mm TH, Oligocene Bridgeboro Limestone, Washington County, Florida (FM-IP WG002). A: aboral. B: oral. C, D: lateral.

ington County, Alabama. The type of *Psammechinus*(*?*) *ocalanus* was collected near Bainbridge Georgia, in what Cooke (1941a) called "questionably Eocene strata".

Discussion.—*Lytechinus floralanus* occurs with *C. cotteaui*, and other, rarer species, in the Oligocene Bridgeboro Limestone at Duncan Church. We herein figure (Fig. 28) a large specimen from Duncan Church (UF 61439) (Fig. 9) that measures 28.7 x 28.4 mm TD, and 12.6 mm TH.

Osborn et al. (2016: table 2) documented *L. floralanus* in the Upper Eocene OLS of Florida, where it occurs with *M. mortoni, W. johnsoni, R. conradi*, and other species, just below the contact with the overlying Bumpnose Limestone in the Brooks Quarries (FM-IP JA021, FM-IP JA025, FM-IP JA030). The proportionately large tubercles readily distinguish *L. floralanus* from *B. pretiosus*, which it occurs within the OLS within the Brooks Quarry. We herein figure (Fig. 29) a specimen from

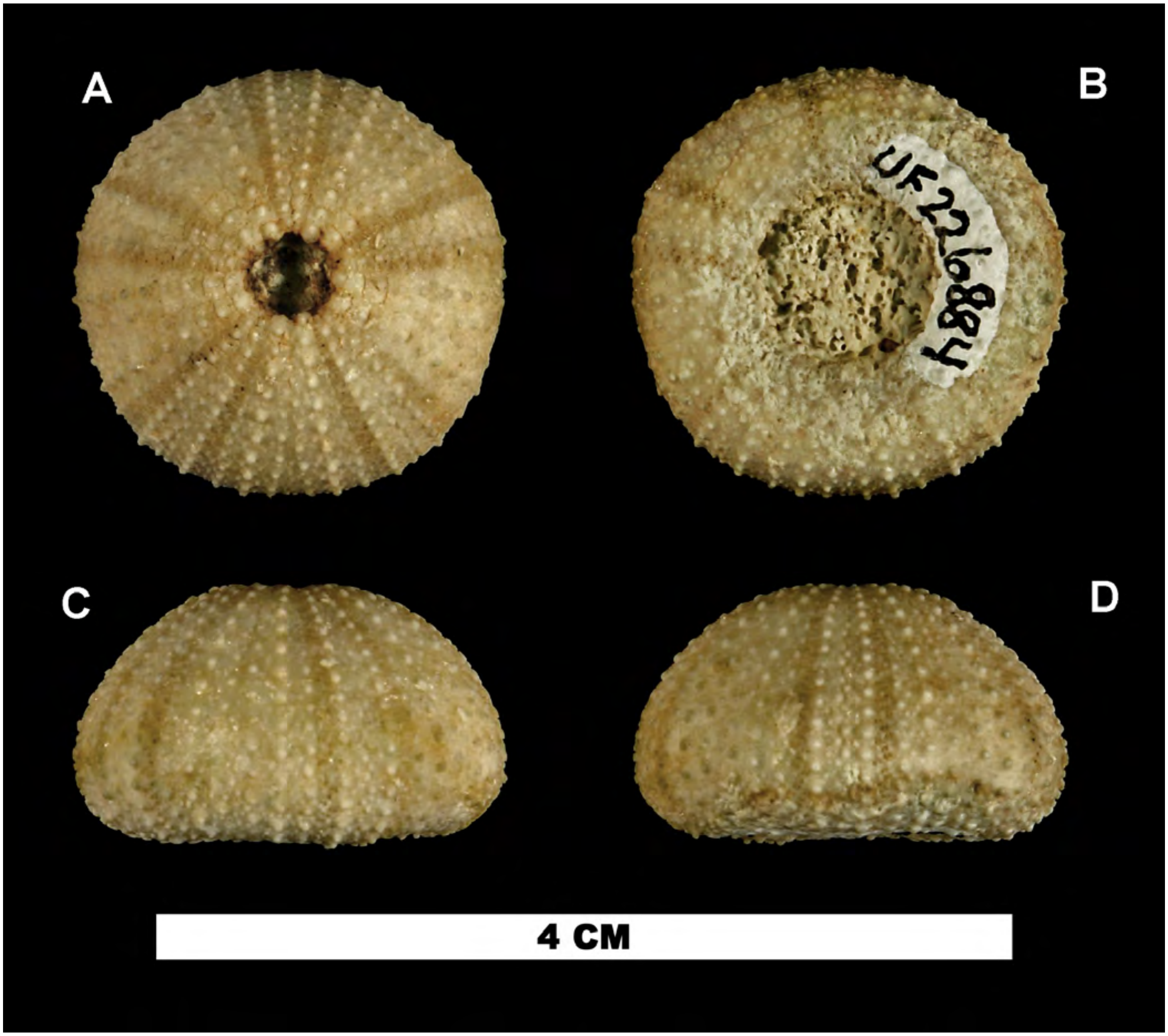


Figure 29: *Lytechinus floralanus* (UF 226884), 20 mm TD, 11 mm TH, Upper Eocene, upper Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C, D: lateral.

this horizon that measures 20.1 x 20.2 mm TD, 11.7 mm TH (UF 226884).

Euechinoidea gen. et. sp. indet.

(Fig. 30)

Occurrence.—Upper Eocene OLS, (occurs with *H. brooksi*), Jackson Blue Spring (FM-IP JA033), east of Marianna, Jackson County.

Discussion.—This taxon is represented by two test fragments (UF 341758, UF 341759) from deep within the Jackson Blue Spring cave system. The specimens were associated with *H. brooksi*, *R. georgiensis,* and other species, and though both specimens are corroded and incomplete, they are sufficient to distinguish the taxon from any known regular urchin in North American deposits. However, they are too incomplete for assignment, even to any higher taxon.

The specimens clearly display large, imperforate, non-crenulate tubercles with pore pairs in arcs of five. Large tubercles form a single column within each ambulacrum. The known fragments do not exhibit a relatively complete interambulacrum

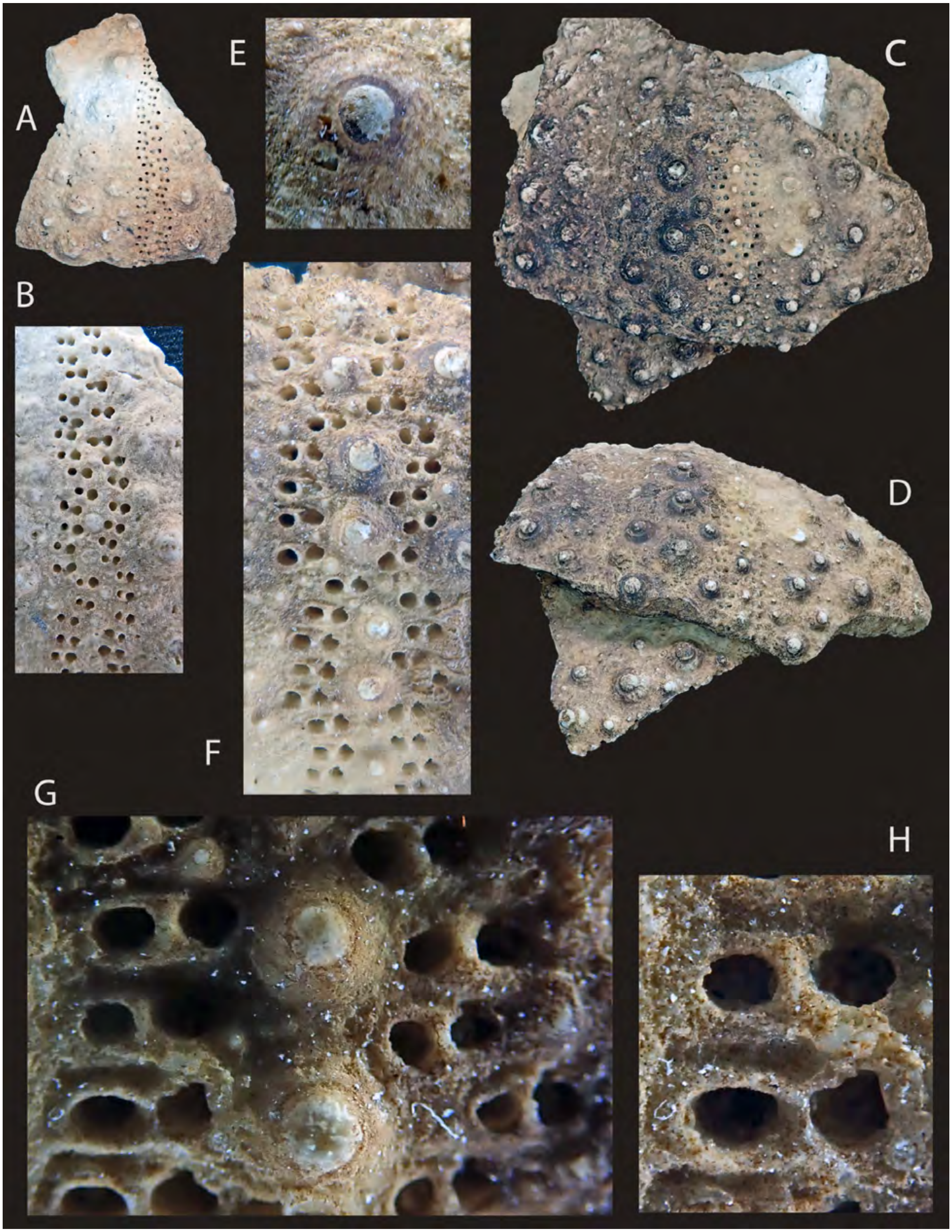


Figure 30: Euechinoidea gen. et. sp. indet. Two test fragments of an undetermined genus of regular urchin from the Ocala Limestone (associated with *Haimea brooksi*) in Jackson Blue Spring (FM-IP JA033), east of Marianna, Jackson County, Florida. A, B: UF 341759; 25.7 mm x 22.7 mm; fragment includes portions of an ambulacrum and interambulacrum. B: close-up of ambulacrum showing pore series. C-H: UF 341758; 34.3 mm x 33.0 mm; two test fragments adhered together in matrix with portions of ambulacra and interambulacra.

or ambulacrum. The largest specimen (UF 341758) represents two fragments in the same block of matrix, which measures 34 mm x 33 mm, indicating this was a rather large species. It is likely the largest non-cidarid regular urchin in Eocene deposits of North America.

The specimens are readily distinguishable from either *A. dixie* from Florida or *Acanthechinus peloria* (Clark in Arnold and Clark, 1927), which is from the Eocene of Jamaica, because these taxa have only two columns of ambulacral or interambulacral primary tubercles. The specimens of the unknown echinoid are unlike the smaller *L. floralanus*. Cenozoic regular urchins are not abundant in the remainder of the eastern Americas and Caribbean Region, and we were able to compare these specimens to most of these taxa. The single column of tubercles in the ambulacrum is like *Triadechinus multiporus* Clark in Arnold and Clark, 1927, from the Eocene of Jamaica, but the triserial pore pair arrangement of *T. multiporus* is very different. Likewise, the fragments cannot be confused with *Stenechinus regularis* Clark in Arnold and Clark, 1927; *Stenechinus perplexus* Clark in Arnold and Clark, 1927; or *Hebertia simplex* Hawkins, 1924, from the Eocene of Jamaica. These three forms, all now placed in *Echinopsis*, have much wider ambulacra, different tuberculation and pore pairs arranged in straight columns, not arcs. Clark in Arnold and Clark (1927) also described *Scoliechinus axiologus* from the Eocene of Jamaica, which Smith and Kroh (2011) asserted belongs in *Lytechinus*.

Leiosoma chondra Clark in Arnold and Clark, 1927, from the Eocene of Jamaica, and *Leiosoma guadalupense* Sánchez-Roig, 1949, from the Eocene of Cuba, are now placed in *Trochalosoma* (Fell and Pawson, 1966), and have triserial pore pairs orally and biserial aborally, readily distinguishing these *Trochalosoma* from the Florida material.

Diadema principeana Weisbord, 1934, the holotype of which is housed at the Paleontological Research Institute (PRI 3807) is readily distinguished from the Florida specimens by its straight ambulacra.

Stomopneustes pristinus Jackson, 1937, from the Oligocene of Veracruz, Mexico, has very large tubercles and triserial pore pairs that readily distinguish this species from the Florida fragments at hand. The remaining Paleogene Euechinoidea of the Caribbean are either too poorly figured and understood (mostly Cuban species of Sánchez-Roig), or too dissimilar from these specimens to warrant comparison. These taxa include *Amblypneustes corrali* Lambert and Sánchez-Roig in Sánchez-Roig, 1949 (Eocene? of Cuba); *Echinopedina cubensis* Cotteau, 1881 (Cuban strata now considered Cretaceous); *Gauthieria sanchezi* Lambert, 1921 (Eocene? of Cuba); *Leiopedina cienagensis* Sánchez-Roig, 1949 (Eocene of Cuba); *Pedina eocenica* Sánchez-Roig, 1949 (Eocene? of Cuba); *Phymosoma conceptionis* Sánchez-Roig, 1952c (Eocene? of Cuba); *Phymosoma gigantea* Sánchez-Roig, 1953b (Eocene? of Cuba); and *Pseudorthopsis rojasi* Sánchez-Roig, 1953b (Eocene of Cuba). In addition, Cooke (1961) described *Phymosoma trinitensis* from the Paleocene of Trinidad, which Smith and Jeffery (2000) assert belongs in *Trochalosoma*.

We include the above discussed taxon in a table of fossil Euechinoidea (non-cidarid regular urchins) from Cenozoic deposits of the remainder of the eastern Americas and Caribbean Region (Table 5).

After the above considerations, we can only refer this taxon to the Euechinoidea Bronn, 1860, which includes all non-cidarid echinoids. Bather (1909: 7) stated: “As regard the application of species names to such fragments, it seems to me that if our descriptions are to be of practical service to stratigraphers, then they must be accompanied by names. A description without a name is soon lost sight of, whereas a name compels attention until at last it finds its proper place, if only as a synonym.” We disagree when insufficient diagnostic features exist in fragments to allow attribution even to order or infraclass. However, to bring attention to the possible existence of a large, unidentified euechinoid in the Florida Paleogene, we include these specimens as a previously undocumented taxon. Given the scarcity of regular urchins in the OLS, it is hoped that additional material will become available to permit formal description in future.

Table 5: A listing of fossil Euechinoidea (non-cidarid regular echinoids) described from the Cenozoic of the eastern Americas and Caribbean region, outside of the eastern United States. Locality provided is the type area for the species.

Amblypneustes corrali Lambert and Sánchez-Roig, 1949	Oligocene, Cuba
Echinopedina cubensis Cotteau, 1881	strata is now considered Cretaceous (Broderman, 1949)
Ellipsechinus palmeri Lambert, Sánchez-Roig, 1949	strata is now considered Cretaceous (Broderman, 1949)
Diadema principeana Weisbord, 1934	Eocene, Cuba, likely not Diadema per Weisbord (1934)
Gauthieria sanchezi Lambert, 1921	Eocene, Cuba
Hebertia jacksoni Sánchez-Roig, 1949	Oligocene Cuba = *Echinopsis* (Fell and Pawson, 1966)
Hebertia simplex Hawkins, 1924	Eocene Jamaica = *Echinopsis* (Fell and Pawson, 1966)
Irenechinus rosei Poddubiuk, 1987	Oligocene, Antigua = *Ortholophus* (Smith and Kroh, 2011)
Leiopedina cienagensis Sánchez-Roig, 1949	Eocene, Cuba
Leiosoma chondra Clark, 1927	Eocene, Jamaica = *Trochalosoma* (Fell and Pawson, 1966)
Leiosoma guadalupense Sánchez-Roig, 1949	Eocene, Cuba = *Trochalosoma* (Fell and Pawson, 1966)
Pedina eocenica Sánchez-Roig, 1949	Eocene, Cuba
Phymosoma peloria Clark, in Arnold and Clark, 1927	Eocene, Jamaica, = *Acanthechinus* (Smith and Kroh, 2011)
Phymosoma conceptionis Sánchez-Roig, 1952	Eocene, Cuba
Phymosoma gigantea Sánchez-Roig, 1952	Eocene, Cuba
Phymosoma trinitensis Cooke, 1961	Paleocene, Trinidad = *Trochalosoma* (Smith and Jeffery 2000)
Psammechinus anguillensis Poddubiuk, 1987	Miocene, Anguilla
Pseudorthopsis rojasi Sánchez-Roig, 1953	Eocene, Cuba
Scoliechnius axiologus Arnold and Clark, 1927	Eocene, Jamaica = *Lytechinus* (Smith and Kroh, 2011)
Stenechinus perplexus Arnold and Clark, 1927	Eocene, Jamaica = *Echinopsis* (Fell and Pawson, 1966)
Stenechinus regularis Arnold and Clark, 1927	Eocene, Jamaica = *Echinopsis* (Fell and Pawson, 1966)
Stomopneustes pristinus Jackson, 1927	Oligocene, Mexico
Triadechinus multiporus Arnold and Clark, 1927	Eocene, Jamaica; type species of genus
Tripneustes (*Eotripneustes*) *tintamarrensis* Poddubiuk, 1987	Lowest Miocene, Tintamarre
Tripneustes tobleri Jeannet, 1928	Miocene, Venezuela

Infraclass **IRREGULARIA** Latreille, 1825
Subterclass **NEOGNATHOSTOMATA** Smith, 1981
Order **ECHINONEOIDA** H.L. Clark, 1925
Family **ECHINONEIDAE** Agassiz and Desor, 1847
Genus ***Amblypygus*** L. Agassiz, 1840

Amblypygus americanus Michelin, 1856
(Figs. 31-33)

Amblypygus americanus Michelin, 1856. p. 222.

Amblypygus americanus (Michelin). Desor, 1858. p. 256.

Amblypygus americanus (Desor). Duncan and Sladen, 1883. p. 13.

Amblypygus merrilli Twitchell in Clark and Twitchell 1915. p. 165. pl. 76, figs. 1a-d. pl. 57, figs. 1a-b. pl. 78, figs. 1a-b.

Amblypygus americanus (Desor). Lambert and Thiéry, 1921. p. 341.

Amblypygus merrilli (Twitchell). Lambert and Thiéry, 1921. p. 341.

Amblypygus americanus (Desor). Jackson, 1922. p. 55.

Amblypygus americanus (Desor). Arnold and Clark, 1927. p. 25. pl. 3, figs. 1-3.

Amblypygus americanus (Desor). Cooke, 1942. p. 10.

Amblypygus americanus (Desor). Cooke, 1959. p. 27. pl. 7, figs. 8, 9.

Amblypygus americanus (Desor). Toulmin, 1977. pp. 338-339. pl. 64, figs. 4, 5.

Amblypygus americanus (Michelin). Donovan and Lewis, 1993. p. 189.

Amblypygus americanus (Michelin). Donovan, 1993. pp. 382-383. fig. 9.1.

Amblypygus americanus (Desor). Osborn et al., 2016. tbl. 2.

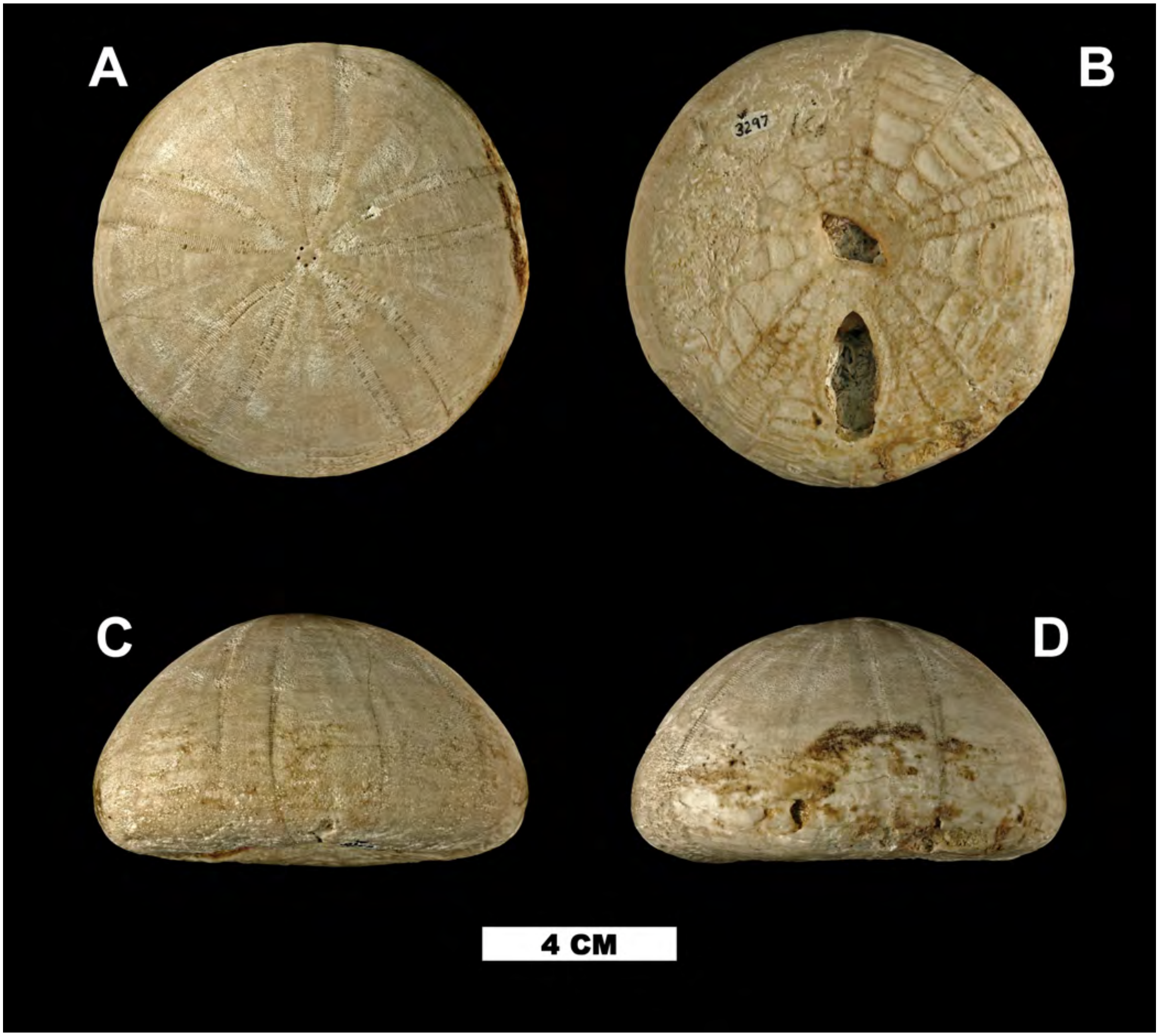


Figure 31: *Amblypygus americanus* (UF 3297), 90 mm TD, 55 mm TH, Upper Eocene *Oligopygus wetherbyi* Zone of Ocala Limestone, Alachua County, Florida (FM-IP AL002). A: aboral. B: oral. C: left side. D: right side.

Occurrence.—Within Florida, *A. americanus* occurs most commonly with *O. wetherbyi* in the upper portion of the Upper Eocene OLS in northern and central peninsular Florida; especially in quarries northwest of Mayo, Lafayette County (FM-IP LF001), and north of Ocala, Marion County. The type locality of *Amblypygus merrilli* (USNM 164934 = *A. americanus*) is Kendrick, Marion County, Florida (USGS 4246). *Amblypygus americanus* also occurs in Jackson County, in the Florida panhandle, where it rarely occurs in the *Oligopygus haldemani* Zone of the upper OLS in the Brooks Quarries, northwest of Marianna (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039), and Eocene portion of the overlying Bumpnose Limestone in the same quarry.

This species is also documented from the Upper Eocene of Georgia (Cooke, 1959) and Jamaica (type locality of *A. americanus*: Michelin, 1856; Desor, 1858; Donovan, 1993; Donovan and Lewis, 1993).

Discussion.—Desor (1858) described this robust species from the Paleogene of Jamaica based on a specimen collected by Michelin and credited it

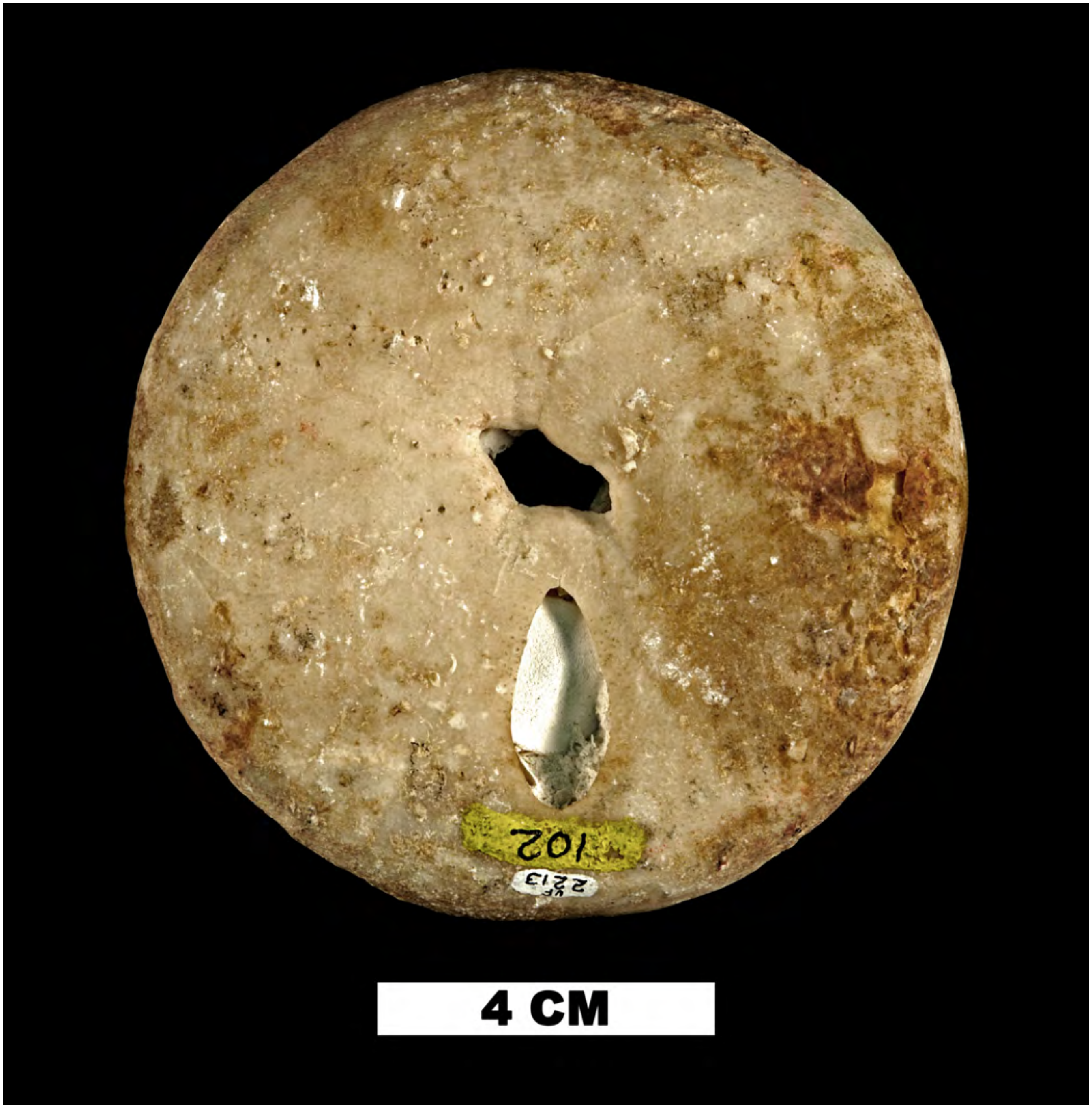


Figure 32: *Amblypygus americanus* (UF 2213), 105 mm TD; oral surface, Upper Eocene Ocala Limestone, Alachua County, Florida (FM-IP 2432).

to “Michelin, mnscr”.

Duncan and Sladen (1883), Jackson (1922), Arnold and Clark (1927), Cooke (1942, 1959), and most subsequent authors credit the species to Desor (1858), likely following Duncan and Sladen (1883), ignoring Desor’s attribution of the species name to Michelin. Clark and Twitchell (1915), Donovan (1993), and Donovan and Lewis (1993) are a few exceptions to this, attributing the name to Michelin as quoted in Desor (1858).

However, Michelin (1856) did indeed name the species two years prior to Desor’s (1858) work. Michelin presented a plaster cast of the holotype of *A. americanus* to the Société Géologique de France, stating (1856: 222, translated from the original French): “this genus is remarkable by a very

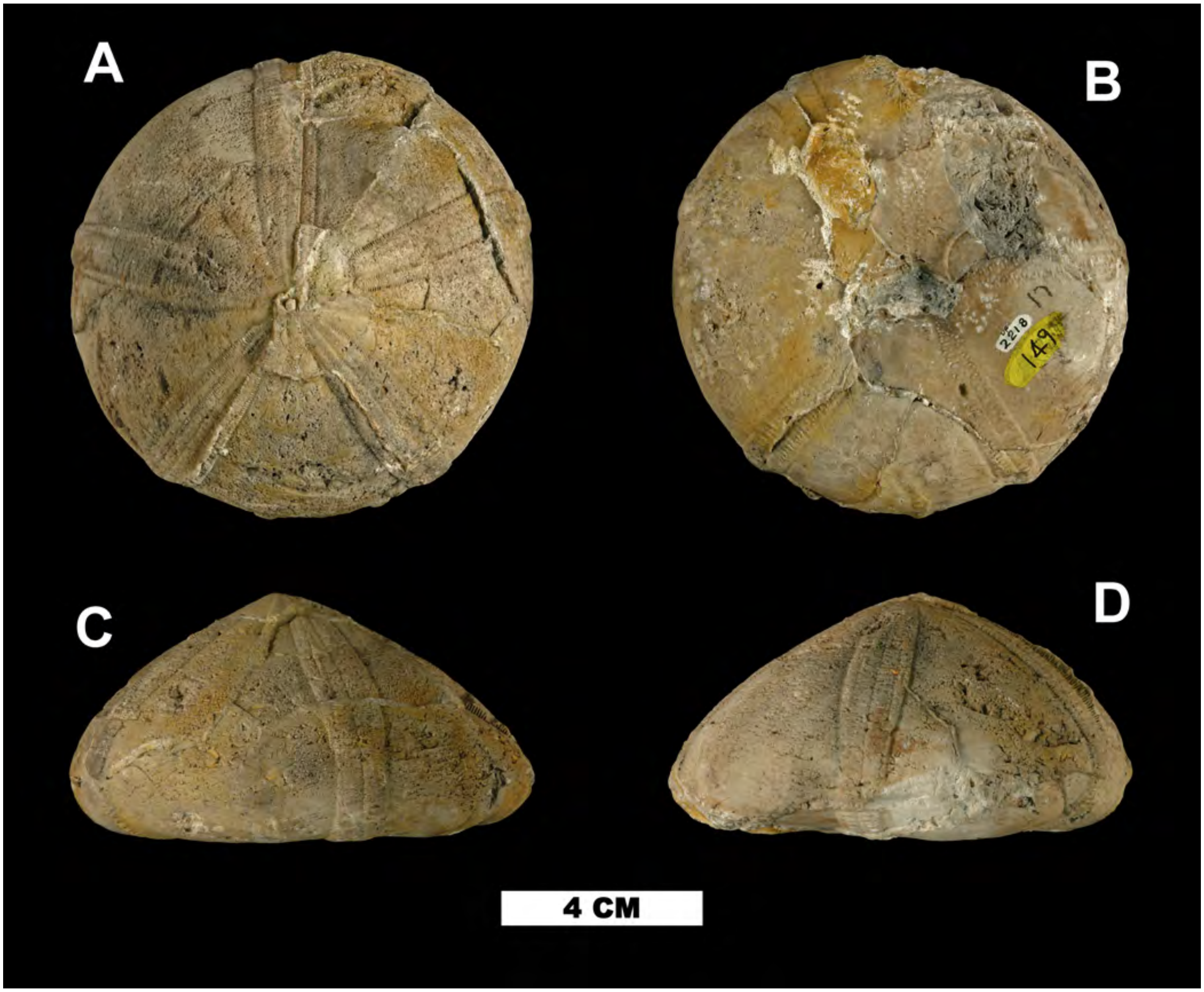


Figure 33: *Amblypygus americanus* (UF 2218), 91 mm TD, 52 mm TH, internal mold, Upper Eocene Ocala Limestone, Alachua County, Florida (FM-IP 2434). A: aboral. B: oral. C: left side. D: right side.

elongated and very large mouth almost like *Echinoneus*. The American species differs from that in that it is rounded and very thick. . . ten centimeters in diameter." Michelin then stated that the cast bears the name *Amblypygus americanus*.

Thus, as stated by Desor (1858) himself, *A. americanus* should be attributed to Michelin (1856) and not Desor (1858). In a departure from Cooke (1959) and several other major monographs, we cite Michelin's (1856) usage as the senior synonym.

Twitchell in Clark and Twitchell (1915), described *Amblypygus merrilli* from the OLS, which he believed to be Oligocene in age, in the Kendrick Lime quarries near Ocala, Florida. However, Cooke (1959) asserted there was little doubt that the Jamaican species (*A. americanus*) and American species (*A. merrilli*) were synonymous, an assertion that has been upheld by subsequent authors.

Amblypygus americanus most commonly occurs in the upper portion of the OLS of peninsular Florida, where it is often associated with *O. wetherbyi* and other species. *A. americanus* occurs more rarely in the panhandle of Florida and southwestern Georgia, where it is associated with *O. haldemani* and the large, star-patterned foraminiferan, *Asterocyclina*. The largest specimen examined, from the Mayo Quarry (FM-IP LF001), Lafayette County, Florida, was 129 mm TL.

Superorder **LUMINACEA** Mongiardino Koch et al., 2022
Order **CLYPEASTEROIDA** A. Agassiz, 1872
Family **OLIGOPYGIDAE** Duncan, 1889
Genus ***Haimea*** Michelin, 1851

Haimea brooksi Osborn et al., 2016
(Figs. 34, 35)

Haimea brooksi Osborn et al., 2016. pp. 18-23. figs. 11, 12.

Occurrence.—This species has not been documented outside of the Upper Eocene OLS of Jackson County, Florida. Osborn et al. (2016) described this taxon from the Brooks Quarry (FM-IP JA039), Sills Pit (FM-IP JA086), and Jackson Blue Spring (FM-IP JA033).

Discussion.—*Haimea brooksi* is common at its type locality (FM-IP JA039) where it occurs with *R. georgiensis*, *O. haldemani, O. rotundus, W. johnsoni,* and many other, rarer echinoid species, including new taxa described herein: *Rhyncholampas mariannaensis* n. sp., *Rhyncholampas bao* n. sp., and *Brissus jonesi* n. sp. As discussed by Osborn et al. (2016), the precise stratigraphic placement of *H. brooksi* within the OLS cannot be determined, as neither excavation in the Brooks (FM-IP JA039) or Sills quarries (FM-IP JA086), nor exposures in Jackson Blue Spring (FM-IP JA033) expose the base of the *Haimea brooksi* Zone. Within the Brooks Quarry, the zone was quarried by dragline below the water level at a depth of up to 24 m, which is 29-30 m below the top of the Eocene exposures within the quarry (Fig. 6). This horizon falls within the *Asterocyclina* Zone named for this abundant, large, star-shaped, foraminiferan, and below the zone of abundance of *Oligopygus haldemani*.

Haimea brooksi can only be confused with *O. haldemani,* with which it occurs at all known localities. However, *Haimea* and *Oligopygus* are only superficially similar. *Haimea* is readily differentiated from *Oligopygus* in having a pentagonal to subpentagonal peristome that is not situated in a transverse circumoral depression, the infundibulum (*sensu* Durham [1955]). In addition, the sutures in *Oligopygus* are sinuous (corrugated *sensu* Kier, 1967), whereas they are smooth and straight in *Haimea*. *Haimea brooksi* is further differentiated from *O. haldemani* by its much more globose test.

Genus ***Oligopygus*** de Loriol, 1887

Oligopygus haldemani (Conrad, 1850)
(Figs. 36-40)

Discoidea haldemani Conrad, 1850. p. 40. pl. 1, fig. 12.
Discoidea haldemani (Conrad). Conrad, 1865. p. 75.
Discoidea haldemani (Conrad). Conrad, 1866. p. 22.
Discoidea haldemani (Conrad). Agassiz, 1883. p. 88.
Oligopygus haldermani (Conrad). Clark and Twitchell, 1915. p. 167. pl. 78, figs. 4a-d, 5a-d.
Oligopygus haldermani (Conrad). Cooke and Mossom, 1929. pl. 3, figs. 3a-b.
Oligopygus colsoni Lambert, 1932. p. 290. pl. 17, figs. 1-4.
Oligopygus haldemani (Conrad). Cooke, 1942. p. 8.
Oligopygus haldemani (Conrad). Cooke, 1945. fig. 5, no. 3.
Oligopygus haldemani (Conrad). Cooke, 1959.p. 29. pl. 8, figs. 6-8.
Oligopygus haldemani (Conrad). Kier, 1967. pp. 83-88. pl. 3, figs 1, 2; pl. 11, figs. 1-6; pl. 23. txt figs. 4, 8, 13-16, 19, 24, 37-39.
Oligopygus haldemani (Conrad). Toulmin, 1977. p. 343. pl. 67, figs. 4-6.
Oligopygus haldemani (Conrad). McKinney and Jones, 1983. pp. 21-29. 8 figs. 1 tbl.
Oligopygus haldemani (Conrad). McKinney, 1984. pp. 407-419. 12 figs. 3 tbls.
Oligopygus haldemani (Conrad). Rice, 1997. pp. 907-912. fig. 3.
Oligopygus haldemani (Conrad). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 3.
Oligopygus haldemani (Conrad). Miller et al., 2008. p. 66.
Oligopygus colsoni (Lambert). Miller et al., 2014.

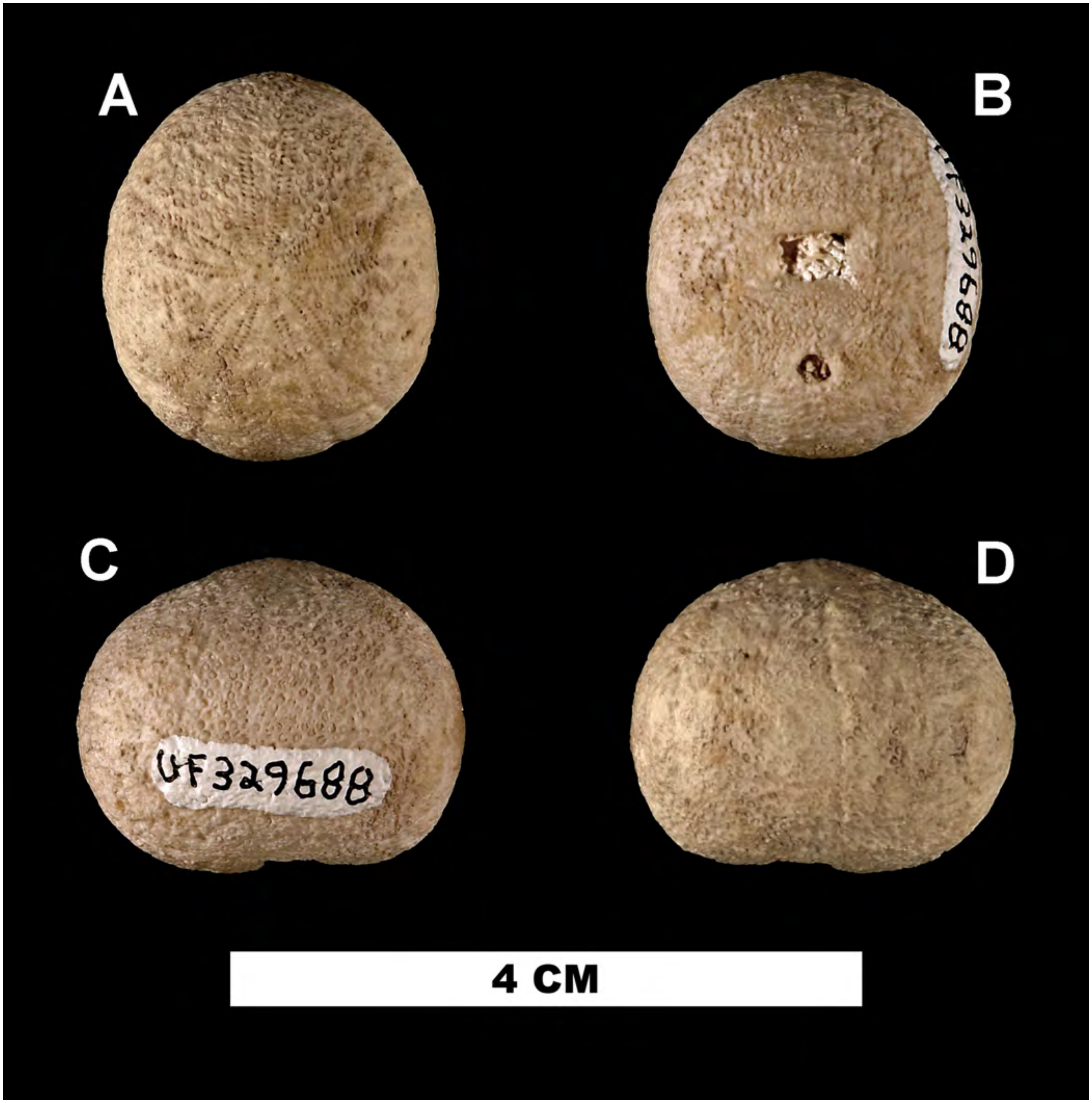


Figure 34: *Haimea brooksi* (UF 329688), 25 mm TL, 21 mm TW, 20 mm TH, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side.

pp. 145-160.
Oligopygus haldemani (Conrad). Osborn et al., 2016. tbl. 2.

Occurrence.—The greatest abundance of this species is undoubtedly in the OLS of Florida (strata formerly included within the Williston Formation of Puri [1957]), although it does occur much more rarely in the Upper Eocene of Georgia. In peninsular Florida, *O. haldemani* occurs stratigraphically below the occurrence of *O. wetherbyi*. Localities for this commonly encountered echinoid are too numerous to list, but notably include quarries such as northwest of Mayo in Lafayette County (FM-IP LF001), the Cemex Quarry west of Center Hill in Sumter County (FM-IP SM010), and the Haile

Figure 35: *Haimea brooksi* (UF 329689), 23 mm TL, 19 mm TW, 19 mm TH, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side.

quarry complex (FM-IP AL004) in Alachua County. *Oligopygus haldemani* is also very abundant in the OLS of the Florida panhandle, where it occurs at numerous localities in Jackson County, including the Brooks Quarries (FM-IP JA009) and Sills Pit (FM-IP JA086).

Discussion.—Kier (1967) stated that *O. haldemani* and *O. wetherbyi* are commonly found together. However, this implied association is likely due to occurrences in mixed spoil from multiple horizons of the OLS often encountered in the limestone quarries of Florida. The two species are not documented together *in situ* in the same horizon.

Oligopygus haldemani and the usually larger *O. wetherbyi* are only superficially similar. The

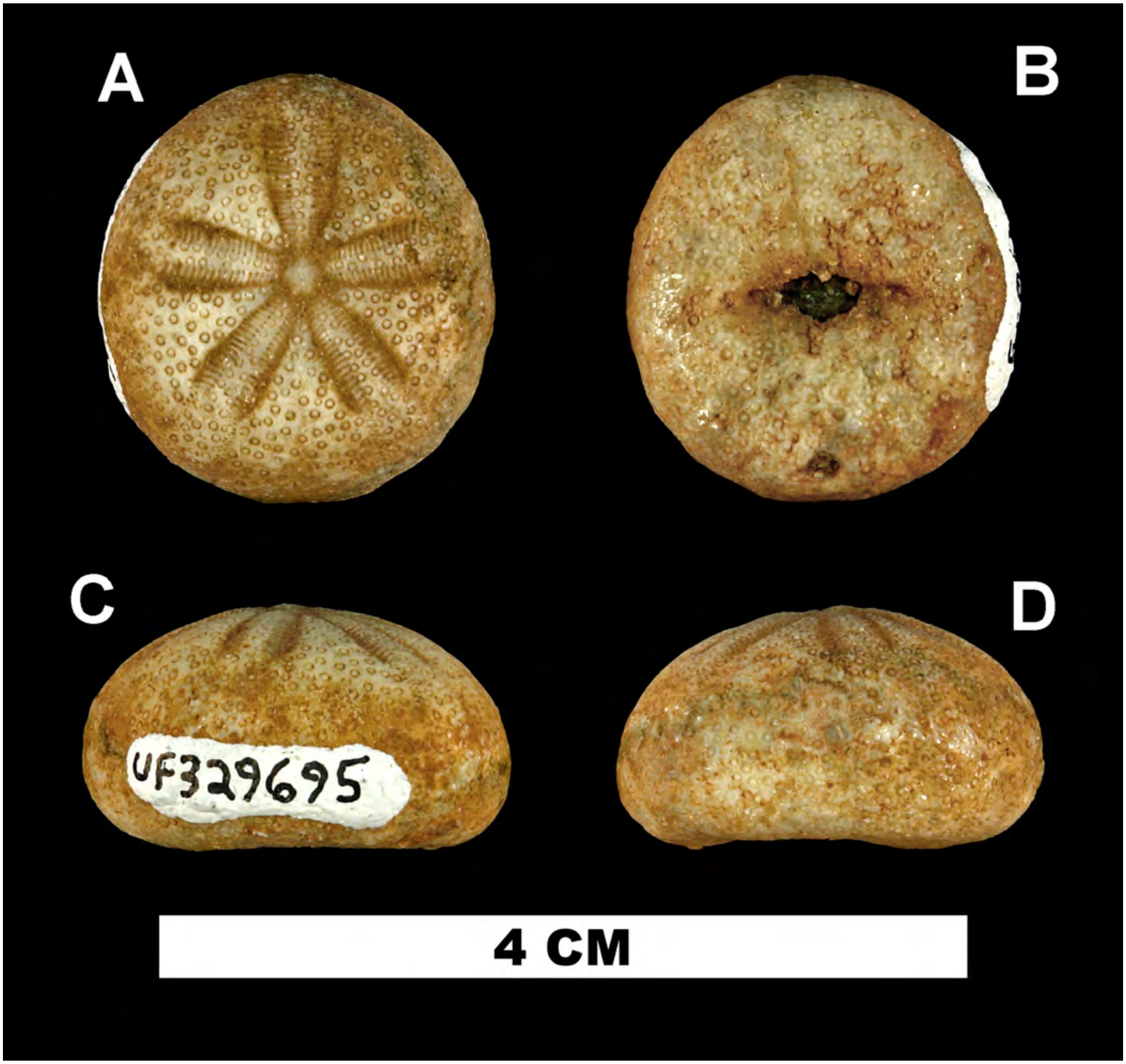


Figure 36: *Oligopygus haldemani* (UF 329695), 21 mm TL, 19 mm TW, 11 mm TH; uppermost bed of Upper Eocene Ocala Limestone in the Marianna Lime Quarry (FM-IP JA031), Jackson County, Florida. A: aboral. B: oral. C: left side. D: right side.

periproct of *O. wetherbyi* is typically located much closer to the peristome than in *O. haldemani*, and this trait is consistent even in smaller specimens of *O. wetherbyi*, which could otherwise be confused with the much smaller *O. haldemani*. In addition, Kier (1967) clarified that the periproct of *O. wetherbyi* is more circular, there are more pore pairs in petals III and V, the test is slightly narrower, and the greatest width is posterior, especially in larger specimens.

Oligopygus haldemani is more superficially like *O. phelani* from the lower portion of the OLS, with specimens of which it had been confused (Fischer, 1951; Cooke, 1959) until Kier (1967) erected the species *O. phelani* for these specimens. The two species are readily differentiated by the deeper infundibulum and more posteriorly situated periproct in *O. haldemani*.

Oligopygus haldemani occurs with *O. rotundus* (the only documented occurrence of stratigraphic range overlap of *Oligopygus* species in the

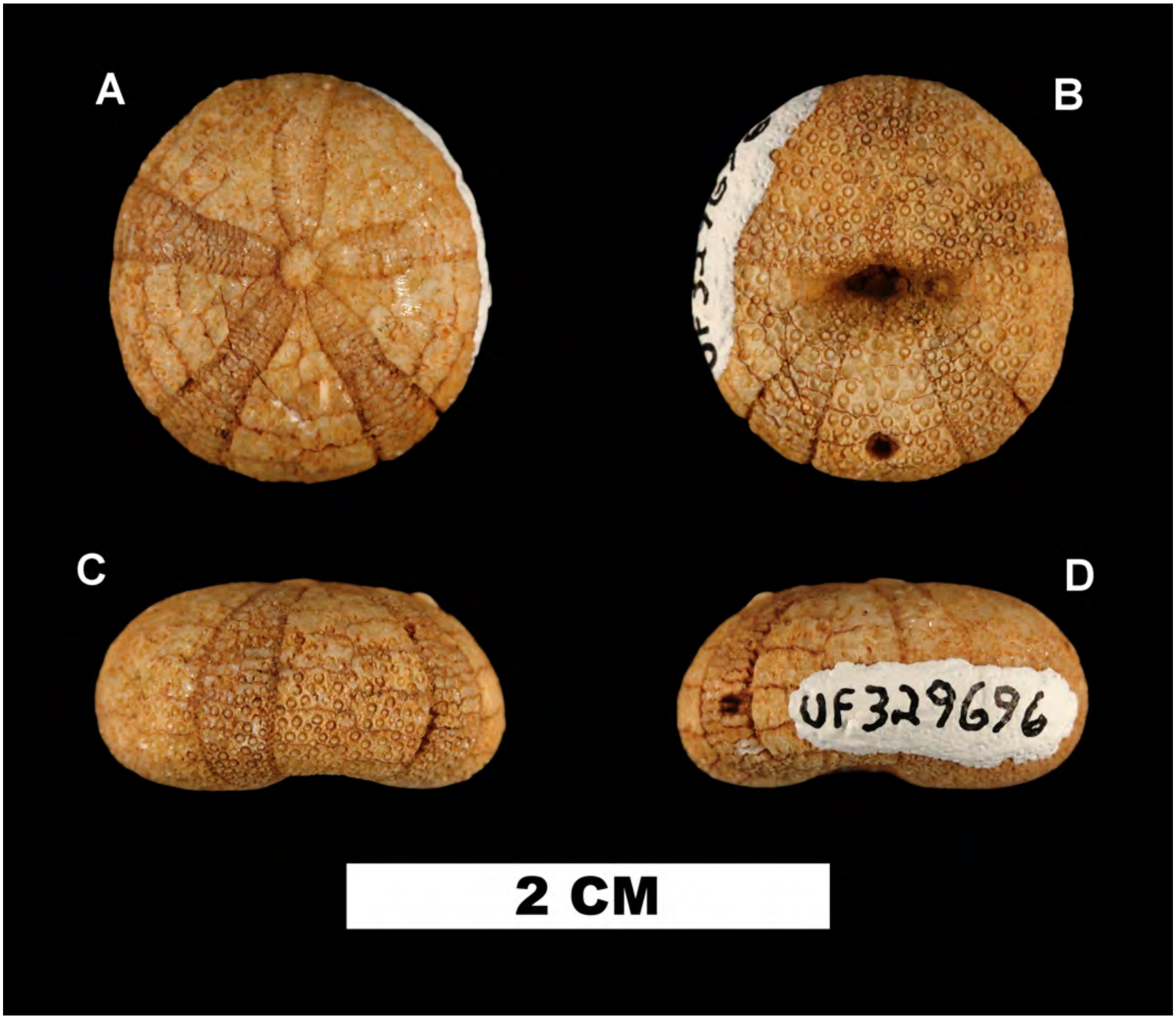


Figure 37: *Oligopygus haldemani* (UF 329696), 16 mm TL, 15 mm TW, 8 mm TH; uppermost bed of Upper Eocene Ocala Limestone in the Marianna Lime Quarry (FM-IP JA031), Jackson County, Florida. A: aboral. B: oral. C: left side. D: right side.

region), as well as the oligopygoid *H. brooksi*, in the lower beds of the OLS in the Brooks Quarry (FM-IP JA039) northwest of Marianna, Jackson County (Osborn et al., 2016). *Oligopygus rotundus* has longer petals and the posterior slope of its infundibulum is much steeper (Cooke, 1959; Kier, 1967).

Two specimens referred in our treatment of *O. haldemani* from near Marianna, Jackson County, were described by Lambert (1932) as *O. colsoni*. He stated that *O. colsoni* is like *O. haldemani* but differed in being less elongate, with a more pronounced ”oral sulcus” (to which we refer as an infundibulum, likely homologous with that of clypeasteroids), less inflated interporiferous zones in the petals, a lower density of pores in the petals, and shorter petals.

Cooke (1942) placed *O. colsoni* in synonymy with *O. haldemani*. Cooke (1959) subsequently surmised that *O. colsoni* was a juvenile specimen of *O. haldemani*, attributing the decreased pore density to the small size of the former. Kier (1967) agreed with Cooke (1959) noting that although he was unable to locate the type of *O. colsoni* (Kier stated that it is not in the Lambert Collection at the Sorbonne, France), he asserted that the specimen

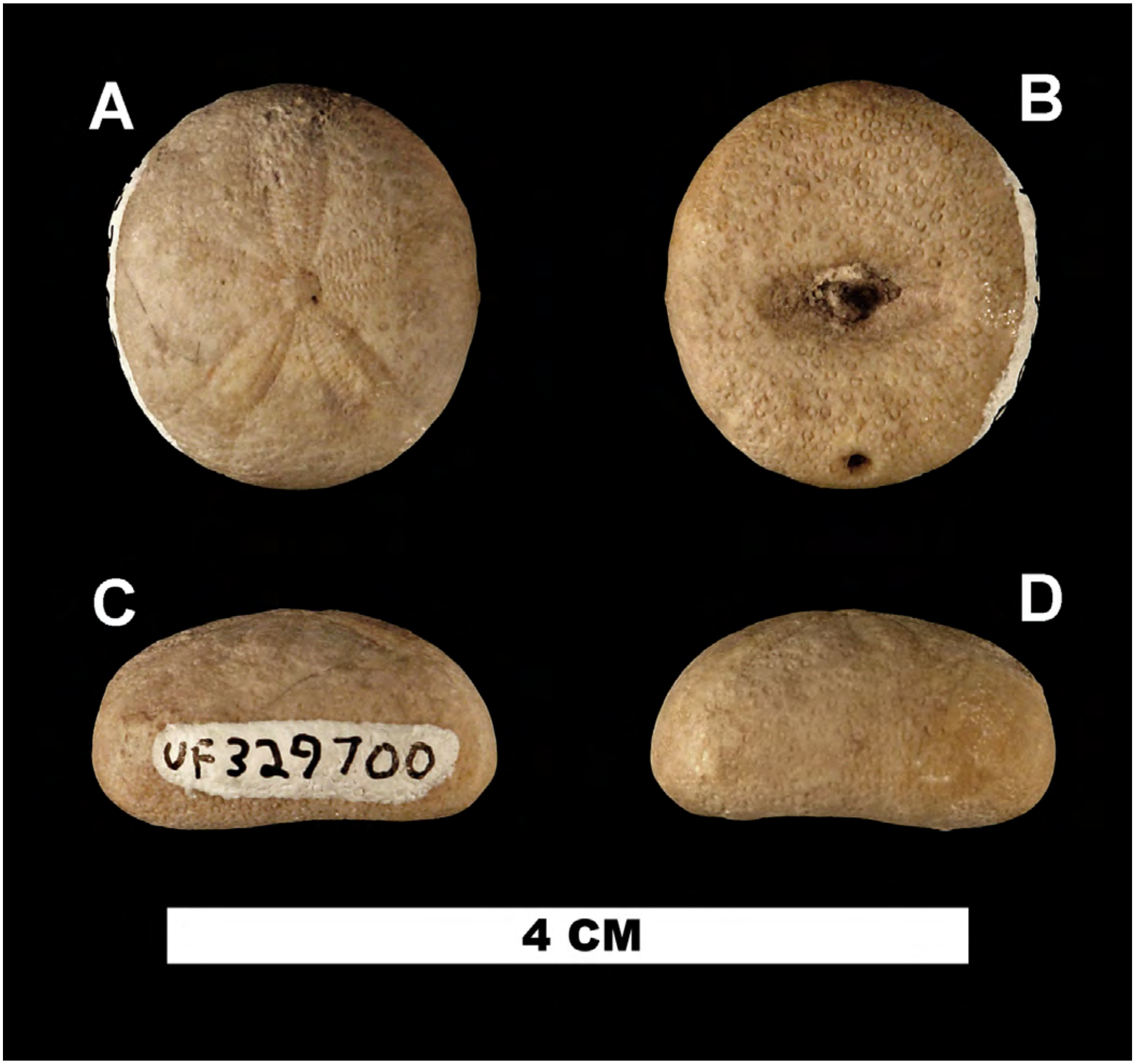


Figure 38: *Oligopygus haldemani* (UF 329700), 19 mm TL, 17 mm TW, 10 mm TH, *Haimea brooksi* Zone, Upper Eocene Ocala Limestone, Marianna Lime Quarry (FM-IP JA039), Jackson County, Florida. A: aboral. B: oral. C: left side. D: right side.

Lambert figured is indistinguishable from small *O. haldemani*.

Miller et al. (2008) compared four morphological measurements from 42 specimens of *O. haldemani* from the Florida panhandle and 148 specimens from peninsular Florida, stating that the only distinction that could be found was when the number of pore pairs in ambulacrum I is plotted against other test measurements. However, they indicated ambiguity in assigning single specimens to either *O. haldemani* or *O. colsoni*, considering the degree of overlap between the populations.

Miller et al. (2014) reversed their earlier (2008) opinion and concluded that *O. colsoni* is a valid taxon and that all populations near Marianna, Jackson County, should be given that name. In doing so, they continued to acknowledge their specimens showed considerable overlap of features and that comparing an individual *O. colsoni* to any given *O. haldemani* (when referencing speci-

Figure 39: *Oligopygus haldemani* (UF 337978), 21 mm TL, 18 mm TW, 10 mm TH, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

mens outside of the type material) is problematic. They indicated that of the five traits Lambert (1932) used to distinguish *O. colsoni* from *O. haldemani*, neither test shape, peristomial infundibulum, inflation of poriferous zones, nor petal length can be used to differentiate the species. However, concerning the density of pore pairs, they calculated a mean pore density of 3.62 for the specimens they recognized as *O. colsoni* and 4.127 for specimens they identified as *O. haldemani*. Again, they stated that overlap of this feature implies that some individuals from either species could be misidentified. It is consistent with the biology of echinoids to suggest that populations of *O. haldemani* in Jackson County are characterized by a slightly higher density of pore pairs. Whether or not this feature, which Miller et al. (2014) admitted has considerable overlap with populations unambiguously assigned to *O.*

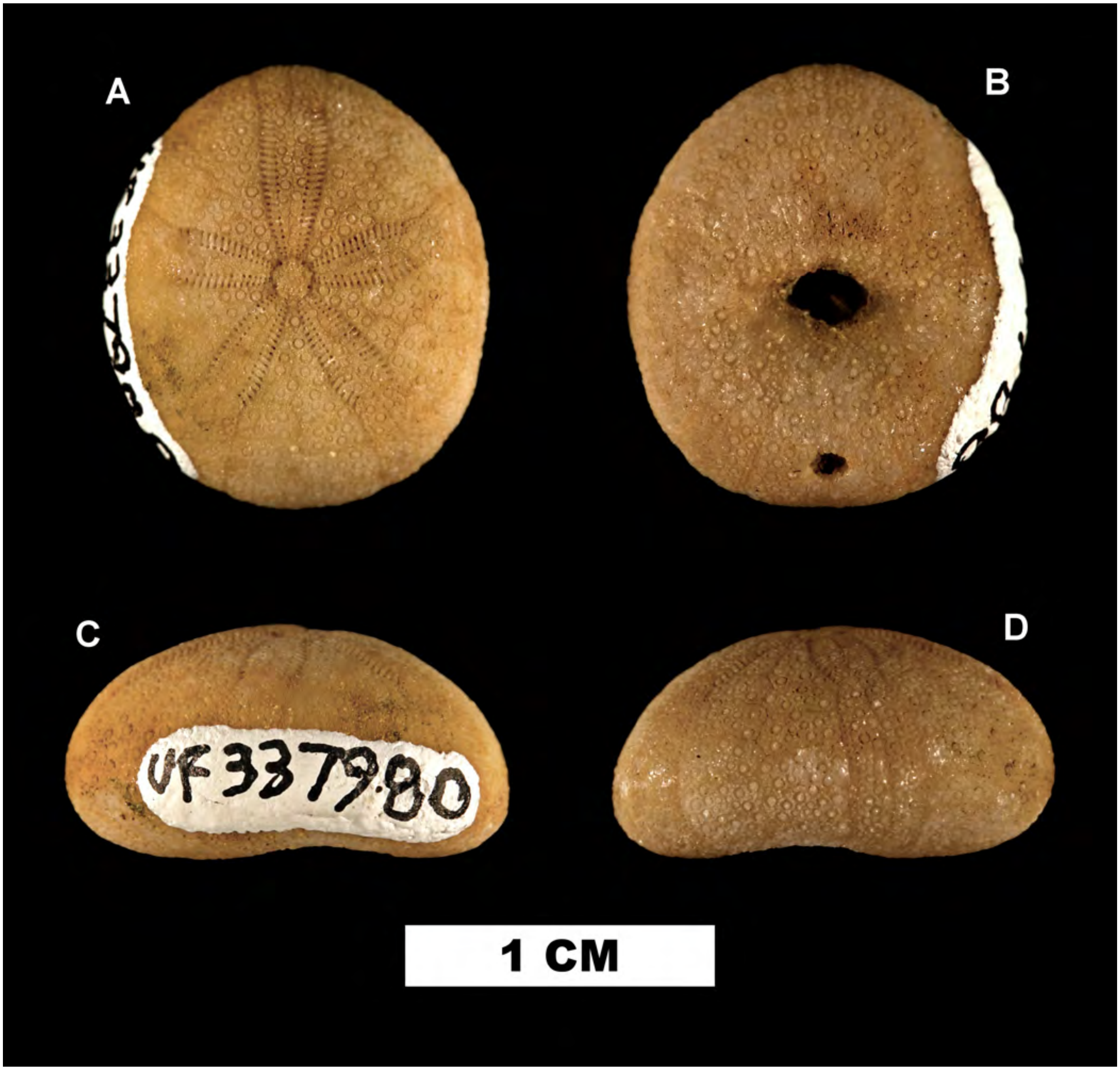


Figure 40: *Oligopygus haldemani* (UF 337980), 15 mm TL, 13 mm TW, 8 mm TH, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

haldemani, is sufficient to distinguish a new species is debatable. Moreover, the proposed *Oligopygus* zonation of Miller et al. (2014) would only be useful if *O. colsoni* is separable from *O. haldemani*, and even Miller et al. (2014) acknowledged it is not.

Kier (1967) noted that of the 140 specimens of *O. haldemani* he examined, the gonopores were small on some individuals and large on others, which led him to propose that the species is sexually dimorphic. This was the first suggestion of a sexually dimorphic oligopygid.

Oligopygus phelani Kier, 1967
(Figs. 41, 42)

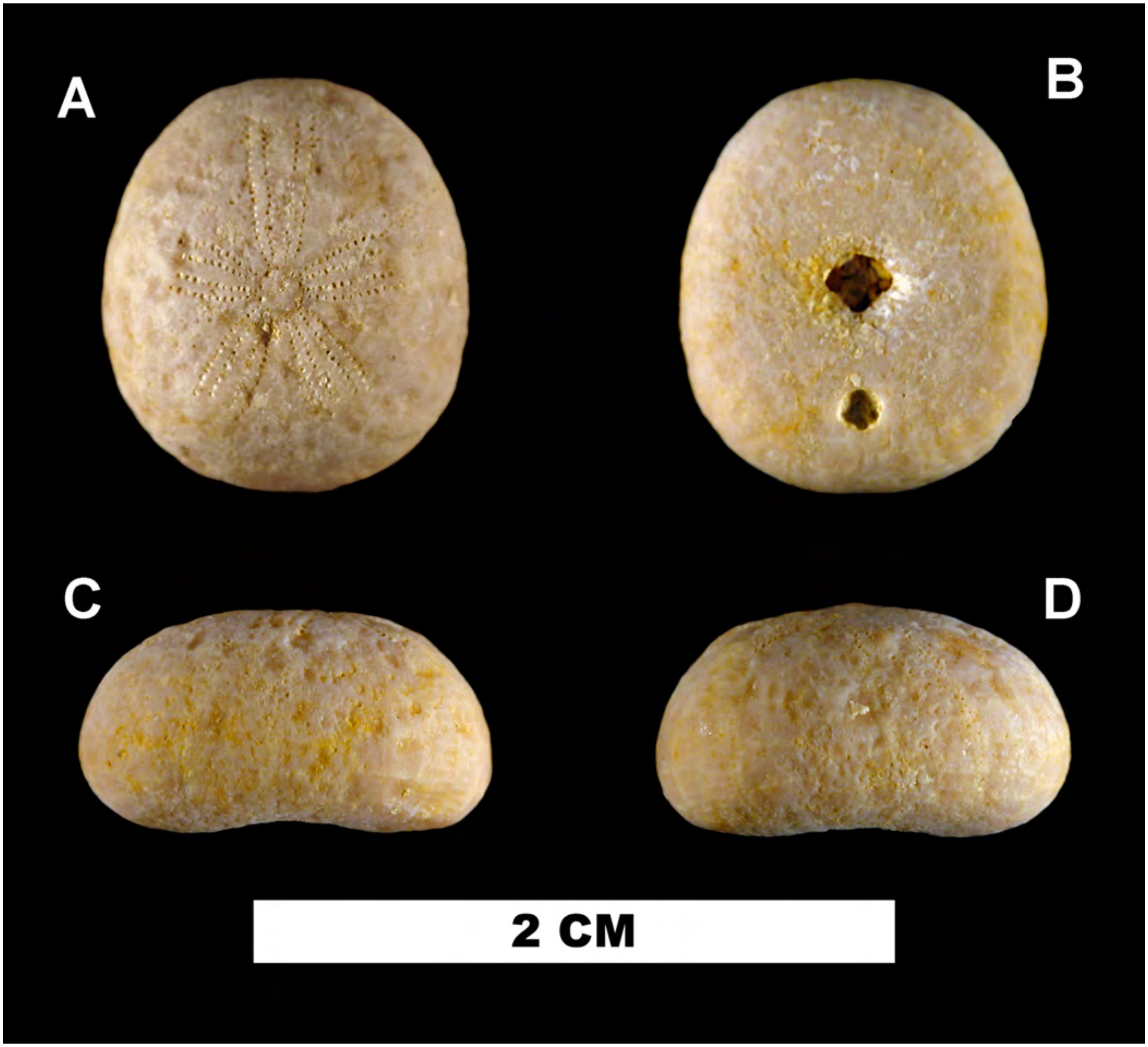


Figure 41: *Oligopygus phelani* (UF 343885), 13 mm TL, 11 mm TW, 7 mm TH, lower portion of Upper Eocene Ocala Limestone, Levy County, Florida (FM-IP LV016). A: aboral. B: oral. C: left side. D: right side.

not *Oligopygus haldemani* (Conrad). Fischer, 1951. p. 56 (not *O. haldemani*).

Oligopygus phelani Kier, 1967. pp. 81-83. pl. 22, txt fig. 9.

Oligopygus phelani (Kier). McKinney and Jones, 1983. pp. 21-29. 8 figs. 1 tbl.

Oligopygus phelani (Kier). McKinney, 1984. pp. 407-419. 12 figs. 3 tbls.

Oligopygus phelani (Kier). Rice, 1997. pp. 907-912. fig. 3.

Oligopygus phelani (Kier). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 2.

Oligopygus phelani (Kier). Osborn et al., 2016. tbl. 2.

Occurrence.—This is the common oligopygid of the lowermost portion of the OLS, in strata formerly known as the Inglis Formation. The type locality is spoil along the Cross Florida Barge Canal south of Inglis. This species is present, though typically never as common as the oligopygids of the upper OLS, at nearly all exposures of the lower OLS,

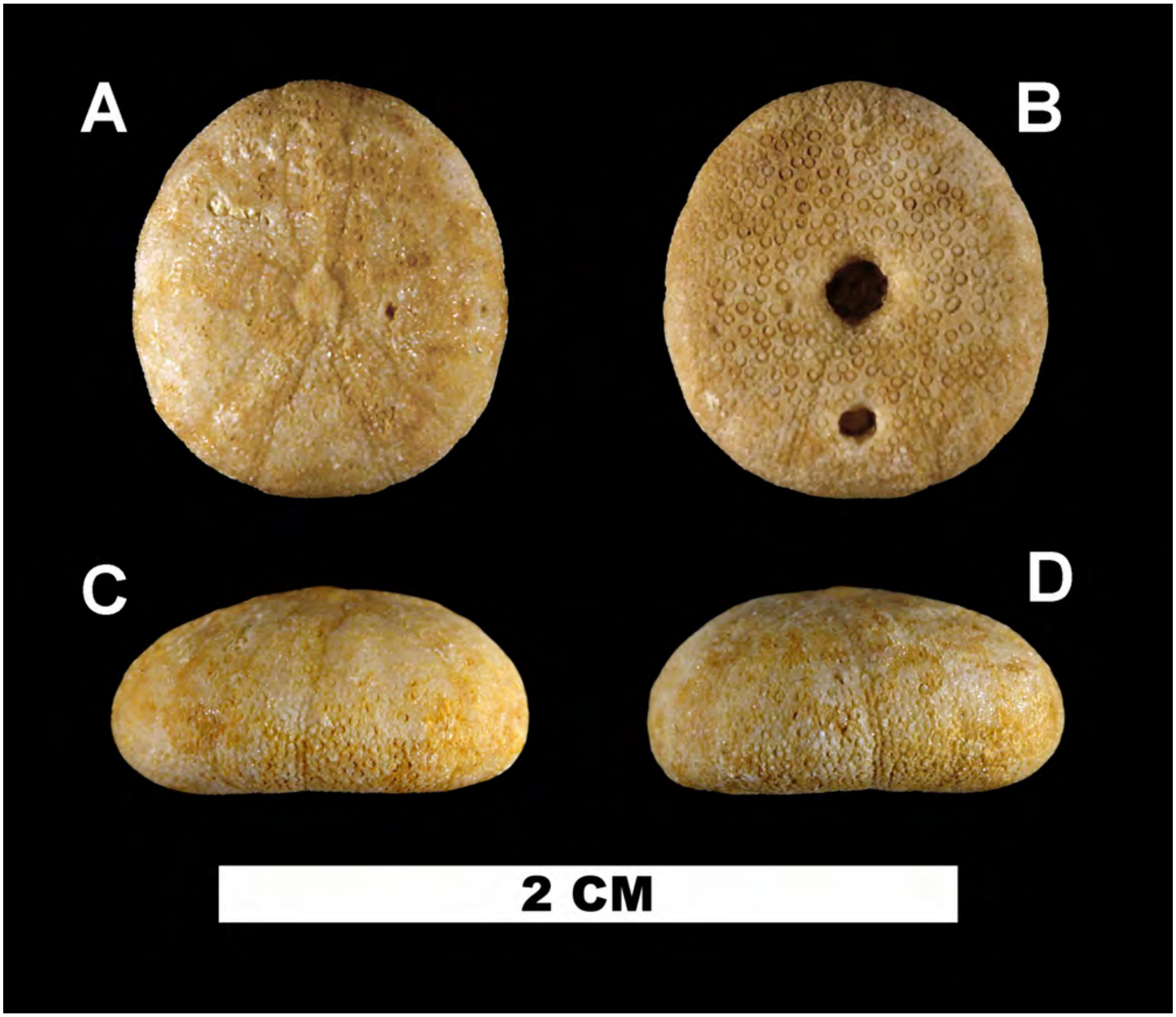


Figure 42: *Oligopygus phelani* (UF 343886), 11 mm TL, 10 mm TW, 5 mm TH, lower portion of Upper Eocene Ocala Limestone, Levy County, Florida (FM-IP LV016). A: aboral. B: oral. C: left side. D: right side.

especially along the Withlacoochee River west of Yankeetown (FM-IP LV024) and small quarries in Levy County (e.g., FM-IP LV114). *Oligopygus phelani* occurs very rarely in the Upper Eocene of Georgia (Carter and Hammack, 1989; Carter and McKinney, 1992).

Discussion.—*Oligopygus phelani* is superficially similar to *O. haldemani* from higher in the OLS, with which it had been historically confused (Fischer, 1951; Cooke, 1959). However, upon close examination the two species are readily differentiated by the deep circum-peristomial infundibulum and more posteriorly situated periproct of *O. haldemani* (Kier, 1967).

Oligopygus phelani appears to be restricted to the lowermost OLS (formerly referred to as the Inglis Formation) in its natural outcropping area near Inglis, in northern Citrus and Levy Counties, Florida. It is present at most exposures of the lower OLS, but never as abundant as the later species *O. wetherbyi* and *O. haldemani* in the horizons within which they occur. As such, although *O. phelani* is recognized as an indicator species, it is perhaps not as good an indicator as the much more abundant *E. mooreanus*, which is also restricted to the lowermost OLS.

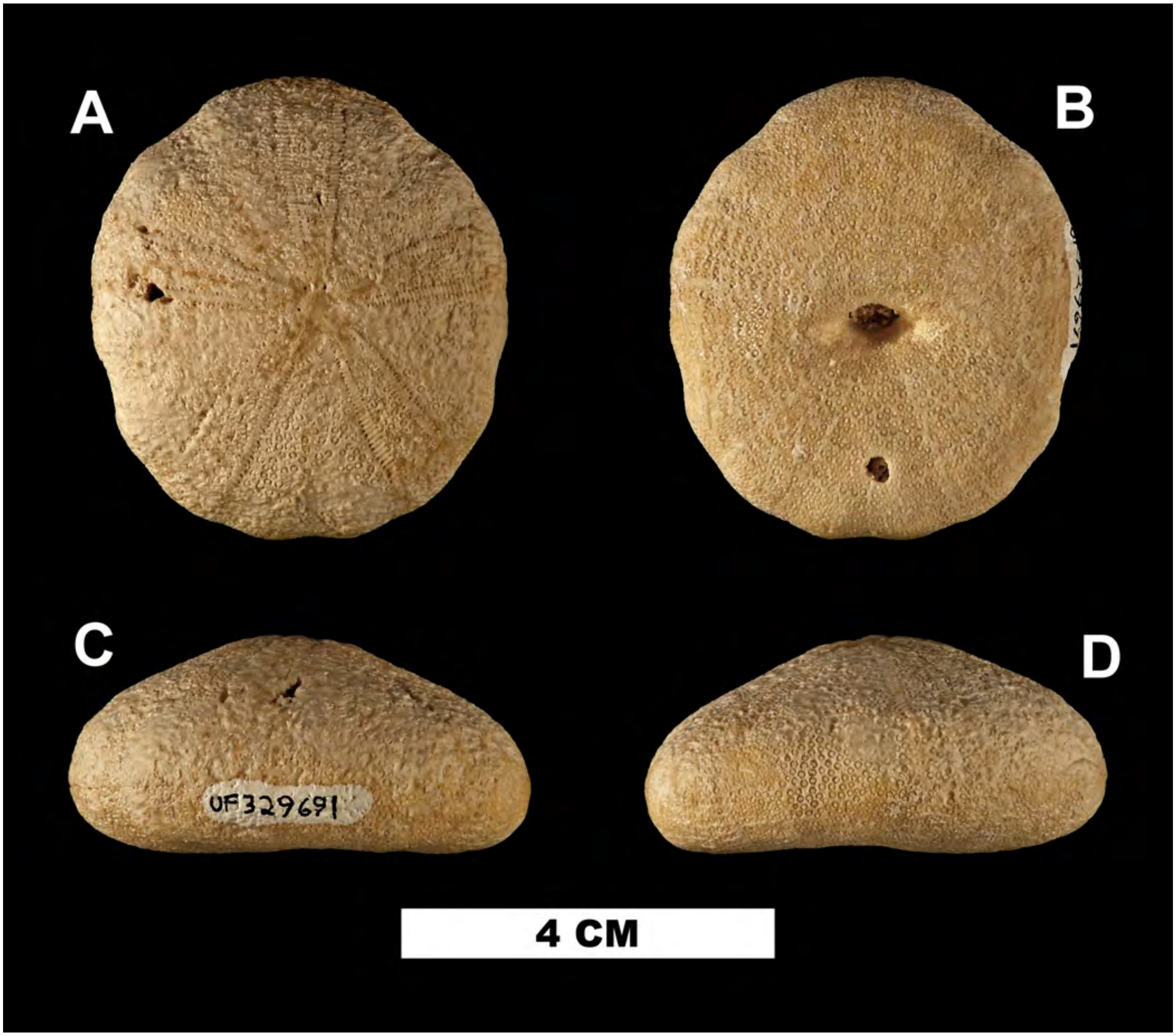


Figure 43: *Oligopygus rotundus* (UF 329691), 50 mm TL, 45 mm TW, 22 mm TH, *Haimea brooksi* Zone, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side.

Oligopygus rotundus Cooke, 1942
(Figs. 43, 44)

Oligopygus rotundus Cooke, 1942. p. 9. pl. 2, figs. 1-3.

Oligopygus rotundus (Cooke). Cooke, 1959. p. 29. pl. 8, figs. 1-5.

Oligopygus rotundus (Cooke). Cooke, 1961. p. 12. pl. 3, figs. 4-6. (not *O. rotundus* per Kier, 1967: 69).

Oligopygus rotundus (Cooke). Kier, 1967. pp. 67-69. pl. 17, figs. 3-5. txt figs. 24, 31, 38, 39.

Oligopygus rotundus (Cooke). Toulmin, 1977. p. 306. pl. 51, figs. 8, 9.

Oligopygus rotundus (Cooke). Buitrón and Sánchez, 1979. p. 123. figs. 2a-c,

Oligopygus rotundus (Cooke). Osborn et al., 2016. tbls. 2, 3.

Occurrence.—Within Florida, this species has only been documented in the OLS in the Brooks Quarry (FM-IP JA039), northwest of Marianna, Jackson County, where it occurs with *O. haldemani* and *H. brooksi*.

The type locality of the species is Geneva

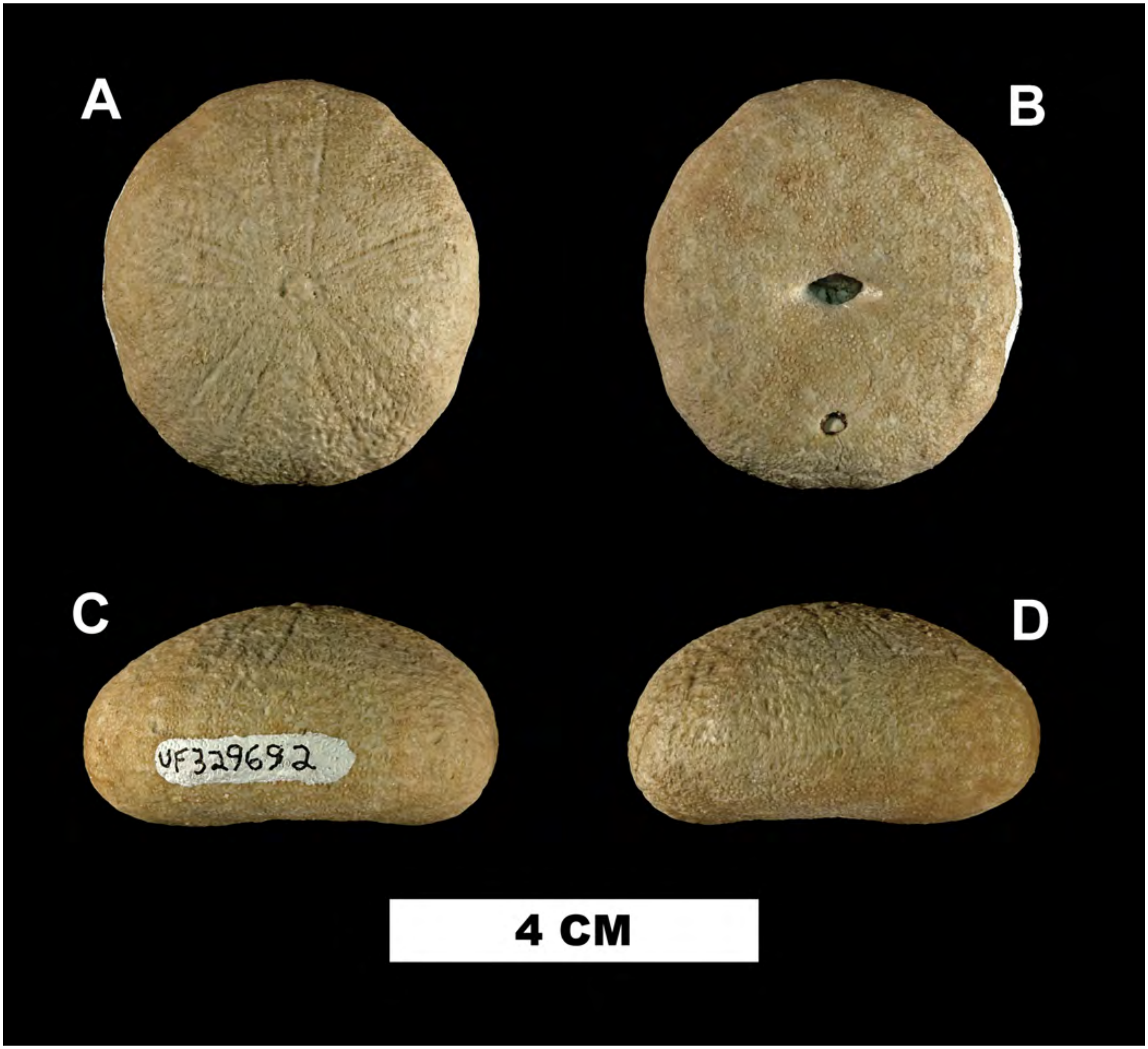


Figure 44: *Oligopygus rotundus* (UF 329692), 44 mm TL, 40 mm TW, 23 mm TH, *Haimea brooksi* Zone, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side.

County, Alabama (Cooke, 1942), where it is rare in the Lisbon Formation. Toulmin (1977) documented the occurrence of *O. rotundus* in the Lisbon Formation in Early County, Georgia. The species was also documented in the Eocene of Mexico (Buitrón and Sánchez, 1979).

Discussion.—Cooke (1942) initially described this species from Middle Eocene strata at Koons Mill, in Geneva County, Alabama. Subsequently, Cooke (1959) added two additional localities in Alabama.

Cooke (1961) also documented specimens of *O. rotundus* from the Eocene of Trinidad and Venezuela. However, Kier (1967) referred these specimens to *O. zyndeli* Jeannet, 1928. Kier (1967: 69) stated that *O. rotundus* is very similar to *O. zyndeli*. However, the peristomial infundibulum in *O. rotundus* is slightly larger and deeper longitudinally. Additional specimens of *O. rotundus* from Jackson County (FM-IP JA039) prove Kier's assessment to be accurate, although the two forms are obviously very closely related.

Oligopygus rotundus was only recently documented in the Upper Eocene OLS in Florida (Osborn et al., 2016), where it occurs in the Brooks Quarry (FM-IP JA039) with a diverse echinoid assemblage including: *H. brooksi, R. georgiensis*, *O. haldemani*, *W. johnsoni*, and others from a horizon within the *Asterocyclina* Zone (*sensu* Puri, 1957), roughly 24 to 29 m below the contact of the upper OLS and the overlying Bumpnose Limestone within the quarry (Fig. 6).

The occurrence in Jackson County, Florida is the first documentation of more than one species of *Oligopygus* occurring in the same horizon in the southeastern United States, where the succession within peninsular Florida is well known: *O. phelani* (lowermost OLS) to *O. haldemani*, and finally to *O. wetherbyi* (uppermost OLS) (Table 3). This stratigraphic succession is now modified to include *O. rotundus* as overlapping with the lower portion of the range of *O. haldemani* in the northern Florida panhandle.

The significant number of specimens from the OLS of Jackson County, allows for a much better understanding of this species. The specimens from Florida are not identical with the holotype of *O. rotundus*, being much larger. The largest specimen is 54.1 mm TL, 49.8 mm TW, 26.3 mm TH; more than twice as large as the holotype. Given this larger size and considering the ontogeny of species within the genus described by Kier (1967), it should come as no surprise that the general form of the test would change throughout growth. The smaller forms are more similar to the holotype. However, as the specimens become larger, they become more pentagonal and often develop shallow indentations in the interambulacra at the ambitus. There is also variation in periproct placement, as some specimens have a periproct much closer to the margin than is typical.

This variation is not evident in the three specimens previously available from the type area in Alabama. If additional material of *O. rotundus* from the type area becomes available, it could provide for a more comprehensive comparison of the populations from Alabama and Florida, but until then, we consider the Florida population to be conspecific.

Oligopygus rotundus has the greatest stratigraphic range of the four species of *Oligopygus* currently documented from North America, spanning from the Middle Eocene (Lisbon Formation of Alabama) to the Upper Eocene (OLS in Jackson County, Florida). In contrast, *O. haldemani*, *O. phelani,* and *O. wetherbyi* are not documented outside of Upper Eocene strata within the region (though *O. wetherbyi* does appear to extend into the Middle Eocene in Jamaica [Donovan, 1993]).

Oligopygus rotundus is superficially like *O. haldemani* in adapical view. However, the species are readily differentiated because the periproct of *O. rotundus* is further from the margin, and its infundibulum is smaller and deeper than in *O. haldemani. Oligopygus rotundus* can be differentiated from *O. wetherbyi* because the periproct of *O. rotundus* is closer to the margin, and it has a smaller and deeper infundibulum. *Oligopygus rotundus* differs from *O. phelani* in having a broader, deeper infundibulum.

Oligopygus wetherbyi de Loriol, 1887
(Figs. 45, 46)

Oligopygus wetherbyi de Loriol, 1887. p. 396. pl. 17, figs. 7-7d.

Oligopygus wetherbyi (de Loriol). Clark and Twitchell, 1915. p. 166. pl. 78, figs. 2a-d, 3a-b.

Oligopygus floridanus Twitchell in Clark and Twitchell, 1915. p. 169. pl. 79, figs. 1a-f.

Oligopygus wetherbyi (de Loriol). Cooke and Mossom, 1929. pl. 3, figs. 2a-b.

Oligopygus wetherbyi (de Loriol). Lambert, 1932. p. 290.

Oligopygus wetherbyi (de Loriol). Cooke, 1942. p. 8.

Oligopygus floridanus (Twitchell). Cooke, 1942. p. 8.

Oligopygus wetherbyi (de Loriol). Cooke, 1945. fig. 5, no. 2.

Oligopygus wetherbyi (de Loriol). Mortensen, 1948. p. 247, fig. 247.

Oligopygus wetherbyi (de Loriol). Cooke, 1959. p. 28. pl. 8, figs. 9-12.

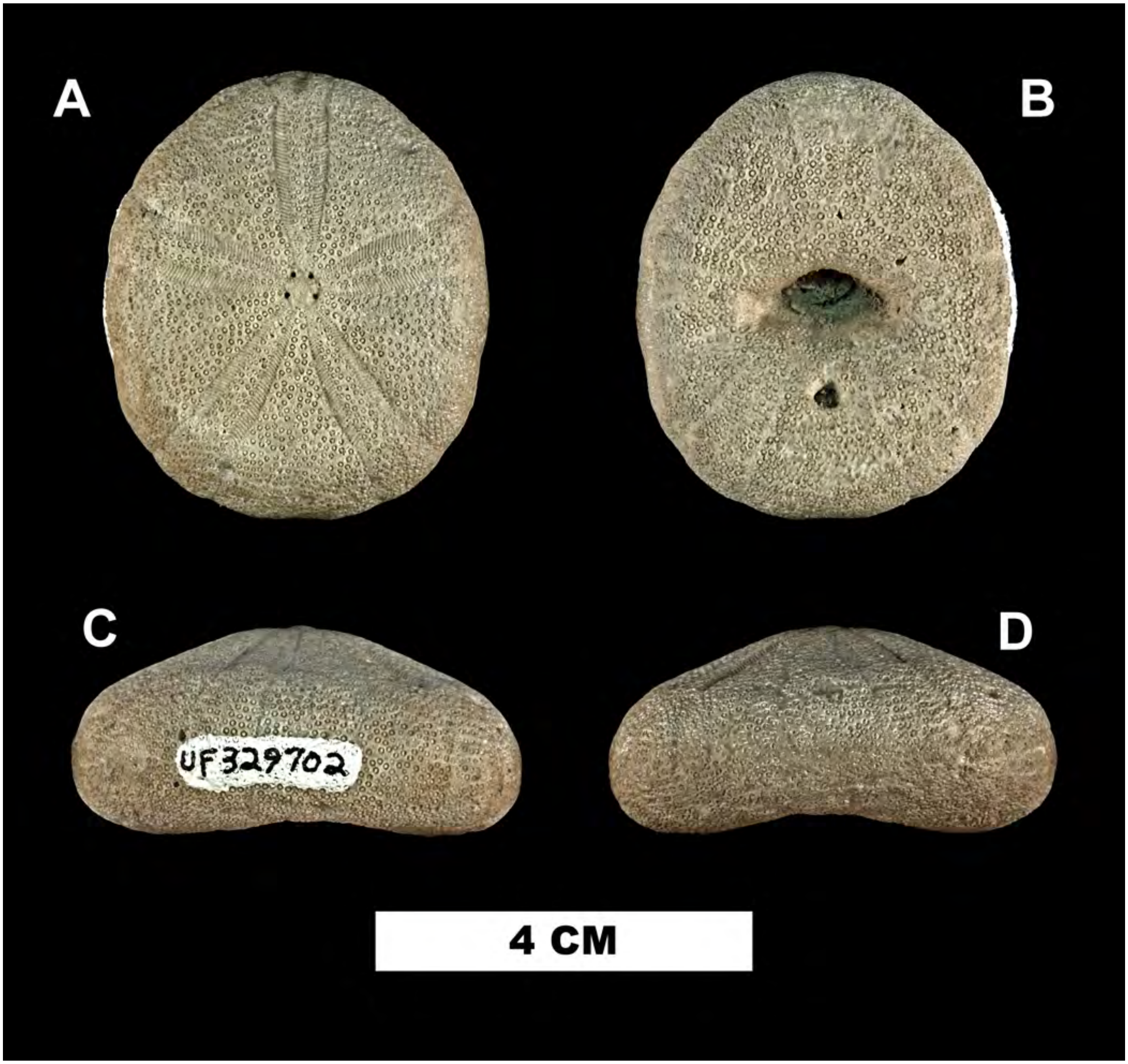


Figure 45: *Oligopygus wetherbyi* (UF 329702), 47 mm TL, 40 mm TW, 21 mm TH, Upper Eocene upper Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

Oligopygus wetherbyi (de Loriol). Wagner and Durham, 1966. p. U448. fig. 334.5.

Oligopygus wetherbyi (de Loriol). Kier, 1967. pp. 54-59. pl.1, figs. 3-5; pl. 4, figs. 1, 2, 4; pl. 5. pl. 8, figs. 1-3; pl. 10, figs. 1, 3-5; pls, 13, 14. pl.16, fig 8. txt. figs. 2, 7a, 11a, 17, 24-26, 30, 38, 39.

Oligopygus wetherbyi (de Loriol). Kier, 1969. txt fig. 2.

Oligopygus wetherbyi (de Loriol). Toulmin, 1977. p. 343. pl. 68, figs.1-3.

Oligopygus wetherbyi (de Loriol). McKinney and Jones, 1983. pp. 21-29. 8 figs. 1 tbl.

Oligopygus wetherbyi (de Loriol). McKinney, 1984. pp. 407-419. 12 figs, 3 tbls.

Oligopygus wetherbyi (de Loriol). Donovan, 1993. p. 384. figs. 9.9, 9.10.

Oligopygus wetherbyi (de Loriol). Rice, 1997. pp. 907-912. fig. 3.

Oligopygus wetherbyi (de Loriol). Oyen and Portell,

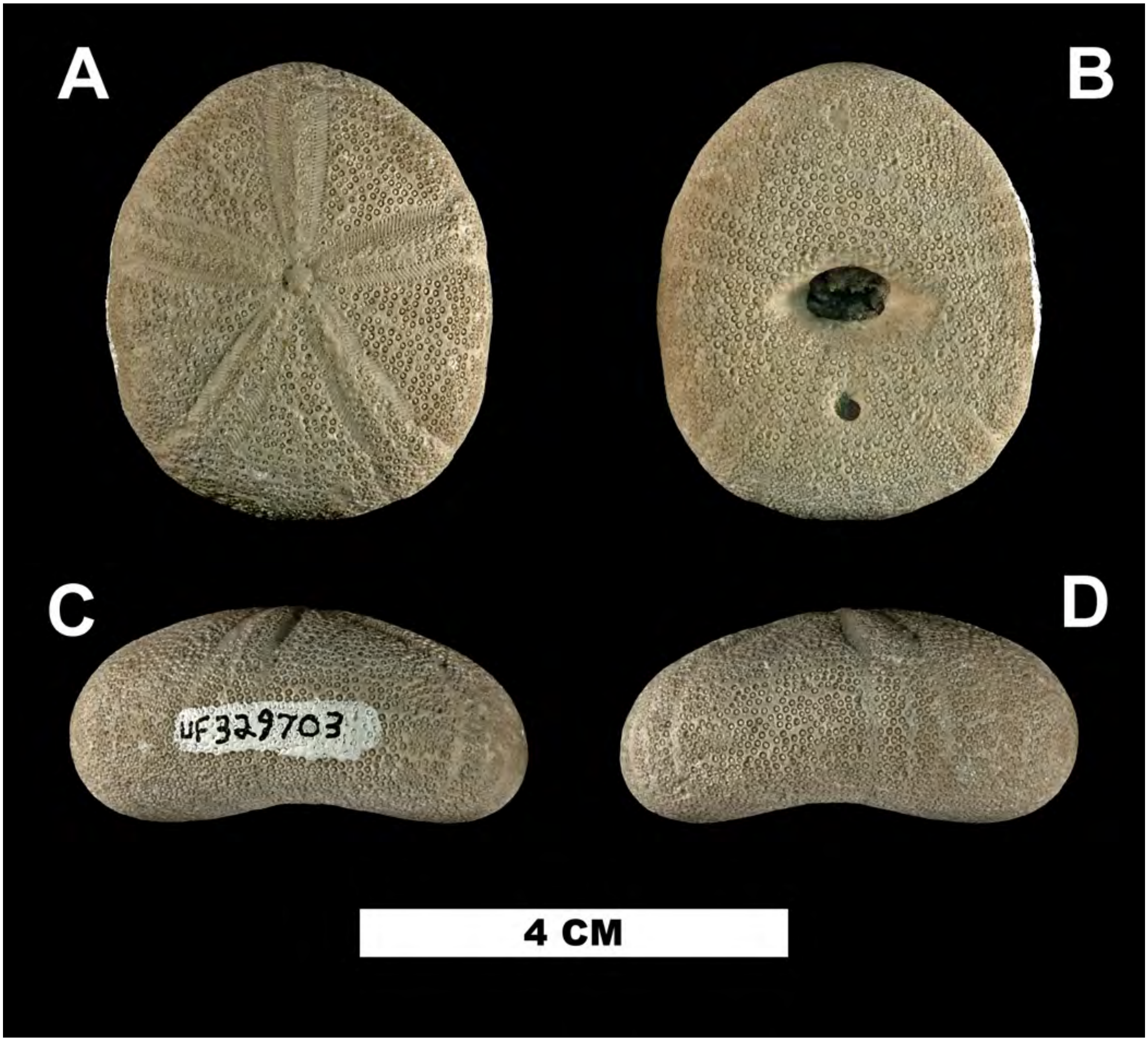


Figure 46: *Oligopygus wetherbyi* (UF 329703), 43 mm TL, 36 mm TW, 20 mm TH, Upper Eocene upper Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

2001. pp. 193-218. pl. I, fig. 4.

Oligopygus wetherbyi (de Loriol). Osborn et al., 2016. tbl. 2.

Occurrence.—This species is a ubiquitous presence in the upper portion of the OLS of peninsular Florida (strata formerly attributed to the Crystal River Formation), especially in quarries north of Ocala, Marion County; north of Branford, Suwannee County (FM-IP SU002); northwest of Mayo, Lafayette County (FM-IP LF001); and west of Dowling Park, Lafayette County (FM-IP LF002).

Oligopygus wetherbyi rarely occurs in the Upper Eocene of Georgia (Carter and McKinney, 1992). It is also documented from the Eocene of Jamaica (Donovan, 1993) and Cuba (Sánchez-Roig, 1949).

Discussion.—*Oligopygus wetherbyi* is one of the key biostratigraphic indicator species of the upper portion of the OLS of Florida where the *Oligopygus wetherbyi* Zone overlies the *Oligopygus haldemani* Zone. *Oligopygus wetherbyi* is often the dominant species in the horizon in which it occurs, commonly occurring with the same echinoid assemblage throughout its range. This assemblage includes *P. mortoni*, *W. cubae*, *E. tanypetalis*, *A. americanus*, *R. conradi*, and other, rarer species.

Oligopygus wetherbyi and *O. haldemani* are superficially similar. The periproct of *O. wetherbyi* is always located much closer to the peristome than in *O. haldemani*, and this trait is consistent even in smaller specimens of the former, which could otherwise be confused with the much smaller *O. haldemani*. Kier (1967) showed that the periproct of *O. wetherbyi* is more circular, there are more pore pairs in petals III and V, the test is slightly narrower, and the greatest width is more posterior (especially in larger specimens) than in *O. haldemani*. In addition, the interambulacral plates are commonly more tumid. *Oligopygus wetherbyi* also attains a greater size than *O. haldemani*. The largest specimen of the former documented by Kier (1967) out of 140 specimens available for his study is 54 mm TL, whereas the largest *O. haldemani*, out of 120 specimens he measured, was 37 mm TL.

Palmer (in Sánchez-Roig, 1949) erected a variety of *Oligopygus floridanus* (= *O. wetherbyi*), called *O. floridanus* var. *laevis*, for some specimens from the Late Eocene of Cuba. However, he did not figure the specimens, so Kier (1967) did not feel comfortable adding them to his synonymy of *O. wetherbyi*, given that the occurrence of *O. wetherbyi* in Cuba is also questionable. Cooke (1961) considered *O. kugleri* from the Eocene of Trinidad to be a subspecies of *O. wetherbyi*. However, Kier (1984) asserted that *O. kugleri* is a distinct species because *O. kugleri* and *O. wetherbyi* are very distinct, with *O. kugleri* having a much higher test, and a much narrower and less depressed peristomial infundibulum.

Suborder **CLYPEASTERINA** L. Agassiz, 1835
Family **CLYPEASTERIDAE** L. Agassiz, 1835
Genus ***Clypeaster*** Lamarck, 1801

THE STATE OF *CLYPEASTER* SYSTEMATICS IN THE REGION

Clypeaster is abundantly represented in Cenozoic faunas of the eastern Americas and Caribbean Region, as well as globally. In endeavoring to describe all Florida forms of *Clypeaster* from the Paleogene, we were compelled to perform a detailed review of the regional taxa (Table 6). More than 400 nominal species of fossil and extant *Clypeaster* have been described and grouped into a variety of subgenera distinguished mainly on gross test morphology (Mortensen, 1948). These subgenera have been recognized as being of little taxonomic value (Durham, 1966; Hopkins, 1988; Mihaljevic et al., 2011; Mooi and van Noordenburg, 2021; Roman, 1952).

It is readily apparent that *Clypeaster* is grossly over-split based on the number of available characters, let alone on fossils. This is especially evident when reviewing the Mediterranean faunas, but it is likewise apparent among the fossil species of the West Indies. In describing *Clypeaster topilanus* from the Oligocene of Mexico, Jackson (1937: 232) expressed frustration over the number of species of *Clypeaster* described at that time: "With all the species assigned to *Clypeaster*, it is annoying to make still another." Yet, he did. Ali (1983) reported that at the time of his writing, 83 species of *Clypeaster* had been documented in Cenozoic strata of the Caribbean Province, which included the southeastern United States. Although this number is undoubtedly inflated (see below), there remains a significant number of species from this region. A great many of these species exist only as single specimens or from single occurrences, which makes assessing their validity even more challenging.

Ali (1983) documented 35 species of *Clypeaster* in the Oligocene of the Caribbean Province, with 26 of these from Cuba alone. Another 17 species occurred in the Miocene of Cuba, five in additional West Indian localities, four from Venezuela (Jeannet, 1928; Casanova, 1955; Kier, 1963), four from the Miocene of Brazil (Marchesini Santos, 1958; Brito and Ramires, 1974), and eight from the Miocene of Florida. Ali (1983) cited Jackson (1917), Gordon (1963) and Kier (1963) to develop his tallies, but this latter number is obviously incorrect, as during the time of his work, only *Clypeaster concavus* Cotteau, 1875 (*sensu*

Table 6: A listing of fossil *Clypeaster* species described from the eastern Americas and Caribbean region. Locality provided is the type area for the species; NA=North America. Distribution of species further discussed herein is provided within the remarks for each species. Durham (1966) placed the genera *Anomalanthus, Bunactus, Coronanthus, Herrerasia, Oranthus, Paratinanthus, Rhaphidoclyphus, Rojaster, Tholeopelta,* and *Zanolettia* in synonymy with *Clypeaster*. Some species designations would have to be resolved if Durham's (1966) synonymies are accepted (such as *Bunactus sanchezi* and *Rojasaster hernandezi*), as these species names are already occupied in the genus *Clypeaster*.

Clypeaster abruptus Sánchez Roig, 1926; Miocene, Cuba
C. antillarum Cotteau, 1875; Miocene, Antigua
C. batheri Lambert, 1915; Miocene, Antigua
C. brodermanni Sánchez Roig, 1949; Oligocene, Cuba
C. canimarensis Palmer, 1949; Pleistocene, Cuba
C. caudatus Jackson, 1922; Miocene, Dominican Republic
C. chiapasensis Mullerried, 1951; Oligocene, Mexico
C. concavus Cotteau, 1875; Miocene, Anguilla
C. concavus puertoricanus Gordon, 1963; Miocene, Puerto Rico
C. cotteaui Egozcue, in Cotteau, 1897; Oligocene, Cuba
C. cryptopetalus Jackson, 1922; Oligocene, Antigua
C. cubensis Cotteau, 1875; Miocene, Cuba
C. dalli (Twitchell, 1915); Pleistocene, Florida
C. densus Sánchez Roig, 1949; Oligocene, Cuba
C. dondolii Fischer, 1985; Miocene, Costa Rica
C. duchassaingi Michelin, 1861; Pliocene, Guadaloupe
C. douvillei Stefanini, 1911; Oligocene, Mississippi
C. elevatus Sánchez Roig, 1949; Miocene, Cuba
C. ellipticus Michelin, 1861, Miocene, Antilles
C. eurychorus Arnold and Clark, 1934; Cenozoic, Jamaica
C. gatuni Jackson, 1917; Miocene, Panama
C. guadalupense Sánchez Roig, 1952; Oligocene, Cuba
C. guillermi Sánchez Roig, 1952; Oligocene, Cuba
C. hernandezi Sánchez Roig, 1949; Oligocene, Cuba
C. herrerae Sánchez Roig, 1926; Miocene, Cuba
C. julli Roman 1952; Miocene, Antigua
C. kugleri Jeannet, 1928; Miocene, Venezuela
C. lamegoi Marchesini Santos, 1958; Miocene, Brazil
C. lamprus H. L. Clark, 1914; Recent, (Pleistocene, Jamaica?)
C. lanceolatus Cotteau, 1897; Oligocene, Cuba
C. lopezriosi Sánchez Roig, 1953; Oligocene, Cuba
C. maoadentroensis Kier, 1992; Pliocene, Dominican Republic
C. maribonensis Sánchez Roig, 1949; Oligocene, Cuba
C. marinanus Jackson, 1937; Oligocene, Mexico
C. meridanensis Michelin, 1850; Miocene, Guadeloupe
C. moronensis Sánchez Roig, 1951; Miocene-Olig., Cuba
C. ovatus Palmer, 1949; Oligocene, Mexico
C. oxybaphon Jackson, 1922; Oligocene, Antigua
C. palmeri Sánchez Roig, 1949; Miocene, Cuba
C. paraensis Brito, 1979; Miocene, Brazil
C. parrae Desmoulins, 1835; Neogene, Cuba and Guadeloupe
C. parvus Michelin, 1861; Miocene, Guadeloupe
C. paulinoi Marchesini Santos, 1958; Miocene, Brazil
C. petersonorum Osborn et al., 2020; Miocene, Florida
C. pileus Israelsky, 1924; Oligocene, Mexico
C. pinarensis Lambert and Sánchez Roig, 1934; Miocene, Cuba
C. placentoides Jackson, 1922; Oligocene, Cuba
C. planipetalus Cotteau, 1897; Oligocene, Antigua
C. planus Sánchez Roig, 1949; Oligocene, Cuba
C. platygaster Jackson, 1922; Oligocene, Cuba
C. polygonalis Sánchez Roig, 1949; Oligocene, Cuba
C. profundus Sánchez Roig, 1949; Oligocene, Cuba
C. rogersi (Morton, 1834); Oligocene, southeastern USA
C. romani Kier, 1964; Pliocene-Pleistocene, SE USA,
C. rosaceus (Linnaeus, 1758); Pliocene-recent, FL and Caribbean,
C. sanchezi Lambert, in Sánchez Roig, 1926; Oligocene, Cuba
C. sandovali Sánchez Roig, 1949; Oligocene, Cuba,
C. sanrafaelensis Palmer, 1949; Oligocene, Cuba,
C. staubi Lambert, 1928; Miocene, Mexico,
C. subdepressus Gray, 1825; Pliocene-recent; SE USA Caribbean
C. sunnilandensis Kier, 1963; Pliocene, Florida
C. tenuicoronae Palmer, 1949; Oligocene, Cuba
C. topilanus Jackson, 1937; Oligocene, Mexico
Anomalanthus elevatus Sánchez Roig, 1952; Oligocene, Cuba
A. gigas Sánchez Roig, 1953; Oligocene, Cuba
A. guadalupense Sánchez Roig, 1952; Oligocene, Cuba
A. oligocenicus Sánchez Roig, 1949; Oligocene, Cuba
A. rojasi Sánchez Roig, 1952; Oligocene, Cuba
A. zanoletti Sánchez Roig, 1952; Oligocene, Cuba
Bunactus aguayoi Sánchez Roig, 1952; Oligocene, Cuba
B. sanchezi Lambert, 1926; Miocene, Cuba,
B. sanchezi altus Sánchez Roig, 1952; Miocene, Cuba
B. sanchezi gigantea Sánchez Roig, 1952; Miocene, Cuba
B. santanae Sánchez Roig, 1952; Oligocene, Cuba
Coronanthus artilesi Sánchez Roig, 1952; Oligocene, Cuba
Co. conceptionis Sánchez Roig, 1952; Oligocene, Cuba
Herrerasia profundus Sánchez Roig, 1952; Miocene, Cuba
Paratinanthus lamberti Sánchez Roig, 1952; Oligocene, Cuba
Rhaphidoclyphus rojasi Sánchez Roig, 1952; Oligocene, Cuba
R. armadilloensis Sánchez Roig, 1953; Oligocene, Cuba
R. costulatus Sánchez Roig, 1952; Oligocene, Cuba
Rojasaster hernandezi Sánchez Roig, 1952; Oligocene Cuba,
R. camagueyanus Sánchez Roig, 1952; Oligocene, Cuba
Tholeopelta herrerae Sánchez Roig, 1951; Oligocene, Cuba
Zanolettia zanolettii Sánchez Roig, 1951; Oligocene, Cuba
Z. gigantea Sánchez Roig, 1952; Oligocene, Cuba

Cooke, 1959) (= *Clypeaster petersonorum* Osborn et al., 2020), was documented from the Miocene of Florida. Ali (1983) noted that the Pliocene strata of the Caribbean Province contained only six species from the southeastern United States and Cuba (Cotteau, 1897; Jackson, 1922; Engel, 1961; Kier, 1963), and four species from Cuba and Florida (Sánchez-Roig, 1949, 1952b; Kier, 1963).

Correcting for the error in count for the Miocene of Florida leaves 75 species of *Clypeaster* in the province by Ali's (1983) count. We have researched 86 species of fossil *Clypeaster* described from eastern North America southward throughout the eastern Americas and eastward through the West Indies and Caribbean region (Table 6).

Sánchez-Roig (1949) documented the occurrence of 35 species of *Clypeaster* in the Cenozoic of Cuba, as well as two species he assigned to *Anomalanthus*, which Durham (1966) reassigned to *Clypeaster*. Sánchez-Roig (1951-1953) subsequently documented another 23 species of *Clypeaster*, as well as several new genera he erected, such as *Herrerasia*, *Rojaster*, and *Zanolettia,* all which Durham (1966) also synonymized with *Clypeaster*. This still left a questionable total of nearly 60 species of *Clypeaster* within Oligocene to Pleistocene strata of Cuba alone. Most of these species were poorly figured, insufficiently described, with type material poorly designated, lost, or unavailable. Many were likely described without considering variation within species, comparison with other candidate taxa in the region, let alone globally, and most of the type specimens figured in Sánchez-Roig's various works are incomplete and lack detail, especially considering the types of characters now suggested to be necessary for full diagnoses (Mooi and van Noordenburg, 2021), as indicated below.

Poddubiuk's (1985) reevaluation of type material of the Upper Oligocene to Middle Miocene species of *Clypeaster* from the Caribbean Islands east of Cuba suggested that the occurrences should be grouped into no more than seven species: *C. batheri*; *C. caudatus* Jackson, 1922; *C. concavus*; *C. cubensis* Cotteau, 1875; *C. julii* Roman, 1952, and *C. oxybaphon* (he listed six, but stated there should be no more than seven valid species). Poddubiuk's PhD thesis (Poddubiuk, 1987) contains discussions on potential junior synonyms of *C. batheri, C. concavus*, and *C. oxybaphon*, and is discussed in the remarks for *C. oxybaphon* below. Poddubiuk (1985, 1987) attributed over-splitting to previous workers describing species based on small sample sizes with few characters and without considering the intraspecific variation (a problem clearly not confined to the Caribbean faunas).

Poddubiuk (1985, 1987) stated that the problem was compounded among Caribbean mid-Cenozoic faunas by two additional factors: 1) most early workers were in Europe (although, most of these species were described by Sánchez Roig in Cuba), basing their species designations on small collections sent to them by collectors and accompanied by minimal locality and/or stratigraphic data; and 2) type specimen repositories are scattered across the Caribbean, USA, and Europe, forcing many workers to rely on poor illustrations and incomplete and often inaccurate descriptions. While we agree with the overall message of these assertions, Poddubiuk's claims concerning this taxonomic history remain unsupported by evidence. Furthermore, it is virtually impossible to apply his findings to the Florida Paleogene occurrences. This is in spite of the fact that several additional papers, including Poddubiuk and Rose (1984), Poddubiuk (1985), and Rose and Poddubiuk (1987) continued to comment, without data concerning synonymies, on the systematics and evolution of *Clypeaster* in the Caribbean region.

Therefore, faced with a multitude of poorly described species, anyone describing a new species of *Clypeaster* from the eastern United States is forced to rely on previous work that is difficult if not impossible to penetrate. For example, such an endeavor proved problematic in describing *C. petersonorum* (Osborn et al., 2020), and even for description of the extant *Clypeaster brigitteae* (Mooi and van Noordenburg, 2021). Mooi and van Noordenburg (2021: 1 and 2) also discussed some of these issues while comparing fossils to extant forms: "... there [are] in excess of 350 nominal fossil *Clypeaster* found in strata from the Eocene to the Recent ... an unwieldy level likely to cause considerable challenges for a complete revision of the group. Some attempts to deal with what appears to be rampant splitting among fossil *Clypeaster* taxa have been made on a local level ... but a full assault on the mountain of paleontological nomenclature on a global scale has yet to be made. With that in mind ... most neontologists have generally ignored the seemingly endless job of dealing with the fossil forms when describing new extant species discovered since Mortensen's (1948) monograph ..." This underscores our sense that providing taxa in open nomenclature is the best that can be done for some of the species we are attempting to document for the Florida Paleogene.

Jackson (1922) provided a key to 19 *Clypeaster* species documented from the Caribbean region at the time. These included: *C. rosaceus* Linnaeus, 1758; *C. concavus,* from the Oligocene of Anguilla and Puerto Rico; *C. caudatus,* from the Miocene of the Dominican Republic; *C. dalli*

Twitchell in Clark and Twitchell, 1915, herein recognized as *C. rosaceus*, from Florida; *C. cubensis* from the Miocene of Cuba and Puerto Rico; *C. parrae* Desmoulins, 1837, from the Cenozoic of Cuba and Guadeloupe; *C. lanceolatus* Cotteau, 1897 from the Oligocene of Cuba, which Cooke (1959) considered a synonym of *C. concavus*; *C. antillarum* Cotteau, 1875, from Miocene of Anguilla and Antigua, which Cooke (1959) considered a synonym of *C. concavus*; *C. planipetalous* Cotteau, 1875, from the Miocene of Antigua; *C. cryptopetalus* Jackson, 1922, from the Miocene of Antigua; *C. cotteaui* from the Oligocene of Cuba and Florida; *C. batheri* from the Miocene of Antigua and Oligocene of Florida; *C. parvus* Michelin, 1861, from the Miocene of Cuba and Antigua; *C. duchassaingi* Michelin, 1861, from an unstated age in Guadeloupe; *C. ambigenus* Lamarck, 1816, from Guadeloupe, which is undoubtedly a misidentification since *C. ambigenus* is a subjective junior synonym of *C. humilis* (Leske, 1778) (Jackson stated Michelin documented it from the Eocene of Georgia, which is also clearly erroneous); *C. placentoides* Jackson, 1922, from the Oligocene of Cuba; *C. meridianensis* Michelin, 1861, from the Miocene of Guadeloupe; *C. oxybaphon* from the Oligocene of Antigua, Puerto Rico and Florida; and *C. platygaster* Jackson, 1922, which Cooke (1959) considered to be a synonym of *C. oxybaphon*, from Cuba.

Poddubiuk (1987) provided a key to differentiate the fossil *Clypeaster* species of Anguilla and Antigua: *C. batheri, C. julii, C. oxybaphon,* and *C. concavus*.

Donovan (1993) provided a very useful key to the Cenozoic species of *Clypeaster* of Jamaica, which included *C. cotteaui*; *C. rosaceus*; *C. concavus*; *C. lanceolatus*, and *C. eurychorus* Arnold and Clark, 1934. Arnold and Clark (1927) also considered two specimens from the Cenozoic of Jamaica to represent *Clypeaster antillarum* Cotteau, 1875. As noted in Osborn et al. (2020), *C. antillarum* has been considered a subjective junior synonym of *C. concavus* (Donovan, 1983: 386; Poddubiuk, 1985: 76). The remaining species of *Clypeaster* documented from the Cenozoic deposits of the eastern Americas are summarized in Table 6.

Within the Cenozoic deposits of the eastern United States, the genus is best represented within the Oligocene, with *C. cotteaui, C. marinanus, C. oxybaphon, C. rogers*i, and three taxa discussed below in open nomenclature: *Clypeaster* sp. A (referred to *C. batheri* by Oyen, 2001); *Clypeaster* sp. B and *Clypeaster* sp. C, both from the basal Suwannee Limestone of Hernando County, Florida. For the record, the Miocene contains only *C. petersonorum* from the Chipola Formation of north Florida; the Pliocene contains *C. sunnilandensis* Kier, 1963, the Plio-Pleistocene *C. romani* Kier, 1964; and the Pleistocene *C. rosaceus* and *C. subdepressus* (Gray, 1825).

It is therefore difficult to assign with confidence any of the newly discovered forms to more than open nomenclature, as they could fall within one of the 86 taxa from the remainder of the eastern Americas (Table 6), and more likely into some of the 38 species from the Oligocene of Cuba described in one of several works by Sánchez-Roig outlined above, the majority of which will likely remain *nomena nuda*. However, we can say that none of Sánchez Roig's figured specimens appear similar to *Clypeaster* sp. B from the Suwannee Limestone. However, we emphasize again that his figures generally do not show views necessary to assess features used classically for the genus, let alone those advocated by more recent workers.

For example, Nisiyama (1968: 34) stated that test shape, position of the periproct, form and relative length of petals, tuberculation, and character of the buccal membrane are of importance in classifying species of *Clypeaster*. Mooi and van Noordenburg (2021) developed these ideas further in reviewing the species of *Clypeaster* found in the Philippines. Their study showed that value can be placed on features seldom observable on fossils, such as spines or spicules. However, other characters such as tubercle and pore pair densities in the poriferous zone, density of tubercles on the aboral surface outside the petals, degree of plate occlusion at the ends of the petals, depth of the infundibulum, certain aspects of the oral plate pattern, detailed morphometerics of periproct position, petal dimensions, TH, TW,

Figure 47: *Clypeaster cotteaui* (UF 337958), 64 mm TL, 50 mm TW, 18 mm TH, Oligocene Bridgeboro Limestone, Washington County, Florida (FM-IP WG002). A: aboral. B: oral. C: left side. D: right side.

internal structure, and other features seldom used to differentiate members of can and should be assessed in fossil taxa. It is our hope to do so with additional fossil material from the Paleogene of Florida so that better characterizations can be made of those taxa we present in open nomenclature, but that we were intent on including so that the diversity of *Clypeaster* in the region would be more accurately represented than in the past.

We provide a tabular key to the Florida species of Paleogene *Clypeaster* in Table 7.

Clypeaster cotteaui Egozcue in Cotteau, 1897
(Figs. 47, 48, Table 7)

Clypeaster cotteaui Egozcue, in Cotteau, 1897. p. 40, pl. 10, figs. 1-1.

Clypeaster cotteaui (Egozcue). Lambert, 1915. p. 24.

Clypeaster cotteaui (Egozcue). Jackson, 1922. p. 41, pl. 6, figs. 6-8.

Clypeaster cotteaui (Egozcue). Cooke, 1942. p. 13.

Clypeaster cotteaui (Egozcue). Sánchez-Roig, 1949. p. 68.

Clypeaster cotteaui (Egozcue). Cooke, 1959. pp. 36-37. pl. 12, figs. 1-3.

Clypeaster cotteaui (Egozcue). Pickering, 1970. pp. 20, 58.

Clypeaster cotteaui (Egozcue). Rose and Poddubiuk,

1987. p. 466. fig. 1. tbl. 1.

Clypeaster cotteaui (Egozcue). Donovan, 1993. p. 388.

Occurrence.—*Clypeaster cotteaui* is the common clypeasteroid of the Bridgeboro Limestone, which outcrops in southwestern Georgia, southeastern Alabama, and Washington County (e.g., FM-IP WG002) in northern Florida. This species is also documented from the type locality in Cuba (Cotteau, 1897). Donovan (1993) tentatively identified it from the Oligocene of Jamaica.

Discussion.—Jackson (1922) recognized *C. cotteaui* from Jamaica and Arnold and Clark (1927) reported a test of uncertain geologic age that they referred to this species from a river near Port Maria, Parish of St. Mary, Jamaica. However, Donovan (1993), in his review of Jamaica's Cenozoic echinoid fauna, suggested that *C. cotteaui* occurred there. Poddubiuk and Rose (1984: table 2) indicated that specimens of *C. cotteaui* listed from Antigua (Lambert, 1915) are conspecific with *Clypeaster batheri* Lambert, 1915. *Clypeaster cotteaui* is therefore undoubtedly represented only in the Oligocene strata of the southeastern United States and Cuba.

Clypeaster cotteaui is the dominant species in the Bridgeboro Limestone (especially the Florala Member) in southwestern Georgia and southeastern Alabama, and in the Duncan Church beds at the Duncan Church Quarry in Washington County. Its very swollen test, with thick rounded margins, deeply concave oral surface, and petals that are wide open distally readily distinguish *C. cotteaui* from any other fossil species in the fauna of the eastern United States (Table 7). *Clypeaster cotteaui* is readily differentiated from *C. rogersi*, which is often found with *C. cotteaui* in mixed spoil of the Marianna and Bridgeboro Limestones in the Duncan Church Quarry (FM-IP WG002), Washington County, Florida, by the much thicker margin, more concave oral surface, and petals that are wide open distally. It is also distinguished from *Clypeaster oxybaphon* Jackson, 1922, with which it also occurs but much more rarely, by the thicker margin, more concave oral surface, and lack of an inframarginal depression on the aboral surface in *C. cotteaui* (Table 7).

Jackson (1922) stated the widely open petals, nearly straight line of inner pores of the pore pairs, and the four pore pairs situated distal to the ends of each column or pore pairs of the petals are features useful in distinguishing *C. cotteaui* from similar *Clypeaster* species of the Caribbean region.

Clypeaster marinanus Jackson, 1937
(Figs. 48-51, Table 7)

Clypeaster marinanus Jackson, 1937. p. 231. pl. 12, fig. 2; pl. 13, fig. 1.

Clypeaster marinanus (Jackson). Caso, 1957. p. 508.

Clypeaster rogersi (Morton). Cooke, 1959. pp. 36-37 (in part, Cooke believed *C. marinanus* to be a synonym of *C. rogersi*).

Clypeaster marinanus (Jackson). Zachos and Molineux, 2007. pp. 79-91. figs. 6 a-b, e.

Occurrence.—Within Florida, this is the common echinoid of the lowermost Oligocene portion of the Bumpnose Limestone in Jackson County, especially in Brooks Quarry near Marianna (FM-IP JA021). A single specimen likely attributable to this species was collected in the Suwannee Limestone at the Cabbage Grove Quarry west of Perry, Taylor County (FM-IP TA001). *Clypeaster marinanus* has not been documented from the Suwannee Limestone of peninsular Florida. Zachos and Molineux (2007) reported it from the Oligocene of Texas. The type locality for the species is the Oligocene Meson Formation in Tamaulipas, Mexico (Jackson, 1937).

Discussion.—This is the first report of the species in Florida. However, the occurrence of a species of *Clypeaster* that is distinct from *C. rogersi* in the Bumpnose Limestone is well documented. Moore (1955: 39) asked C. Wythe Cooke to examine *Clypeaster* specimens from the Bumpnose Limestone. Cooke agreed that the specimens represented a new species closely related to *C. rogersi*. Cooke (1959) failed to mention this occurrence of a *Clypeaster* from the Bumpnose Limestone, even as he placed Jackson's *C. marinanus* in synonymy with *C. rogersi*. Cooke (1959) also stated that spec-

Table 7: Tabular key of the Paleogene *Clypeaster* of Florida. Key follows Mooi and van Noordenburg (2021).

Species of *Clypeaster*	Distribution[1]	Test outline	Average TW as % of TL	Average margin height as %TH[2]	Average TH as % TL	Degree to which petals are open distally	Width petal III as % petal length[3]	Length petal III as % of TL	Margin inflated, with proximal depression of aboral surface[4]	Oral surface concavity	# Primary tubercles between inner and outer pore of respiratory tube foot[5]
cotteaui	FL, GA, CB	Ovate-subpentagonal	83.6 (78-89)	66.3 (63-69)	29.4 (26-32)	All wide open	57.2 (53-63%)	34.2 (33-36)	No	Deeply concave	5-7
marinanus	AL, FL, MX, TX	Supentagonal	90.1 (86-92)	35.4 (31-48)	16.6 (14-20)	All somewhat open	58 (50-65)	26.5 (23-28)	No	Nearly flat	5-7
oxybaphon[6]	FL, CB	Ovate-subpentagonal	70-90	50-90	14-22	All nearly closed	45-60	25-35	Yes	Variably concave	9-12
rogersi[7]	AL, GA, FL, MS, NC	Ovate-subpentagonal	89.1 (82-95)	53.4 (45-67)	22.3(17-28)	All usually wide open[8]	53.4 (47-68)	31.8 (28-34)	No	Nearly flat	5-8
sp. A	FL	Elongate subpentagonal	75.4	44	21	All wide open[9]	42.9	34.7	No	Concave	6-8
sp. B	FL	Subpentagonal	91.1(85-95)	36.4(33-41)	19.6(18-26)	All wide open	53.4 (41-59)	32.9 (31-34)	No	Slightly concave	7-9
sp. C	FL	Subpentagonal	91.6	41.2	13.6	All wide open	60.3	31.3	No	Nearly flat	Not discernable

[1] Standard U.S. postal service state abbreviation, plus "CB" = Caribbean, "MX" = eastern Mexico.
[2] Measurement taken at anterior margin as in figure, lower right.
[3] Measurement taken at widest point of petal III in ambulacrum III.
[4] In *C. oxybaphon*, the margin is inflated relative to the rest of the distal part of the aboral surface so that the distal ends of the petals are below the level of the margin.
[5] Number of tubercles in poriferous zone between adjacent pore pairs near midpoint of petal IIIa, where poriferous zone is generally widest.
[6] Data supplemented with measurements from Poddubiuk (1987), only range provided, but not averages.
[7] Populations sampled from the Marianna Limestone in FL, MS, and AL.
[8] Petal in ambulacrum III sometimes slightly closed distally.
[9] Petal III slightly more closed than other petals.

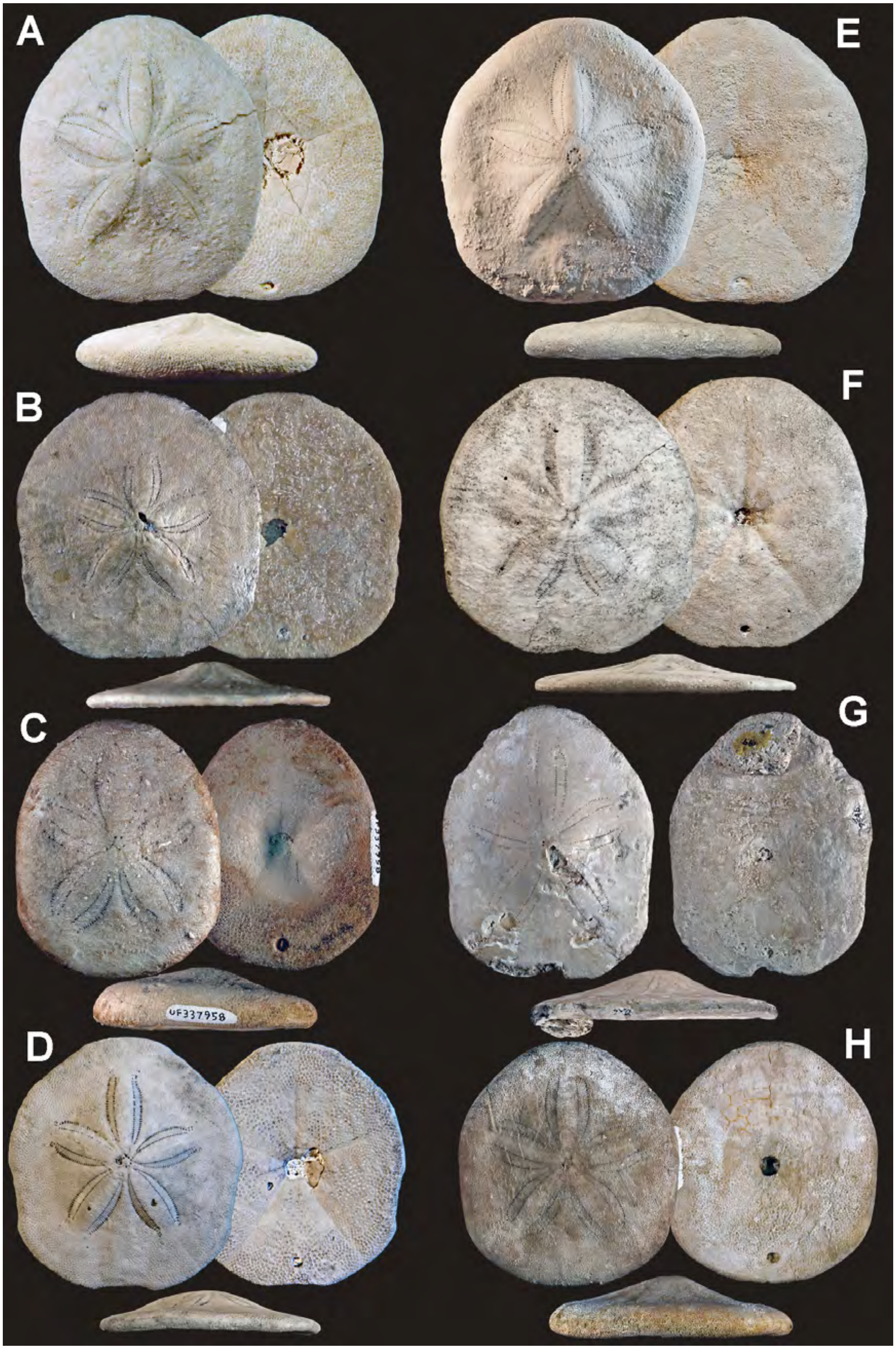


Figure 48: Comparison of Oligocene species of *Clypeaster* from Florida. Aboral, oral and leftside views shown for all. A: *Clypeaster rogersi*, (UF 337962) Marianna Limestone, Jackson County, (FM-IP JA029). B: *Clypeaster*

(**Fig. 48 caption cont.**) *marinanus* (UF 337995) Bumpnose Limestone, Jackson County, (FM-IP JA021). C: *Clypeaster cotteaui* (UF 337958) Bridgeboro Limestone, Washington County, (FM-IP WG002). D: *Clypeaster* sp. B. (UF 338008) Suwannee Limestone, Hernando County, (FM-IP HE038). E: *Clypeaster* cf. *C. oxybaphon* (UF 342868) Bridgeboro Limestone, Washington County, (FM-IP WG002). F: *Clypeaster* sp. C. (UF 338011) Suwannee Limestone, Hernando County, (FM-IP HE019). G: *Clypeaster* sp. A. (UF 2546) Suwannee Limestone, Suwannee County, (FM-IP SU002). H: *Clypeaster rogersi* (UF 27190) Suwannee Limestone, Polk County (FM-IP PO017).

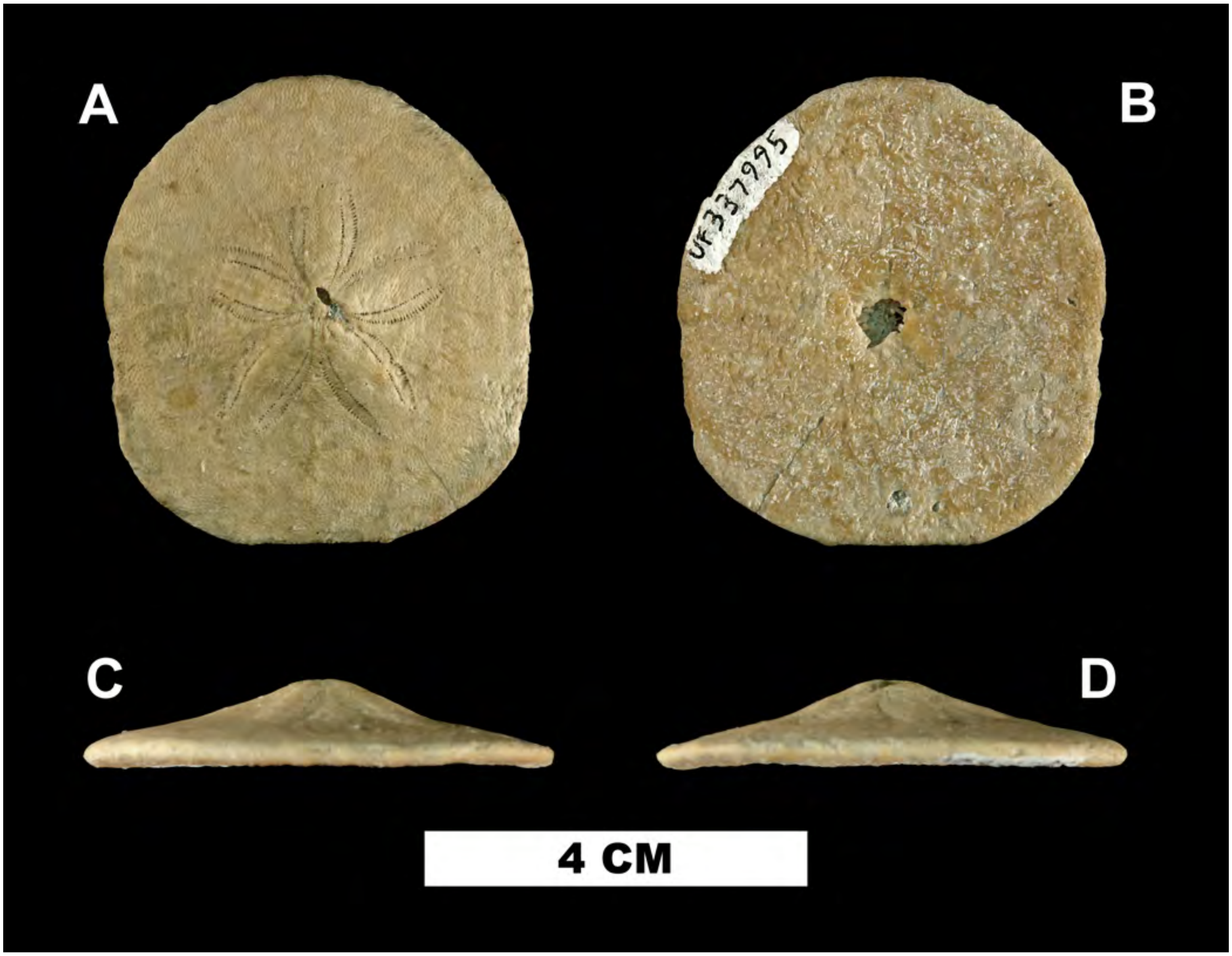


Figure 49: *Clypeaster marinanus* (UF 337995), 49 mm TL, 45 mm TW, 8 mm TH, Lower Oligocene Bumpnose Limestone, Jackson County, Florida (FM-IP JA021). A: aboral. B: oral. C: left side. D: right side.

imens from the Suwannee Limestone and Meson Formation of Mexico (= *C. marinanus* for the Mexican occurrence) tend to have slightly wider interporiferous zones and a thinner margin than the typical Marianna Limestone specimens of the species (he did not mention the distinctly shorter petals of *C. marinanus*).

Huddlestun (1993: 66, 67) reiterated the point made by Moore (1955: 39) and stated the Bumpnose Limestone does not contain *C. rogersi*, but rather contains a smaller, undescribed, probably ancestral species. Osborn et al. (2016) tentatively considered this an undescribed species. It was during the process of assessing that assumption and examining a significant number of specimens from the Bumpnose Limestone near Marianna, Florida, and Brooklyn, Alabama, that we realized these specimens cannot be differentiated from *C. marinanus*.

Figure 50: *Clypeaster marinanus* (UF 337996), 41 mm TL, 38 mm TW, 9 mm TH, Lower Oligocene Bumpnose Limestone, Jackson County, Florida (FM-IP JA021). A: aboral. B: oral. C: left side. D: right side.

Jackson (1937) described *C. marinanus* as closest in form to *C. rogersi*, but different in having a flatter test, thinner margin, less sunken infundibulum around the peristome, and shorter, narrower, and less curved ambulacra. These attributes are here recognized as features distinguishing *C. marinanus* from *C. rogersi* (Table 7).

While *C. marinanus* is the characteristic echinoid of the Bumpnose Limestone, it also occurs in the correlative Red Bluff Formation of southwestern Alabama and the Suwannee Limestone in the Cabbage Grove Quarry west of Perry, Taylor County (FM-IP TA001). It has not been documented in the typical Suwannee Limestone of peninsular Florida.

Clypeaster oxybaphon Jackson, 1922
(Figs. 48, 52, Table 7)

Clypeaster oxybaphon Jackson, 1922. p. 44. pl. 7, figs. 3, 4; pl. 8, figs. 1-3.

Clypeaster oxybaphon (Jackson). Cooke, 1942. p. 13. pl. 8, fig. 7.

Clypeaster oxybaphon (Jackson). Sánchez-Roig, 1949. p. 81.

?Clypeaster polygonalis Sánchez-Roig, 1949. p. 84, pl. 7, figs. 1, 2.

?Clypeaster pinarensis Lambert and Sánchez-Roig in Sánchez-Roig, 1949. p. 86. pl. 12, figs. 1, 2.

?Clypeaster profundus Sánchez-Roig, 1949. p. 91.

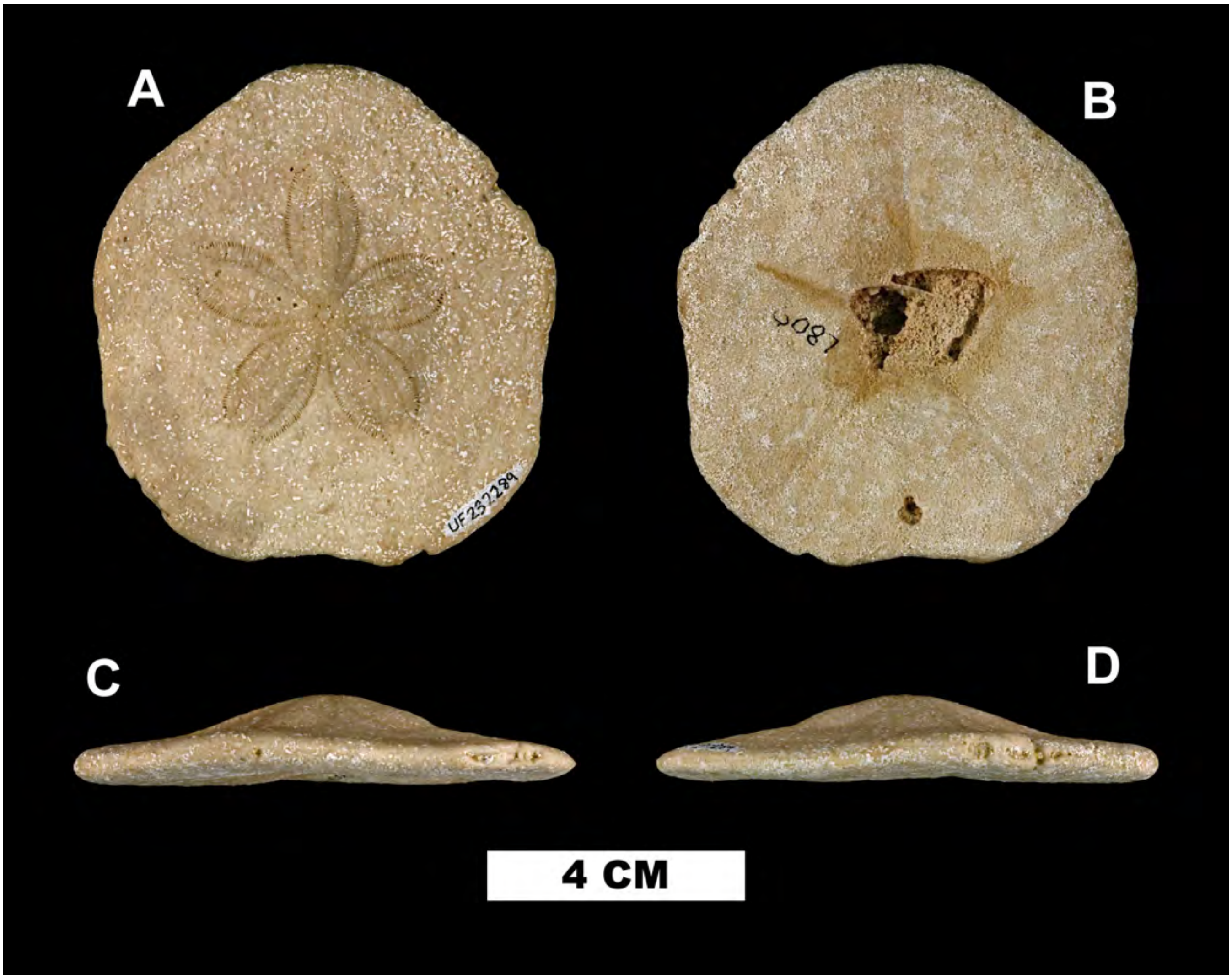


Figure 51: *Clypeaster marinanus* (UF 232289), 77 mm TL, 71 mm TW, 12 mm TH, Lower Oligocene Suwannee Limestone, Taylor County, Florida (FM-IP TA001). A: aboral. B: oral. C: left side. D: right side.

pl. 6, figs. 1-3.

Clypeaster oxybaphon (Jackson). Caso, 1957. p. 505. figs. 6-8.

Clypeaster oxybaphon (Jackson). Cooke, 1959. p. 35. pl. 11, fig. 1.

Clypeaster oxybaphon (Jackson). Gordon, 1963. pp. 636-637. txt fig. 2d. pl. 79, figs. 3, 4.

Clypeaster oxybaphon (Jackson). Rose and Poddubiuk, 1987. p. 466. fig. 1. tbl. 1.

Clypeaster oxybaphon (Jackson). Poddubiuk, 1987. pp. 58-60, 278-279. pls. 91-94.

Clypeaster oxybaphon (Jackson). Donovan, 2004. pp. 144-145. figs. 2, 3, 4.

Clypeaster cf. *oxybaphon* (Jackson). Zachos and Molineux, 2007. pp. 79-91.

Occurrence.—Within Florida, this species only rarely occurs in the Bridgeboro Limestone at the Duncan Church Quarry, Washington County (FM-IP WG002). Zachos and Molineux (2007) tentatively referred fragmentary material from the Oligocene at Damon Mound, northwestern Brazoria County, Texas to this species. *Clypeaster oxybaphon* is much more commonly distributed in Oligocene strata throughout the Caribbean region, including Antigua (type locality: Jackson, 1922), Cuba, Jamaica, Panama, and Puerto Rico (Cooke, 1959; Gordon, 1963).

Discussion.—Cooke (1959) first documented the presence of *C. oxybaphon* in the Oligocene of Washington County (FM-IP WG002), noting that the shape of the petals, thickened margin, broad

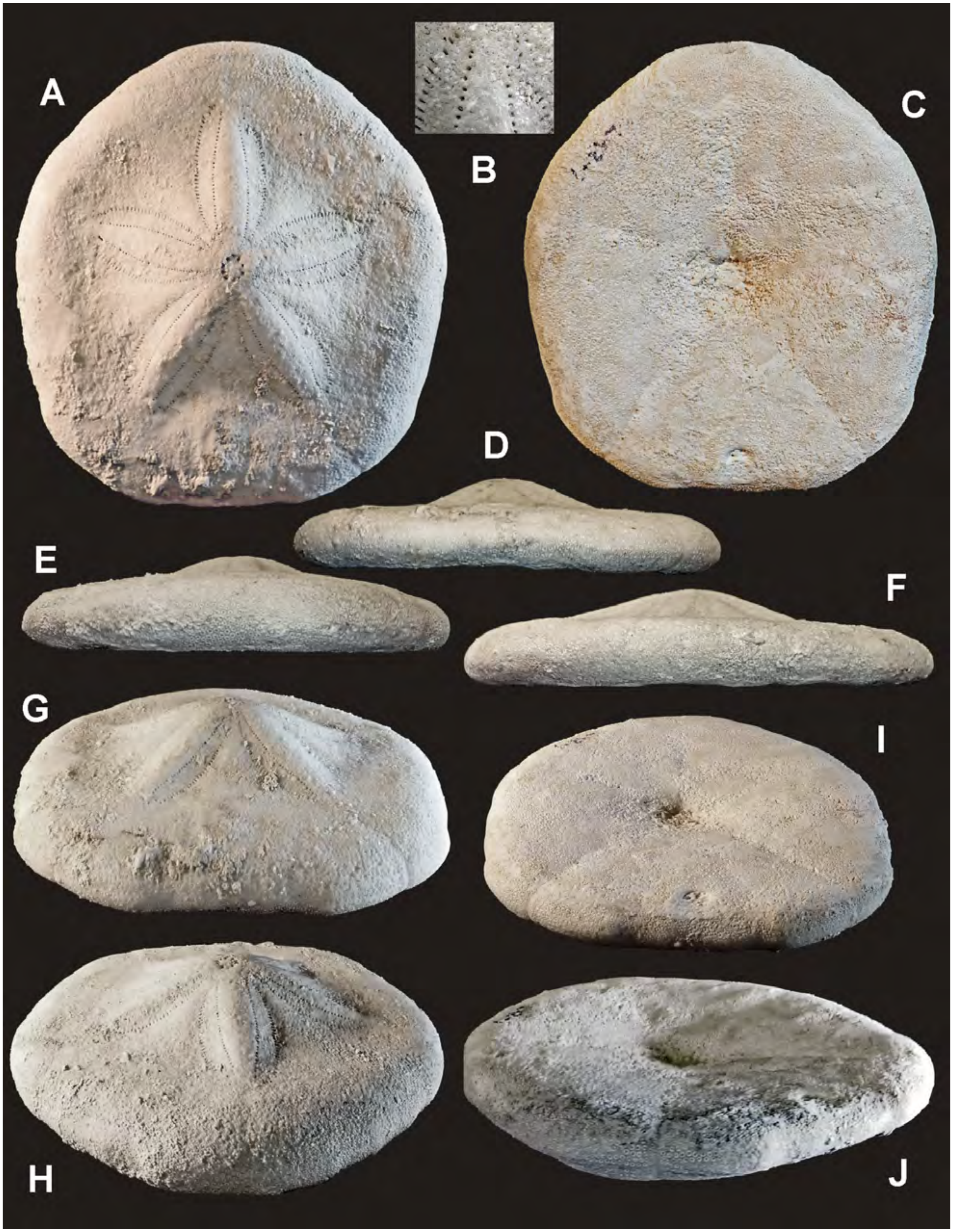


Figure 52: *Clypeaster* cf. *C. oxybaphon* (UF 342868), 74 mm TL, 69 mm TW, 16 mm TH, Oligocene Bridgeboro Limestone, Washington County, Florida (FM-IP WG002). A: aboral. B: distal end of petal III. C: oral. D: posterior. E: anterior. F: left side. G: tilted aboral viewpoint from posterior. H: tilted aboral viewpoint from anterior. I: tilted oral viewpoint from posterior. J: oblique oral viewpoint from posterior.

posterior truncation, and nearly flat lower surface were consistent features of the species. Although there is a submarginal, aboral depression in all the specimens Cooke (1959) had available, he noted that the degree of inflation of the apical region is variable.

The depressed submargin and lower test of *C. oxybaphon* readily differentiate it from the more inflated *C. cotteaui*, which also has much thicker margins but without the periperal depression between the margin and the petaloid area. Additionally, the petals of *C. cotteaui* are wide open distally, whereas they are nearly closed in *C. oxybaphon* (Table 7). The petaloid area is variably slightly inflated, as evidenced by the Bridgeboro Limestone specimens, and noted by Gordon (1963) concerning Puerto Rican specimens. The Bridgeboro Limestone tests have petals that are more open distally than typical *C. oxybaphon*, but not nearly as widely open as those of *C. rogersi*.

Cooke (1959) considered *C. platygaster* Jackson, 1922; *C. polygonalis* Sánchez-Roig, 1949; *C. pinarensis* Lambert and Sánchez-Roig, 1934; and *C. profundus* Sánchez-Roig, 1949, to be subjective junior synonyms of *C. oxybaphon*. However, Cooke (1959) stated that the three species of Sánchez-Roig, all from Cuba, are too poorly figured for complete assessment, and Gordon (1963) agreed, and Poddubiuk (1987) agreed with all these synonymies except for *C. platygaster*. Poddubiuk (1987:279) noted: "A numerical study of Cuban and Puerto Rican material available to the author suggests that although *C. oxybaphon* and *C. platygaster* are very closely related, the latter can be distinguished by greater petal closure, if not absolutely on the basis of oral surface concavity, Jackson's original diagnostic character." We follow Poddubiuk and do not include *C. platygaster* in the synonymy of *C. oxybaphon* above.

Caso (1957) documented the presence of *C. oxybaphon* in Mexico, but Gordon (1963) disagreed with her identification. Caso's designation should remain questionable until the specimen is reexamined.

Within the Bridgeboro Limestone of Washington County, *C. oxybaphon* occurs with the much more common *C. cotteaui*, as well as *L. floralanus, A. mossomi,* and other, rarer species.

Clypeaster rogersi (Morton, 1834)

(Figs. 48, 53-60, Table 7)

Scutella rogersi Morton, 1834. p. 77. pl. 13, fig. 3.
Lagana rogersi (Morton). Agassiz, 1840. p. 6.
not *Scutella rogersi* (Morton). Agassiz, 1841. p. 85. pl. 19a, figs. 1-4 (= *Periarchus quinquefarius*).
Scutella jonesi Forbes in Lyell, 1845. p. 574. txt fig.
not *Mortonia rogersi* (Morton). Desor, 1858. p. 231. (=*Periarchus quinquefarius*).
?*Mortonia turgida* Conrad, 1865. p. 184.
Clypeaster rogersi (Morton). Conrad, 1866. p. 22.
Clypeaster jonesi (Forbes). Conrad, 1866. p. 22.
Mortonia tumidus (Conrad). Conrad, 1866. pp. 22, 37.
Clypeaster tumidus (Conrad). Conrad, 1866. pp. 22, 37.
Scutella (Mortonia) rogersi (Morton). Gregorio, 1890. p. 250. pl. 43, fig. 16 (not description or figs. 17-20 = *Periarchus quinquefarius*).
Clypeaster douvillei Stefanini, 1911. p. 682. pl. 22, figs. 1a-c.
Clypeaster rogersi (Morton). Clark and Twitchell, 1915. p. 136. pl. 64, figs. 2a-d, 3a-d (includes additional references).
Clypeaster rogersi (Morton). Cooke, 1926. pl. 97, fig. 7.
Clypeaster rogersi (Morton). Cooke and Mossom, 1929. pl. 7, fig. 7.
Clypeaster rogersi (Morton). Cooke, 1942. p. 12.
Clypeaster brodermanni Sánchez-Roig, 1949. p. 74. pl. 9, figs. 1-3.
Clypeaster aff. *rogersi* (Morton). Sánchez-Roig, 1949. pp. 82, 83. pl. 8, fig. 4.
Clypeaster rogersi (Morton). Cooke, 1959. pp. 36-37. pl. 12, figs. 4-6.
Clypeaster rogersi (Morton). Pickering, 1970. pp. 20, 57.
Clypeaster rogersi (Morton). Dockery, 1980. p. 191. pl. 80, figs. 6, 7.
Clypeaster rogersi (Morton). Kier, 1997. pp. 8, 10. pl. 6, figs. 3, 4.
Clypeaster rogersi (Morton). Oyen and Portell, 2001.

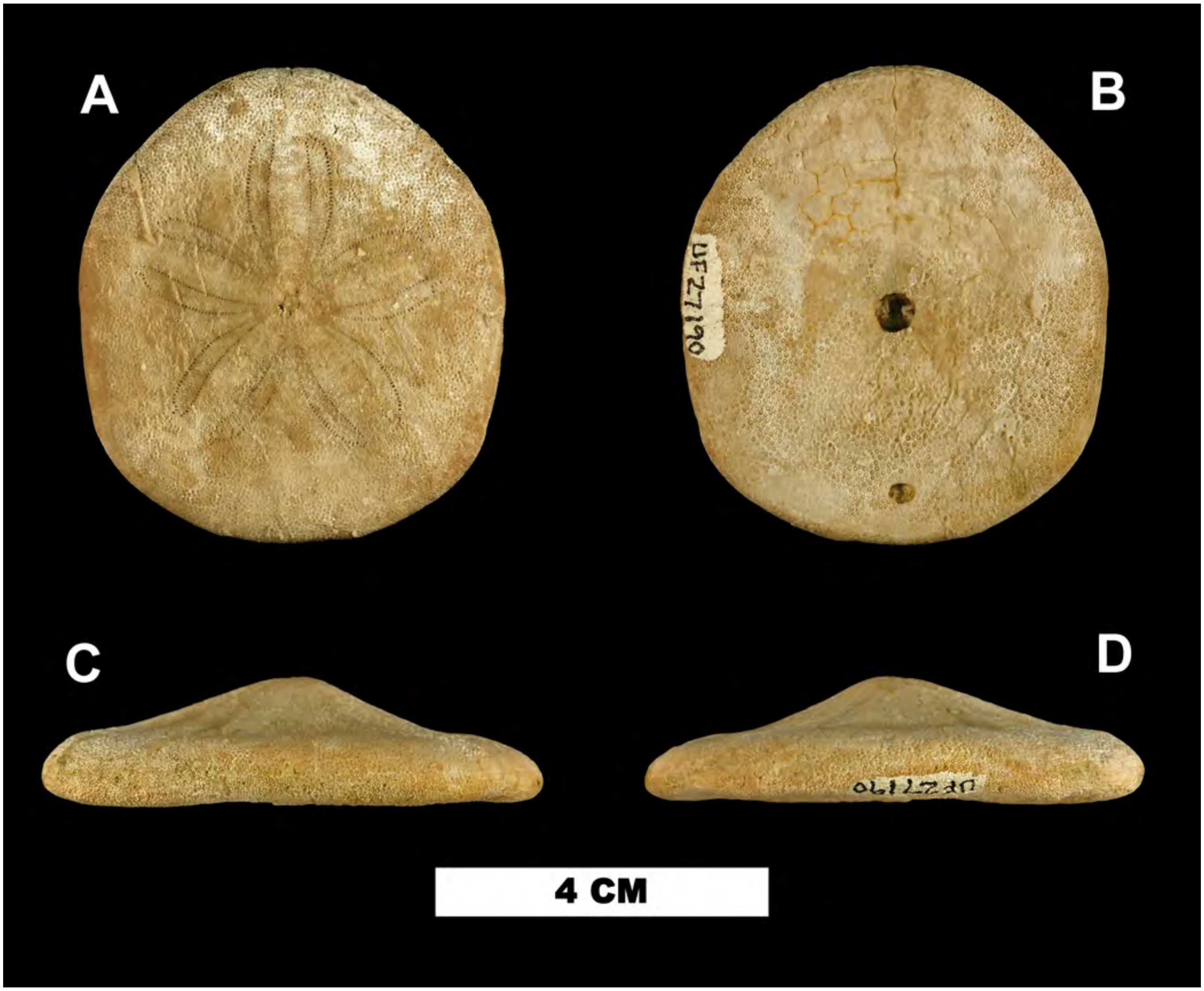


Figure 53: *Clypeaster rogersi* (UF 27190), 59 mm TL, 52 mm TW, 17 mm TH, Lower Oligocene Suwannee Limestone, Polk County, Florida (FM-IP PO017). A: aboral. B: oral. C: left side. D: right side.

pp. 193-218. pl. I, fig. 7.

Occurrence.—This is the ubiquitous sand dollar of the Lower Oligocene Marianna Limestone throughout the Gulf Coastal Plain, commonly collected in the Marianna Limestone in the Florida panhandle, especially in Jackson and Washington Counties. Notable localities include the Duncan Church Quarry (FM-IP WG002), Washington County, and the Brooks Quarries (FM-IP JA013, FM-IP JA019, FM-IP JA026, FM-IP JA029) northwest of Marianna, Jackson County. Moldic specimens are frequent in the dolomitic facies of the Marianna Limestone in the bed and banks of Dry Creek, south of Marianna, Jackson County (FM-IP JA010). The only specimens that appear to belong to this species from the Suwannee Limestone are from the Terramar Quarry in Polk County (FM-IP PO017). Specimens from the lower Suwannee Limestone in the Brooksville Rock Quarry (now Vulcan Quarry) northwest of Brooksville (FM-IP HE038), Hernando County, are discussed as *Clypeaster* sp. B.

Clypeaster rogersi is very abundant in the Marianna Limestone of Alabama, the Marianna and Glendon Limestones of Mississippi, and Lower

Figure 54: *Clypeaster rogersi* (UF 31970), 67 mm TL, 61 mm TW, 11 mm TH, Lower Oligocene Suwannee Limestone, Polk County, Florida (FM-IP PO017). A: aboral. B: oral. C: left side. D: right side.

Oligocene strata of Georgia. Kier (1997) recorded three fragments of this species from the River Bend Formation (*sensu* Ward, 2007) of North Carolina. *Clypeaster rogersi* has also been reported from the Oligocene of Cuba (Sánchez-Roig, 1949; Cooke, 1959).

Discussion.—*Clypeaster rogersi* is the most widespread species in Oligocene deposits of the eastern United States, distributed eastward from the banks of the Mississippi River in Vicksburg, Mississippi, southward to Florida, and northward to North Carolina. It is also the characteristic echinoid of the Marianna Limestone, the dominant Lower Oligocene unit of the Gulf Coast. Described and figured by Morton (1834), it was among the first echinoids documented from the Cenozoic deposits of North America.

It should come as no surprise that a species with a lineage that dates back nearly 200 years should have some amount of taxonomic complication. Louis Agassiz (1841: pl. 19a, figs. 1-4) created the first instances of this when he figured a specimen of *Periarchus quinquefarius* Say, 1825 as *C. rogersi*. Desor (1858) repeated this error, compounding it by founding the new genus *Mortonia* for what was *P. quinquefarius* but citing Morton's figure of *C. rogersi*. Gregory (1892) first explicated the errors of Agassiz (1841) and Desor (1858), and Clark and Twitchell (1915: 137) stated the confusion between *C. rogersi* and Say's *P. quinquefarius* "was found to be in a tangle requiring significant labor to unravel". Thankfully, Clark and Twitchell (1915)

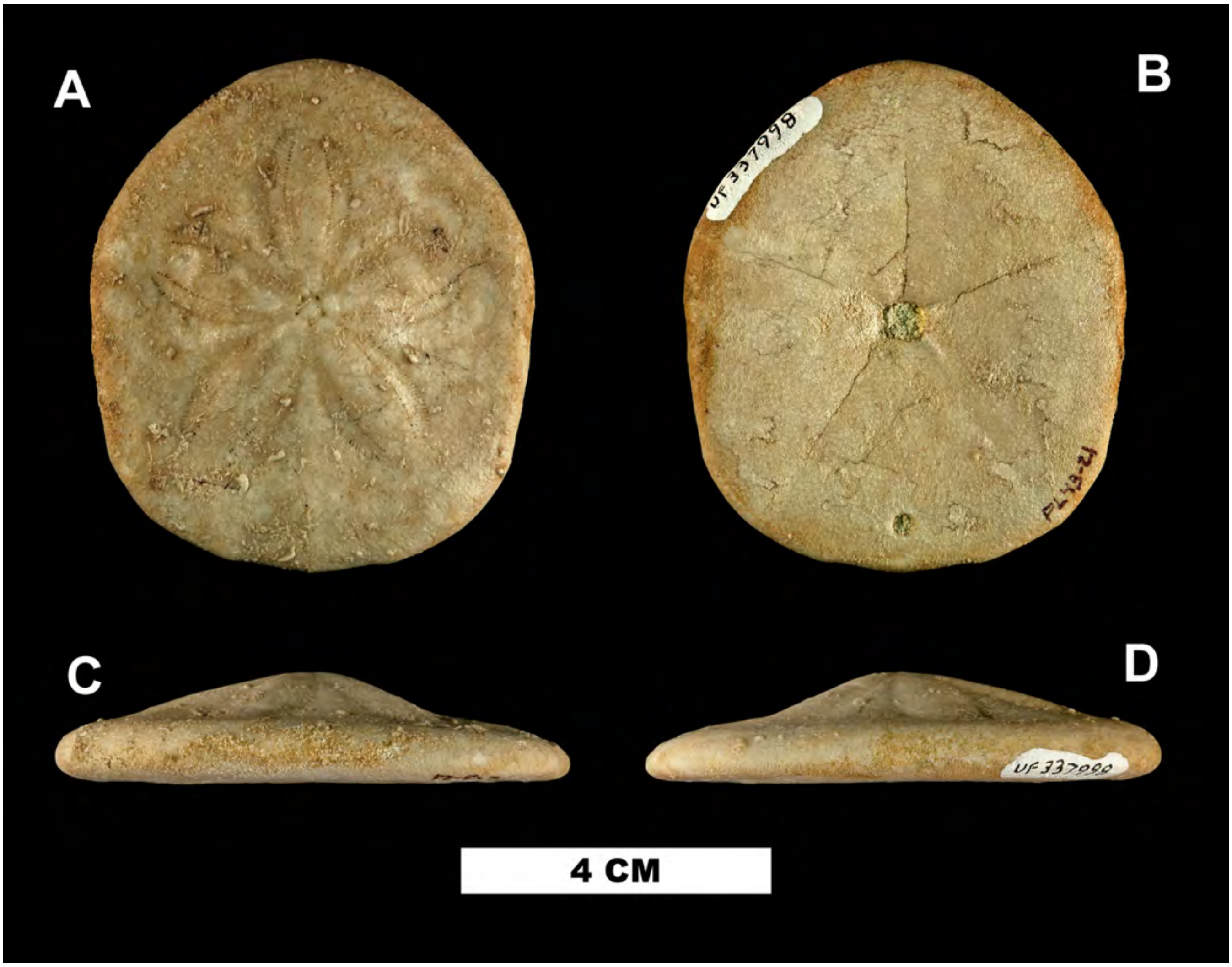


Figure 55: *Clypeaster rogersi* (UF 337998), 66 mm TL, 57 mm TW, 14 mm TH, Lower Oligocene Marianna Limestone, Washington County, Florida (FM-IP WG033). A: aboral. B: oral. C: left side. D: right side.

persisted and corrected the synonymies of both *C. rogersi* and *P. quinquefarius*.

Forbes, in Lyell (1845), described *Scutella jonesi* from specimens Lyell collected near Jonesboro, Georgia, and his figures of *S. jonesi* clearly depict *C. rogersi*. Subsequently, Conrad (1865) described *Mortonia turgida* from Jasper County, Mississippi, which he stated was allied to *C. rogersi*, but was larger, more elevated medially, and with a greater depression around the peristome. However, he did not figure the form. Conrad (1866) likely had the intent to change the name of his *M. turgida*, as within a year of describing the species he listed *M. tumida* (Conrad) from Mississippi, and not *M. turgida*. Conrad (1865: 184) described *M. turgida* from Jasper County, Mississippi. Considering the species has not been further described or discussed since, it is worth reproducing Conrad's description and comments on the species here: "*Mortonia turgida*: suboval or subpentagonal, swelling medially, with a convex outline; thin on the submarginal portion of the disc; ambulacra elliptical. Allied to *C. rogersi*, but larger, thinner round the central prominence, more elevated medially, the depression about the mouth greater, and the anus smaller. It bears about the same relation to *Cl. rogersi* as *Sismondia alta* bears to *S. lyelli*."

In his notes (Conrad, 1866: 37) he listed *Mortonia tumida* in reference to the work in which he described *M. turgida*. He then subsequently changed

Figure 56: *Clypeaster rogersi* (UF 337962), 63 mm TL, 53 mm TW, 13 mm TH, Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA029). A: aboral. B: oral. C: left side. D: right side.

the name to *C. tumidus* (Conrad, 1866: 22). This is not to be confused with the modern Pacific form *Clypeaster tumidus* Tenison-Woods, 1878, which is apparently a homonym of *C. tumidus* Conrad, 1866, which seems to be an available name despite the confusion Conrad himself introduced. Conrad (1866) did not provide a rationale for his species redesignation from *turgida* to *tumida,* then finally to *tumidus*. Presumably, he was attempting to introduce agreement in gender with the genus name, which is masculine. The fact that he gave his species two different names does not alter the fact of homonymy suggested above.

In any case, variation within collections of *C. rogersi* was starting to be reflected in taxonomic usage. When Conrad (1866) developed his checklist, he documented three species from three states based on minimal differences among the three: *C. rogersi* from Alabama, *C. jonesi* from Georgia, and *C. tumidus* from Mississippi, all from strata that were, at that time, considered to be Eocene in age. All are now recognized as *C. rogersi*.

Stefanini (1911) described *Clypeaster douvillei* from strata now recognized as the Marianna Limestone in Jasper County, Mississippi (the same locality information given by Conrad for his *M. turgida* discussed above).

Clark and Twitchell (1915) and Cooke (1942, 1959) considered *C. jonesi, C. douvillei*, and *C. turgida* junior synonyms of *C. rogersi* and emphasized the great variability of *C. rogersi*. However, *C. turgida* (which, given the account above,

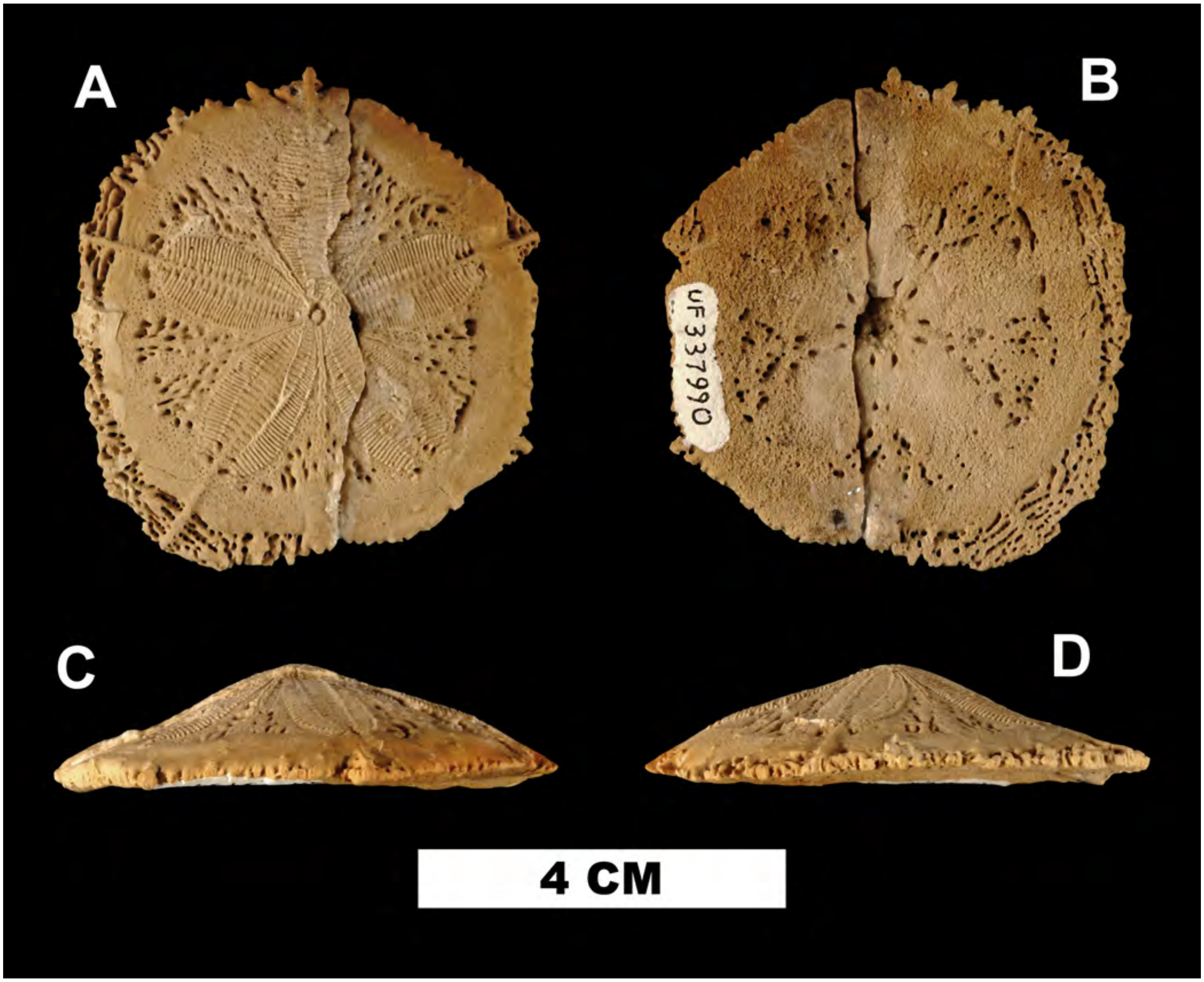


Figure 57: *Clypeaster* cf. *C. rogersi* (UF 337990), 55 mm TL, 52 mm TW, 13 mm TH, internal mold showing internal structure, dolomitic portion of Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: aboral. B: oral. C: left side. D: right side.

should probably be emended to *C. turgidus*) and *C. douvillei* were described for specimens with a higher test, deeper infundibulum, and thinner margin than typical *C. rogersi*. Considering the proximity of the type localities, and relatively similar descriptions (both distinguished from *C. rogersi* by similar traits), they undoubtedly described the same form from the population of *Clypeaster* in the Glendon Limestone that overlies the Marianna Limestone in Mississippi and contains typical *C. rogersi*. If subsequent workers resurrect Conrad's *Mortonia turgida* for these forms with a thinner margin, more elevated test and often more concave oral surface, Stefanini's *C. douvillei* would likely be a subjective junior synonym of *C. turgida*, and not of *C. rogersi*. These subjective junior synonyms of *C. rogersi* are further discussed in the remarks for *Clypeaster* sp. B, below.

Clark and Twitchell (1915) stated that *C. rogersi* is the most abundant American *Clypeaster* and documented the variability in marginal outline, tumidity of the aboral surface, and concavity of the oral surface. Cooke (1959) noted that though the shape and size of *C. rogersi* is variable, the shape of the petals is relatively constant. However, the variability expressed by Cooke included the thinner-margined and shorter-petaled *C. marianus* from northern Florida and Mexico, as well as *Clypeaster* sp. B from the Suwannee Limestone of

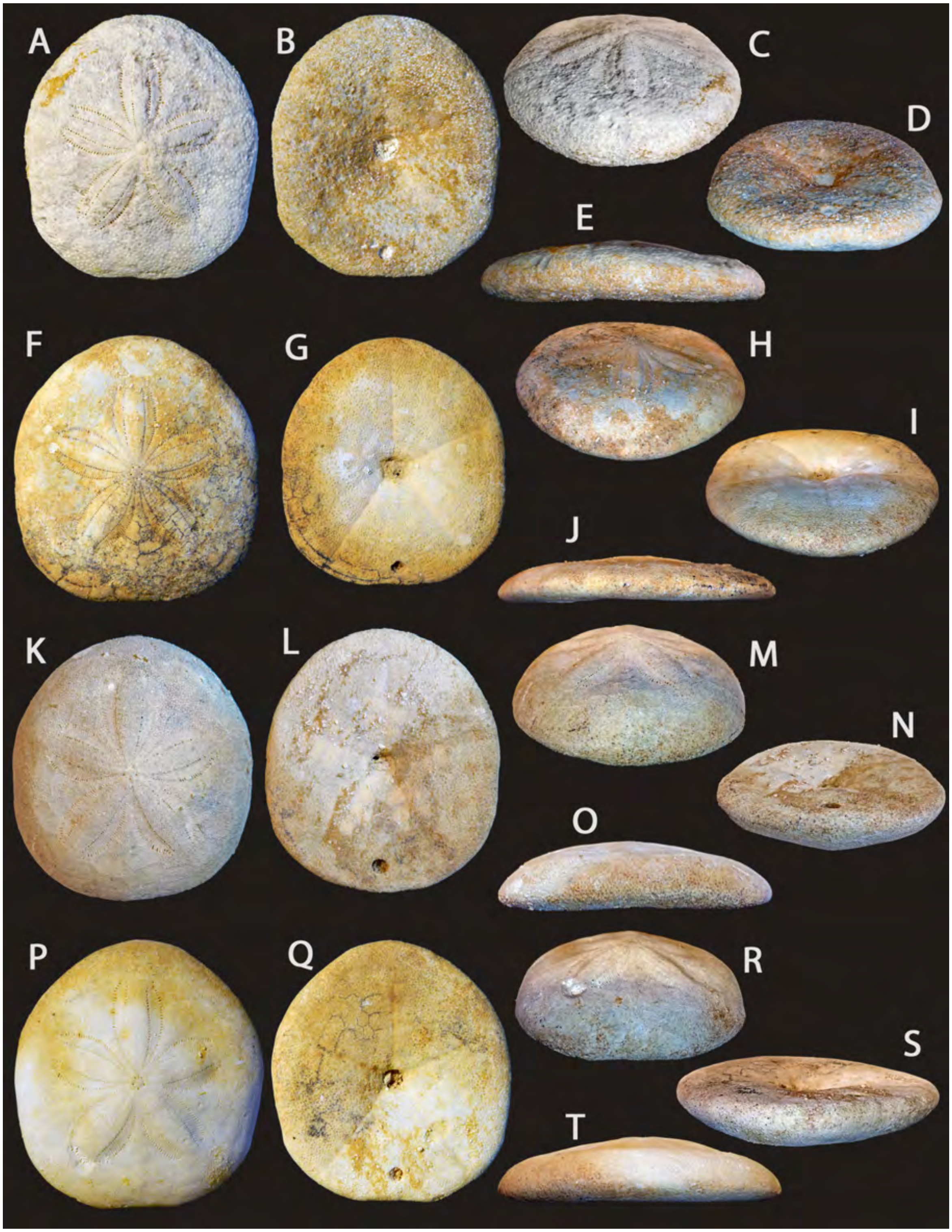


Figure 58: Series of *Clypeaster rogersi* showing variation in test thickness and oral surface concavity, from the Lower Oligocene Marianna Limestone, quarry southeast of Brooklyn (FM-IP ZA181), Conecuh County, Alabama. A-E: UF 338015; 49.2 mm TL, 43.2 mm TW, 11.9 mm TH; A: aboral. B: oral. C: tilted aboral viewpoint from anterior. D: tilted oral viewpoint from posterior; concavity around peristome deeper than typical. E: left side. F-J: UF 338016; 55.6 mm TL, 50.9 mm TW, 9.4 mm TH; F: aboral. G: oral. H: tilted aboral viewpoint from anterior. I: tilted oral viewpoint from anterior. J: lateral. K-O: UF 338014; 58.8 mm TL, 52.6 mm TW, 14.5 mm TH; K: aboral. L: oral. M: tilted aboral viewpoint from posterior. N: tilted oral viewpoint from posterior. O: left side. P-T: UF 338017; 61.2 mm TL, 56.1 mm TW, 13.6 mm TH; P: aboral. Q: oral. R: tilted aboral viewpoint from posterior. S: oblique oral viewpoint from posterior. T: left side.

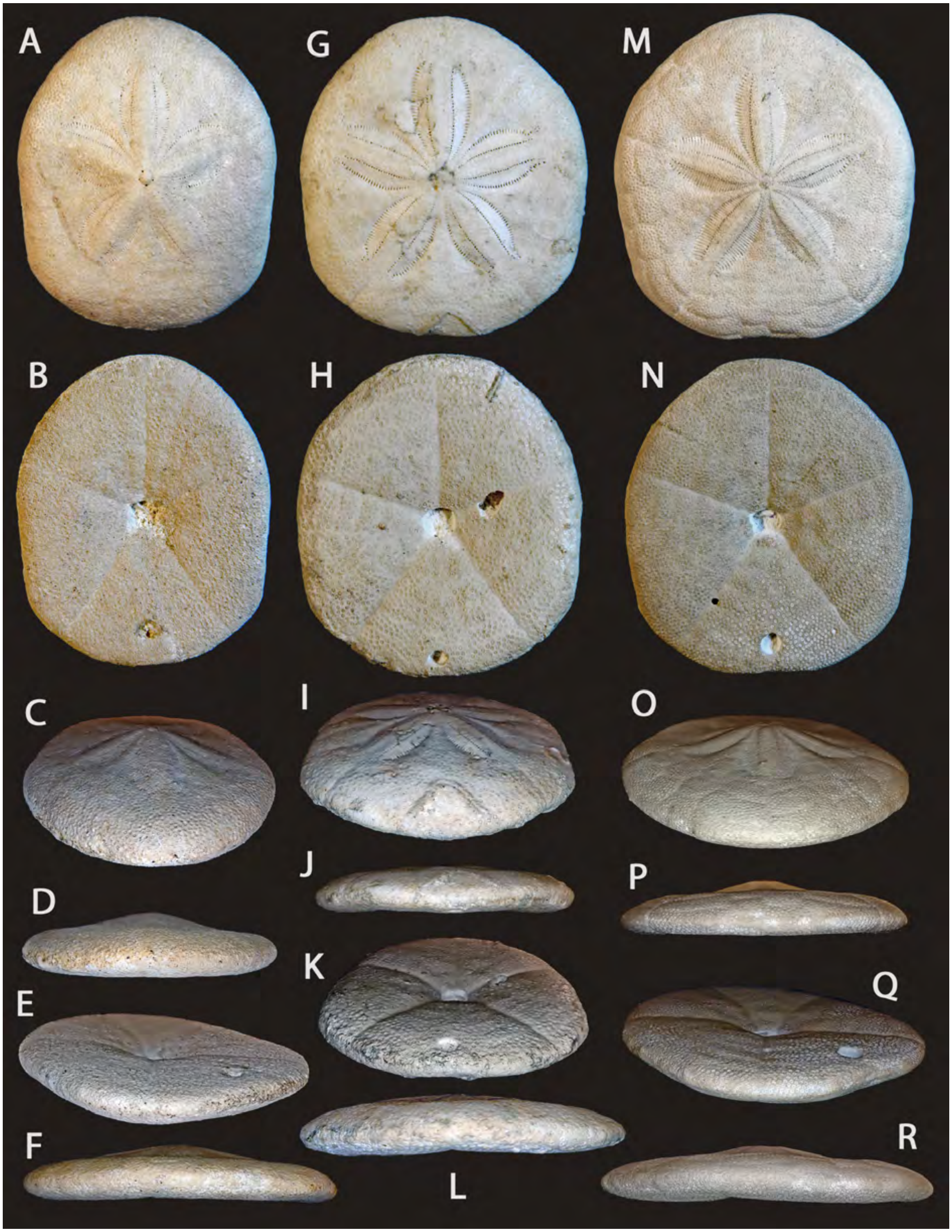


Figure 59: Series of *Clypeaster rogersi* showing variation in test thickness and oral surface concavity, from the Lower Oligocene Marianna Limestone, Smith County Lime Quarry, MS (FM-IP ZZ104). A-F: UF 338020; 39.1 mm TL, 32.4 mm TW, 7.4 mm TH; A: aboral. B: oral. C: tilted aboral viewpoint from anterior. D: anterior. E: oblique oral viewpoint from anterior. F: left side. G-L: UF 338019; 44.8 mm TL, 40.0 mm TW, 8.2 mm TH; G: aboral. H: oral. I: tilted aboral viewpoint from posterior. J: posterior. K: tilted oral viewpoint from posterior. L: left side. M-R: UF 338018; 50.7 mm TL, 46.5 mm TW, 9.1 mm TH; M: aboral. N: oral. O: tilted aboral viewpoint from anterior. P: posterior. Q: oblique oral viewpoint from posterior. R: left side.

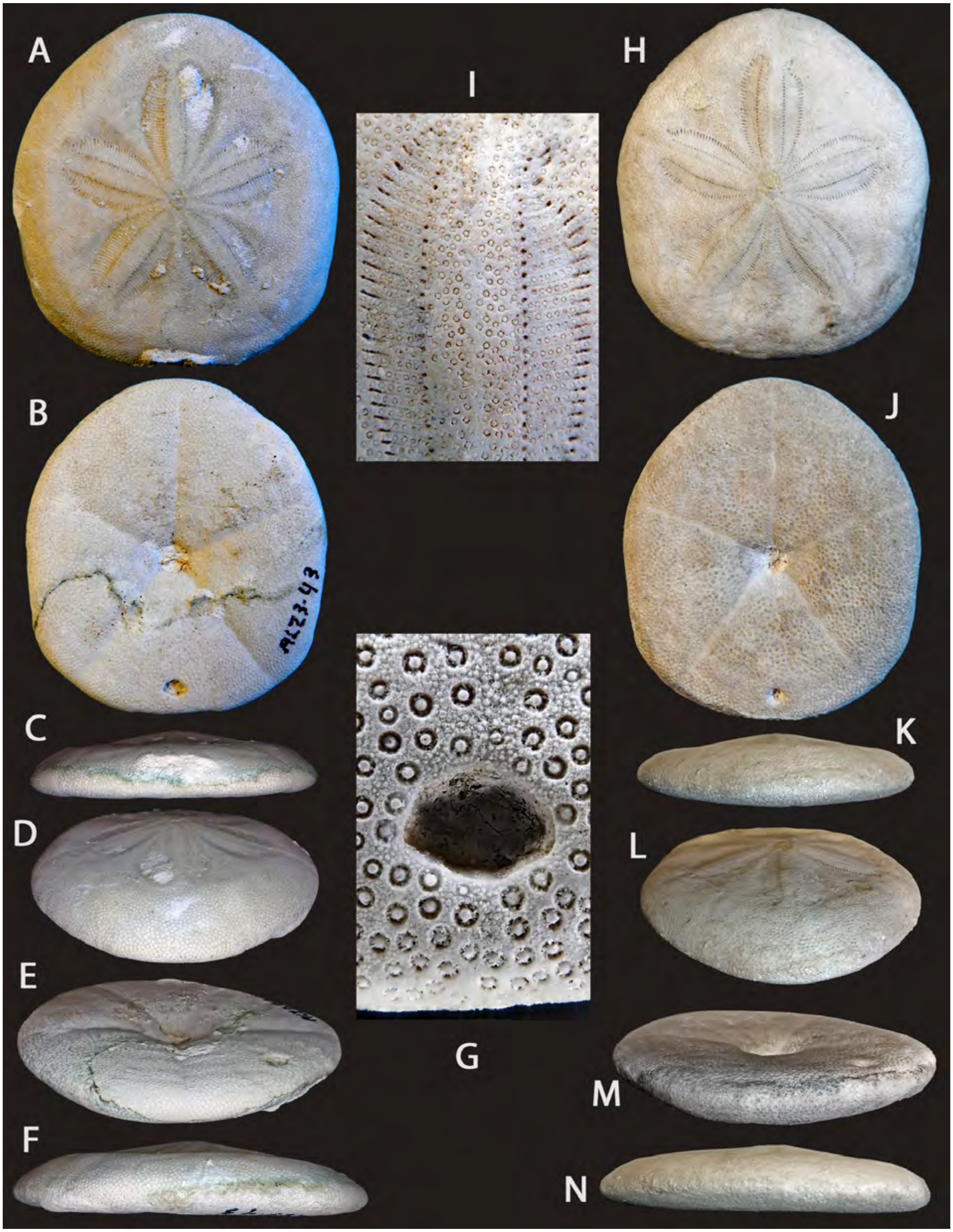


Figure 60: Two specimens of *Clypeaster rogersi* from the Lower Oligocene Marianna Limestone, St. Stephens, Washington County, Alabama (FM-IP ZA192). A-G: UF 338022, 50.9 mm TL, 10.9 mm TW, 10.9 mm TH; A: aboral. B: oral. C: anterior. D: tilted aboral viewpoint from anterior. E: oblique lateral viewpoint from posterior. F: left side. G: periproct. H-N: UF 338021, 64.8 mm TL, 56.7 mm TW, 11.7 mm TH; H: aboral. I: distal end of petaloid portion of ambulacrum III. J: oral. K: anterior. L: tilted aboral viewpoint from posterior. M: oblique lateral viewpoint from posterior. N: left side.

Florida.

Cooke (1959) stated that the specimen of *C. rogersi* from the Suwannee Limestone (*Clypeaster* sp. B) and Meson Formation of Mexico (herein referred to *C. marinanus*) have shorter petals, a thinner margin, and often have a more inflated apical area than typical *C. rogersi*. The first two of these characteristics are true of *C. marinanus* and the second two are accurate for the population from the lower Suwannee Limestone in the Vulcan Quarry west of Brooksville (FM-IP HE038) here referred to *Clypeaster* sp. B. When these populations are removed from the synonymy, *C. rogersi* remains variable, but more restrictedly so (Table 7). The typical form is a thick-margined, relatively flat, cookie-like form with a nearly flat to very slightly concave oral surface, and as such, the species is a common element in the Marianna Limestone of northern Florida, Alabama, and Mississippi. As mentioned above, the Glendon Limestone of Mississippi contains a *Clypeaster* intermediate between typical *C. rogersi* and what we discuss as *Clypeaster* sp. B. Within the Suwannee Limestone, the only specimens that appear to belong to *C. rogersi* are from the Terramar Quarry in Polk County (FM-IP PO017) (Figs. 53, 54).

Clypeaster rogersi has a thicker margin with longer petals than *C. marinanus*. It lacks the aboral submarginal depression of *C. oxybaphon* and has a lower test with a much less concave oral surface than *C. cotteaui* (Fig. 48) (Table 7). Twitchell in Clark and Twitchell (1915), indicated that *C. cotteaui* has straighter and more widely divergent poriferous zones than *C. rogersi*. See the remarks for *Clypeaster* sp. B below for features differentiating it from *C. rogersi*.

***Clypeaster* sp. A**

(Figs. 48, 61, Table 7)

not *Clypeaster batheri* (Lambert). Oyen, 2001. p. 96. figs. 3-12, F-G.

Occurrence.—Suwannee Limestone north of Branford, in Suwannee County (FM-IP SU002).

Discussion.—A single specimen (UF 2546) from the Lower Oligocene Suwannee Limestone of Suwannee County, Florida is distinct from all other species of *Clypeaster* described from North America. The specimen was initially discussed by Oyen (2001) as *Clypeaster batheri* Lambert, 1915. However, this fossil is clearly not conspecific with *C. batheri*, as further discussed below. Oyen (2001) also identified another specimen (UF 5341) as *C. batheri*, but this specimen consists of a test fragment that cannot be attributed to this species with confidence.

Oyen (2001) briefly described the complete specimen (UF 2546) but his description is nearly verbatim from Jackson's (1922) description for *C. batheri.* The specimen has a heavily eroded oral surface, but it is sufficiently preserved to be distinguished from *C. batheri*. The holotype of *C. batheri* (NHM E12860) measures 52 mm TL, 44 mm TW, and 15 mm TH (Jackson, 1922). The specimen from the Suwannee Limestone (UF 2546) is very large for an Oligocene *Clypeaster* (113 mm TL, 85 mm TW, and 23 mm TH), and is much narrower (width is 75% length vs 84.6% in the type of *C. batheri*), and lower (height is 21% length vs 28.8% in the type of *C. batheri*) than *C. batheri*. *Clypeaster* sp. A is also much more peaked apically, as the maximum height rises from a much thinner margin than in *C. batheri* (Table 7). The thicker margin of *C. batheri* also distinguishes these two forms, as do the petals of *C. batheri*, which are not as widely open distally. *Clypeaster batheri* is more like *C. cotteaui* than *Clypeaster* sp. A.

Clypeaster sp. A is also much larger, narrower, with a much more "peaked" apical system than *C. rogersi*, and it does not have a swollen margin with depressed submarginal periphery on the aboral surface like *C. oxybaphon*. *Clypeaster* sp. A also lacks the thin margin and short petals of *C. marinanus*. Furthermore, it is much narrower, with a more concave oral surface than *Clypeaster* sp. B, from the lowermost Suwannee Limestone, Hernando County, Florida (Table 7).

The single specimen was collected in 1969 from an area that is still actively quarried (O'Brien Mine: FM-IP SU002). However, current operations have exposed only a thin horizon of Suwannee Limestone with an abundance of *R. gouldii*, and

Figure 61: *Clypeaster* sp. A., (UF 2546), 114 mm TL, 86 mm TW, 24 mm TH, Lower Oligocene Suwannee Limestone, Suwannee County, Florida (FM-IP SU002). A: aboral. B: oral. C: left side. D: right side.

although the site has been extensively collected, no additional specimens of *Clypeaster* sp. A have been discovered. Lacking additional material to determine the variability of the taxon, we can only document its existence in the hope that future collecting will provide further specimens adequate to determine if it is indeed a new species, or conspecific with one of the myriad *Clypeaster* taxa already known from New World fossil and Recent localities. In addition, a much better understanding is critically needed of the 40 or so taxa of Cuban *Clypeaster* described in the works of Sánchez-Roig alone (Table 6), as it is possible that *Clypeaster* sp. A might be assigned to one of those.

Clypeaster sp. B

(Figs. 48, 62-66, Table 7)

not *Clypeaster rogersi* (Morton). Cooke, 1959. pp. 36-37 (in part, discussion of *C. rogersi* in Suwannee Limestone is likely *Clypeaster* sp. B).

Occurrence.—This form occurs in the lower beds of the Suwannee Limestone in the Vulcan Quarry (FM-IP HE038), Hernando County, Florida (Fig. 8).

Discussion.—Specimens of *Clypeaster* are very common in the lowermost beds of the Suwannee Limestone in the quarries west of Brooksville, Hernando County, especially in the Vulcan Quarry (FM-IP HE038). A collector familiar with specimens typical of *C. rogersi* from the Marianna Limestone (holotype ANSP 1070), especially from the type area of the species west of Claiborne, Alabama, will quickly notice some of the other specimens from there are very different. These examples, herein referred to in open nomenclature as *Clypeaster* sp. B, typically have a thinner margin, are more tumid centrally on the aboral surface, and a more concave oral surface than typical *C. rogersi* (Table 7). The concavity of the oral surface is most pronounced in smaller specimens (as in UF 338001, 54 mm TL, 50 mm TW) but much less so in larger specimens (UF 337999, 82 mm TL, 73 mm TW).

The widest point of *Clypeaster* sp. B is anterior of the apical area, the distal end of ambulacrum III being on average 66.4% of the distance from the center of the apical area to the anterior margin (the same average for *C. marinanus* is 55%). However, the distance of the periproct from the posterior margin is highly variable, ranging from 5.5% to 9% TL.

Cooke (1942) recognized the differences between the Florida specimens and typical *C. rogersi,* though he still considered them synonymous. However, he noted the Florida specimens have a thinner margin and are more tumid centrally than is customary for *C. rogersi*. Nevertheless, Cooke (1942: 12 and 13) stated: “these features can be matched in selected individuals from Alabama and Mississippi”. This is true, but specimens of *C. rogersi* from the Marianna Limestone of the Gulf Coast only rarely display these traits, whereas *Clypeaster* sp. B is dominant and typical for the specimens in the basal Suwannee Limestone west of Brooksville.

Cooke (1959) stated specimens of *C. rogersi* from the Suwannee Limestone (that is, *Clypeaster* sp. B) and Meson Formation of Mexico (referred here to *C. marinanus*) have shorter petals, a thinner margin, and often have a more inflated apical area than typical *C. rogersi*. The first two of these characteristics are true of *C. marinanus* and the second two are accurate for the population from the lower Suwannee Limestone in the Vulcan Quarry (FM-IP HE038) referred to *Clypeaster* sp. B. As noted in the remarks for *C. marinanus* and *C. rogers*i above, removal of these forms from the range of variation in *C. rogersi*, the species remains more variable than other regional species of *Clypeaster*, but readily recognizable as the typical flat, thick, cookie-like form of the Marianna Limestone of the Gulf Coast (reference holotype: ANSP 1070).

While determining the identity of the thin specimens with short ambulacra from the Bumpnose Limestone was rather straight forward given their similarity to *C. marinanus*, assigning a species name to *Clypeaster* sp. B is less straightforward, as the forms in synonymy with *C. rogersi* would attest.

Scutella jonesi, from Lower Oligocene strata in eastern Georgia (Forbes in Lyell, 1845), is clearly a typical *C. rogersi*, as noted by Clark and Twitchell (1915) and Cooke (1942, 1959), being recognized as a junior synonym of *C. rogersi* since Clark and Twitchell (1915).

As noted above, Conrad (1866) intended to emend his *M. turgida* to *C. tumidus*. Although Conrad’s statement that *M. turgida* is more elevated medially than *C. rogersi* implies an affinity with the Suwannee Limestone specimens, as was typical for Conrad, he didn’t provide catalog information for a type, potential or otherwise, and it is not listed in the catalog of type specimens in the Philadelphia Academy of Sciences, which houses most of Conrad’s collection. The type is therefore unavailable for examination (Richards, 1968). Conrad’s species has been recognized as a subjective junior synonym of *C. rogersi* since Clark and Twitchell (1915), and has not been further described, discussed, or figured. While Conrad’s description is tantalizingly close to *Clypeaster* sp. B, *M. turgida* is otherwise unrecognizable and is only questionably included in our synonymy of *C. rogersi* (following Clark and Twitchell, 1915; Cooke, 1942, 1959). Stefanini (1911) stated that *M. turgida* is a *nomen nudum* and then described another *Clypeaster* from the same general area (Jasper County, Mississippi) as Conrad’s *M. turgida*, which does not clarify the issue.

Stefanini (1911) subsequently described what would become recognized as yet another junior synonym of *C. rogersi* (Clark and Twitchell, 1915; Cooke, 1942, 1959), when he named *C. douvillei* from strata now recognized as the Marianna Lime-

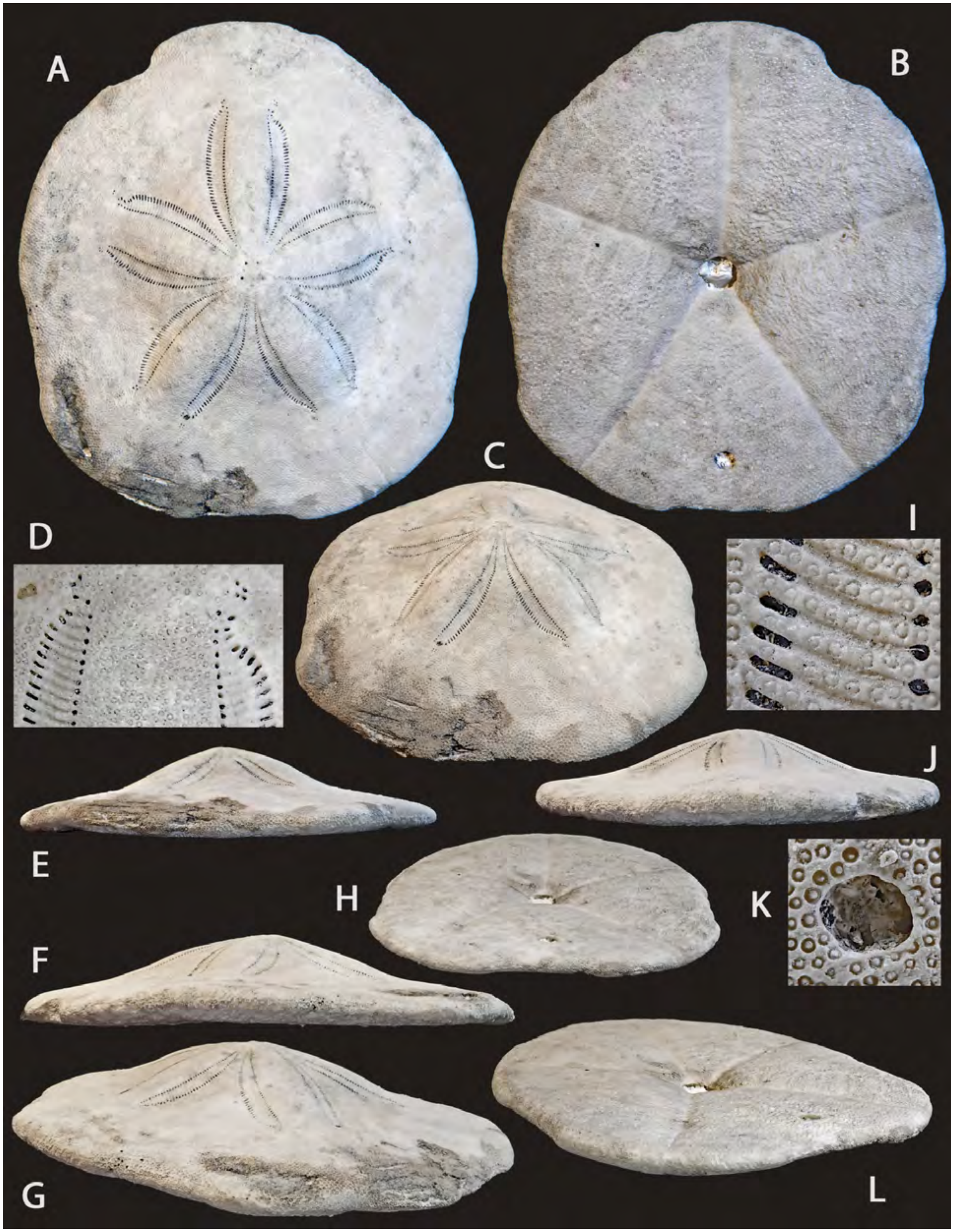


Figure 62: *Clypeaster* sp. B., (UF 337999), 82 mm TL, 74 mm TW, 16 mm TH, Lower Oligocene, basal beds of Suwannee Limestone, Vulcan Quarry (FM-IP HE038), west of Brooksville, Hernando County, Florida. A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: distal end of petaloid portion of ambulacrum III. E: posterior. F: left side. G: oblique lateral viewpoint from posterior. H: tilted oral viewpoint from posterior. I: pore-pairs at widest point of ambulacrum III. J: anterior. K: periproct. L: oblique oral viewpoint from posterior.

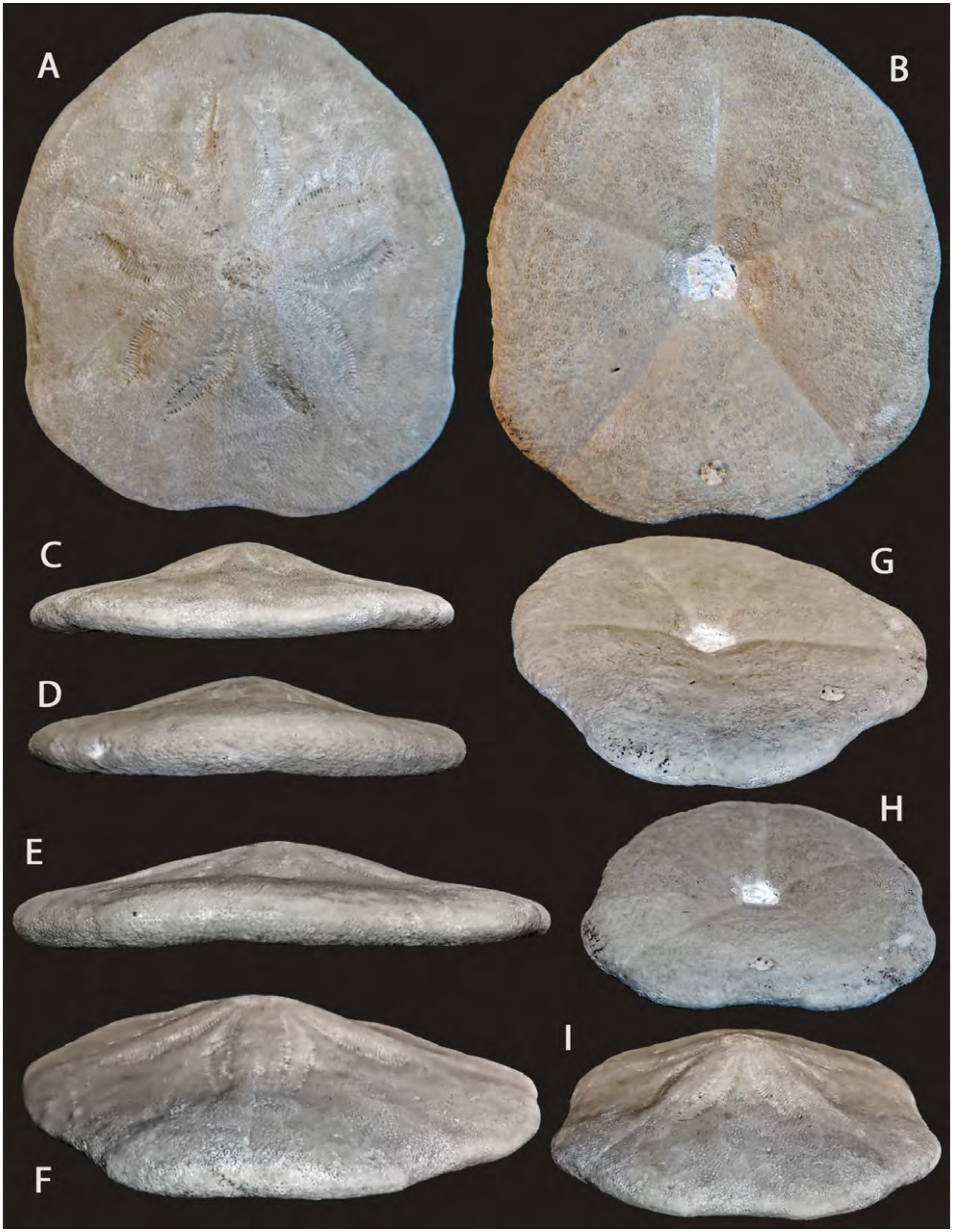


Figure 63: *Clypeaster* sp. B., (UF 338000), 59 mm TL, 53 mm TW, 13 mm TH, Lower Oligocene, basal beds of Suwannee Limestone, Vulcan Quarry (FM-IP HE038), west of Brooksville, Hernando County, Florida. A: aboral. B: oral. C: anterior. D: posterior. E: left side. F: oblique lateral viewpoint from posterior. G: oblique oral viewpoint from posterior. H: tilted oral viewpoint from posterior. I: tilted aboral viewpoint from posterior.

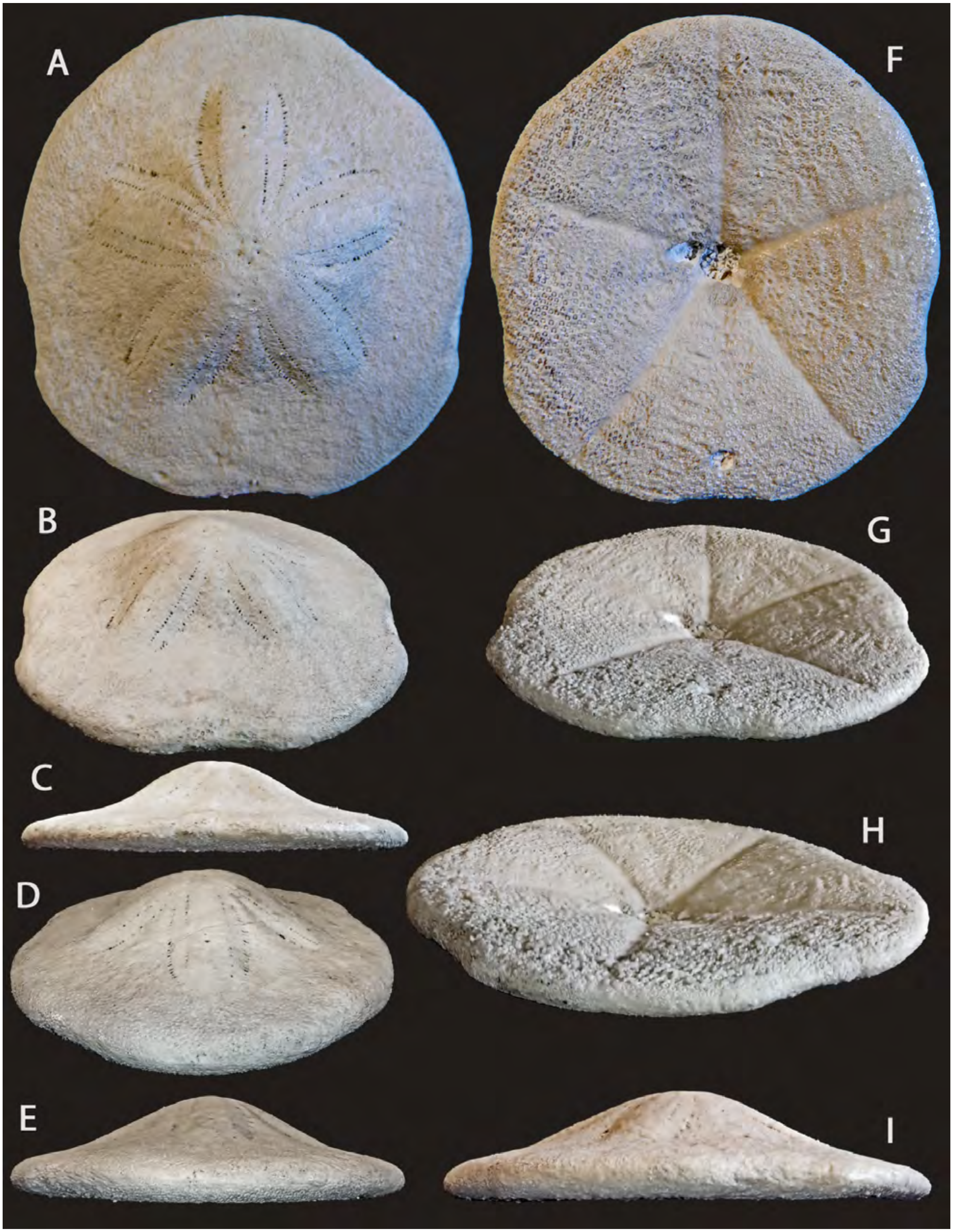


Figure 64: *Clypeaster* sp. B., (UF 338001), 54 mm TL, 50 mm TW, 12 mm TH, Lower Oligocene, basal beds of Suwannee Limestone, Vulcan Quarry (FM-IP HE038), west of Brooksville, Hernando County, Florida. A: aboral. B: tilted aboral viewpoint from posterior. C: posterior. D: tilted aboral viewpoint from anterior. E: anterior. F: oral. G: tilted oral viewpoint from posterior. H: oblique oral viewpoint from posterior. I: left side.

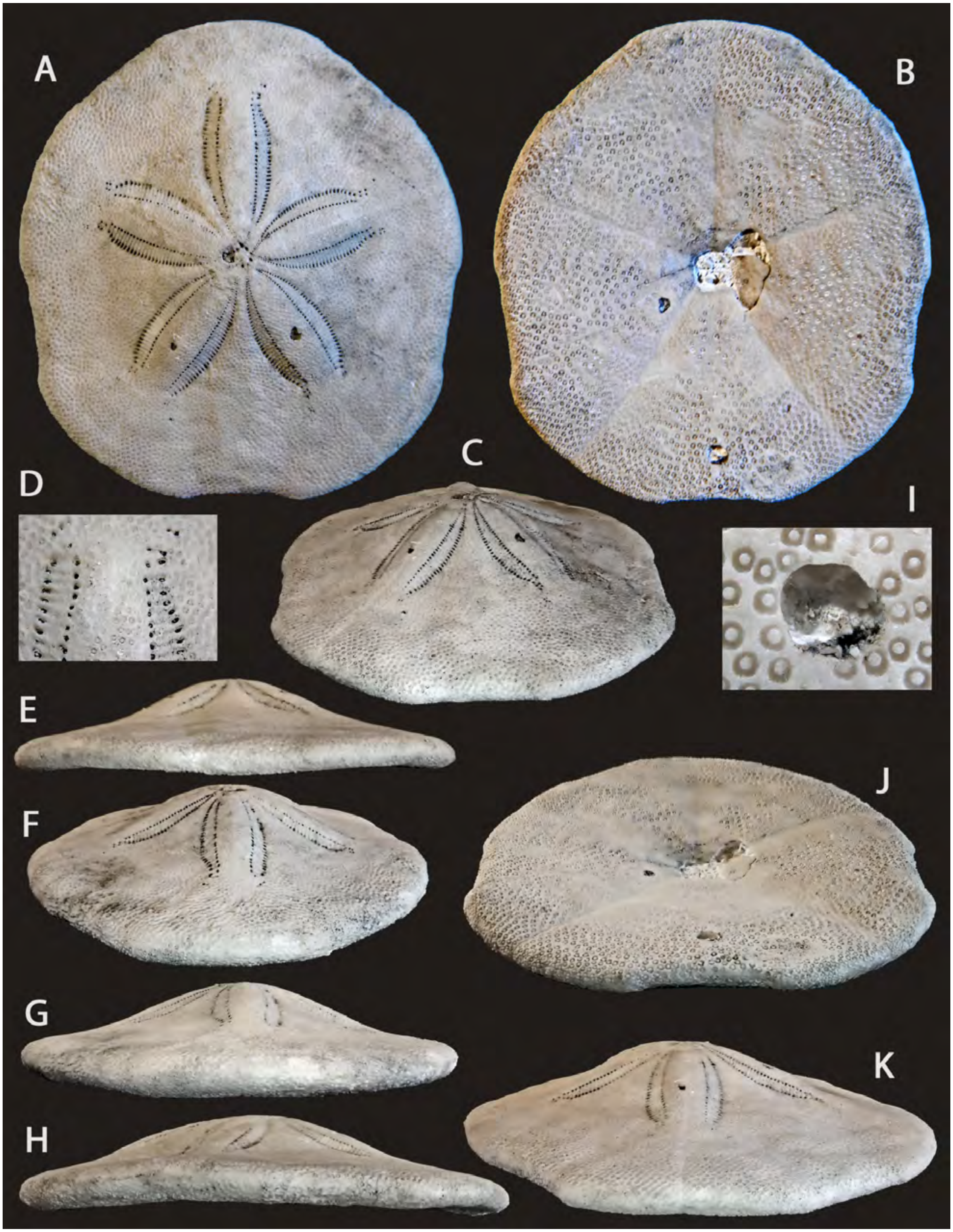


Figure 65: *Clypeaster* sp. B., (UF 338008), 49 mm TL, 45 mm TW, 9 mm TH, Lower Oligocene, basal beds of Suwannee Limestone, Vulcan Quarry (FM-IP HE038), west of Brooksville, Hernando County, Florida. A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: distal end of petaloid portion of ambulacrum III. E: posterior. F: tilted aboral viewpoint from anterior. G: anterior. H: left side. I: periproct. J: tilted oral viewpoint from posterior. K: oblique lateral viewpoint from posterior.

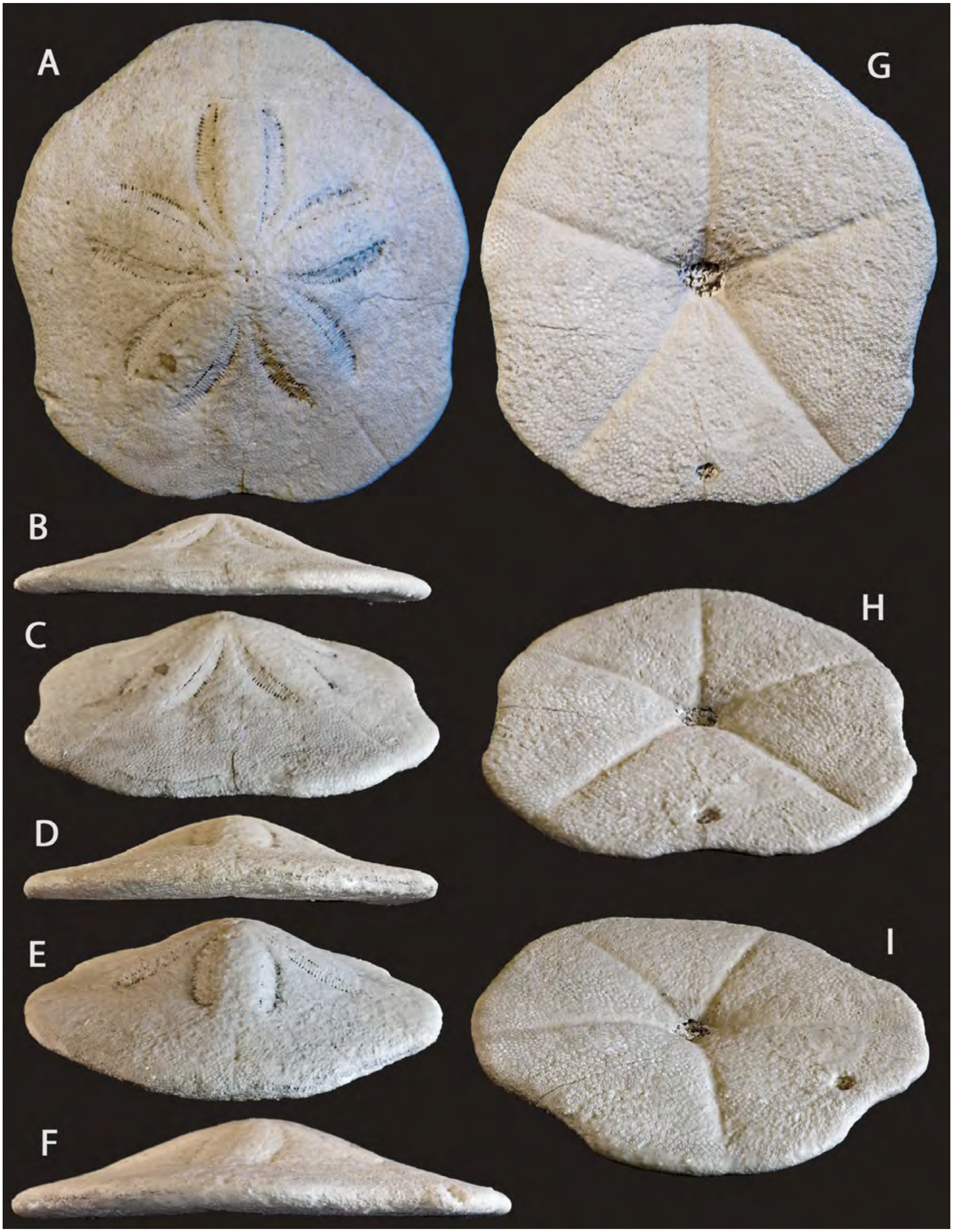


Figure 66: *Clypeaster* sp. B., (UF 338009), 64 mm TL, 60 mm TW, 13 mm TH, Lower Oligocene, basal beds of Suwannee Limestone, Vulcan Quarry (FM-IP HE038), west of Brooksville, Hernando County, Florida. A: aboral. B: posterior. C: tilted aboral viewpoint from posterior. D: anterior. E: tilted aboral viewpoint from anterior. F: left side. G: oral. H: tilted oral viewpoint from posterior. I: oblique oral viewpoint from posterior.

stone in Jasper County, Mississippi. Unfortunately, neither Conrad nor Stefanini provided more specific locality information than Jasper County, Mississippi for their respective specimens.

The specimen Stefanini figured is incomplete but shows a *C. rogersi* with a slightly thinner than typical margin, and more elevated apical area (the same traits Conrad used to distinguish his *C. turgida*/*tumidus* from *C. rogersi*). Subsequent recognition of Conrad's *M. turgida* would likely require Stefanini's *C. douvillei* to be a subjective junior synonym of *C. turgida*, and not of *C. rogersi*. According to Stefanini (1911), the holotype of *C. douvillei* is in the École Nationale Supérieure des Mines de Paris. However, we have not yet been able to examine this material, and this needs to be done before assigning a species name to *Clypeaster* sp. B. We only questionably include *C. douvillei* in the synonymy of *C. rogersi* above (following Clark and Twitchell, 1915; Cooke, 1942, 1959).

***Clypeaster* sp. C**

(Figs. 48, 67, Table 7)

Occurrence.—Lower Oligocene Suwannee Limestone, Vulcan Quarry (FM-IP HE019), northwest of Brooksville, Hernando County, Florida.

Discussion.—A single (UF 338011) specimen of *Clypeaster* with a distinctly thin, flat, test with broad petals that are wide open distally, was collected in the zone of *R. gouldii* roughly 10 m above the basal Suwannee Limestone (zone of *Clypeaster* sp. B) in the Vulcan Quarry (FM-IP HE019) northwest of Brooksville, Hernando County.

Clypeaster sp. C is characterized by a low, nearly flat test that cannot be confidently attributed any species listed in Table 6. It occurs in the same quarry as *Clypeaster* sp. B, but from a soft limestone, rich in *R. gouldii*, roughly 10 m above the basal Suwannee Limestone bed containing *Clypeaster* sp. B.

Clypeaster sp. C is readily distinguished from *C. rogersi* and *Clypeaster* sp. B by its exceptionally thin, flat, test (Table 7). The specimen measures 83.5 mm TL, 76.5 mm TW, 11.4 mm TH. The flat test is reminiscent of *C. marinanus*, but the latter has much shorter petals, with ambulacrum III on average equal to 26.5% TL vs 31.3% in *Clypeaster* sp. C., which also has much broader, distally open petals than *C. marinanus* (Table 7).

Additional specimens are necessary to fully describe this species. Considering that the Suwannee Limestone is heavily collected in the Brooksville area, it is possible that specimens have already been collected and await recognition. We hope that by highlighting this specimen as distinct from any we have been able to study, collectors will examine their material and bring additional examples to light.

Order **ECHINOLAMPADACEA** Mongiardino Koch et al., 2018
Suborder **CASSIDULOIDA** Agassiz and Desor, 1847
Family **EURHODIIDAE** Souto et al., 2019
Genus ***Eurhodia*** Haime in d'Archiac and Haime, 1853

Eurhodia patelliformis (Bouvé, 1851)

(Fig. 68)

Catopygus patelliformis Bouvé, 1851. p. 2. 2 txt figs.
Cassidulus patelliformis (Bouvé). Desor, 1858. p. 290.
"*Cassidulus" patelliformis* (Bouvé). Cotteau, 1888. p. 521.
Cassidulus patelliformis (Bouvé). Stefanini, 1911. p. 700.
Cassidulus (*Rhynchopygus*?) *patelliformis* (Bouvé). Clark and Twitchell, 1915. p. 143. pl. 66, figs. 3a-d.
Cassidulus (*Rhynchopygus*) *depressus* Twitchell in Clark and Twitchell, 1915. p. 144. pl. 66, figs. 4a-e, 5a-b.
Procassidulus patelliformis (Bouvé). Lambert and Thiéry, 1921. p. 362.
Procassidulus depressus (Twitchell). Lambert and Thiéry, 1921. p. 362.
Eurhodia patelliformis (Bouvé). Cooke, 1942. p. 35. pl. 5, figs. 1-4.
Cassidulus (*Rhynchopygus*) *depressus* Twitchell. Sánchez-Roig, 1949. p. 141.

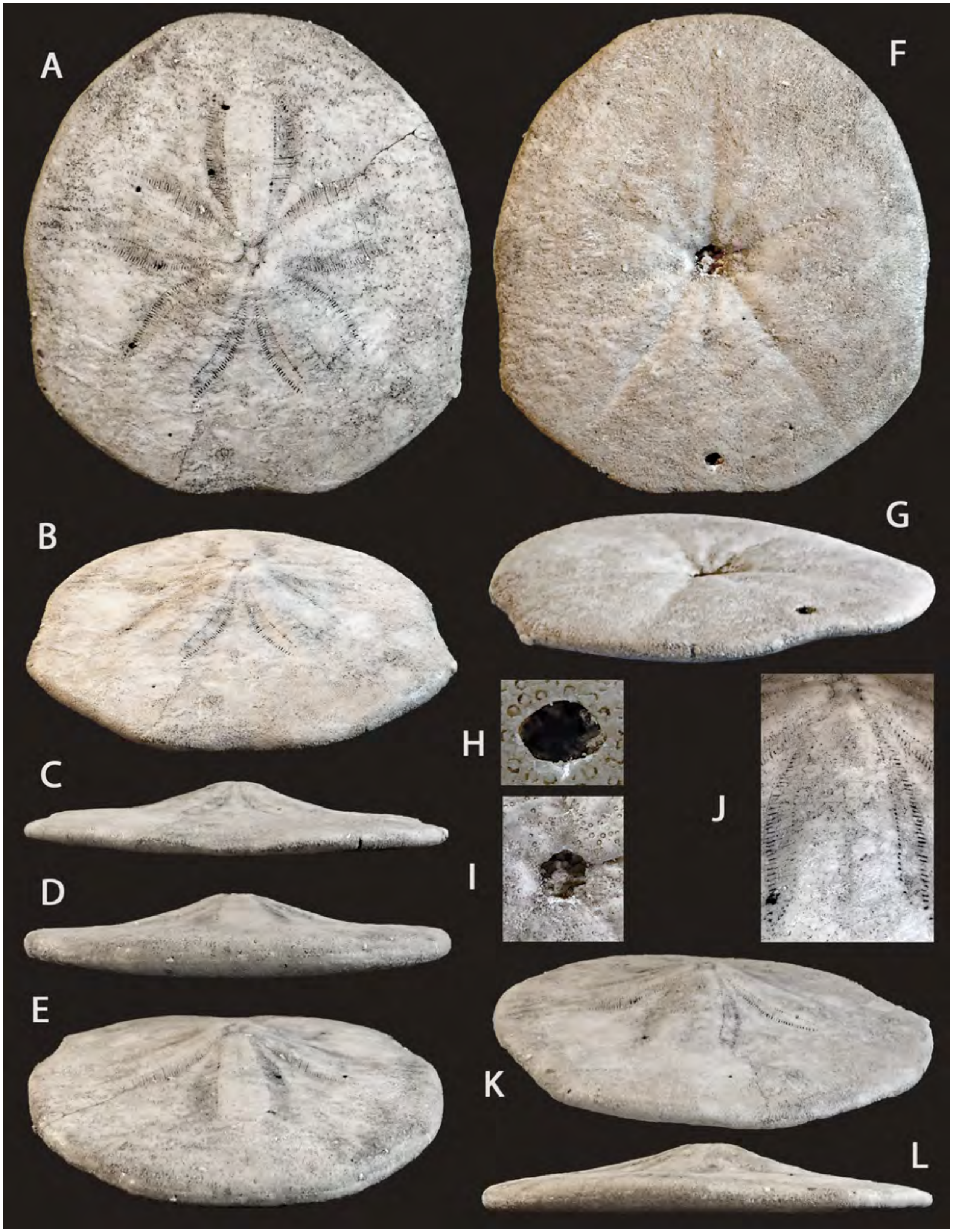


Figure 67: *Clypeaster* sp. C., (UF 338011), 83 mm TL, 76 mm TW, 11 mm TH, Lower Oligocene Suwannee Limestone, ~10 m above quarry floor, Vulcan Quarry (FM-IP HE019) west of Brooksville, Hernando County, Florida. A: aboral. B: tilted aboral viewpoint from posterior. C: posterior. D: anterior. E: tilted posterior viewpoint from anterior. F: oral. G: oblique oral viewpoint from posterior. H: periproct. I: peristome. J: ambulacrum V. K: oblique lateral viewpoint from posterior. L: left side.

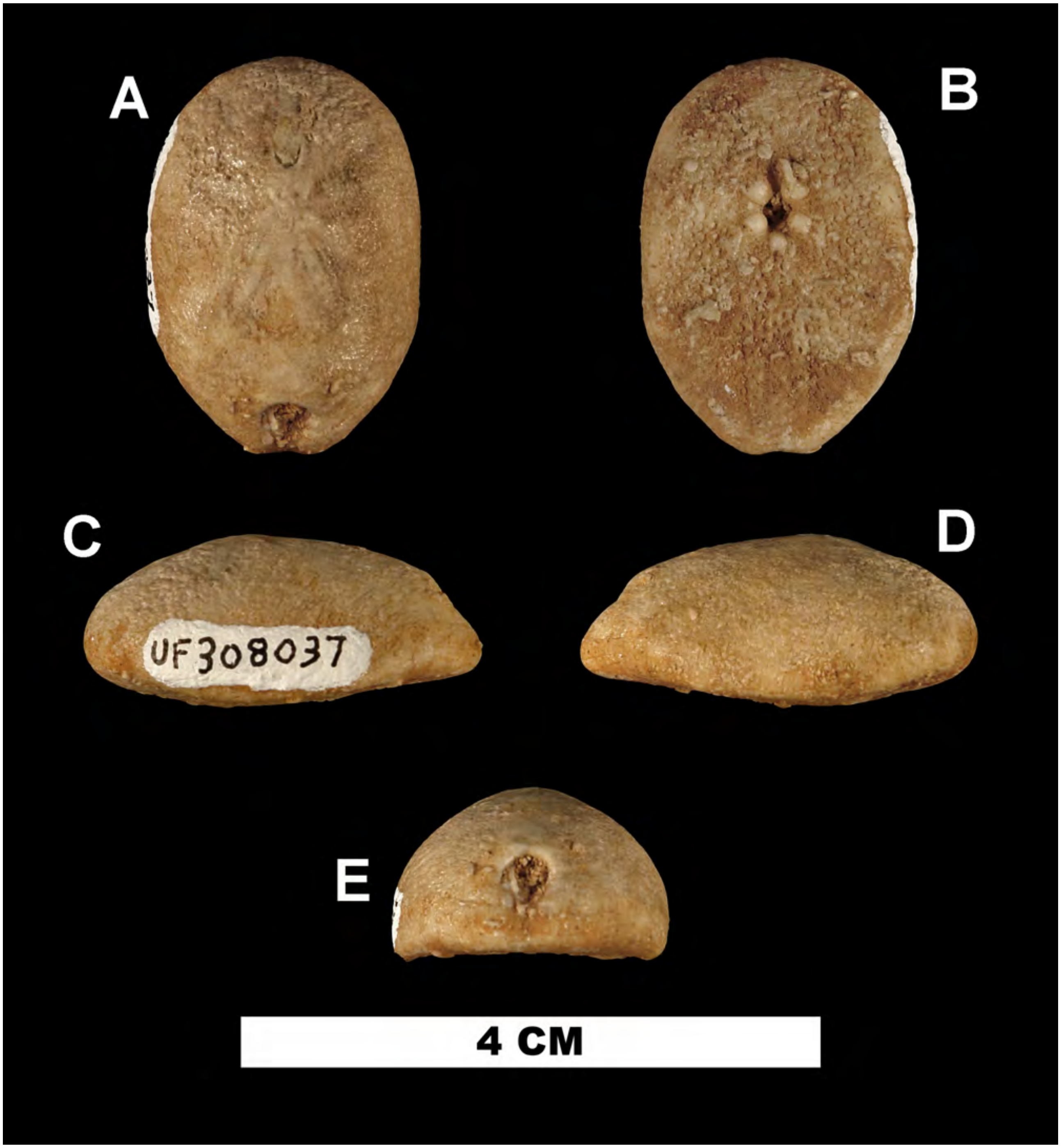


Figure 68: *Eurhodia patelliformis* (UF 308037), 27 mm TL, 18 mm TW, 11 mm TH, upper portion Upper Eocene Ocala Limestone, Dixie County, Florida (FM-IP DI013). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Eurhodia patelliformis (Bouvé). Cooke, 1959. p. 64. pl. 22, figs. 7-10.
Eurhodia patelliformis (Bouvé). Toulmin, 1977. p. 341. pl. 65, fig. 4-6.
Eurhodia patelliformis (Bouvé). Osborn et al., 2016. tbl 2.

Occurrence.—This is an Upper Eocene species that occurs throughout *Oligopygus haldemani* and *Oligopygus wetherbyi* Zones of the OLS, but has not been documented from the *Oligopygus phelani* Zone in the lower portion of the unit. *Eurhodia patelliformis* occurs at numerous localities in Jackson County, notably the Brooks Quarries northwest of Marianna (FM-IP JA009, JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039). It is also present west of Dowling Park, Lafayette County (FM-IP LF002); south of Tennille (FM-IP DI001), Dixie County, and the O'Brien Quarry north of Branford, Suwannee County (FM-IP SU002), among other localities.

Eurhodia patelliformis also occurs in the Yazoo Formation of Alabama (Toulmin, 1977) and the upper OLS of Georgia. The type locality of *E. patelliformis* and *Cassidulus depressus* Twitchell in Clark and Twitchell, 1915 (subjective junior synonym of *E. patelliformis*) is in Baker County, Georgia. Sánchez-Roig (1949) documented specimens he attributed to *Cassidulus* (*Rhynchopygus*) *depressus* Twitchell in Clark and Twitchell, 1915, in Cuban strata, which Cooke (1959) included in the synonymy of *E. patelliformis*.

Discussion.—Bouvé (1851) described *Catopygus patelliformis* from the Paleogene strata of Georgia and though his description is somewhat limited, he figured the species well. Twitchell in Clark and Twitchell (1915), better described the species and stated the holotype was likely collected in Baker County, Georgia.

This small species of *Eurhodia* is commonly found in northern Florida where it is often associated with *O. haldemani* and *W. johnsoni* in Jackson County. We figure a specimen (UF 308037) from Brooks Quarry (FM-IP JA009) that measures 27 mm TL, 18.5 mm TW, and 11 mm TH (Fig. 68).

Family **CASSIDULIDAE** L. Agassiz and Desor, 1847

Genus ***Rhyncholampas*** A. Agassiz, 1869

The State of *Rhyncholampas* Systematics in the Region

Many species of *Rhyncholampas* are recognized in the Cenozoic strata of the eastern United States. Here, a discussion concerning *Rhyncholampas* is provided to clarify what we consider to be a member of this genus.

Smith and Kroh (2011) noted that *Rhyncholampas* is usually distinguished from *Cassidulus* by its larger test, broader, lanceolate petals, generally more posterior periproct, and more developed phyllodes with more occluded plates. However, Smith and Kroh (2011) also stated that these differences are largely size related, and it was not clear that there is sufficient evidence to merit keeping the two genera separate.

Souto et al. (2019: 651) brought some clarity by providing emended diagnoses for *Cassidulus* and *Rhyncholampas*. Their diagnosis for *Rhyncholampas* was: "Small to large cassidulids of varying test shape. Anterior paired petals tulip or leaf-shaped; posterior petals bowed. Paired petals with unequal number of pores in a and b columns (difference up to four pore pairs in anterior paired petals, up to ten pore pairs in posterior paired petals). Poriferous zones with three or more reduced primary tubercles. Periproct transverse, with prominent aboral hood. Posterior region of test sometimes truncated. Six to ten interambulacral plates between basicoronal plate 5 and base of periproct. Interambulacrum 5 naked zone usually wide, finely pitted, although pits vary from absent to large. Bourrelets bulged or pointed; bourrelet 5 often convex, projecting towards peristome. Outer column of anterior phyllodes with five to 12 phyllopores per half; posterior phyllodes with eight to 12 phyllopores per half; occluded plates often scattered. Phyllopores in large specimens often disorganized throughout phyllodes. Sphaeridia concealed by thin layer of stereom (fossils could have lost pit covering or pits in some species possibly open)."

Mooi (1990a) pointed out that as with *Cassidulus*, any treatment of fossil species must take into consideration comparison with the Recent type species of the genus. Although Kier (1962) accomplished a substantial revision of the cassiduloid echinoids, including examination of types, considerable work remains to assign members of the Cassidulidae, which has been a dumping ground for species and genera of uncertain affinities. The phylogenic analysis of Souto et al. (2019) concluded by mentioning species they considered of undetermined genus affinities, such as *R. conradi* and *R. carolinensis* (Twitchell in Clark and Twitchell, 1915), which we retain in *Rhyncholampas*.

Kier (1962: 174 and 180) moved *Cassidulus sabistonensis* (Kellum, 1931), *C. georgiensis, C. alabamensis* (Twitchell in Clark and Twitchell, 1915), *C. ericsoni,* and *C. gouldii* to *Rhyncholampas*. Cooke (1959) considered *C. conradi*, with its subspecies *C. conradi carolinensis*, to belong to the subgenus *Plagiopygus*. Kier (1962: 186) considered *Plagiopygus* a synonym of *Rhyncholampas*, which consequently moved *R. conradi* into *Rhyncholampas*. Kier (1962) left *Cassidulus trojana* in *Cassidulus* from the fossil fauna of the region. However, Carter and Beisel (1987) placed *C. trojana* in *Eurhodia*, in part because of the lack of naked areas on the oral surface, larger oral tubercles, and the presence of pits on the oral surface near the peristome. Nevertheless, Souto et al. (2019) subsequently placed this species in *Rhyncholampas*, with which we agree.

The result is that the Cenozoic deposits of eastern North America contain no species in *Cassidulus*. Under older usage of the name [i.e., pre-Kier (1962) and Carter and Beisel (1987)], *Cassidulus* was very well represented with seven species and three subspecies (Cooke, 1959). Therefore, there is a dramatic difference between the cassiduloid taxonomy of the present monograph and that of Cooke (1959).

The genus *Rhyncholampas*, as currently recognized, contains 15 species in the eastern United States, ranging from the Middle Eocene to Upper Pleistocene: *R. alabamensis* (Twitchell in Clark and Twitchell, 1915), Oligocene; *R. ayresi* Kier, 1963, Pleistocene; *R. carolinensis* (Twitchell in Clark and Twitchell, 1915), Eocene; *R. chipolanus* Oyen and Portell, 1996, Miocene; *R. conradi* (Conrad, 1850), Eocene; *R. ericsoni* (Fischer, 1951), Eocene; *R. evergladensis* (Mansfield, 1932), Pliocene; *R. fontis* (Cooke, 1942), Eocene; *R. georgiensis* (Twitchell in Clark and Twitchell, 1915), Eocene; *R. gouldii,* Oligocene; *R. meansi* Osborn et al., 2020, Pleistocene; *R. sabistonensis* (Kellum, 1931), Pleistocene; *R. trojana* (Cooke, 1942), Eocene; and *Rhyncholampas bao* n. sp., which occurs in the same strata as *R. mariannaensis* n. sp.

Therefore, the Cenozoic fauna of the eastern United States currently includes 15 species of *Rhyncholampas*, and the Cenozoic strata of the remainder of the eastern Americas and Caribbean region potentially includes at least 11 additional species. Many of these taxa, especially the Cuban forms described by Sánchez-Roig, are poorly described and figured, most with inaccessible or lost holotypes that will likely remain poorly understood. Remarks on many of these species are included in the discussion below for *Rhyncholampas mariannaensis* n. sp.

Rhyncholampas conradi (Conrad, 1850)
(Figs. 69-71, 88)

Catopygus conradi Couper MS, Conrad, 1850. p. 39, pl. 1, fig. 9.

Nucleolites lyelli Conrad, 1850. p. 40, pl. 1, fig. 14.

Cassidulus lyelli (Conrad). Conrad, 1865. p. 75.

Pygorhynchus lyelli (Conrad). Cotteau, 1888. p. 550.

Cassidulus conradi Couper in Conrad. Stefanini, 1911. p. 700.

Cassidulus (*Pygorhynchus*) *conradi* (Conrad). Clark and Twitchell, 1915. p. 145. pl. 67, figs. 1a-f.

Cassidulus (Rhynchopygus) lyelli (Conrad). Clark and Twitchell, 1915. p. 141. pl. 65, figs. 4a-d.

Rhyncholampas lyelli (Conrad). Lambert and Thiéry, 1921. p. 370.

Rhyncholampas conradi (Conrad). Lambert and Thiéry, 1921. p. 370.

Cassidulus (*Paralampas*) *conradi* (Conrad). Cooke, 1942. p. 33.

Cassidulus (Paralampas) lyelli (Conrad). Cooke, 1942. p. 33.

Cassidulus conradi lyelli (Conrad). Cooke, 1959. p. 60. pl. 25, figs. 1, 2.

Cassidulus (*Plagiopygus*) *conradi* (Conrad). Cooke, 1959. p. 59-60. pl. 25, figs. 3-6.

Rhyncholampas conradi (Conrad). Kier, 1962. p. 186 (considered *Plagiopygus* a synonym of *Rhyncholampas*).

Cassidulus conradi (Conrad). Toulmin, 1977. pp. 399-340. pl. 65, figs.1-3.

Rhyncholampas conradi (Conrad). Osborn et al., 2016. tbl. 2.

Occurrence.—Within Florida, *R. conradi* occurs throughout the *Oligopygus haldemani* and

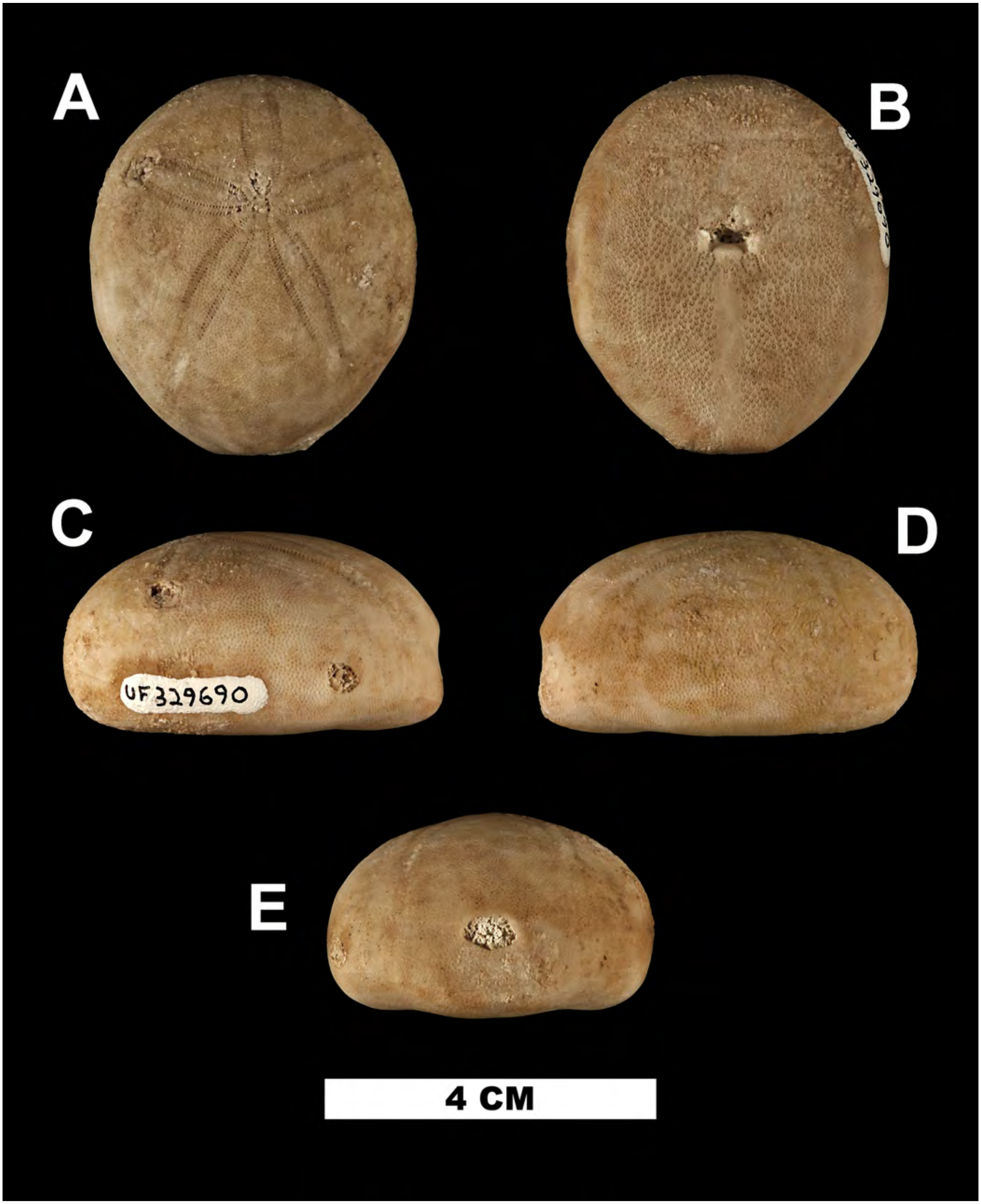


Figure 69: *Rhyncholampas conradi* (UF 329690), 46 mm TL, 40 mm TW, 24 mm TH, Upper Eocene upper Ocala Limestone in Marianna Lime Quarry, Jackson County, Florida (FM-IP JA009). A: aboral. B: oral. C: left side. D: right side. E: posterior.

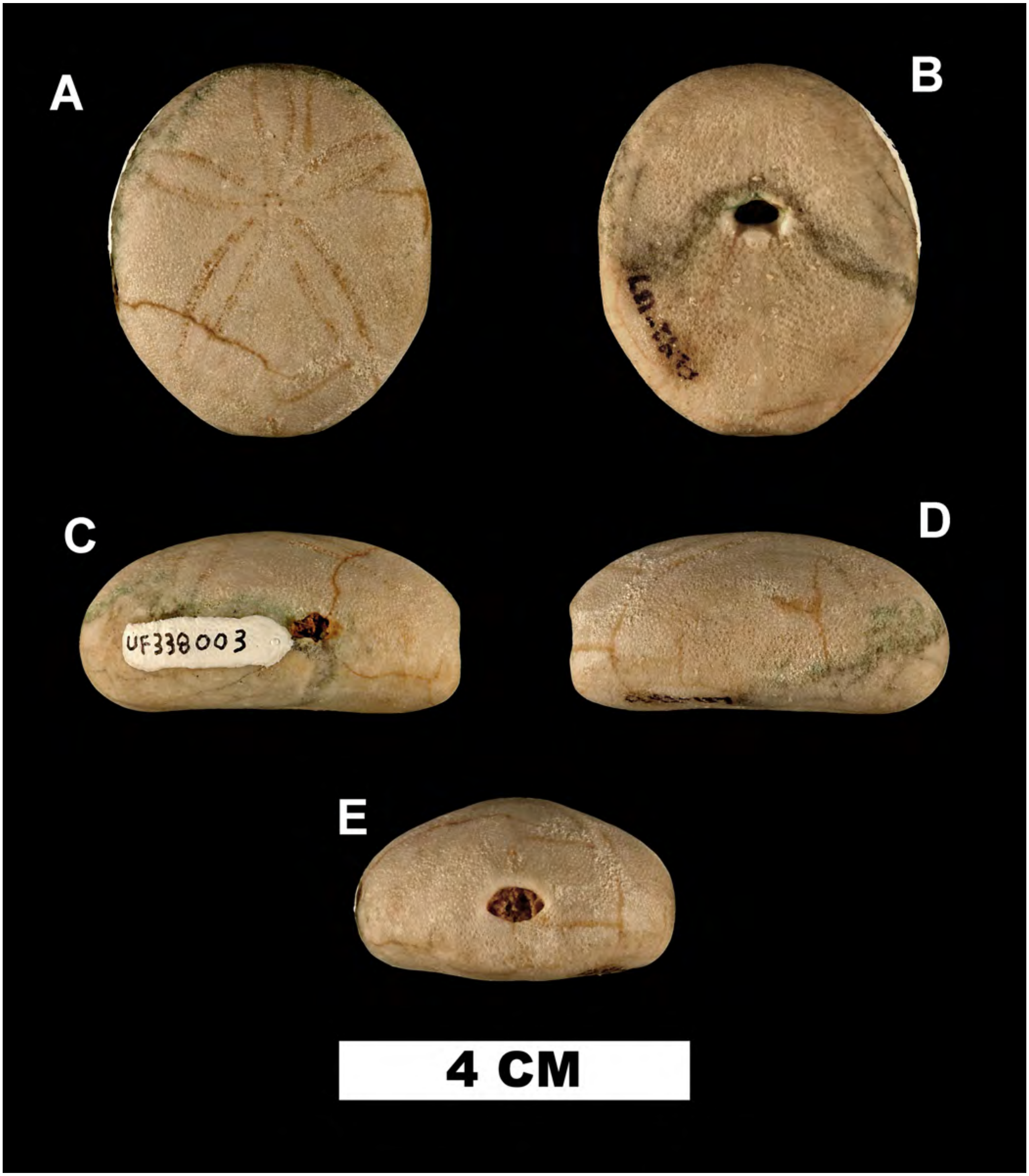


Figure 70: *Rhyncholampas conradi* (UF 338003), 41 mm TL, 35 mm TW, 19 mm TH, *Oligopygus wetherbyi* Zone Upper Eocene, upper Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: right side. E: posterior.

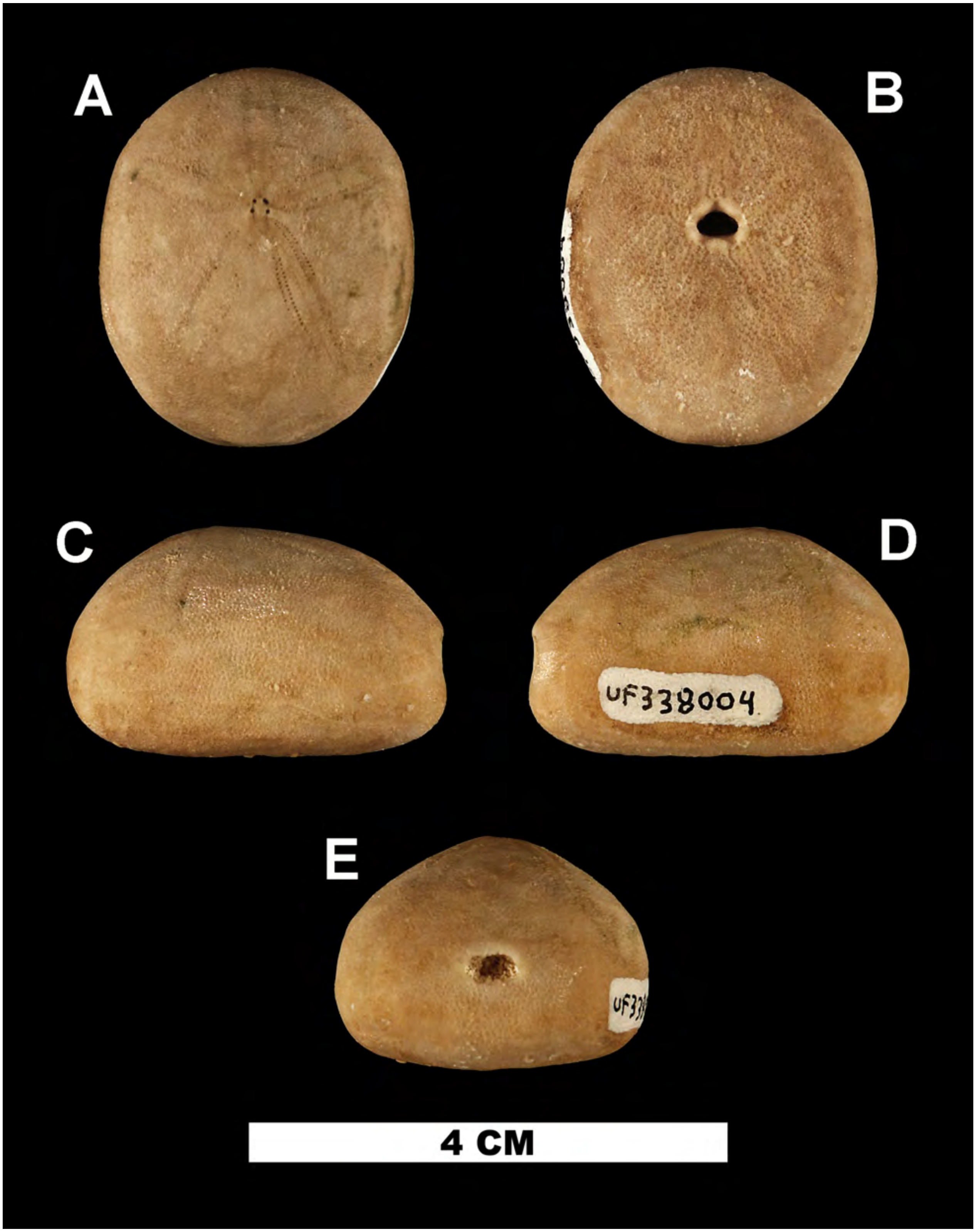


Figure 71: *Rhyncholampas conradi* (UF 338004), 32 mm TL, 27 mm TW, 20 mm TH, *Oligopygus wetherbyi* Zone Upper Eocene, upper Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Oligopygus wetherbyi Zones of the OLS and is especially abundant in Jackson County (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039) where it occurs with *O. haldemani*. The species also occurs south of Tennille (FM-IP DI001), Dixie County, west of Dowling Park, Lafayette County (FM-IP LF002); northwest of Mayo, Lafayette County (FM-IP LF001), and north of Branford near O'Brien (FM-IP SU002), to name only a few localities.

Rhyncholampas conradi also occurs in the Upper Eocene of Alabama (Toulmin, 1977) and Georgia (Carter, 1987a, 1989; Cooke, 1959).

Discussion.—This species was named in honor of Timothy Abbott Conrad, the individual to whom the name is also attributed. However, Conrad (1850) named the species from the white limestone of Palmyra, Lee County, Georgia, stating that the collector, J. Hamilton Couper, Esq., specifically requested the species name. Conrad (1850) was merely honoring the request of the collector, and as it remains only practice, and not an ICZN rule, not to name a new species after oneself, this was not unusual for the time. Conrad (1850) attributed the species name to an unpublished manuscript of Mr. Couper.

Conrad (1850) also described *Nucleolites lyelli* from an internal mold collected in burrstone in Baker County, Georgia. Cooke (1942) indicated that specimens of *Rhyncholampas lyelli* Conrad, 1850 from Florida are higher in front than behind, thus differentiating them from those in Georgia, which are uniformly inflated. He stated that this difference is likely not of specific importance as other species in the genus show considerable variation in tumidity. This is accurate, as discussed in the remarks for *R. gouldii* and *R. georgiensis* below.

Cooke (1959) considered *R. lyelli* to be a subspecies of *R. conradi* and stated that although *R. lyelli* is more ovate and less truncate posteriorly than *R. conradi,* it is otherwise indistinguishable from *R. conradi*. We do not recognize *R. lyelli* as a distinct species, nor do we consider it worth retaining it as a subspecies as asserted by Cooke (1959). Both *R. conradi* and *R. lyelli* share the same stratigraphic horizon in the OLS and specimens of both morphotypes (specimens with distinctly constricted posteriors and more ovate specimens) are often found at the same locality from the same horizon, with smaller specimens tending to be more nearly ovate.

It is possible, therefore, to make a substantial collection of *Rhyncholampas* from this stratum, select more ovate, smaller forms and call them *R. lyelli*, as well as separate out specimens that are more truncated posteriorly and somewhat larger that would be called *R. conradi*, but such selectivity would ignore clear intermediates between the forms throughout the rest of the population. As implied by Cooke (1959) when he made *R. lyelli* a subspecies, *R. conradi lyelli*, there is no empirical support to maintain *R. lyelli* as distinct species or subspecies, so we consider it a subjective junior synonym of *R. conradi.*

Fischer (1951) documented the occurrence of *R. conradi lyelli* in the *Oligopygus phelani* Zone of the lower portion of the OLS in Levy County. However, Cooke (1959) referred those specimens to *R. georgiensis*. We are unaware of verified occurrences of *R. conradi* from the *Oligopygus phelani* Zone.

Rhyncholampas ericsoni (Fischer, 1951)
(Figs. 72, 73, 88)

Cassidulus ericsoni Fischer, 1951. p. 65. txt figs. 6-10; pl. 2, figs. 1, 2; pl. 3, figs. 1-3.

Cassidulus ericsoni (Fischer). Cooke, 1959. pp. 57-58. pl. 24, figs. 13-16.

Rhyncholampas ericsoni (Fischer). Kier, 1962. pp. 174, 180.

Rhyncholampas ericsoni (Fischer). Toulmin, 1977. pp. 345-346. pl. 69, figs.7-9.

Rhyncholampas ericsoni (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—This species has not been documented outside the *Oligopygus phelani* Zone of the OLS of Florida (formerly the Inglis Formation). The type locality is along the Withlacoochee River in Levy County, but the species also occurs westward at the mouth of the river (FM-IP LV024) and is found

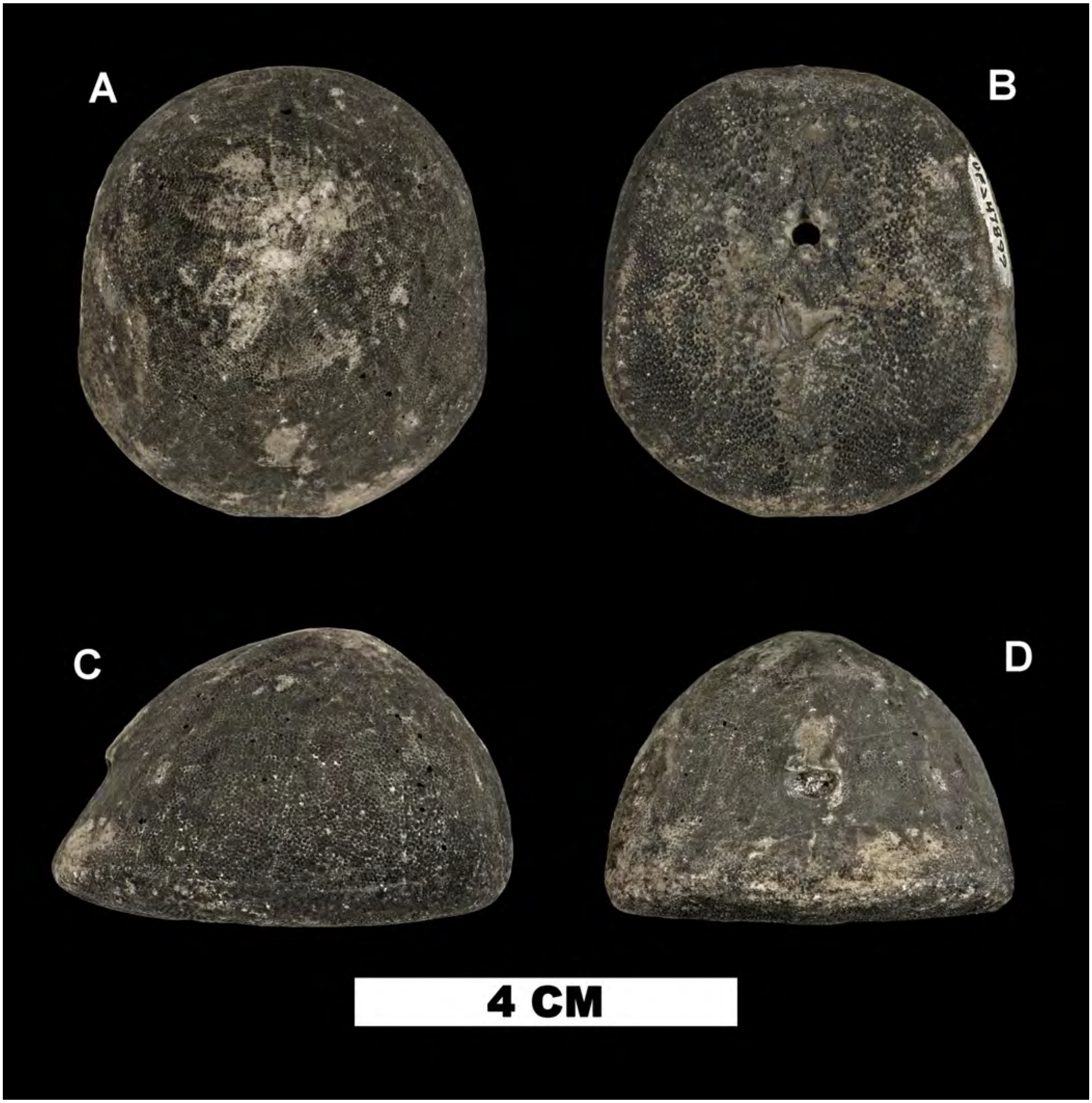


Figure 72: *Rhyncholampas ericsoni* (UF 247899) holotype, 48 mm TL, 43.5 mm TW, 32 mm TH, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, Citrus County, Florida (FM-IP CI052). A: aboral. B: oral. C: right side. D: posterior.

along the banks of the Cross Florida Barge Canal south of Inglis (FM-IP CI001) and in numerous small quarries in Levy County (FM-IP LV114).

Discussion.—*Rhyncholampas ericsoni* is similar in general appearance to *R. gouldii* but its periproct is much farther towards the anterior (Cooke, 1959). *Rhyncholampas ericsoni* occurs with *R. georgiensis* (form described by Fischer [1951] as *R. globosus*), but its lower, less rotund, and slightly more elongate test readily differentiates it from *R. georgiensis*. See the discussion for *R. mariannaensis* n. sp. for distinction of these two taxa.

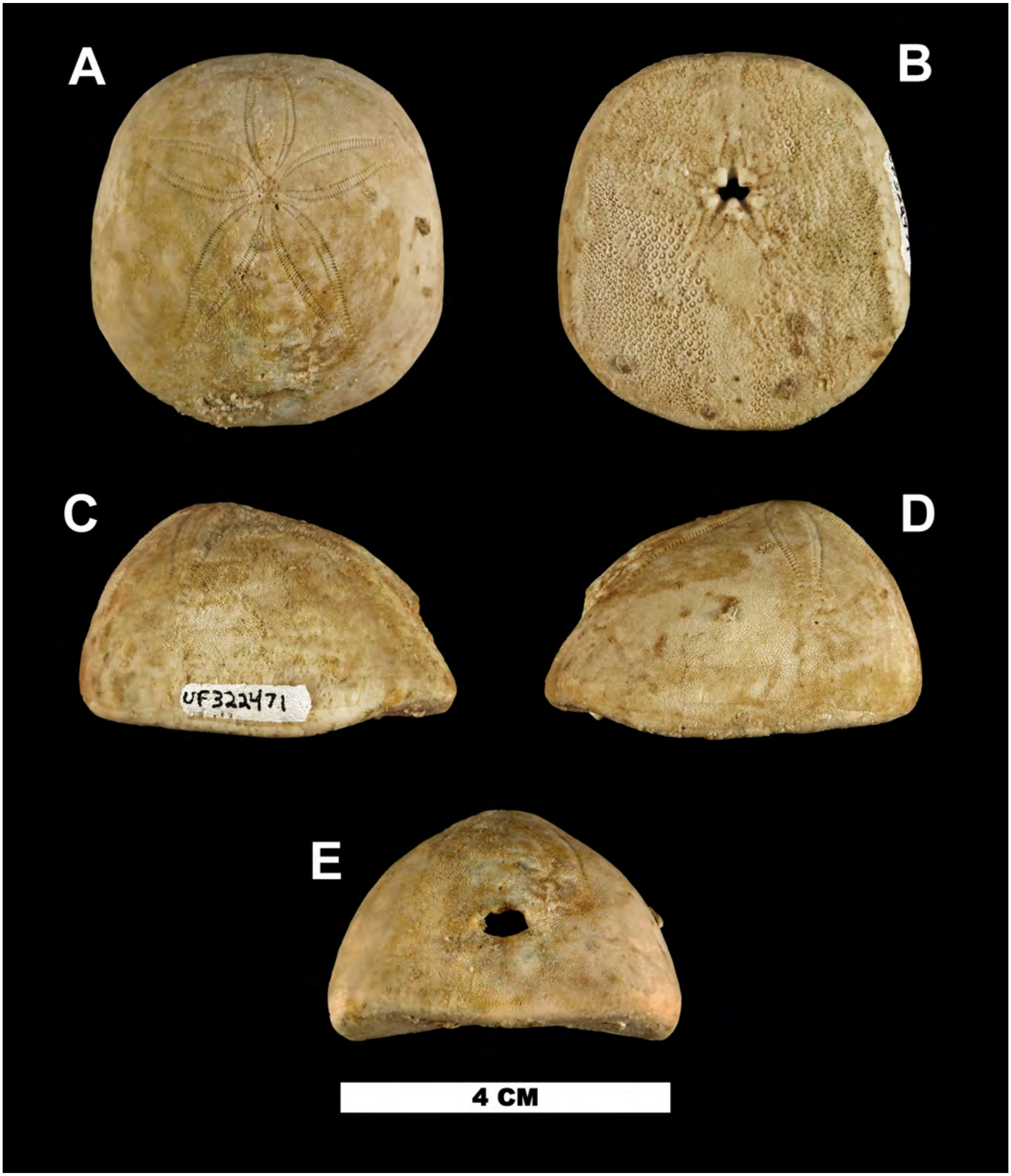


Figure 73: *Rhyncholampas ericsoni* (UF 322471), 44.7 mm TL, 42.1 mm TW, 27.5 mm TH, *Oligopygus phelani* Zone, Upper Eocene lower Ocala Limestone, Citrus County, Florida (FM-IP 6341). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Rhyncholampas fontis (Cooke, 1942)
(Figs. 74)

?*Cassidulus* (*Galerolampas*) *fontis* Cooke, 1942. p. 35. pl. 2, figs. 26-29.

Echanthus georgiensis (Twitchell). Cooke, 1959. pp. 62-63. pl. 26, figs. 13-16 (in part, Cooke considered *R. fontis* a subj. jr. syn. of *E. georgiensis*).

Rhyncholampas fontis (Cooke). Souto et al., 2019. pp. 643, 652. tbl. 4.

Occurrence.—This species is not documented outside of its type locality, 487 m below the surface in a well drilled near Falling Waters, 4 mi. south of Chipley (Station 8872g, E. C. Butler collector), in Washington County (Cooke, 1942). Cooke (1942) surmised the specimen came from Lower Eocene or Paleocene strata.

Discussion.—The type (USNM 498997) is the only known specimen of the species, and although it is exceptionally unlikely it would be found while surface collecting in Florida, we include it herein for completeness.

Cooke (1959) subsequently placed *Cassidulus fontis* in synonymy with *Gitolampas georgiensis*, stating that the periproct of *C. fontis* was likely vertical prior to being crushed and distorted.

However, as indicated by Zachos (2017), the type of *C. fontis* has better developed bourrelets and a transverse peristome, with no evidence of it being crushed along a vertical axis as stated by Cooke (1959). *Cassidulus fontis* is therefore not conspecific with *G. georgiensis*, and we recognize this form as a distinct species within *Rhyncholampas*. Souto et al. (2019) confirmed this genus assignment.

The holotype of *R. fontis* (USNM 498997) was recovered from well washings originating from an unknown formation and was included in a larger lot of fossils that Zachos (2017) stated is now lost, so associated faunas are not available to assist in stratigraphic assignment. Additional material of this species may be collected in the future, enabling better understanding of this form.

Although the holotype is slightly crushed, it is not severe enough to distort its overall test morphology. The specimen is much lower than any other *Rhyncholampas* currently recognized within the Paleogene strata of the region. With TW equal 92% of TL, the species is also more nearly circular in aboral view than any other *Rhyncholampas* known from the Paleogene of the region.

Rhyncholampas georgiensis (Twitchell in Clark and Twitchell, 1915)
(Figs. 75-79, 88)

Cassidulus (*Pygorhynchus*) *georgiensis* Twitchell in Clark and Twitchell, 1915. p. 170, pl. 79, figs. 2a-d.

Rhyncholampas georgiensis (Twitchell). Lambert and Thiéry, 1921. p. 370.

Cassidulus (*Paralampas*) *lyelli* (Conrad). Cooke, 1942. p. 33 (in part, Cooke believed *R. georgiensis* a subjective junior synonym of *C. lyelli*).

Cassidulus (*Paralampas*) *globosus* Fischer, 1951. p. 71. pl. 4, figs. 1-5. txt figs. 8-10.

Cassidulus georgiensis globosus (Fischer). Cooke, 1959. p. 61. pl. 25, figs.11-13.

Cassidulus (*Plagiopygus*) *georgiensis* (Twitchell). Cooke, 1959. pp. 60-61. pl. 25, figs. 14-17.

Rhyncholampas georgiensis (Twitchell). Kier, 1962. p.180.

Rhyncholampas georgiensis (Twitchell). Osborn et al., 2016. fig. 2.

Occurrence.—Apart from the type locality near Bainbridge, Georgia, *R. georgiensis* occurs abundantly in two distinct localities in Florida. It occurs with *O. haldemani* in the OLS of northern Florida, especially near Marianna, Jackson County (FM-IP JA039). It also occurs in the *Oligopygus phelani* Zone near the base of the OLS (*C. globosus* of Fischer [1951]) in Levy County, notably 3.2 km southwest of Gulf Hammock (type locality of *C. globosus*), and along the Withlacoochee River west of Yankeetown (FM-IP LV024).

Discussion.—When Twitchell in Clark and Twitchell (1915), described *R. georgiensis*, he noted

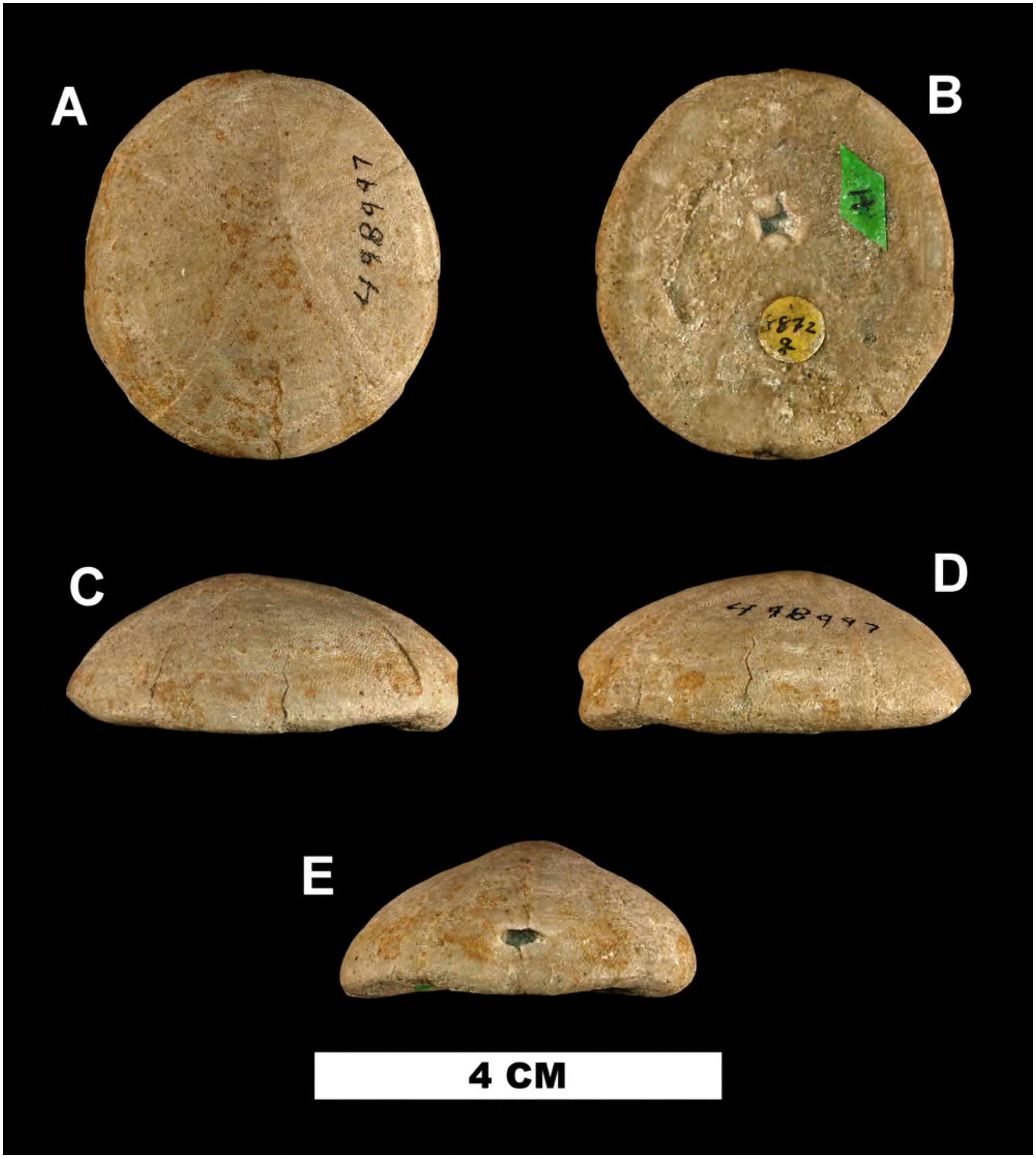


Figure 74: Holotype of *Cassidulus* (*Galerolampas*) *fontis* (= *Rhyncholampas fontis*) (USNM 498997), 38.7 mm TL, 35.8 mm TW, 16 mm TH, likely Early Eocene or Paleocene (per Cooke, 1942), well near Falling Waters, 4 mi. south of Chipley, Washington County, Florida. A: aboral. B: oral. C: left side. D: right side. E: posterior.

its rarity (represented by three specimens at the time), and provided two occurences for the species: the Flint River near Bainbridge, Georgia and 4 km north of Cuthbert, Georgia. However, the exact position of the second locality is unknown. It is unfortunate that he formed its name from a state in which it is far less abundant and widespread than in the OLS of Florida.

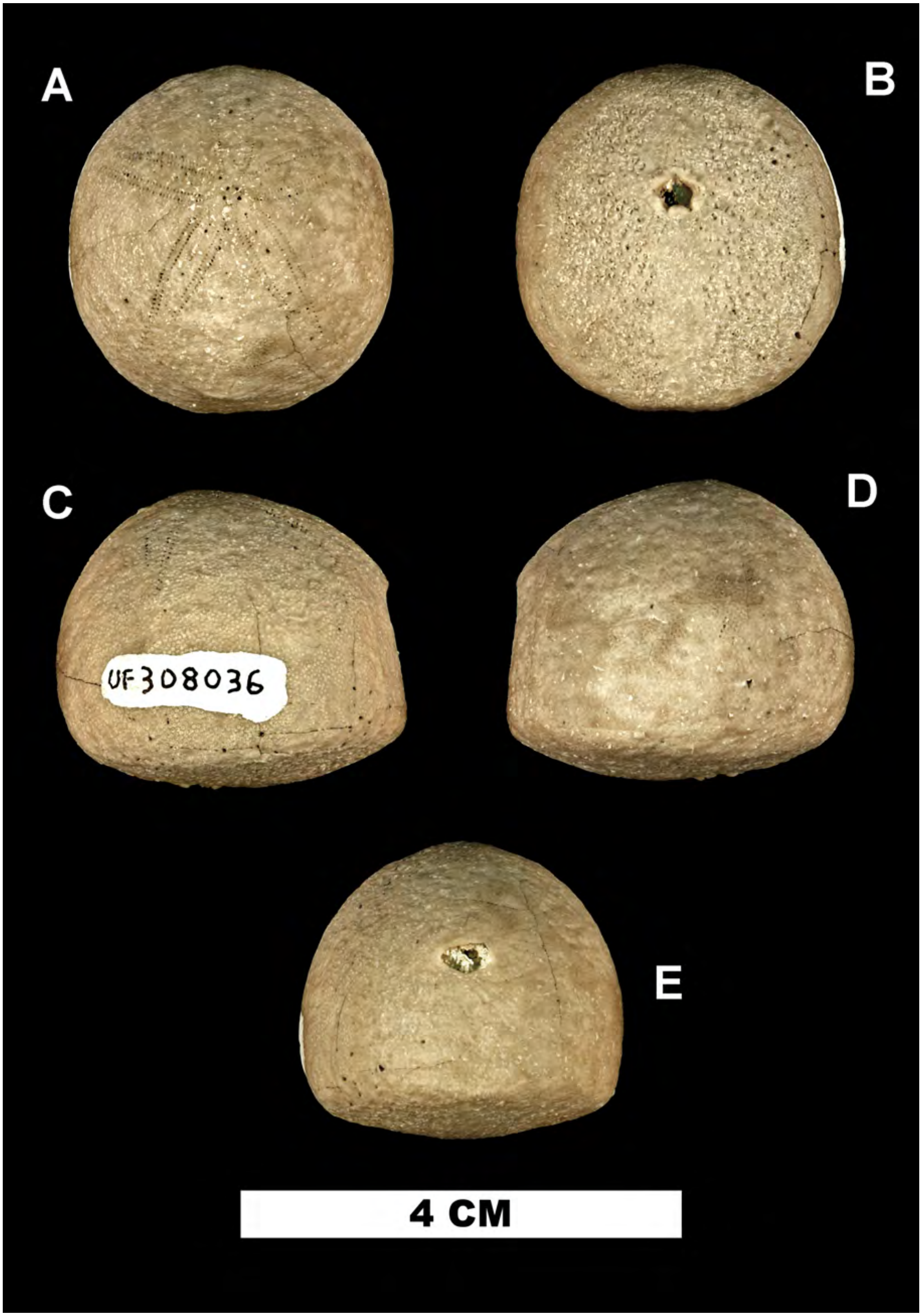


Figure 75: *Rhyncholampas georgiensis* (UF 308036), 32 mm TL, 30.5 mm TW, 28 mm TH, *Oligopygus phelani* Zone of Upper Eocene lower portion of Ocala Limestone, Levy County, Florida (FM-IP LV114). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 76: *Rhyncholampas georgiensis* (UF 329686), 28 mm TL, 26 mm TW, 23 mm TH, *Haimea brooksi* Zone of Upper Eocene, Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side. E: posterior.

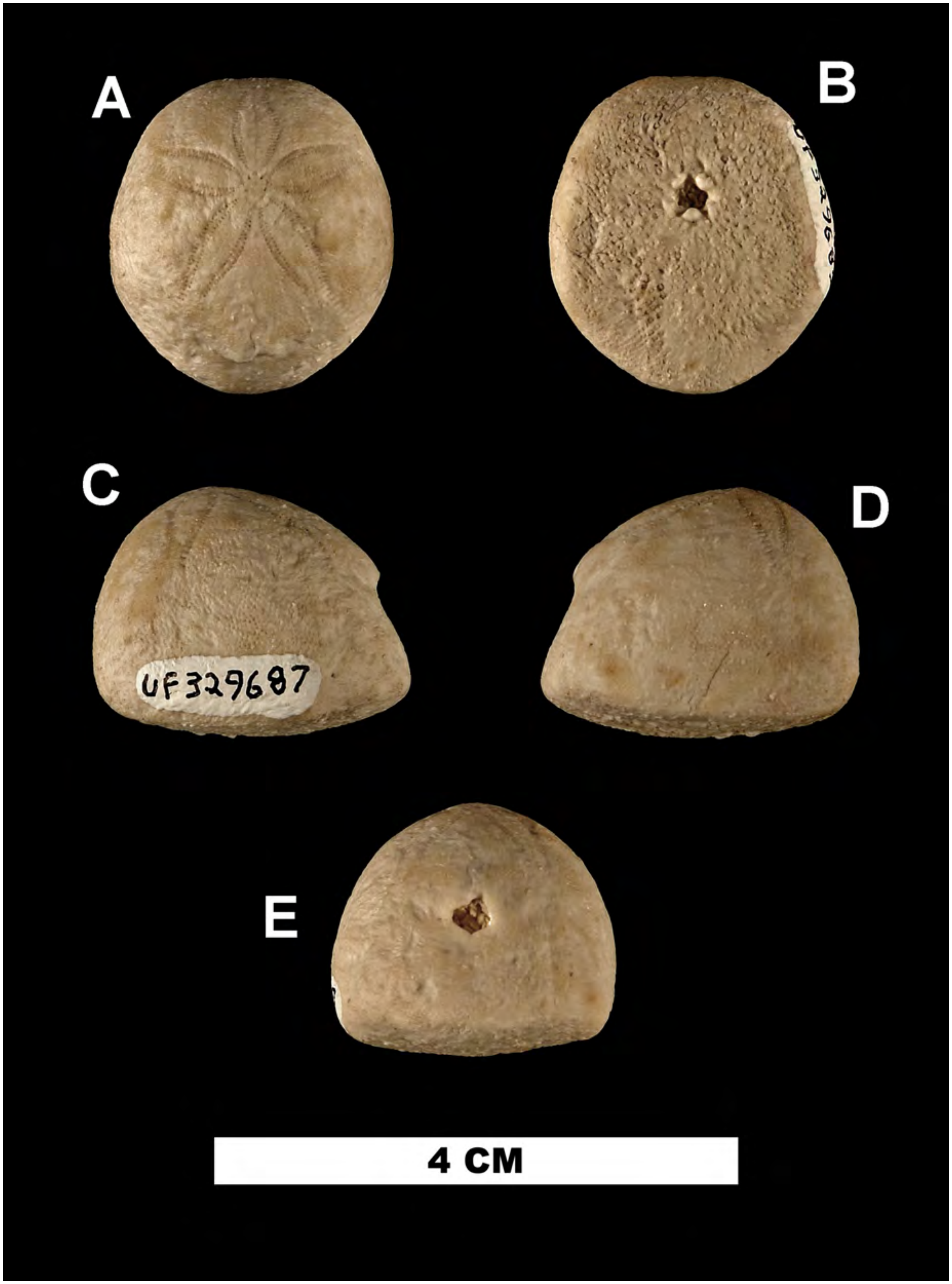


Figure 77: *Rhyncholampas georgiensis* (UF 329687), 24.5 mm TL, 22 mm TW, 19.5 mm TH, *Haimea brooksi* Zone of Upper Eocene, Ocala Limestone, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 78: Holotype of *Cassidulus globosus* (= *Rhyncholampas georgiensis*), UF 248491 (with original catalog number of I-5346 still on specimen), *Oligopygus phelani* Zone, Upper Eocene lower Ocala Limestone, Levy County, Florida (FM-IP LV014). A: aboral. B: oral. C: left side. D: posterior.

Rhyncholampas georgiensis largely occurs in two areas within the region: in the *Oligopygus haldemani* Zone of the OLS of northern Florida (especially Jackson County) and southwestern Georgia (the typical *R. georgiensis*), and the more southerly area in northern Citrus and southern Levy Counties, especially near Inglis, on the western Florida Peninsula (occurrences previously attributed

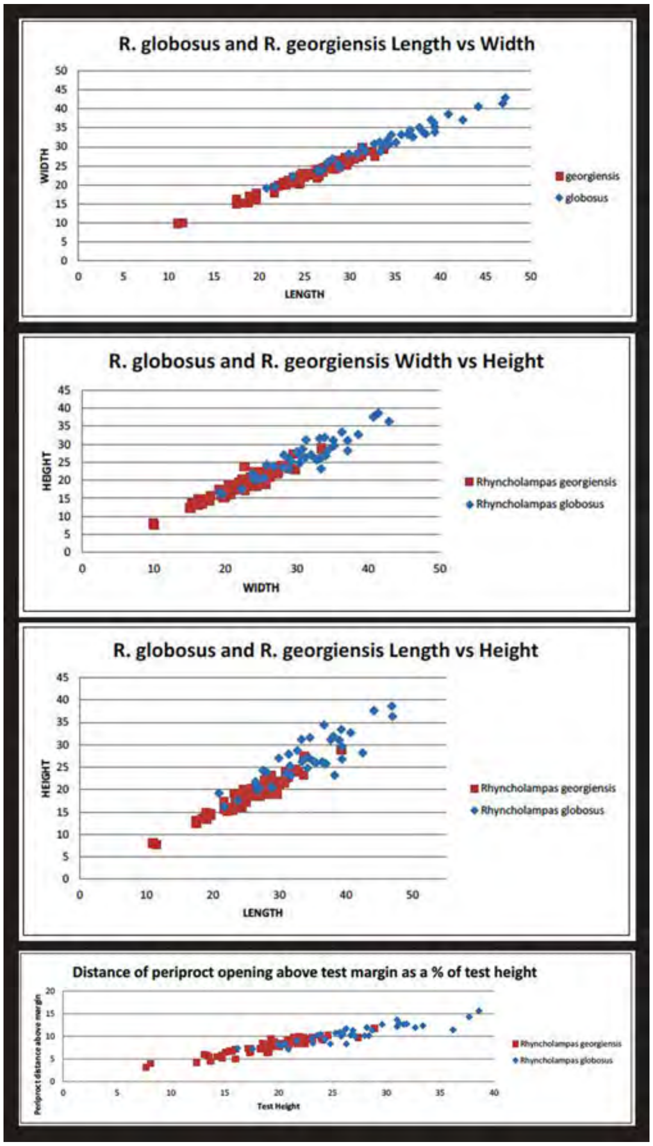


Figure 79: Comparison of various dimensions of 71 specimens of *Rhyncholampas georgiensis* from the *Haimea brooksi* Zone of the Ocala Limestone in the Brooks Quarry (FM-IP JA039), Marianna, Jackson County, Florida, and 41 specimens of *Rhyncholampas globosus* from the *Oligopygus phelani* Zone of the lower Ocala Limestone near Inglis (FM-IP LV114), Levy County, Florida. These similarities prompted us to herein designate *R. globosus* as a subjective junior synonym of *R. georgiensis*.

to *R. georgiensis globosus* in the *Oligopygus phelani* Zone of the lowermost OLS).

When Fischer (1951) described *R. globosus*, it appears he was unaware of *R. georgiensis* as he did not mention it in his consideration of other *Rhyncholampas* from the region (he compared his *R. ericsoni* to *R. trojana, R. alabamensis, R. gouldii,* and *R. lyelli*). He stated *R. globosus* is most like *R. lyelli*, from which he differentiated it by its greater size, relative height, and inflation. Had Fischer (1951) compared his *R. globosus* with *R. georgiensis*, he would likely have realized their similarities. Subsequently, Cooke (1959) designated *R. globosus* as a subspecies of *R. georgiensis* and noted that *R. globosus* is much more highly inflated than the type of *R. georgiensis,* but little more so than many specimens from Bainbridge, Georgia, the type locality of the species. We present comparisons of TH, TW, TL, and distance of periproct above the margin of these two forms (Fig. 79).

This variation in TH among different, widely separated populations is not unique in *Rhyncholampas*. McKinney et al. (2014) documented variation in TH within populations of *R. gouldii*. We likewise recognize the variation in *R. georgiensis* and do not recognize the subspecific designation of *globosus* for the Levy County specimens.

Rhyncholampas georgiensis is readily differentiated from any of its congeners in the Upper Eocene of the region by its proportionately higher test and very inflated appearance, sharply truncated anterior margin, and an oral surface that is not at all concave or depressed. See the remarks for *R. mariannaensis* n. sp., for discussion on distinguishing these two species.

Rhyncholampas gouldii (Bouvé, 1846)
(Figs. 80-82)

Pygorhynchus gouldii Bouvé, 1846. p. 192.

Pygorhynchus gouldii (Bouvé). Bouvé, 1847a. p. 437.

Pygorhynchus gouldii (Bouvé). Bouvé, 1847b. p. 142.

Nucleolites mortoni Conrad, 1850. p. 40. pl. 1, fig. 11.

Pygorhynchus gouldii (Bouvé). Bouvé, 1851. p. 2. 2 txt figs.

Pygorhynchus gouldii (Bouvé) Desor, 1858. p. 299.

Ravenelia gouldii (Bouvé). McCrady, 1859. p. 282.

Pygorhynchus gouldii (Bouvé). Cotteau, 1888. p. 550.

Nucleolites mortoni (Conrad). Boyle, 1893. p. 200.

Pygorhynchus gouldii (Bouvé). Stefanini, 1911. p. 696.

Cassidulus (*Pygorhynchus*) *gouldii* (Bouvé). Clark and Twitchell, 1915. p. 171, pl. 79, figs. 3a-d; pl. 80, figs. 1a-f, 2a-d.

Procassidulus (*Bardouinia*) *gouldii* (Bouvé). Lambert and Thiéry, 1921. p. 363.

Cassidulus (*Cassidulus*) *gouldii* (Bouvé). Cooke, 1942. p. 31.

Cassidulus (*Cassidulus*) *gouldii* (Bouvé). Cooke, 1959. pp. 57-58. pl. 24, figs. 5-12.

Rhyncholampas gouldii (Bouvé). Kier, 1962. pp. 174, 180.

Cassidulus gouldii (Bouvé). Pickering, 1970. pp. 29, 36, 66. tbl. 1.

Rhyncholampas gouldii (Bouvé). Carter and Beisel, 1987. pp. 1080-1083. fig. 1. 3.

Rhyncholampas gouldii newbernensis Kier, 1997. pp. 6-8. fig. 3. pl. 5, figs. 1-7.

Rhyncholampas gouldii (Bouvé). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 8.

Rhyncholampas gouldii (Bouvé). McKinney et al., 2014. pp. 215-219.

Occurrence.—This species is exceptionally abundant within the Suwannee Limestone at numerous Florida localities in Alachua, Columbia, Gadsden, Hamilton, Hernando, Hillsborough, Jefferson, Pasco, and Suwannee Counties. In the northern portion of the state, *Rhyncholampas gouldii* is commonly preserved as molds in the dolomitic facies of the Suwannee Limestone and equivalent units (Huddlestun, 1993). This is the most ubiquitous echinoid of the Suwannee Limestone.

Rhyncholampas gouldii also occurs in the Oligocene of Georgia (Huddlestun, 1993), North Carolina (Kier, 1997), and Mississippi (McKinney et al., 2014).

Discussion.—Bouvé (1846) described *Pygorhynchus gouldii* from Paleogene strata of Georgia but did not figure the species. This led to confusion, as Conrad (1850) subsequently described *Nucleolites mortoni* from an intenal mold from Palmyra, in Lee County, Georgia, which is clearly the same species. Bouvé (1851) quickly remedied this by redescribing and figuring his species while explaining that Conrad's species was synonymous.

Clark and Twitchell (1915) subsequently also figured Bouvé's type specimen and noted that though this species was considered rare at the time it was documented, it was by then known to be one of the most seen of all American Cenozoic echinoids, especially so in Florida where they noted its abundance and highly variable form. In fact, Clark and Twitchell (1915) stated this species is so variable that extreme specimens differ in so many details that they would likely be described as distinct species if not for the intermediate forms found within large quantities of material, just as noted above for taxa such as *R. conradi*.

Kier (1997) described a subspecies, *R. gouldii newbernensis*, from the Oligocene Trent Formation near New Bern, North Carolina. This stratum has since been referred to the Upper Oligocene River Bend Formation (Ward, 2007). Kier distinguished *R. gouldii newbernensis* from *R. gouldii gouldii* by the following: 1) longer petals; 2) peristome slightly higher and wider; 3) lower test; and 4) higher periproct. Nevertheless, Kier (1997) used the overlap in most of these characters between the two taxa to prevent their consideration as separate species.

As discussed by McKinney et al. (2014) in their study of populations of *R. gouldii* from five locations in Florida, Mississippi, and North Carolina, this species demonstrates extraordinary variation in test shape among and within separated populations. Given this fact, we see no value in retaining the subspecies *newbernensis*, as there is no evidence whatsoever that it a separately evolving lineage worth recognizing.

In the Suwannee Limestone of peninsular Florida, *R. gouldii* is often present in profusion and associated with *G. mossomi* and *P. mansfieldi* throughout much of the unit.

Rhyncholampas trojana (Cooke, 1942)
(Figs. 83, 84)

Cassidulus (*Cassidulus*) *trojanus* Cooke, 1942. p.

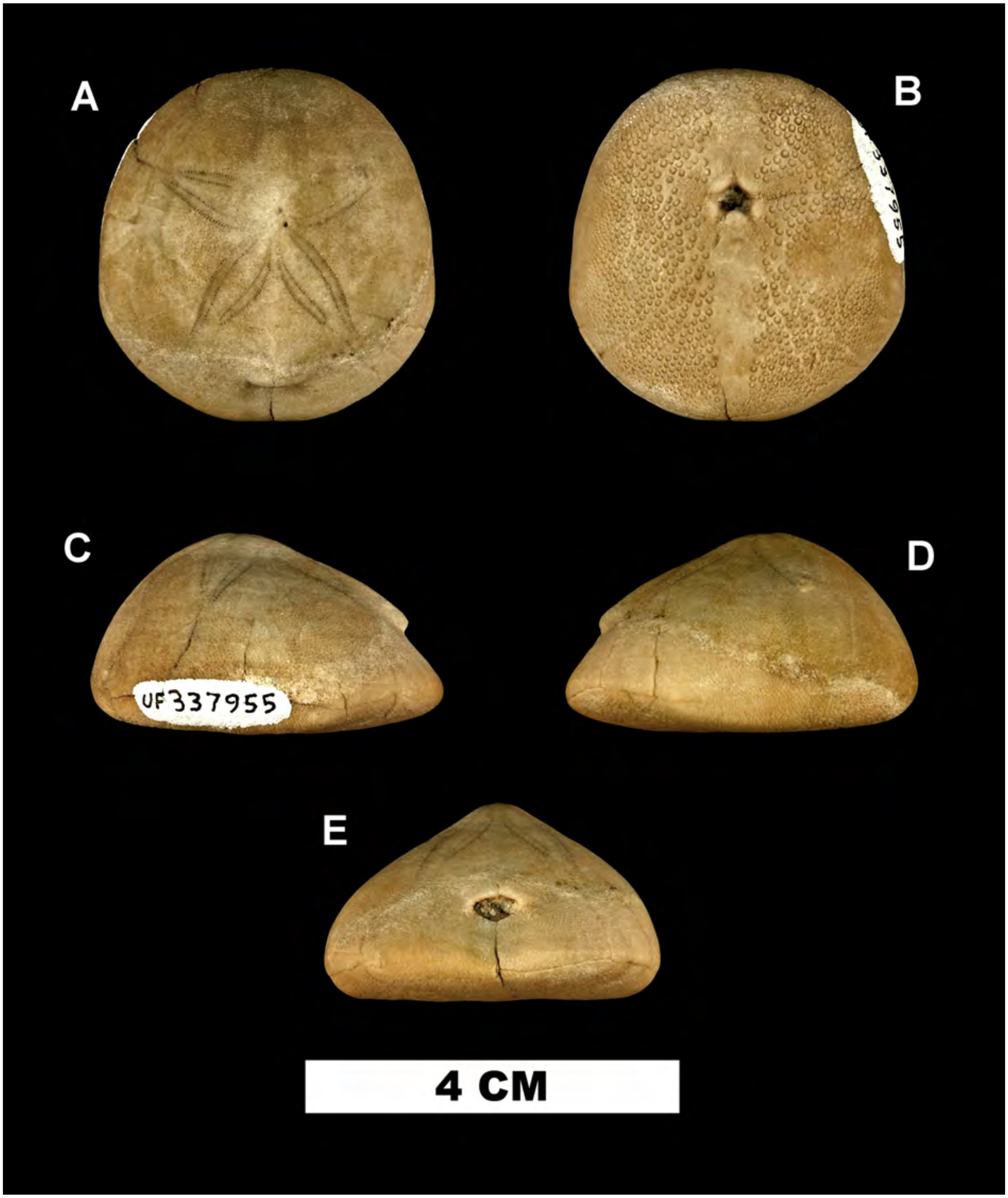


Figure 80: *Rhyncholampas gouldii* (UF 337955), 38 mm TL, 36.5 mm TW, 21 mm TH, Lower Oligocene Suwannee Limestone, Hernando County, Florida (FM-IP HE038).

32. pl. 2, figs. 22-25.

Cassidulus trojanus (Cooke). Cooke, 1959. pp. 58-59. pl. 24. figs. 1-4.

Cassidulus trojanus (Cooke). Kier, 1962. p. 175.

Eurhodia trojana (Cooke). Carter and Beisel, 1987. pp. 1080-1083.

Eurhodia trojanus (Cooke). Osborn et al., 2016. tbl. 2.

Rhyncholampas trojanus (Cooke). Souto, 2018. p. 59.

Cassidulus trojanus (Cooke). Souto et al., 2019. pp. 625, 651. figs. 11-13, 16.

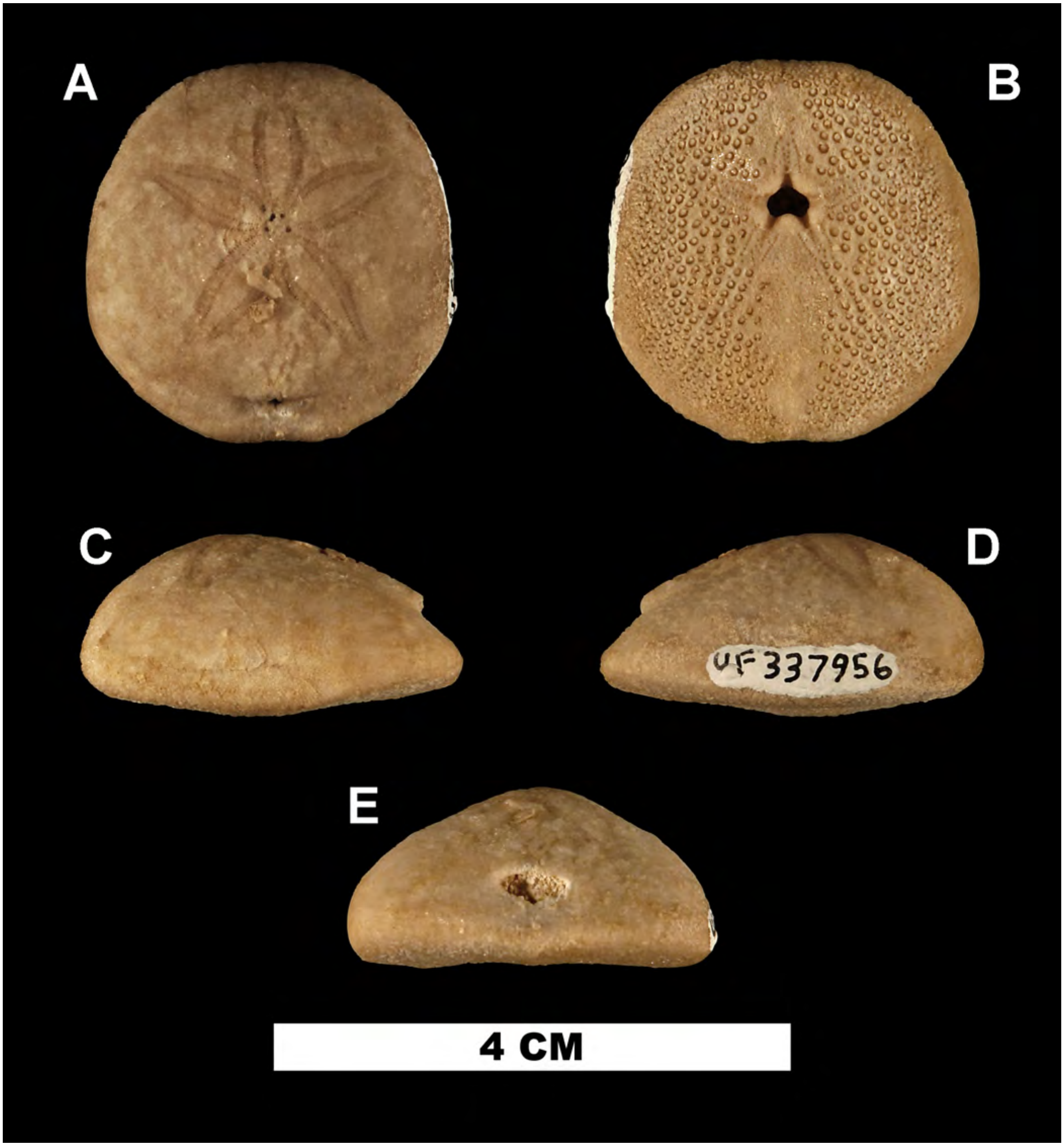


Figure 81: *Rhyncholampas gouldii* (UF 337956), 30.5 mm TL, 29 mm TW, 14 mm TH (a very low specimen), Lower Oligocene Suwannee Limestone, Hernando County, Florida (FM-IP HE038). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Rhyncholampas trojana (Cooke). Souto et al., 2019. p. 651.

Occurrence.—*Rhyncholampas trojana* is most commonly found in the uppermost beds of the OLS where it is associated with *W. eldridgei* in the *Rotularia vernoni* Zone, especially west of Dowling Park, Lafayette County (FM-IP LF002); northwest of Mayo, Lafayette County (FM-IP LF001), Cemex Quarry near Center Hill, Sumter County

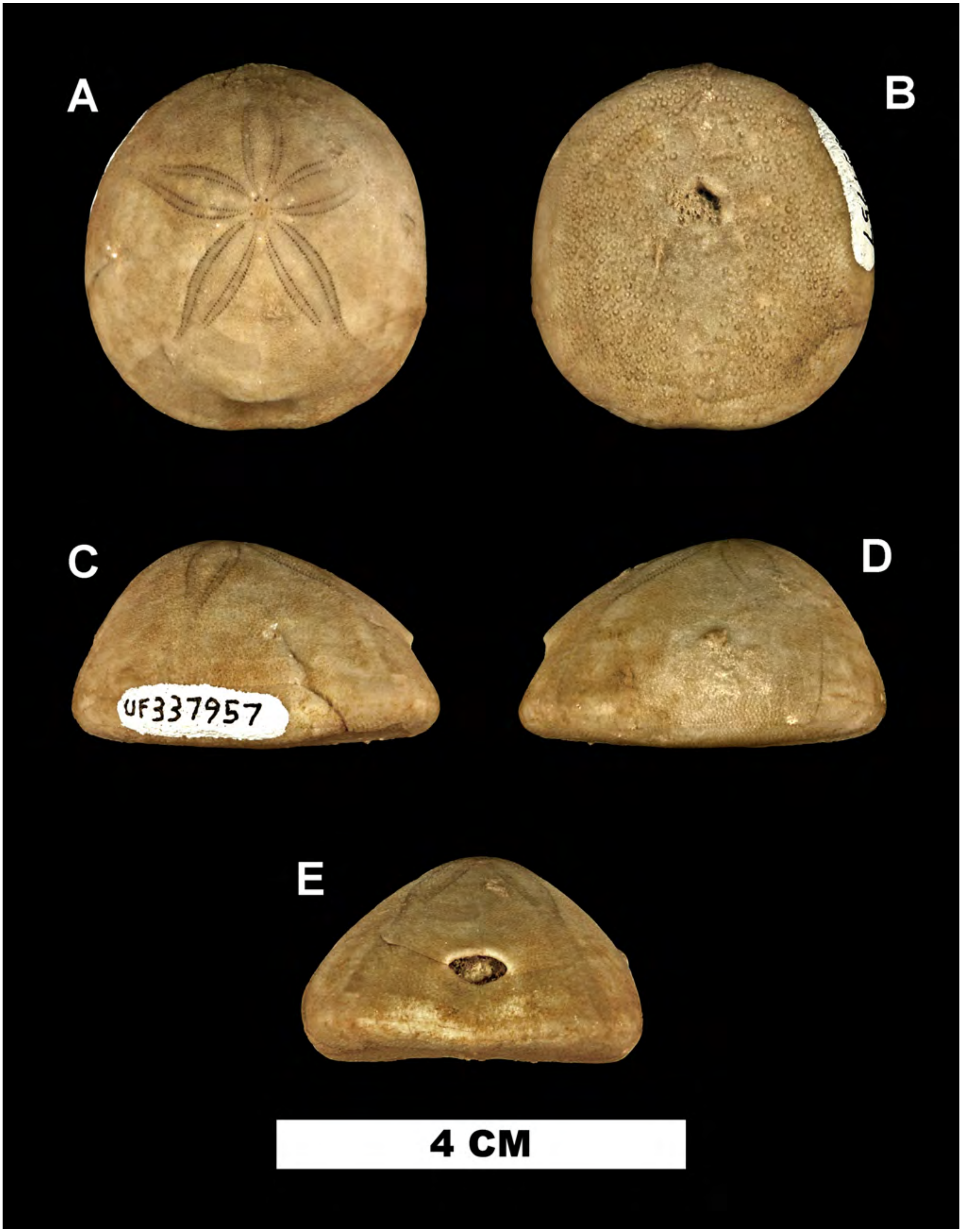


Figure 82: *Rhyncholampas gouldii* (UF 337957), 35 mm TL, 33 mm TW, 20 mm TH, Lower Oligocene Suwannee Limestone, Hernando County, Florida (FM-IP HE038). A: aboral. B: oral. C: left side. D: right side. E: posterior.

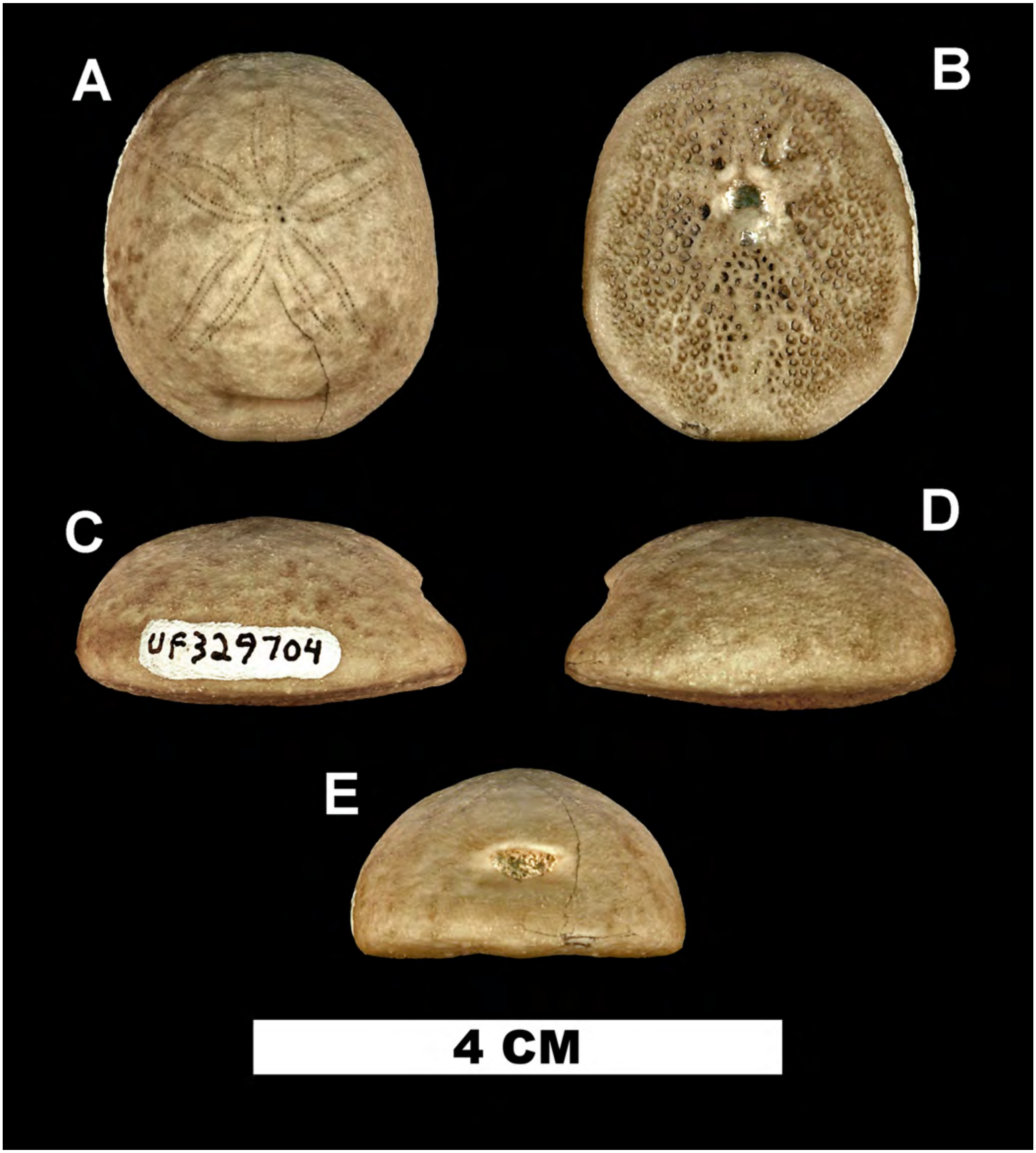


Figure 83: *Rhyncholampas trojana* (UF 329704), 28.5 mm TL, 24 mm TW, 13.5 mm TH, uppermost portion of Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: right side. E: posterior.

(FM-IP SM010), and north of Branford, Suwannee County (FM-IP SU002). The type locality is along the Suwannee River below Troy Springs, Lafayette County.

Rhyncholampas trojana also occurs in the OLS of Georgia (Cooke, 1959).

Figure 84: *Rhyncholampas trojana* (UF 329705), 27.5 mm TL, 23 mm TW, 13 mm TH, uppermost portion of Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Discussion.—*Rhyncholampas trojana* cannot be confused with the much smaller and narrower *E. patelliformis*, with which it has been considered a congener, and often occurs within the OLS of northern Florida. *Eurhodia patelliformis* has a more sharply truncated posterior margin. *Rhyncholampas trojana* is more easily confused with *R. gouldii*, from the overlying Lower Oligocene Suwannee Limestone. The two species often co-occur in mixed spoil in northern Florida quarries, or in outcrops

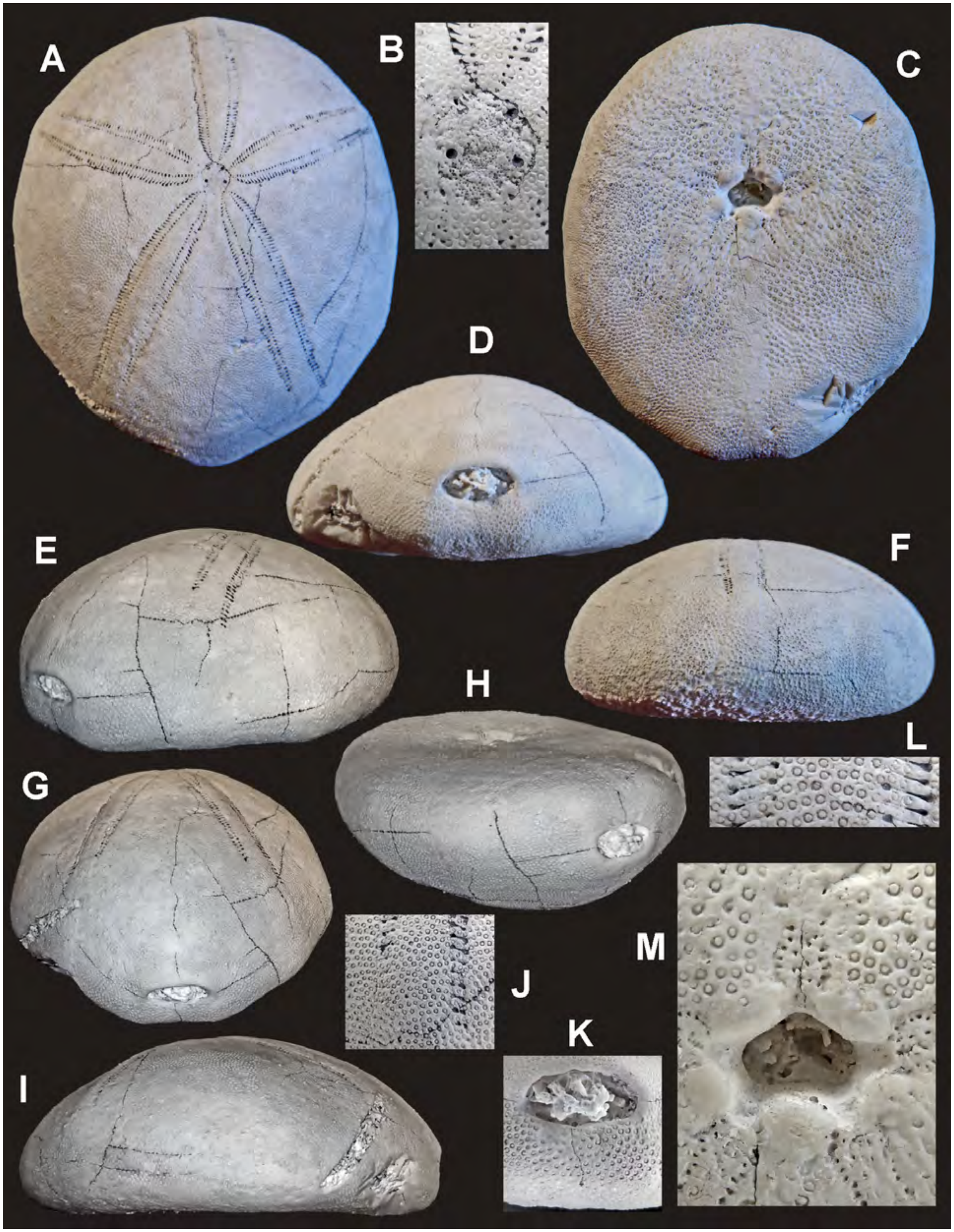


Figure 85: *Rhyncholampas bao* n. sp., holotype (UF 342094), 60.3 mm TL, 52.1 mm TW, 24.9 mm TH, Upper Eocene, Ocala Limestone, *Haimea brooksi* Zone, Brooks Quarry, northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: apical area. C: oral. D: posterior. E: oblique lateral viewpoint from posterior. F: anterior. G: tilted aboral viewpoint from posterior. H: oblique oral viewpoint from posterior. I: left side. J: distal end of petaloid portion of ambulacrum I. K: periproct. L: pore-pairs at widest point of ambulacrum I. M: peristome and phyllodes.

in very close proximity to the Eocene/Oligocene boundary, where the Suwannee Limestone often immediately overlies the *Wythella eldridgei* Zone in the uppermost OLS.

Carter and Beisel (1987) discussed the importance of the large, deep pits in the interambulacrum of the nearly flat oral surface of *R. trojana*. These pits are absent in the more gently concave oral surface of *R. gouldii*. Species of *Rhyncholampas* have a prominent naked area on the oral surface that extends from near the peristome to very near the posterior margin that is diagnostic in comparing *R. gouldii* to *R. trojana*. In contrast, *R. trojana* has an oral surface that is rather evenly adorned with comparatively large tubercles and no such naked area.

As discussed by Carter and Beisel (1987), misidentification of these two species can lead to confusion on the part of paleontologists and geologists attempting to make age determinations of the strata with which they are concerned. The differences can be subtle, so this confusion can lead to errors because *R. gouldii* is considered an indicator of the Oligocene strata of the region.

The traits discussed above also led Carter and Beisel (1987) to assign this species to *Eurhodia*. Mooi (1990b: 696) stated that re-examination of Carter and Beisel's characters, with comparison to the type species of *Cassidulus* and *Rhyncholampas*, is needed before *R. trojana* can be correctly placed, an assertion applicable to many cassiduloids, which is overall, a poorly studied group with uncertain phylogenetic relationships. Phylogenetic analyses of Recent species, combined with fossil taxa, especially those that are the type species for their genera (Souto et al., 2019), is essential to establish a basis for ongoing treatment of the fossil species. Previous attempts, such as that of Suter (1994a, b) failed largely due to a lack of understanding of homologies within the group, as well as evident non-monophyly that makes identification of appropriate outgroups extremely problematic.

Souto et al. (2019) stated that Carter and Beisel's (1987) assertion that *R. trojana* belongs in *Eurhodia* was not correct. The traits they used (i.e., deep pits in the naked zone and concave oral surface) are not present in the type species of *Eurhodia*. Souto et al. (2019) then placed *trojana* into *Rhyncholampas*, and we follow this assignment.

Rhyncholampas trojana has traits that suggest placement in *Eurhodia*, *Rhyncholampas*, and *Cassidulus* and debate will continue among some echinologists who weigh one characteristic more heavily than another. Nevertheless, the species itself is relatively easy to identify, and appears to be restricted to the *Wythella eldridgei* Zone in the uppermost OLS.

Rhyncholampas bao n. sp.
(Figs. 85-88)

Diagnosis.—Large *Rhyncholampas* (TL average 56.1 mm TL, largest 60.8 mm TL) with low test, TH on average 45.3% TL and 54% TW, posterior margin sharply truncated with oral edge of periproct on average 18.7% above the posterior margin; posterior end of prominent aboral hood over periproct forms furthest point of posterior margin of test, with long, straight, narrow, only slightly widened halfway along, but petals extending nearly to ambitus.

Description.—Based on holotype (UF 342094), four paratypes (UF 342095, UF 342096, UF 342097, UF 342098), and non-type specimens. Test large, holotype largest specimen: 60.3 mm TL, 52.1 mm TW, 24.9 mm TH; smallest specimen (UF 342098): 29.1 mm TL, 25.3 mm TW, 13.3 mm TH; ten additional specimens range from 49 to 60 mm TL (avg. 56.1 mm TL). Test wide, width 86.4% TL in holotype, average 84%; low: TH 41.2% TL and 47.7% TW in holotype, average TH is 45.3% TL and 54% TW; highest point posterior of apical system, greatest width posterior of apical system, point of greatest length on posterior is above ambitus at prominent aboral hood over periproct which overhangs posterior margin of test. Posterior ambitus sharply truncated, shallow sinus extends from periproct to posterior ambitus. Apical system monobasal with four gonopores, anterior (center of apical system on average 69.3% TL from posterior margin).

Petals narrow, long, nearly straight (only

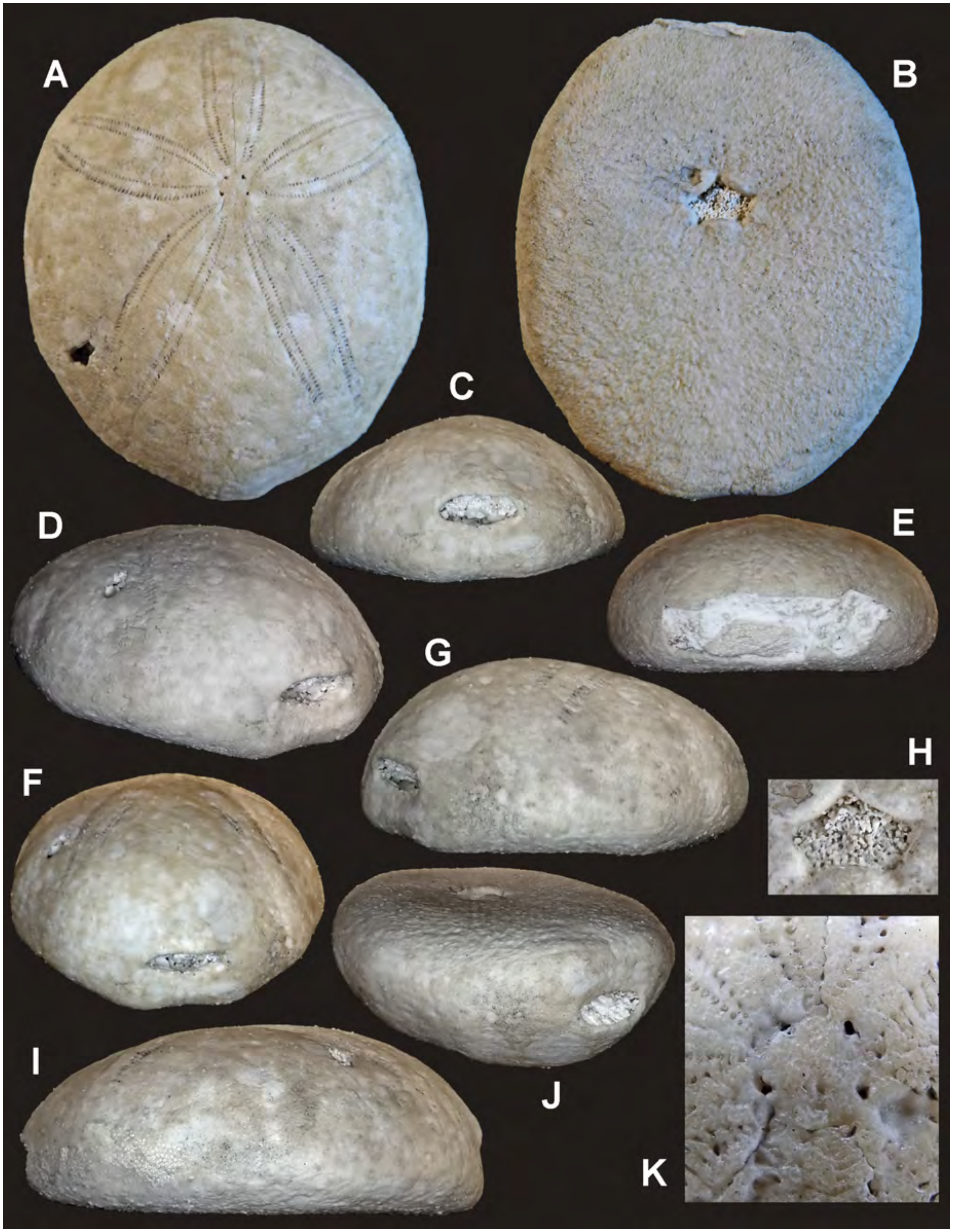


Figure 86: *Rhyncholampas bao* n. sp., paratype (UF 342095), 58.9 mm TL, 50.1 mm TW, 23.6 mm TH, Upper Eocene, Ocala Limestone, *Haimea brooksi* Zone, Brooks Quarry, northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: posterior. D: oblique lateral viewpoint from posterior. E: anterior. F: tilted aboral viewpoint from posterior. G: oblique lateral viewpoint from posterior. H: peristome. I: left side. J: oblique oral viewpoint from posterior. K: apical area.

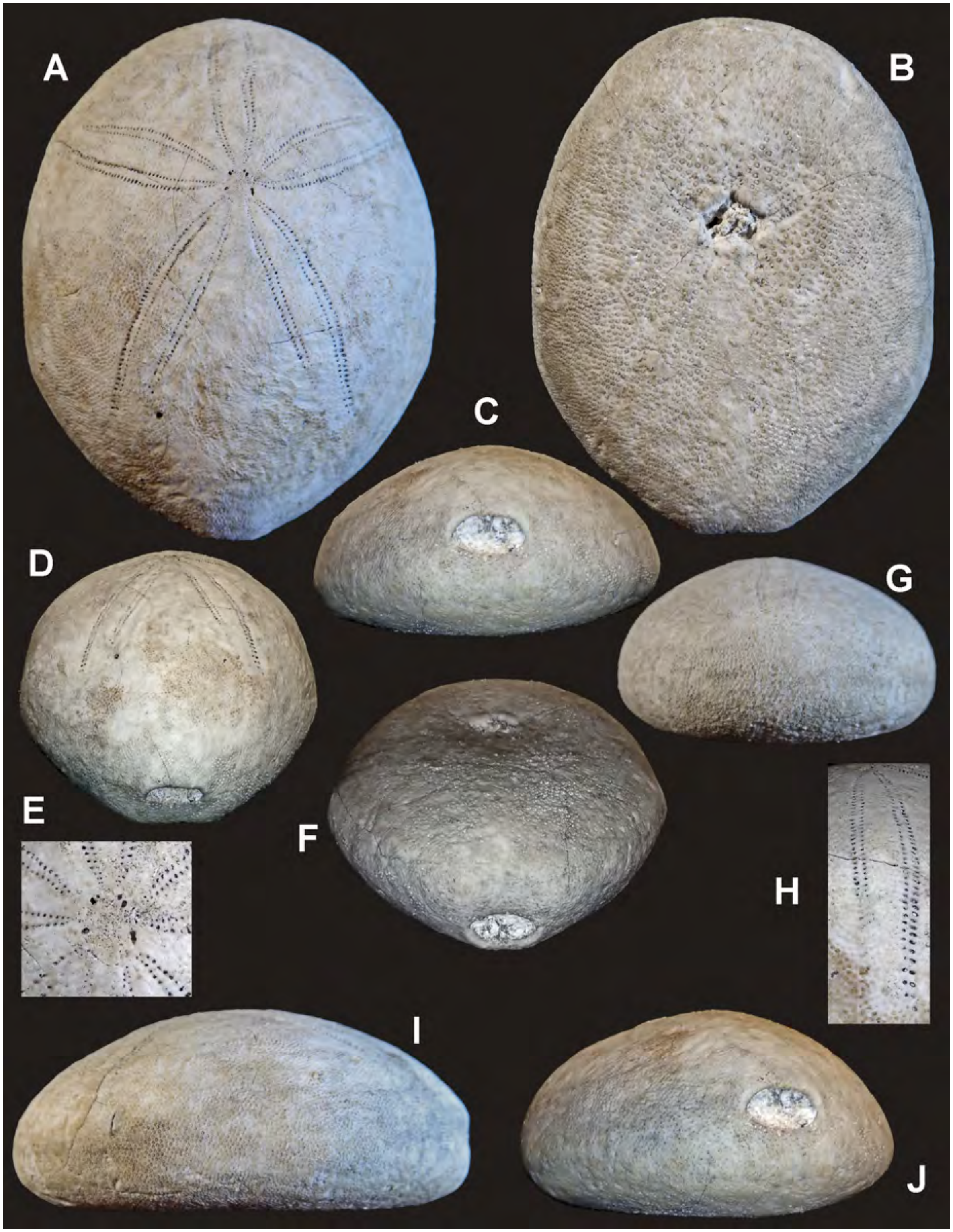


Figure 87: *Rhyncholampas bao* n. sp., paratype (UF 342096), 58.6 mm TL, 46.5 mm TW, 26.1 mm TH, Upper Eocene, Ocala Limestone, *Haimea brooksi* Zone, Brooks Quarry, northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: oral. C: posterior. D: tilted aboral viewpoint from posterior. E: apical area. F: oblique oral viewpoint from posterior. G: anterior. H: ambulacrum I. I: left side. J: oblique lateral viewpoint from posterior.

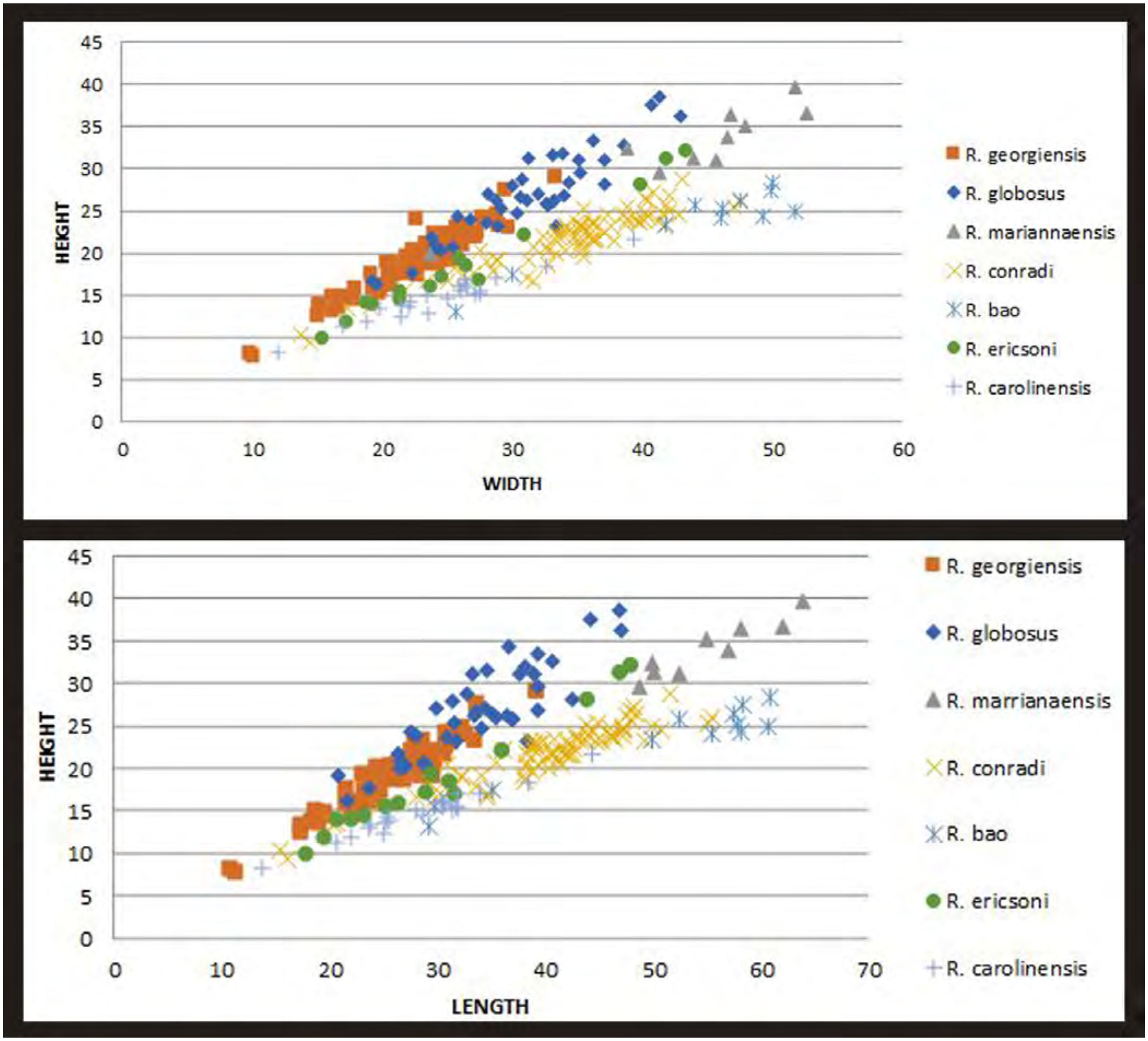


Figure 88: Comparison of test height and test width (top) and test length (bottom) of Eocene *Rhyncholampas* species from the eastern United States.

slightly widened at their midpoint; most pronounced in smaller specimens), pore pairs almost parallel, open distally; average petal length as a percentage of TL is: I: 44.0%, II: 33.5%, III: 34.2%, IV: 35.2%, V: 43.5% (petal length taken from distal end of longest pore-pair column, if columns are of unequal length); pore pair columns of petal I, II, IV and V usually of unequal length, petal I and V more so; anterior pore pair columns of petal I and IV longer; posterior pore pair columns of petal II and IV longer; pore pair columns of petal III usually equal: anterior pore pair columns of petal I and V have, on average, six more pore pairs than the posterior series; pore pair columns of petal II and IV have, on average, four more pore pairs than the anterior series; both pore pair columns of petal III usually equal; ambulacra with unipores between end of petals and peristome.

Periproct transversely elongate, width on average 49.7% its height, with prominent aboral hood that usually extends over posterior margin of test.

Adoral edge of periproct on average 18.7% above the posterior margin, shallow sinus below periproct leads to truncated posterior margin.

Oral surface nearly flat, only in smallest specimen (29 mm TL) is there slight, but noticeable, concavity in peristomial area; larger tubercles than aboral surface; narrow naked area in interambulacrum V from peristome to posterior margin with minimal pitting, greatest width of naked area on average 8.9% TW, 8.4% TW in holotype, naked area tapers posteriorly.

Peristome pentagonal, wider than high, peristome height on average 63.5% width; anterior, posterior edge of peristome on average 55.8% from posterior margin. Five pronounced, vertical bourrelets, each convex towards peristome. Phyllodes with unipores, on average 39% width of peristome at widest point, occluded plates usually present; two buccal pores present.

Zoobank Nomenclatural Act.—F527F287-DB04-4585-859A-A91D25229B67

Discussion.—*Rhyncholampas bao* n. sp. has not been documented outside of its type locality in the northwesternmost pit in the Brooks Quarry (FM-IP JA039) northwest of Marianna, Jackson County, Florida, where it occurs in the OLS in material dredged from 24 m below the top of the Eocene stratum in the quarry (Fig. 6). It is found in association with *H. brooksi, O. haldemani O. rotundus*, *R. georgiensis*, *W. johnsoni,* and other, rarer species including *Brissus jonesi* n. sp. and *Rhyncholampas mariannaensis* n. sp.

While attempting to place these specimens into *R. conradi*, we quickly realized this was untenable, and they could not be placed with confidence in any other currently described species from the Americas. It is possible that if these specimens occurred with otherwise typical specimens of *R. conradi*, we could consider them outliers of *R. conradi*'s typical form. This taxon occurs stratigraphically below the occurrence of *R. conradi* within the Brooks quarry and is typically much larger than the *R. conradi* which occur above it (other than one small specimen that is 29 mm TL, ten additional specimens range from 49 to 60 mm TL vs 81 *R. conradi* that ranged from 15.4 to 55.1 mm TL). It is further distinct from *R. conradi* by its much lower test (TH on average 41.2% TL and 47.7% TW in *Rhyncholampas bao* n. sp., compared to 54.7% TL and 63% TW in 81 specimens of *R. conradi* we measured) (Fig. 88). TW as a percentage of TL is similar in these two forms, being on average 86.2% in *R. conradi* and 84% in *Rhyncholampas bao* n. sp. (Fig. 88). In addition, the periproct of *R. conradi* is on average 28% above the posterior margin of the test, whereas in *Rhyncholampas bao* n. sp. it is significantly lower at 18.7%.

Other than the remarkably low test of this species and long narrow petals that are typically only very slightly bowed (widened medially), the most striking characteristic is the very posterior high point of the test that in many larger specimens gives the test a striking "humped" posterior portion of the test, visible from a lateral viewpoint. The oral surface is nearly flat, and only in the smallest specimen (29 mm TL) is there a slight, but noticeable, concavity in the peristomial area.

The low test of this species is like that of *R. fontis*, which has an even lower test (though the holotype and only known specimen is slightly crushed) with a TH 41% TL and 44% TW. However, *R. fontis* is a nearly circular species when viewed aborally, with a TW 92% TL.

We complete a review of species of *Rhyncholampas*, and potential *Rhyncholampas*, from the remainder of the eastern Americas in the discussion for *R. mariannaensis* n. sp., below and of these forms, *Rhyncholampas bao* n. sp. is most like *R. ellipticus* (Clark in Arnold and Clark, 1927) which Clark designated as the type species of his new genus *Anisopetalus* (subsequently recognized as a subjective junior synonym of *Rhyncholampas*). Though the holotype of this species is 50 mm in length, Clark noted the remaining six specimens he had available were much smaller, from 26 to 41 mm in length. *Rhyncholamaps ellipticus* has a low test (holotype TH 40% TL and 51% TW), but it is narrower than *Rhyncholampas bao* n. sp. (TW 78% TL vs 84% in *R. bao* n. sp.), and the highest point of the test is much more anterior. The figures of the species provided by Arnold and Clark (1927) also appear to show a much more concave oral surface

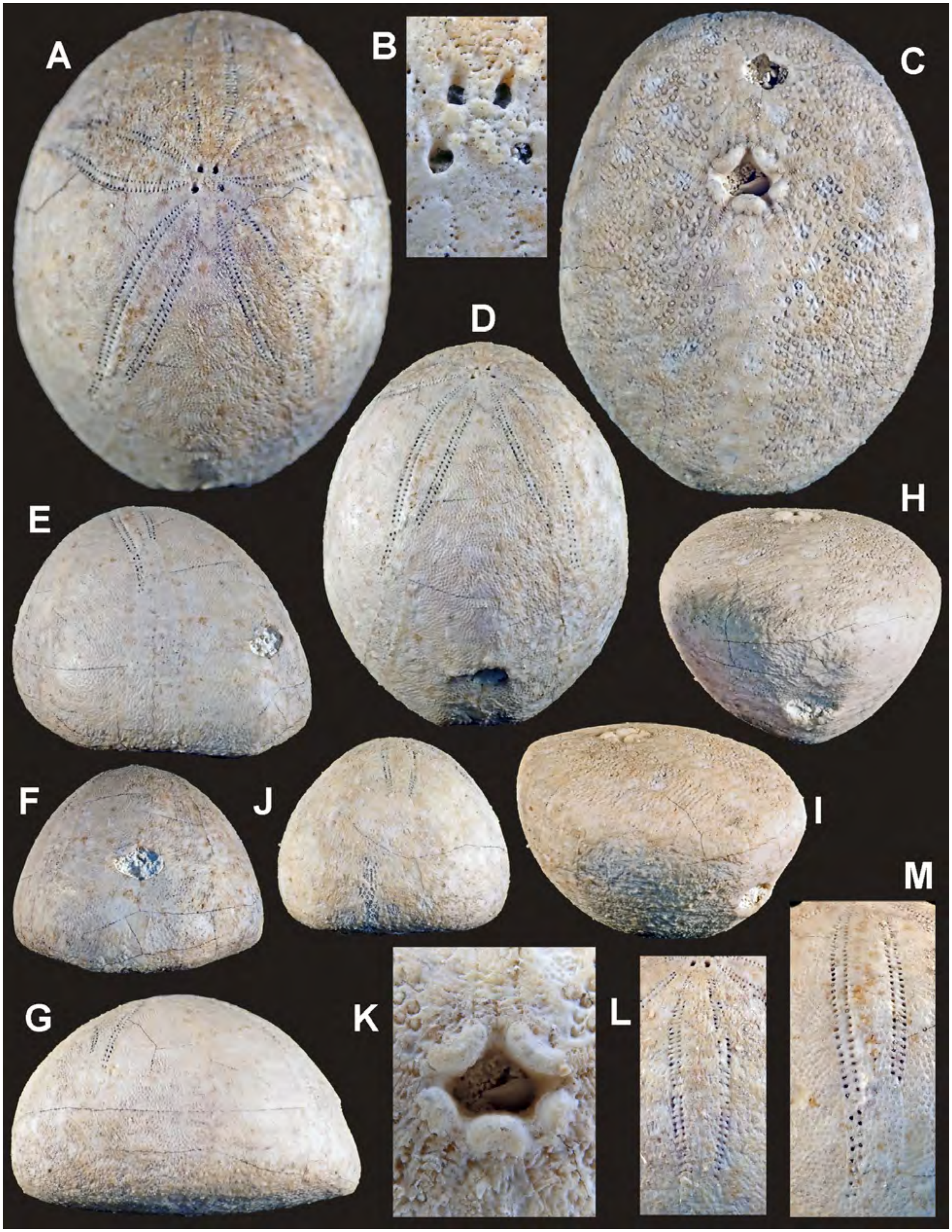


Figure 89: *Rhyncholampas mariannaensis* n. sp., holotype (UF 338027), 49.8 mm TL, 38.8 mm TW, 32.6 mm TH, Upper Eocene Ocala Limestone, *Haimea brooksi* Zone, Leon Brooks Quarry (FM-IP JA039), Marianna, Jackson County, Florida. A: aboral. B: apical area. C: oral. D: tilted aboral viewpoint from posterior. E: oblique posterior viewpoint. F: posterior. G: left side. H: tilted oral viewpoint from posterior. I: oblique oral viewpoint from posterior. J: anterior. K: peristome. L: petaloid portion of ambulacrum III. M: petaloid portion of ambulacrum V.

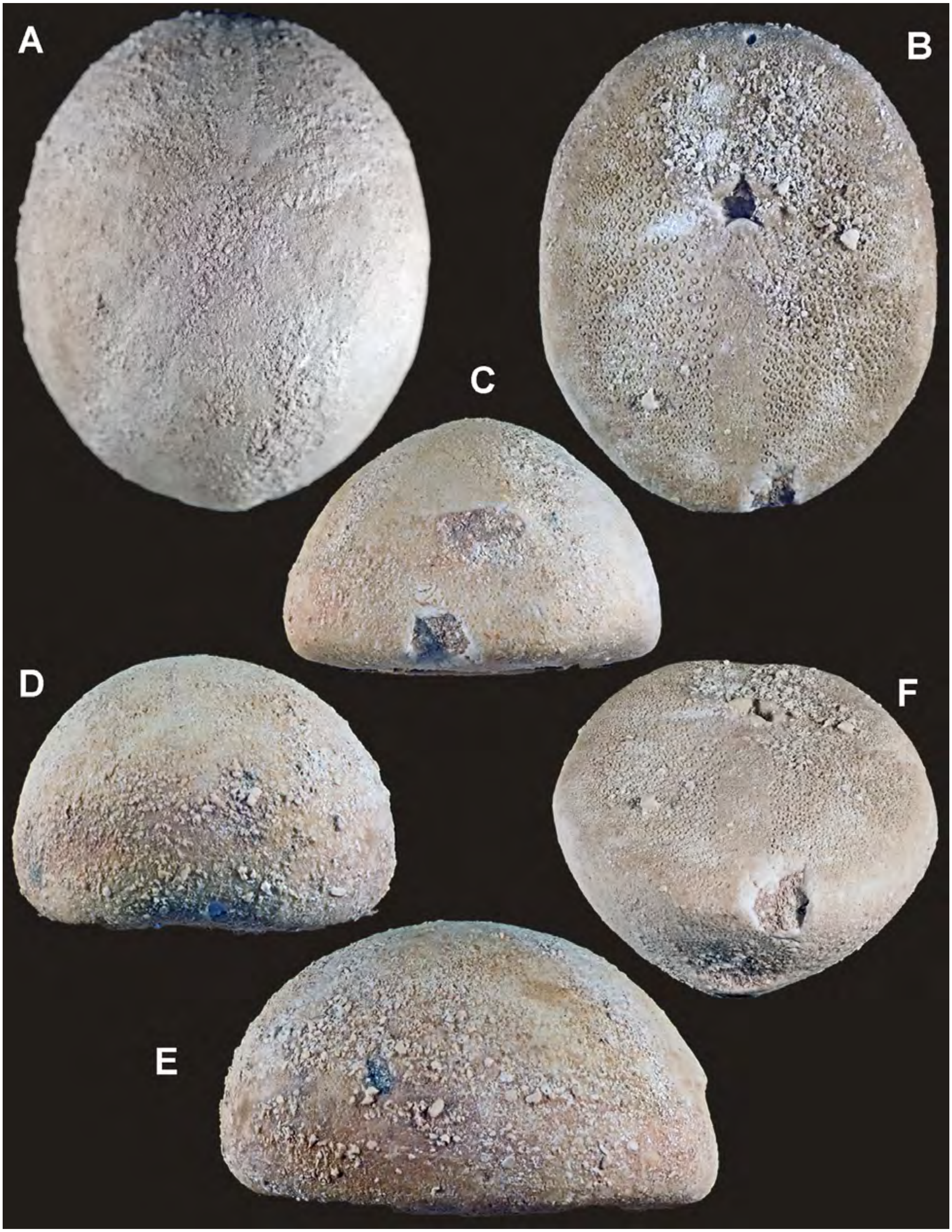


Figure 90: *Rhyncholampas mariannaensis* n. sp., paratype (UF 342090), 56.7 mm TL, 46.5 mm TW, 33.4 mm TH, Upper Eocene Ocala Limestone, *Haimea brooksi* Zone, Leon Brooks Quarry (FM-IP JA039), Marianna, Jackson County, Florida. A: aboral. B: oral. C: posterior. D: anterior. E: left side. F: tilted oral viewpoint from posterior.

in *R. ellipticus* than *R. bao* n. sp. *Rhyncholampas bao* n. sp. is not comparable to any other species of *Rhyncholampas* currently documented from the eastern Americas or Caribbean region, as reviewed in the remarks for *R. mariannaensis* n. sp.

Etymology.—The new species is named for their resemblance to bao, a type of Chinese steamed meat or vegetable filled bun.

Material and Occurrence.—Holotype (UF 342094), four paratypes (UF 342095, UF 342096, UF 342097, UF 342098), from the type locality in the OLS, where it occurs with *H. brooksi* and *O. haldemani* in material dredged from 24 m below the top of the Eocene stratum in the most northwestern pit in the quarry complex of Leon Brooks, northwest of Marianna, Jackson County, Florida (FM-IP JA039).

Rhyncholampas mariannaensis n. sp.
(Figs. 88-91)

Diagnosis.—*Rhyncholampas* with TW on average 80.1% TL; highest point posterior of apical system; TH on average 65.4% TL and 84% TW; adoral edge of periproct on average 33.9% TH above posterior margin; naked area along oral interambulacrum 5 on average 15.5% TW.

Description.—Description based on holotype (UF 338027), three paratypes (UF 342090, UF 342091, UF 342092), and several non-type specimens. Test large (holotype 49.8 mm TL, 38.8 mm TW, 32.6 mm TH, largest specimen [UF 342091] 64.6 mm TL, 52.0 mm TW, 39.6 mm TH); elongate, narrow (holotype TW 77.9 % TL; average 80.1%), high (holotype TH 65.4% TL, average 61.5% TL); highest point posterior of apical system; greatest width along transverse line posterior of apical system; posterior ambitus sharply truncated, anterior vertical to slightly overhung. Apical system monobasal, four gonopores, anterior (center of apical system 63.5% TL from posterior margin of test in holotype; 63.8% average). Petals lanceolate, moderately open distally, posterior petals widened about halfway their length; petals I and V longest, III shortest (petal length taken from distal end of longest pore-pair column, if columns are of unequal length), average petal length as a percentage of TL is: ambulacrum I: 43.5%; II: 36.8%; III: 36.4%; IV: 37.2%; V: 43.2%. Columns of pore pairs in petals of ambulacra I, II, IV and V usually of unequal lengths, most pronounced in petals I and V; anterior pore pair column of ambulacra I and IV longer; posterior columns of pore pairs in ambulacra II and IV longer; pore pair columns of petal in ambulacrum III usually equal; pore counts of petals of holotype follows: I: 44 and 47, II: not counted, III: 44 and 44, IV: 34 and 42, V: 49 and 41; ambulacra single-pored beyond petals.

Periproct transversely elongate, width on average 50.8% of its height (upper portion of periproct of holotype damaged), with prominent aboral hood. Adoral edge of periproct on average 33.9% TH above the posterior margin, 34.6% TH in holotype; shallow sinus below periproct proceeding to truncate posterior margin.

Oral surface flat, not concave, with larger tubercles than on aboral surface; broad naked area in interambulacrum 5 from peristome to posterior margin with minimal pitting, greatest width of naked area on average 15.5% TW, 15.7% TW in holotype. Peristome pentagonal, wider than long, 4.6 mm wide, 3.3 mm long on holotype, peristome height on average 71.7% width; anterior, posterior edge of peristome 60.4% TL in holotype, average 58.5%. Five pronounced, vertically oriented bourrelets, convex towards peristome. Phyllodes with unipores, on average 47% width of peristome at widest point, occluded plates usually present; two buccal pores present.

Zoobank Nomenclatural Act.—F3FBFDF8-5D2F-48AB-98A3-9EF6FDF36638

Discussion.—This species has not been documented outside of its type locality in the Brooks Quarry in Jackson County, Florida (FM-IP JA039) (Fig. 6). Here, it occurs in material dredged from 24 m below the top of the Eocene stratum in the northwesternmost pit in the quarry complex, in an horizon of *Asterocyclina*-rich limestone with a diverse echinoid assemblage, initially discussed in Osborn et al. (2016). This assemblage includes *H. brooksi, O. haldemani, O. rotundus, W. johnsoni, R. georgiensis, Brissus jonesi* n. sp., *Rhyn-*

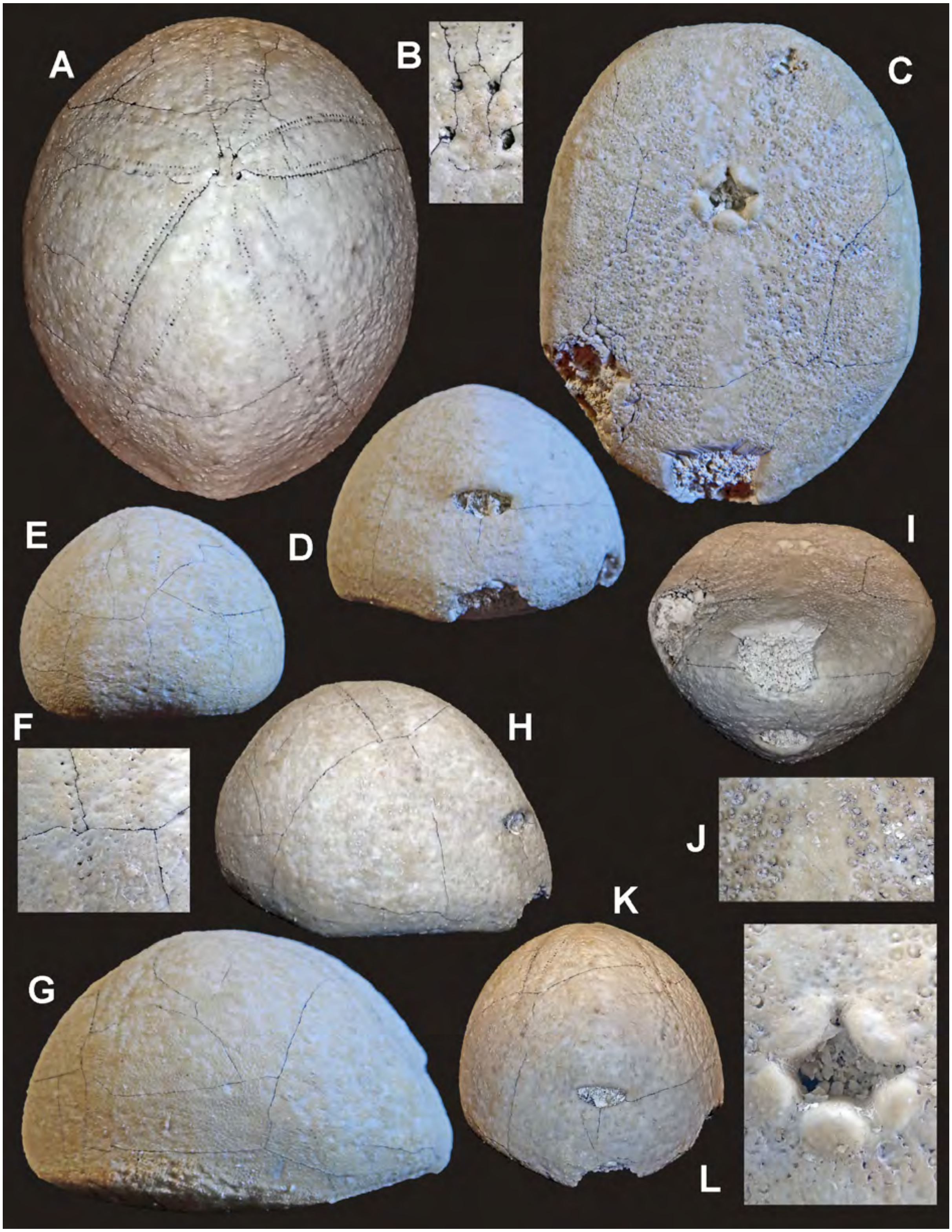


Figure 91: *Rhyncholampas mariannaensis* n. sp., paratype (UF 342091), 64.6 mm TL, 52.0 mm TW, 39.6 mm TH, Upper Eocene Ocala Limestone, *Haimea brooksi* Zone, Leon Brooks Quarry (FM-IP JA039), Marianna, Jackson County, Florida. A: aboral. B: apical. C: oral. D: posterior. E: anterior. F: distal end of petal V. G: left side. H: oblique lateral viewpoint from posterior. I: oblique oral viewpoint from posterior. J: naked medial area of oral surface just posterior of peristome. K: tilted aboral viewpoint from posterior. L: peristome.

cholampas bao n. sp., and many other, rarer species (Table 1).

Within this assemblage, *R. mariannaensis* n. sp. could only be confused with *R. georgiensis*, from which it is readily distinguished by its much greater size (known specimens of *R. mariannaensis* n. sp. range from 48-64 mm TL, and the largest specimen of *R. georgiensis* known to us is 33 mm TL) and narrower test (average TW of *R. georgiensis* is 88.5% TL; average TW *R. mariannaensis* n. sp. is 80.1% TL; holotype is 77.9% TL). However, as shown in Fig. 88, TW vs TL is not a very useful feature for distinguishing regional species of Eocene *Rhyncholampas*. Perhaps most significantly, the periproct of *R. mariannaensis* n. sp. is on average 33% TH above the posterior margin, whereas in *R. georgiensis* it is on average 40% TH above the posterior margin (Fig. 79). Differences in TH vs TW are also apparent in these two species: TH is on average 83.5% TW in *R. georgiensis* and 73.7% in *R. mariannaensis* n. sp. (Fig. 88). In addition, TH is on average 74% TL in *R. georgiensis*, and 61.5% in *R. mariannaensis* n. sp. (Fig. 88).

The large, high test of *R. mariannaensis* n. sp. is distinguished from the relatively lower test of *R. conradi*, which occurs in strata immediately above the horizon of *R. mariannaensis* n. sp. (TH on average 54.7% TL and 63% TW in *R. conradi* and 61.5% TL and 73.7% TW in *R. mariannaensis* n. sp.). Furthermore, the periproct is on average only 28% TH above the posterior margin in *R. conradi*, whereas it is 33.9% TH in *R. mariannaensis* n. sp.

Other than *R. conradi* and *R. georgiensis*, of the regional species *R. mariannaensis* n. sp. could only be confused with *R. ericsoni*, which occurs in the lowermost portion of the OLS near Inglis in Citrus and Levy Counties. *Rhyncholampas ericsoni* has a smaller and proportionately lower and wider test: TH is 66.6% TL in the holotype of *R. ericsoni* and on average 61.5% TL in *R. mariannaensis* n. sp. (Fig. 88). In addition, TH is 73.5% TW in the holotype of *R. ericsoni* and on average 83.9% TW in *R. mariannaensis* n. sp. (Fig. 88). However, the test of *R. ericsoni* is quite variable: the range of 12 measured specimens revealed a test width from 52.5-66.8% TL, with an average of 59.8%; TH ranged from 52.5-66.5% TL (average of 59.8%) and 60.7-73.9% TW (average of 68.6%). The average TH of *R. mariannaensis* n. sp. is therefore significantly higher relative to width than in *R. ericsoni*. In addition, the periproct of *R. mariannaensis* n. sp. is lower (on average 33.9 % TH above the margin) than *R. ericsoni* (on average 40.1% TH above margin).

Rhyncholampas contains comparatively few species in the remainder of the eastern Americas and Caribbean region, and we will endeavor to compare *R. mariannaensis* n. sp. to all of them. These species include *R. candidoi* Garrafielo and Carreira, 1994, from the Miocene of Brazil; *R. cervantesi* Sánchez-Roig, 1949, from the Oligocene of Cuba, and *R. rodriguezi* Lambert and Sánchez-Roig in Sánchez-Roig, 1926, from the Oligocene to Miocene of Cuba (Souto et al., 2019). The large, high, narrow test of *R. mariannaensis* n. sp. readily distinguishes it from these small Cuban taxa.

Five species of *Anisopetalus* have been described from the eastern Americas and this genus has since been considered a junior synonym of *Rhyncholampas* (Kier, 1966b: U515), requiring comparison with *R. mariannaensis* n. sp.: *Anisopetalus brodermanni* Sánchez-Roig, 1952c; *A. cookei* Sánchez-Roig, 1952c (Souto et al. [2019] stated this species is likely not a *Rhyncholampas* but did not reassign it), and *A. caobaense* Sánchez-Roig, 1952c, all three of which are from the Eocene of Cuba. These taxa were figured adequately enough by Sánchez-Roig (1952c) to readily distinguish them from *R. mariannaensis* n. sp.

Anisopetalus ellipticus Clark in Arnold and Clark, 1927 (not to be confused with *Cassidulus ellipticus* Kew, 1920, from the Eocene of California and Mexico which Souto et al., 2019, stated should be reassigned to *Eurhodia*), was described from the Eocene of Jamaica, but the low test of this species readily differentiates it from *R. mariannaensis* n. sp. *Anisopetalus oliveirae* Marchesini Santos, 1958, was described from the Miocene of Brazil but it can not be confused with *R. mariannaensis* n. sp.

Echinanthus parallelus Azpeitia in Cotteau, 1897, from the Eocene of Cuba, and *E. antillarum* Cotteau, 1875, St. Bartholomew, and Cuba, were placed in *Parapygus* by Jackson (1922) and subsequently reported from the Eocene of Jamaica by Arnold and Clark (1927). Donovan (1993) questionably attributed both species to *Rhyncholampas*, but stated they require further study. Judging by the figures of these two species, Donovan was correct, but given their dissimilarity to *Rhyncholampas*, we do not place them in that genus, and they are likewise not comparable to *R. mariannaensis* n. sp.

Six species from the Oligocene-Miocene of Cuba were named to *Procassidulus* in the works of Sánchez-Roig. Kier (1962, 1966b) considered *Procassidulus* a junior synonym of *Rhynchopygus*, which Kier (1962) stated is largely distinguished from *Cassidulus* by its tetrabasal apical system, whereas *Cassidulus* and *Rhyncholampas* have monobasal apical systems. As shown by Smith and Kroh (2011), *Rhynchopygus* has strongly developed bourrelets, whereas *Cassidulus* has bourrelets largely confined to the vertical sides of the peristome, and *Rhyncholampas* has very weakly developed bourrelets. Smith and Kroh (2011) state *Procassidulus* to be very similar to *Rhynchopygus* in petal form, phyllode structure, and in having an invaginated periproct. It differs in lacking the strongly pronounced tongue-like projection above the periproct opening. Sánchez-Roig did not characterize the apical system, nor did he figure *Procassidulus avilensis* Palmer in Sánchez-Roig, 1949, or *P. habanensis* Sánchez-Roig, 1949, both from the Oligocene of Cuba.

However, *P. brodermanni* Sánchez-Roig, 1949, from the Oligocene, *P. circularis* Palmer in Sánchez-Roig, 1949, also from the Oligocene, and *P. jeanneti* Sánchez-Roig, 1949, from the Miocene, are figured well enough to determine they likely do not belong in *Procassidulus* or *Rhynchopygus* and are potentially *Rhyncholampas.* Though we did not examine any of these specimens, and we are not prepared to assert the genus placement for any of them, we compared them with *R. mariannaensis* n. sp., and there is no way to confuse *R. mariannaensis* n. sp. with any of these small forms.

Judging by Sánchez-Roig's understanding of *Procassidulus*, it is likely *P. avilensis*, *P. habanensis*, and *P. echevarriai* Sánchez-Roig, 1953b, from the Oligocene of Cuba could also be *Rhyncholampas*, along with *Paralampas conceptionis* Sánchez-Roig, 1953b, from the Eocene of Cuba. None of these taxa could be confused with *R. mariannaensis* n. sp.

Although *Cassidulus* is not currently recognized in the Cenozoic faunas of the eastern United States, many species have been placed in the genus in the remainder of the eastern Americas and Caribbean region. These will require additional study to determine if they should be reassigned to *Rhyncholampas*, and include: *C. mestieri* Kier, 1966a and *C. senni* Kier, 1966a, two small species that appear to be good *Cassidulus*, from the Eocene of Barbados. These bear no resemblance to *R. mariannaensis* n. sp.

Rhyncholampas falconensis (Jeannet, 1928), from the Miocene of Venezuela, was originally placed in *Eurhodia*, but considered a *Cassidulus* by Cooke (1961) and subsequently *Rhyncholampas* by Souto et al. (2019). We agree that this species appears to be a *Rhyncholampas*, though it bears no resemblance to *R. mariannaensis* n. sp.

Cassidulus (*Rhynchopygus*) *zanolettii* Sánchez-Roig, 1952d, was described from the Eocene of Cuba and may belong to *Eurhodia*, as does *Nucleopygus tamarindensis* Sánchez-Roig, 1952d, also from the Cuban Eocene. *Cassidulus rojasi* Sánchez-Roig, 1953b, from the Oligocene of Cuba, as well as *C. sphaeroides* Arnold and Clark, 1934 and *C. platypetalus* Arnold and Clark, 1934, both from the Eocene of Jamaica, could belong in *Rhyncholampas*. Sánchez-Roig (1949) described *Cassidulus* (*Pygorhynchus*) *riveroi* from the Oligocene (potentially Miocene according to Souto et al. [2019]) of Cuba, and which Souto et al. (2019) asserted is a *Rhyncholampas*; and *Catopygus rodriguezi* Lambert and Sánchez Roig in Sánchez Roig (1926) from the Miocene (and potentially Oligocene according to Souto et al. [2019]) of Cuba, which Souto et al. (2019) also asserted is a *Rhyncholampas*. Perhaps a few of these taxa can be assigned to *Rhyncholampas*, but none of these comparatively small taxa bears resemblance to *R. mariannaensis* n. sp.

Etymology.—Named in honor of the city of Marianna, Jackson County, Florida.

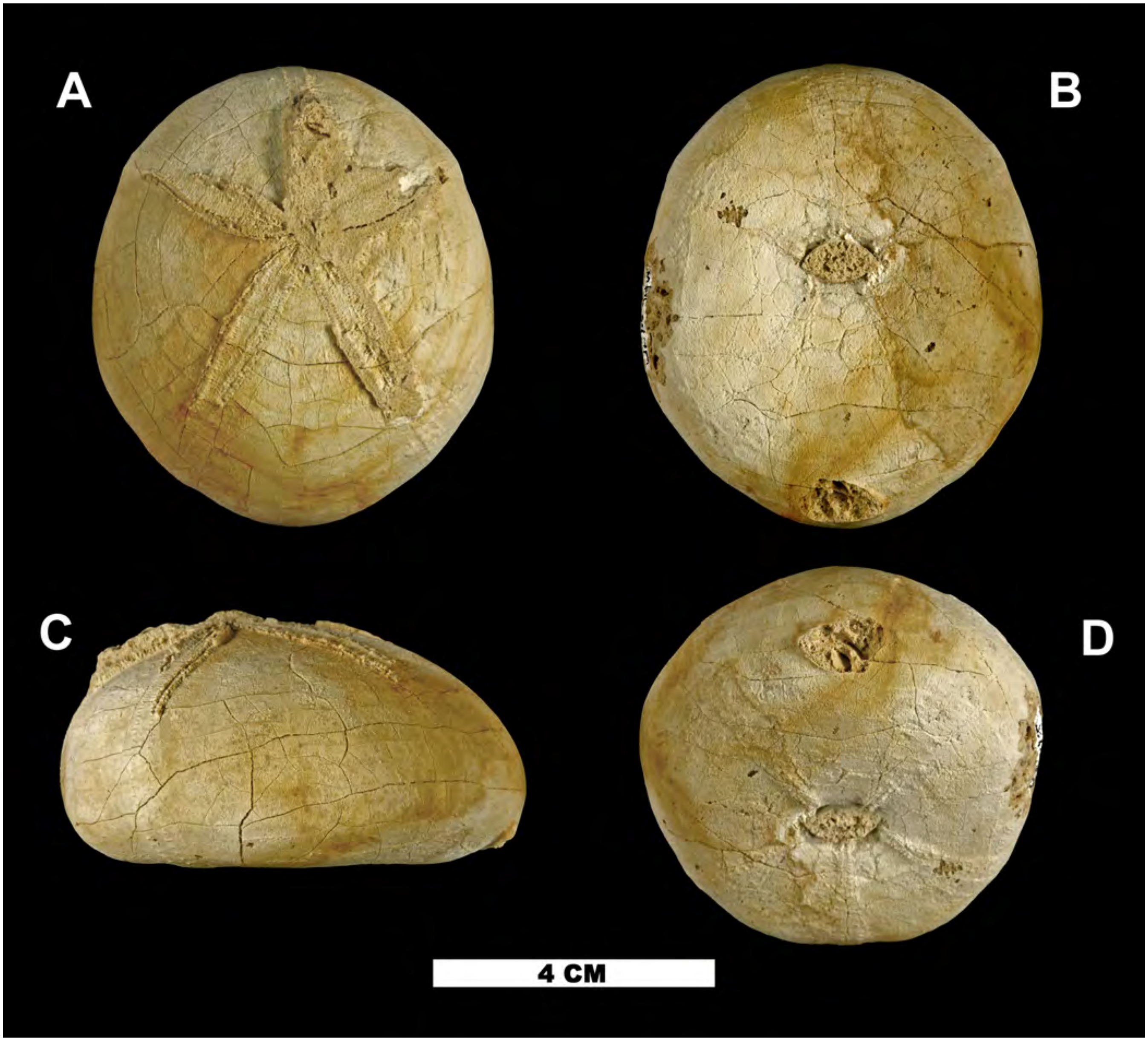


Figure 92: *Echinolampas* cf. *E. aldrichi* (UF 112504), 67 mm TL, 58 mm TW, 33.5 mm TH, internal mold from the dolomitic portion of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA014). A: aboral. B: oral. C: left side. D: oblique posterior viewpoint tilted upward from oral surface showing periproct placement.

Material and Occurrence.—Holotype (UF 338027) and paratypes (UF 342090 and UF 342091), from the type locality in the OLS, where it occurs with *H. brooksi* and *O. haldemani* in material dredged from 24 m beneath the top of the Eocene stratum in the most northwestern pit in the quarry complex of Leon Brooks, northwest of Marianna, Jackson County, Florida (FM-IP JA039).

Suborder **ECHINOLAMPADOIDA** Kroh and Smith, 2010

Family **ECHINOLAMPADIDAE** Gray, 1851
Genus ***Echinolampas*** Gray, 1825

Echinolampas aldrichi Twitchell in Clark and Twitchell, 1915
(Fig. 92)

Echinolampas aldrichi Twitchell in Clark and Twitchell, 1915. p. 173. pl. 81, figs. 1. a-d, 2.

Echinolampas (*Miolampas*) *aldrichi* (Twitchell). Lambert and Thiéry, 1921. p. 383.

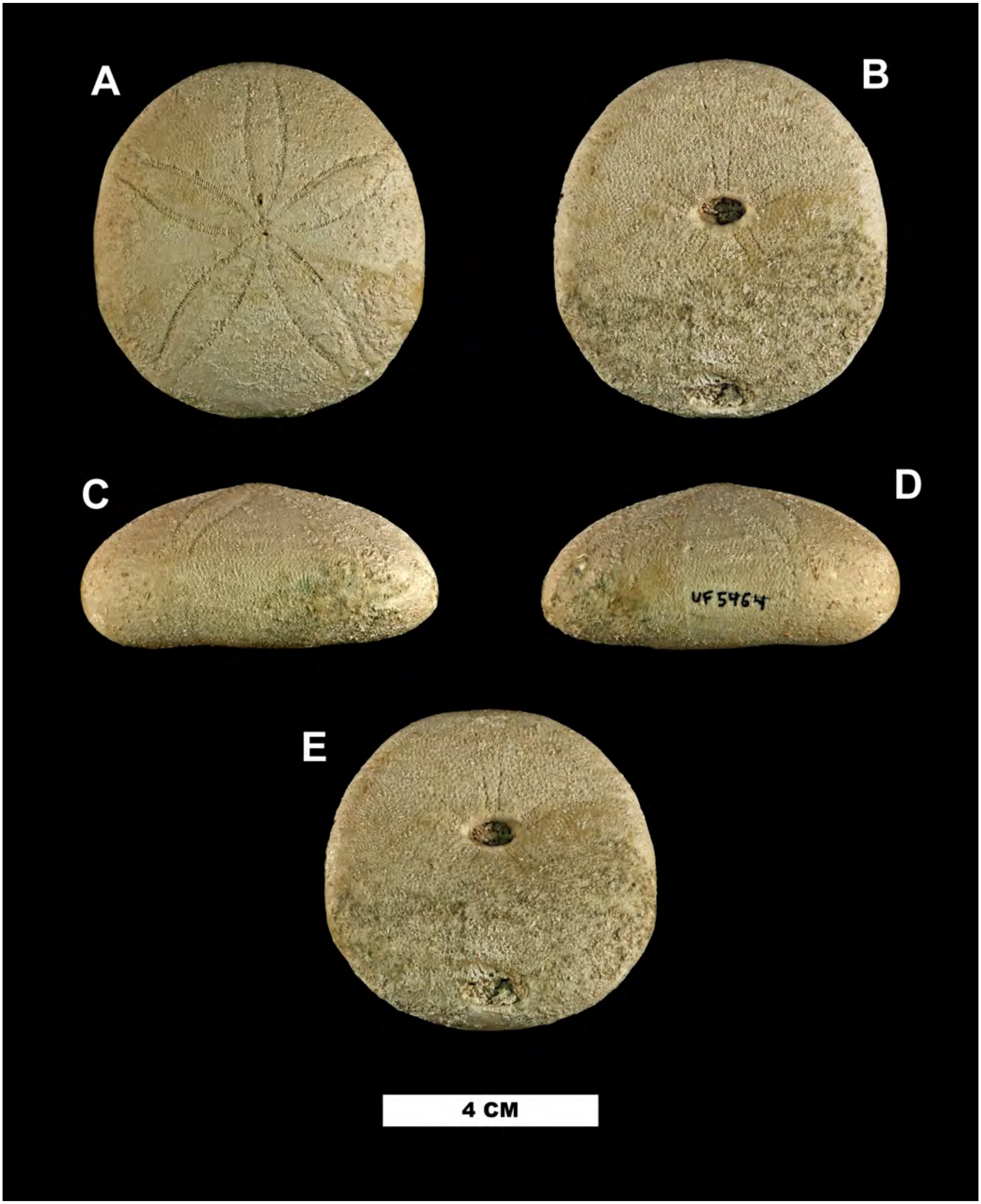


Figure 93: *Echinolampas tanypetalis* (UF 5464), 70 mm TL, 65 mm TW, 34 mm TH, upper portion of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: right side. E: tilted oral viewpoint from posterior.

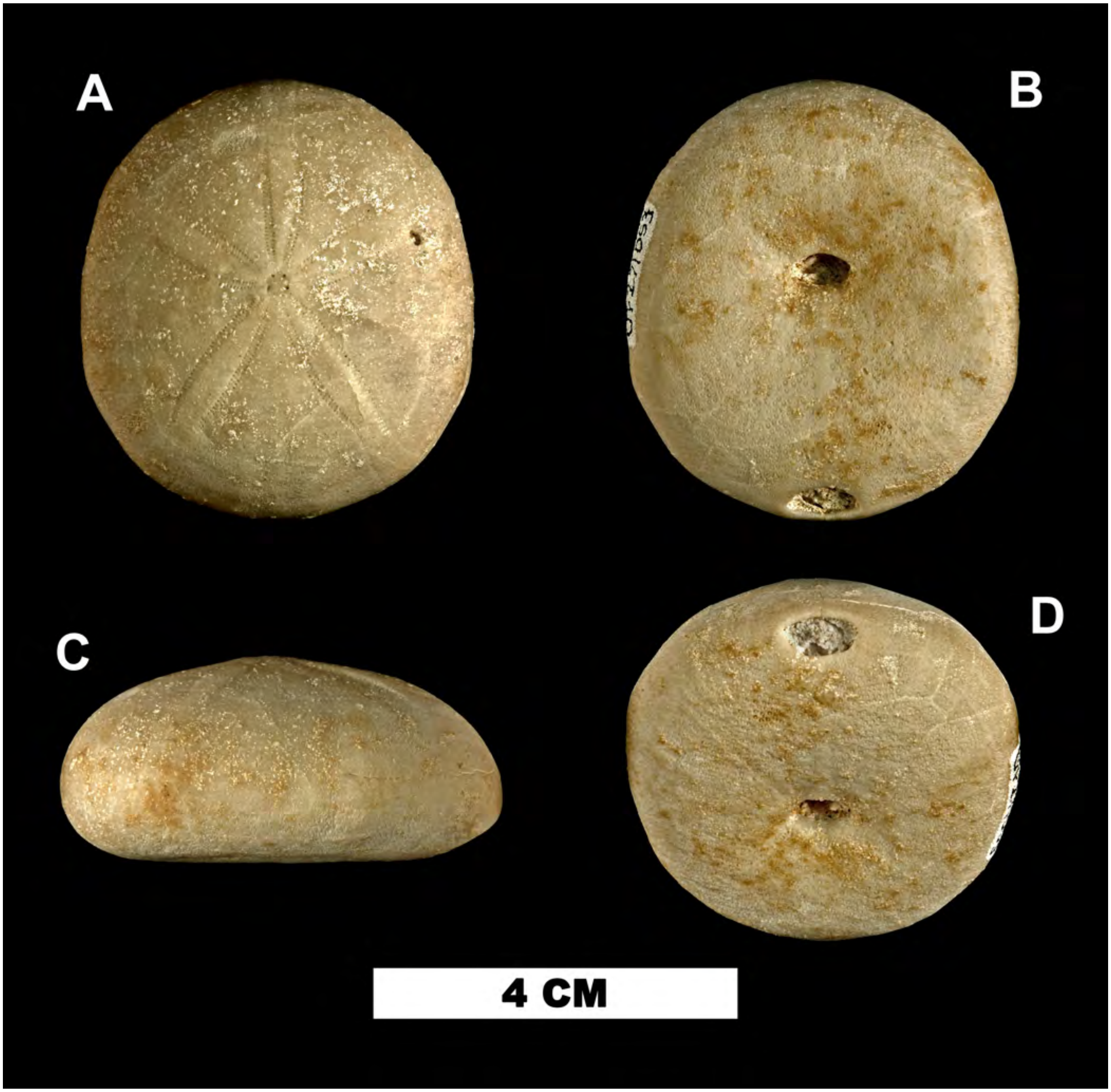


Figure 94: *Echinolampas tanypetalis* (UF 271053), 50 mm TL, 44.5 mm TW, 23 mm TH, Upper Eocene Ocala Limestone, Alachua County, Florida (FM-IP AL004). A: aboral. B: oral. C: left side. D: tilted oral viewpoint from posterior.

Echinolampas aldrichi (Twitchell). Cooke, 1942. p. 38.

Echinolampas aldrichi (Twitchell). Cooke, 1959. pp. 55-56. pl. 22, figs. 11-13.

Echinolampas aldrichi (Twitchell). Gordon, 1963. p. 637. pl. 81, figs. 1, 2.

Echinolampas sp. cf. *E. aldrichi* (Twitchell). Donovan et al., 2005. p. 323. fig. 1.

Echinolampas aldrichi (Twitchell). Osborn and Ciampaglio, 2014. p. 142.

Echinolampas aldrichi (Twitchell). Martinez-Melo, 2019. pp. 5-8. figs. 6, 7.

Echinolampas aldrichi (Twitchell). Buitrón-Sánchez et al., 2019. p. 53, figs. 2a, b, c.

Occurrence.—Specimens of *E. aldrichi* (e.g., UF 112389) were collected from a dolomitic facies of the Marianna Limestone, in the Oakdale Quadrangle between Marianna and Altha in southern Jackson County (FM-IP JA014). This is the first documented record of this species in Florida.

The species is found in greatest abundance in the Upper Oligocene Chickasawhay Limestone in southwestern Alabama and southeastern Mississippi, and rarely occurs in the Upper Oligocene River Bend Formation of North Carolina. The type locality is in the Chickasawhay Limestone, near Gainestown, Clarke County, Alabama.

Echinolampas aldrichi also occurs in the Oligocene of Chiapas, Mexico (Durham, 1969); the Miocene of Palenque, Chiapas, Mexico (Martinez-Melo, 2019); Oligocene of Veracruz, Mexico (Buitrón-Sánchez, 2019); the Oligocene of Puerto Rico (Cooke, 1959; Gordon, 1963), and the Middle Miocene of Belize (Donovan et al., 2005).

Discussion.—Twitchell in Clark and Twitchell (1915), described this robust species from the holotype collected by T. H. Aldrich in the St. Stephens Limestone (now considered to be the Chickasawhay Limestone) near Gainestown, Alabama. However, as the occurrences noted above attest, this species is now known to have a much broader distribution. In Florida, *E. aldrichi* is known only from internal molds collected in dolomitic facies of the Marianna Limestone, south of Marianna, where it occurs with *C. rogersi* and *S. americanus.* This is the only species of *Echinolampas* in the Oligocene strata of the region and cannot be confused with any other element of the fauna. We figure one specimen (UF 112504) from this deposit that measures 66 mm TL, 58 mm TW, 33 mm TH (Fig. 92), but the collections include numerous specimens.

Echinolampas tanypetalis Harper and Shaak, 1974
(Figs. 93-96)

Echinolampas tanypetalis Harper and Shaak, 1974. pp. 166-169. txt fig. 2. tbl. 1, pl. 1.
Echinolampas tanypetalis (Harper and Shaak). Osborn et al., 2016. tbl. 2.

Occurrence.—This species has not been documented outside of the *Oligopygus wetherbyi* Zone of the OLS of Florida. The type locality is a quarry west of Dowling Park (FM-IP LF002), in Lafayette County. The species also occurs in quarries northwest of Mayo (FM-IP LF001), Lafayette County and south of Tennille (FM-IP DI001), Dixie County.

Discussion.—Harper and Shaak (1974) differentiated *E. tanypetalis* and the Oligocene *E. aldrichi* by the lower test and more anterior apical system of *E. tanypetalis*, and its longer petals that have pore pairs almost perpendicular to the petal axis. The pore pairs of *E. aldrichi* are distinctly oblique (approximately 35° towards the ambitus from the petal axis). Furthermore, the peristome of *E. tanypetalis* is further forward.

This species is rare, which would account for it remaining undocumented for so long in the OLS (an otherwise historically heavily collected unit), but persistent collecting in the *Oligopygus wetherbyi* Zone of the OLS will usually provide specimens, especially in the more northerly exposures of the *Oligopygus wetherbyi* Zone in Lafayette and Dixie Counties. We figure four specimens, the largest of which (UF 5464) is from the type locality, and measures 70 mm TL, 65 mm TW, 34 mm TH (Fig. 93).

Suborder **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 macneili Cooke, 1959
(Figs. 97-100)

Echinocyamus macneili Cooke, 1959. p. 32. pl. 9, figs. 6-8.
Echinocyamus macneili (Cooke). Kier, 1966a. p. 7, figs. 10A, B; 11A, B; 13A.
not *Echinocyamus parvus* (Emmons). Zachos, 2005. p. 220. figs. 2.4-6.
not *Echinocyamus parvus* (Emmons). Osborn et al., 2016. tbl. 3.

Occurrence.—Within Florida, *E. macneili* is

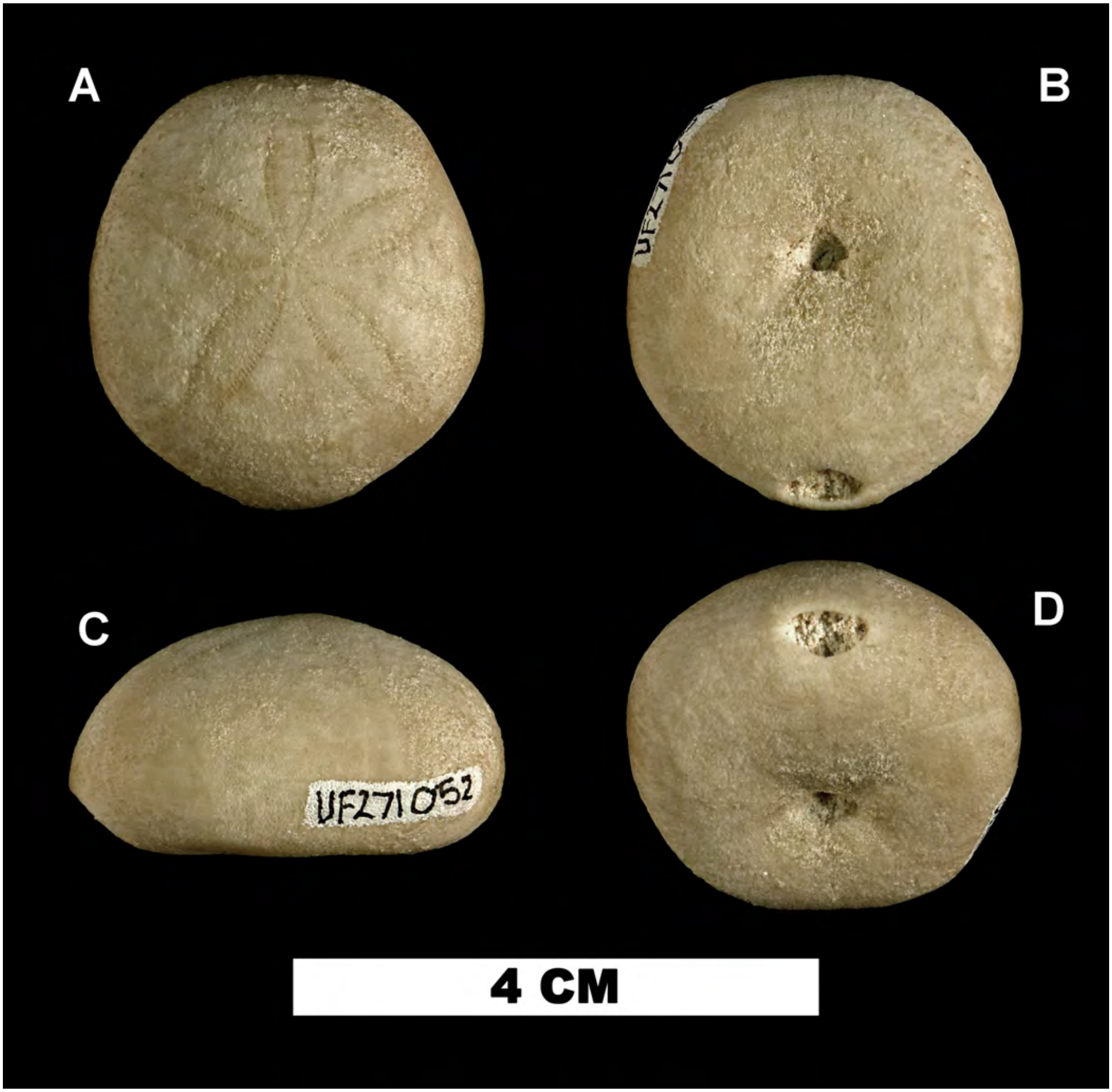


Figure 95: *Echinolampas tanypetalis* (UF 271052), 32 mm TL, 29 mm TW, 17 mm TH (small specimen for the species), Upper Eocene Ocala Limestone, Alachua County, Florida (FM-IP AL004). A: aboral. B: oral. C: right side. D: tilted oral viewpoint from posterior.

known only from the subsurface, where it was obtained from the OLS in Florida Geological Survey core W-19663 between 244 and 256 m depth (FM-IP OK005) in Okaloosa County. The type locality for the species is in the basal Upper Eocene Moodys Branch Formation where it is associated with *Periarchus lyelli* (Conrad, 1834) along a creek (presumably Fall Creek) flowing into the Conecuh River in the NE¼ sec. 32, T. 4 N, R. 15 E., southwest of Andalusia, Covington County, Alabama.

Discussion.—The holotype of *E. macneili* (USNM 862297; Fig. 99) was collected in the basal Upper Eocene Moodys Branch Formation, as noted above. The species is abundant at the type locality near the upper portion of the “*Scutella* bed” (dense

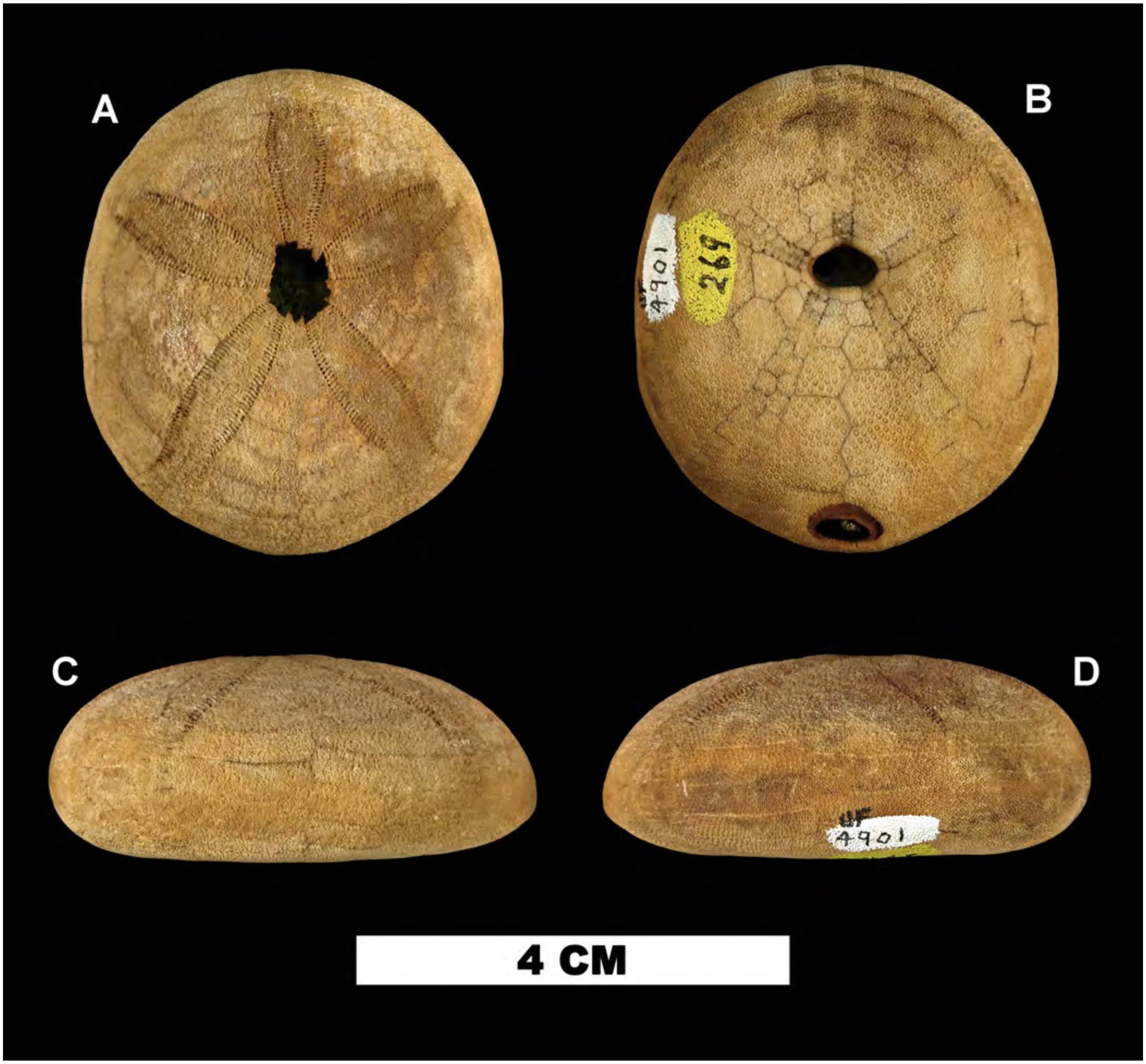


Figure 96: *Echinolampas tanypetalis* (UF 4901), 44.5 mm TL, 40 mm TW, 18 mm TH, specimen with some oral surface plate details, Upper Eocene Ocala Limestone, Levy County, Florida (FM-IP LV005). A: aboral. B: oral. C: left side. D: right side.

concentration of *P. lyelli*) atop the bank just north of Fall Creek. The recognition of *E. macneili* from the OLS in the Okaloosa County well material discussed herein is the first documentation of *Echinocyamus* in Florida and the first known occurrence of *E. macneili* outside of its type locality. Although internal structure of this species seems not to have ever been mentioned in the literature, preparation of a pair of specimens show that it has strongly developed internal supports, and the species is therefore attributable to *Echinocyamus*, and not *Fibularia*.

Cooke (1959) stated that the lateral profile of *E. macneili* is like that of *Echinocyamus parvus* Emmons, 1858, but the upper surface is higher and more rounded. Unfortunately, Cooke compared *E. macneili* to specimens of *Echinocyamus* from the Thomas Farm site north of Jacksonville, Onslow County, NC that are not definitively *E. parvus* (Emmons, 1858). With issues such as this, and to ensure clarity concerning our comparative material, a short summary of the taxonomy of the genus in the Eocene of North America is necessary.

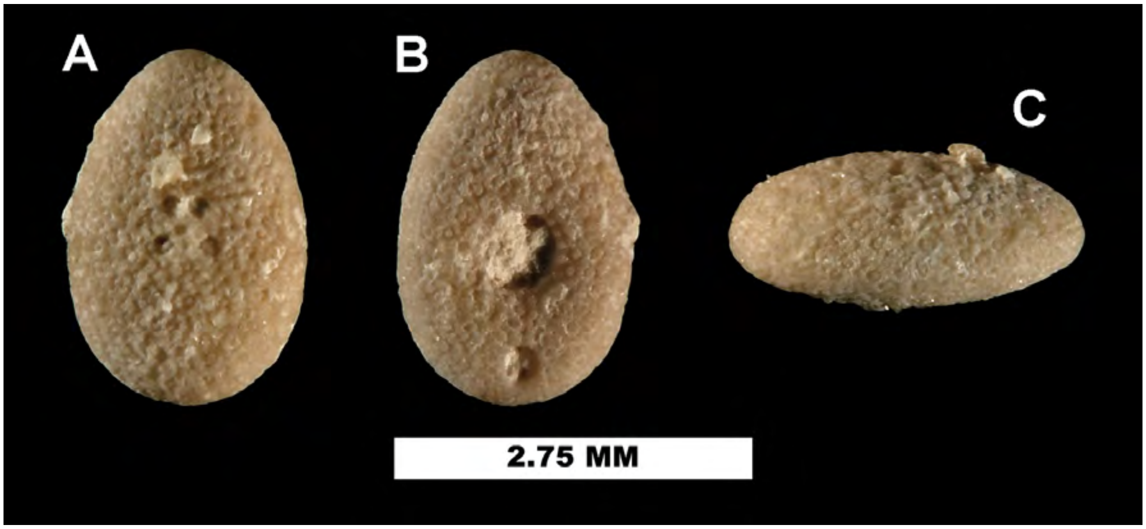


Figure 97: *Echinocyamus macneili* (UF 297039 #12), Upper Eocene Ocala Limestone, from 800-840 ft. depth in core from Fred Gannon Rocky Bayou State Park (FM-IP OK005), Okaloosa County, Florida. A: aboral. B: oral. C: right side.

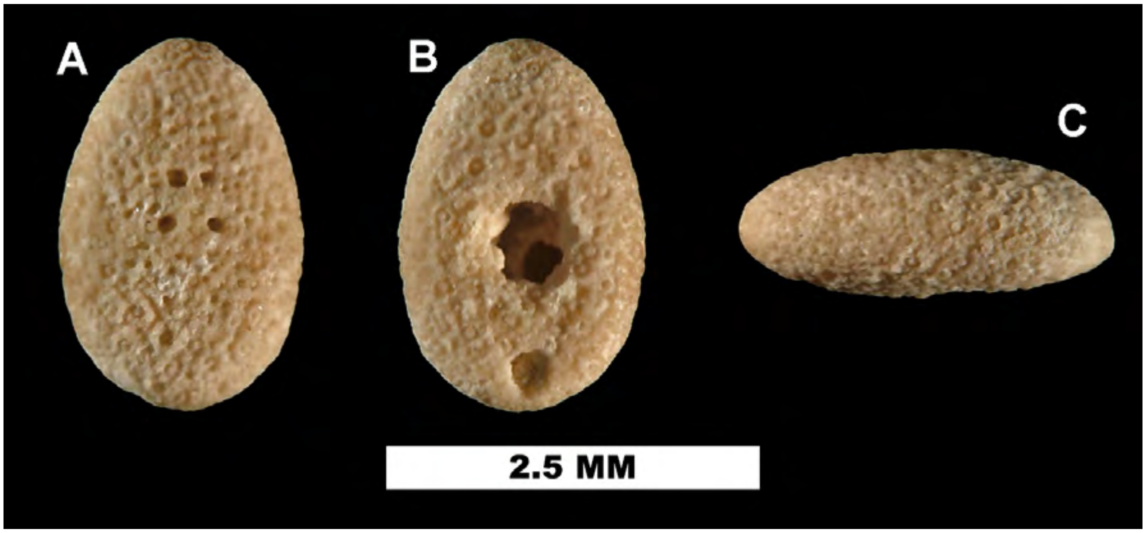


Figure 98: *Echinocyamus macneili* (UF 297039 #13), Upper Eocene Ocala Limestone, from 800-840 ft. depth in core from Fred Gannon Rocky Bayou State Park (FM-IP OK005), Okaloosa County, Florida. A: aboral. B: oral. C: right side.

Echinocyamus parvus Emmons, 1858, the first *Echinocyamus* reported from North America, was described from the Eocene of Craven County, North Carolina, in strata now known as the Middle to Upper Eocene Castle Hayne Limestone. Meyer (1886) described *Echinocyamus huxleyanus* from a single damaged specimen collected at Claiborne, Alabama, in strata subsequently recognized as the Middle Eocene Gosport Sand (Cooke, 1942). The holotype of *E. huxleyanus* (USNM 559484) has been broken, but examination of the fragments remaining shows that they have no relationship with *E. parvus*. The type of *E. huxleyanus* has apparently not been consulted in revisionary works such as Clark and Twitchell (1915), Cooke (1942), and more recently, Zachos (2005), leading to incorrect synonymy with *E. parvus*. Determination of what *E. huxleyanus*, a species from Alabama, represents falls outside the scope of the present work except to note that it is not part of the synonymies of any *Echinocyamus* discussed here, and that it is almost undoubtedly not attributable to the genus.

Cooke (1959) described *E. macneili* from the basal Upper Eocene Moodys Branch Formation

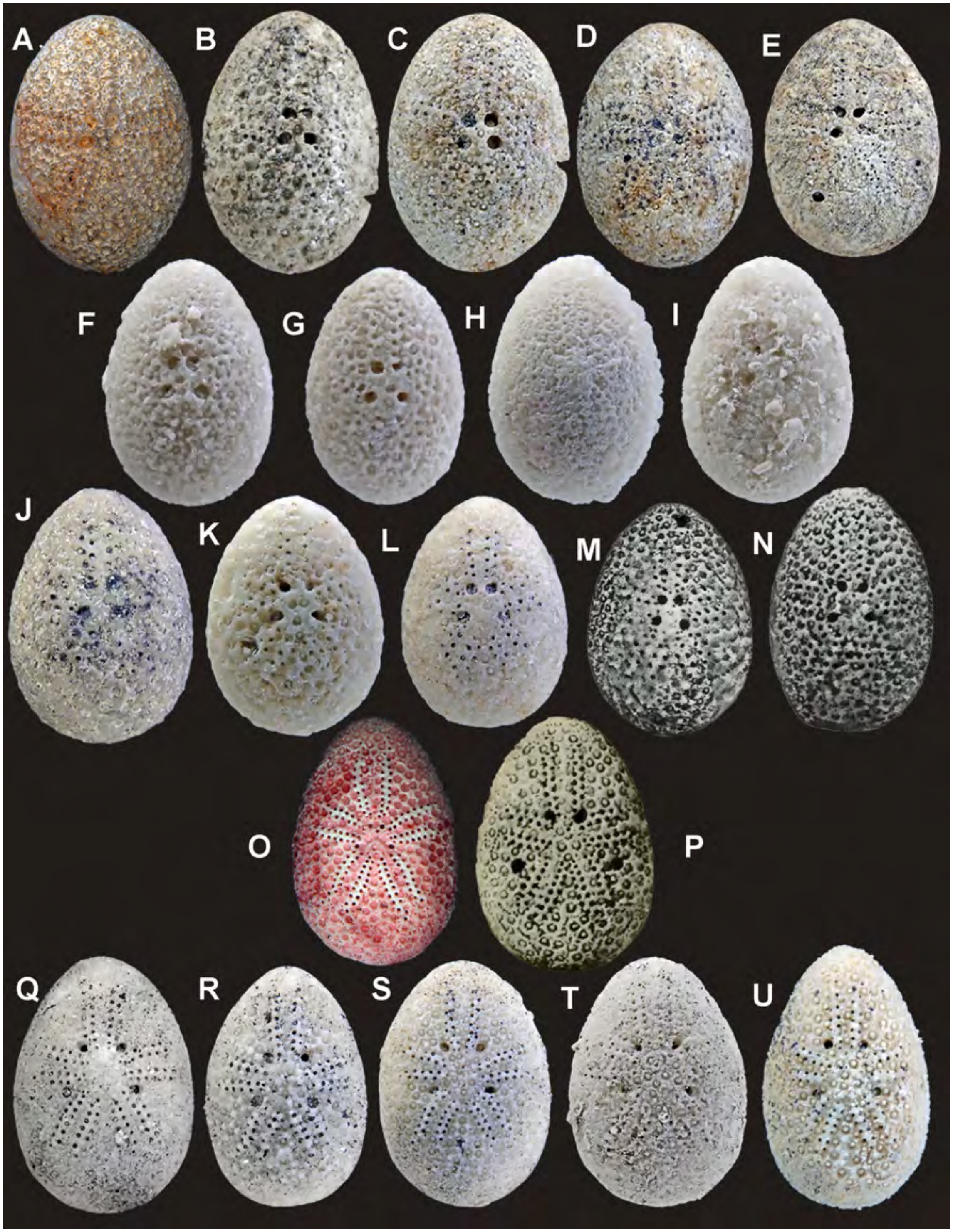


Figure 99: Comparison of aboral surfaces of female specimens of regional Eocene *Echinocyamus* emphasizing gonopore arrangement. A: *E. macneili*, holotype (USNM 562297), 5.6 mm TL, 4.0 mm TW, 2.4 mm TH, Upper Eocene Moodys Branch Formation, creek flowing into Conecuh River, Covington County, Alabama. B-E: *E. macneili* (from lot UF 338023) Upper Eocene Moodys Branch Formation, screened from *Periarchus lyelli* bed, Conecuh River at mouth of Fall Creek, above Brooklyn Rd. (very near the type locality of the species) west of Andalusia, Covington County, Alabama (FM-IP ZA145); all females. B: 3.2 mm TL, 2.1 mm TW, 1.3 mm TH. C: 4.2 mm TL, 2.9 mm TW, 1.5 mm TH. D: 4.9 mm TL, 3.6 mm TW, 1.9 mm TH. E: 5.3 mm TL, 3.9 mm TW, 1.6 mm TH. F-I: *Echinocyamus* cf. *E. macneili* (from lot UF 297039) Upper Eocene Ocala Limestone, from 800-840 ft. depth in core from Fred Gannon Rocky Bayou State Park (FM-IP OK005), Okaloosa

(**Fig. 99 caption cont.**) County, Florida. F: 2.6 mm TL, 1.8 mm TW, 1.1 mm TH. G: 2.3 mm TL, 1.5 mm TW, .9 mm TH. H: 4.5 mm TL, 3.2 mm TW, 1.4 mm TH. I: 5.3 mm TL, 3.7 mm TW, 1.9 mm TH. J-L: *Echinocyamus* cf. *E. parvus*, (from lot UF 338024) upper sequence three (of Zullo and Harris, 1987), late zone of Kier (1980) of the Middle to Upper Eocene Castle Hayne Limestone, Lanier Pit south of Maple Hill, Pender County, North Carolina (FM-IP ZN039). J: 3.4 mm TL, 2.5 mm TW, 1.3 mm TH. K: 3.5 mm TL, 2.5 mm TW, 1.4 mm TH. L: 3.6 mm TL, 2.6 mm TW, 1.3 mm TH. M, N: *Echinocyamus* cf. *E. parvus*; specimens identified as *E. parvus* in Kier (1980), Lanier Quarry (see F-H above); M: USNM 264054. N: USNM 264055. O: *E. bisexus*, holotype (USNM 650722), a male, Middle Eocene, Lake City Formation; USGS test well number 5, near Brunswick, Glynn County, Georgia. P: *E. bisexus* (USNM 650720) from Kier (1968); female, from the type locality, test well level 1130-1135 ft., Middle Eocene Lake City Formation, Glynn County, Georgia. Q-T: *Echinocyamus* cf. *E. bisexus*, (from lot UF 338025) upper sequence three (of Zullo and Harris, 1987), late zone of Kier (1980) of the Middle to Upper Eocene Castle Hayne Limestone, Martin Marietta Richland Quarry, near Catherine Lake, Onslow County, North Carolina (FM-IP ZN126). Q: 6.0 mm TL, 4.2 mm TW, 2.2 mm TH. R: 6.4 mm TL, 4.2 mm TW, 2.5 mm TH. S: 6.6 mm TL, 4.5 mm TW, 2.1 mm TH. T: 7.6 mm TL, 5.5 mm TW, 2.7 mm TH. U: *Echinocyamus* cf. *E. bisexus*, (from lot UF 338026), upper sequence three (of Zullo and Harris, 1987), late zone of Kier (1980) of the Middle to Upper Eocene Castle Hayne Limestone, Trent River, boat ramp at Trenton, Jones County, North Carolina (FM-IP ZN125): 5.4 mm TL, 3.4 mm TW, 1.6 mm TH.

in Alabama. Kier (1968) described *Echinocyamus bisexus* from a Georgia test well in the Middle Eocene Lake City Formation (subsumed into the Avon Park Formation by Miller 1986). We discuss the implications of these descriptions in more detail, below.

Zachos (2005) suggested that *Echinocyamus meridonalis* Meyer, 1887 was a juvenile *P. lyelli*, and went on to assert that *E. bisexus, E. huxleyanus,* and *E. macneili* are junior synonyms of *E. parvus*. This action effectively assigned all Eocene *Echinocyamus* in North America to one highly variable species (but see errors noted above with respect to *E. huxleyanus*, which we will not consider further). It became important to compare our test well material to each form. While doing so, differences among the species became evident (except for *E. parvus* as discussed below), leading us to maintain *E. macneili* as a separate species.

Echinocyamus parvus is likely the least understood *Echinocyamus* in North America, making synonymies challenging. Emmons (1858) described *E. parvus* from a single specimen (the holotype was uncataloged, poorly figured, and has since been lost) collected in the Eocene of Craven County, North Carolina, in strata now referred to the Middle to Upper Eocene Castle Hayne Limestone. His figure, a hand drawing of the oral surface done at natural size, lacks detail but could be interpreted as the oral surface of an *Echinocyamus*. At the time of his description, the sense of *Echinocyamus* and *Fibularia* were reversed from the presently accepted nomenclature, so this adds yet another layer of difficulty over what Emmons meant with his drawing. Distinction between the two genera is difficult (though not impossible), without reference to the internal structure. Emmons leaves us to guess what that might have been for his *E. parvus*, and we will likely never be sure what Emmons meant by the name ”*Echinocyamus*”.

Emmons’ (1858: 307) description of *E. parvus* is: “Test small, oval, with rounded sides; avenues dorsal; mouth sub-central, rounded, large, with a crenulated margin; vent between the mouth and hinder margin; genital pores apparently four. The mouth is large in proportion to the size of the body and the vent is situated half way between the mouth and margin.” This description, though inadequate for determing his concept of *Echinocyamus*, is almost sufficient to distinguish it from other small taxa found in the Castle Hayne Limestone. However, it is clearly not sufficient to distinguish it from subsequently described species of *Echinocyamus* from the region.

Clark and Twitchell (1915) stated that the holotype of *E. parvus* was lost. They did not figure the species and merely reiterated Emmons’ description.

Kellum (1926) documented *E. parvus* from the Castle Hayne Limestone at Thomas Farm, 10 mi. northwest of Jacksonville, Onslow County, North Carolina. Kellum did not figure the specimens, nor indicate what led him to the identification, but considering that Emmons’ description is not diagnostic, nor is his figure, and the holotype of *E. parvus* had been lost, it is likely Kellum made his specific identification solely based on what he perceived to be the genus designation and locality. That is, an *Echinocyamus* from the Castle Hayne Limestone must be *E. parvus*.

Cooke (1942) reported on Kellum's specimens (he documented five) from Onslow County, North Carolina, and figured one (USNM 499002). Cooke cautioned the figured specimen could not be compared to the type specimen, because it appeared to be lost. He noted that his image showed a specimen wider posteriorly and narrower anteriorly than Emmons' figure.

Cooke (1959) figured the same specimen, and again listed Kellum's locality as the only locality for *E. parvus* in North Carolina. Cooke (1959) provided the most complete description of what workers continued to call "*E. parvus*", but it must be remembered that at this point, the only specimens available for study since Emmons' described the type specimen, was the material in the USNM first documented by Kellum (1926) from Onslow County. Whether or not this is *E. parvus* remains an open question.

Kier (1968) described *E. bisexus* from the Middle Eocene Lake City Formation (now Avon Park Formation) in a Georgia test well and noted that *E. bisexus* most resembled the concept of *E. parvus* in use at the time. He stated that both species have a similar shape, periproct position, and peristome size, but that *E. bisexus* differs in having longer petals with more pore pairs and a smaller madreporite (he did not mention differences in gonopore position). Again, Kier was comparing his new species with material in the USNM identified as *E. parvus* by Kellum (1926).

Kier (1980) subsequently recorded 67 specimens of *E. parvus* and 13 specimens of *E. bisexus* from the Castle Hayne Limestone in the Lanier Quarry, near Maple Hill, Pender County, North Carolina. He redescribed "*Echinocyamus parvus*" from this material, whether or not it actually represents *E. parvus* of Emmons (1858). Kier (1980) also documented disparity in gonopore size, with some specimens having very small gonopores and others very large ones, interpreting this as sexual dimorphism.

Kier (1980: pl. 10, figs. 5-10) figured three specimens (USNM 264053-55) he identified as *E. parvus* from the Lanier Quarry. Of these, two (USNM 264054 and 264055) appear to be females with large gonopores and are distinguished from *E. macneili* by their gonopores being situated further apart, though not partway adoral along the interambulacrum like *E. bisexus* (Fig. 99). We refer to the specimens in Kier's (1980: pl. 10, figs. 5-10) as *Echinocyamus* cf. *E. parvus* in view of the analysis above. Kier (1980: 34) lists USNM 499002 (the same specimen from Onslow County collected by Kellum [1926] and figured by Cooke [1942, 1959]) as one of his figured specimens, however, it does not seem to appear among his figures.

The stratigraphy and locality-based identification of Kellum (1926), followed by Cooke (1942, 1959) and Kier (1968, 1980) was reasonable prior to Kier (1980) because only *E. parvus* had been documented from the Castle Hayne Limestone. That is only the specimens from Thomas Farm, north of Jacksonville, North Carolina were known, and they all appeared to belong to one species. However, when Kier (1980) documented both *E. bisexus* and another that he attributed to *E. parvus* by comparing it to the Thomas Farm material, in the Castle Hayne Limestone at the Lanier Quarry, this circumstantial approach to identification of *E. parvus* was rendered invalid. We can no longer ascertain that the holotype of *E. parvus* is distinct from what Kier (1968) subsequently named *E. bisexus.* We figure the latter species from two additional localities in the Castle Hayne Limestone of North Carolina (Fig. 99) and note that *E. bisexus* is far more common in the Castle Hayne Limestone than the form Kellum (1926) identified as *E. parvus* from Thomas Farm.

The only solution, other than finding the missing holotype, is to discover and describe new material from the type locality of *E. parvus*, possibly by additional collecting. Emmons (1858) stated the type locality of *E. parvus* is Craven County, North Carolina, which is vague, but he provided clues to perhaps two specific localities. Within his report, Emmons discussed two exposures of Eocene "marl" in Craven County. One is on the south bank of the Neuse River on the Biddle Plantation (Biddle Landing on the Neuse River) and the other is on the plantation of William B. Wadsworth at Core Creek. He also indicated the fossil fauna associated with *E. parvus*, although he did not state what additional echinoids might be a part of that fauna. Interestingly, he noted that the small comatulid crinoid *Microcrinus conoideus* Emmons, 1858 was collected with *E. parvus*.

Unfortunately, our research has not yet yielded records of comutalid crinoids (or *Echinocyamus*) at Biddle Landing. This leaves the Wadsworth Marl at the Wadsworth Plantation at Core Creek. Emmons (1858: 105) stated that a crinoid is abundant in the Wadsworth Marl, which also lends evidence that the type locality of *E. parvus* is at the Wadsworth Plantation at Core Creek, Craven County, North Carolina. Wadsworth wrote a letter to Emmons (1858), included in the latter's report, detailing how he utilized the marl dug on his plantation as fertilizer, suggesting that the marls was not a natural exposure on Core Creek, but excavations on the Wadsworth Plantation near Core Creek.

Wadsworth's Plantation is shown south of Core Creek, roughly midway between Rock Landing and Biddle Landing on the Neuse River, on a beautiful map hand-drawn by Jeremy Francis Gilmer (1818-1883) during the Civil War (between 1861 and 1865: "Reconnaissance of the country between Newbern and Goldsboro between the Trent and the Neuse Rivers"). Unfortunately, there are no current marl pits or other exposures of the Castle Hayne Limestone in this area. Therefore, although we have a suggestion as to where to search for additional specimens in the type area, until exposures become available, or the holotype is discovered, we see no viable way to identify positively any specimen as *E. parvus*. As a result, we maintain that specimens referred to as *E. parvus* from the Castle Hayne Limestone by Kellum (1926), Cooke (1942, 1959), and Kier (1980) (Fig. 99) can only be referred to as *Echinocyamus* cf. *E. parvus*. Consequently, no other species can be placed in junior synonymy.

Test width (TW) as a percentage of test length (TL) is very similar in these taxa: 70.2% for Richlands Quarry *E. bisexus*, 70.8% for Lanier Quarry *Echinocyamus* cf. *E. parvus*, 70.1% for type locality *E. macneili*, and 72.1% for Florida *E. macneili*. However, as noted by Cooke (1959), the test of *E. macneili* is higher than that of *Echinocyamus* cf. *E. parvus* (Fig. 100). The average TH as a percentage of TL for type locality *E. macneili* is 40%, and Florida *E. macneili* is 40.9%; whereas the average of *E. bisexus* from the Richlands Quarry was 36%, and *Echinocyamus* cf. *E. parvus* from the Lanier quarry was 38.3%. TH vs TW revealed similar results, with TH of *E. macneili* from the type locality being on average 57.2% TW. The Florida *E. macneili* is 59.3%, but in Richland Quarry *E. bisexus* TH is only 51.4% TW; specimens of *E. parvus* from the Lanier quarry were closer to *E. macneili* with TH 53.5 % TW.

However, TH is not the characteristic that best distinguishes *E. macneili*, *Echinocyamus* cf. *E. parvus*, and *E. bisexus*. The gonopores of females of *E. macneili* are closer together than in *Echinocyamus* cf. *E. parvus*, and much closer together than that of *E. bisexus* (Fig. 99). We compared female specimens (specimens with larger gonopores) of regional *Echinocyamus*, including the available holotypes. This includes *E. macneili* from its type locality, *Echinocyamus* cf. *E. parvus* from the Castle Hayne Limestone, *E. bisexus* from the Castle Hayne Limestone, and specimens we recognize as *E. macneili* from Okaloosa County, to explore differences in gonopore arrangement of these species (Fig. 99). This comparison confirms we have more than one species of *Echinocyamus* in the regional Eocene strata.

To reiterate, *Echinocyamus macneili* is readily distinguished from *E. bisexus* in not only having a higher test, but by differences in gonopore arrangement in females of these two species. In *E. macneili*, the four enlarged gonopores are closer together in the apical area than any other regional Eocene species of *Echinocyamus*. In *E. bisexus*, the gonopores are placed well outside the apical area part of the way down their respective interambulacra (Fig. 99).

Cooke (1959) alluded to possible sexual dimorphism in *E. macneili* in his description. Due to the large gonopores, he considered the holotype of *E. macneili* (Fig. 99) to be a female. The species seems very likely to be sexually dimorphic (females with large gonopores, males with gonopores that are barely discernable without magnification) when comparing multiple specimens from the type locality and from the specimens we studied from the Okaloosa County Well Core (UF 297039, UF 307764).

Osborn et al. (2016) followed Zachos (2005) in recognizing *E. parvus* (and not *E. macneili*) in the Moodys Branch Formation of Alabama (Osborn et al., 2016: table 3). In retrospect, this was an error that we have corrected in the synonymy above.

As mentioned above, although *E. macneili* is not known from surface exposures in Florida, it was abundant in Florida Geological Survey Core W-19663, being represented by two lots: UF 297039 (14 tests) and UF 307764 (15 tests).

Genus ***Fibularia*** Lamarck, 1816

Fibularia vaughani (Twitchell in Clark and Twitchell, 1915)
(Figs. 101-104)

Echinocyamus vaughani Twitchell in Clark and Twitchell, 1915. p. 160, pl. 74, figs. 1a-f.
Echinocyamus vaughani (Twitchell). Lambert and Thiéry, 1925. p. 576.
Echinocyamus vaughani (Twitchell). Cooke and Mossom, 1929. pl. 3, figs. 4a-b.
Fibularia vaughani (Twitchell). Cooke, 1942. p. 7.
Fibularia vaughani (Twitchell). Cooke, 1945. fig. 5, no. 4.
Fibularia vaughani (Twitchell). Fischer, 1951. p. 55. txt fig. 1.
Fibularia vaughani (Twitchell). Cooke, 1959. p. 30. pl. 9, figs. 23-27.
Fibularia vaughani (Twitchell). Osborn et al., 2016. tbl. 2.

Occurrence.—This is the common microechinoid of the OLS of Florida, and more rarely in Georgia. It occurs in sporadic abundance in the *Oligopygus haldemani* Zone of the OLS, especially northwest of Mayo, Lafayette County (FM-IP LF001) (Figs. 101, 102). It is common in the *Oligopygus phelani* Zone in the lower portion of the OLS, especially along the banks of the Withlacoochee River (FM-IP LV024), Levy County (Figs. 103, 104); Cross Florida Barge Canal (FM-IP CI001), south of Inglis, Citrus County, and in small pits near Inglis, Levy County.

Discussion.—Twitchell in Clark and Twitchell (1915), described this species as *Echinocyamus vaughani* from strata believed to be lower Oligocene at the time, but now recognized as the Upper Eocene OLS, along the Flint River in Georgia. *Fibularia vaughani* appears to be restricted to the OLS of Florida and Georgia, and it cannot be confused with any other species within the OLS.

Detailed examination of the type, including plate patterns of both the aboral and oral surfaces, strongly suggest that this species should not be placed in *Fibularia*. Aspects of these patterns strongly ally *F. vaughani* with members of *Fibulariella* Mortensen, 1948, presently considered to be rotulids. A revision of these minute taxa is in progress, but it is almost certain that placement in *Fibularia* is not the final word on the systematics of *F. vaughani*.

Family **NEOLAGANIDAE** Durham, 1954

The State of Neolaganid Systematics in the Region

Durham (1954) erected the family Neolaganidae to contain New World laganids whose basicoronal plates are arranged in a pentagon and not in a star-like pattern (i.e., no points on the distal part of the interambulacral basicoronals, and with large ambulacral basicoronals almost equal in length to the interambulacral basicoronals). He also erected numerous new genera to contain many species of laganids including *Cubanaster* Sánchez Roig, 1952e, *Neolaganum* Durham, 1954, *Weisbordella* Durham, 1954, and *Wythella* Durham, 1954. Kier (1967) subsequently erected *Pentedium* but left its family attribution in question, stating it likely belonged to a new family. *Pentedium* is distinguished from the neolaganids in having five, instead of four genital pores.

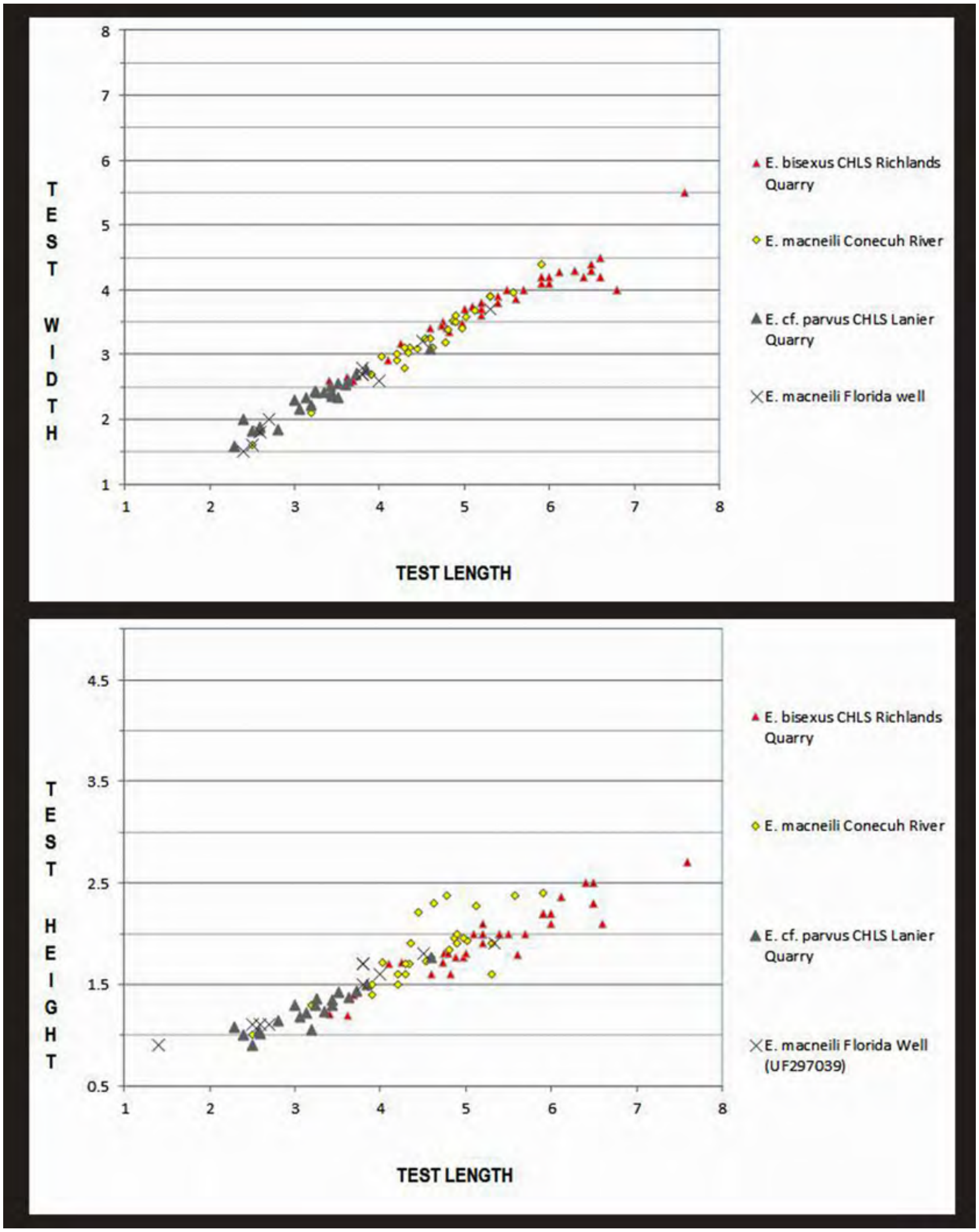


Figure 100: Comparison of regional Eocene *Echinocyamus*: comparisons of test length, width, and height of *Echinocyamus macneili* from the Moodys Branch Formation at the type area, Conecuh River west of Andalusia, Covington County, Alabama. (FM-IP ZA145); *Echinocyamus* cf. *E. bisexus* from the Castle Hayne Limestone, Martin Marietta Quarry near Catherine Lake, Onslow County, North Carolina (FM-IP ZN126); *Echinocyamus* cf. *E. parvus* from the Castle Hayne Limestone, Lanier Pit, Pender County, North Carolina (FM-IP ZN039), and *E. macneili,* Upper Eocene Ocala Limestone, from 800-840 ft. depth in core from Fred Gannon Rocky Bayou State Park (OK005), Okaloosa County, Florida. Although test width (TW) as a percentage of test length (TL) is very similar in these specimens: 70.2% for Richlands Quarry *E. bisexus*, 70.8% for Lanier Quarry *Echinocyamus* cf. *E. parvus*, 70.1% for type locality *E. macneili*, and 72.1% for Florida *E. macneili*; the test of *E. macneili* is higher than its congeners. The average test height (TH) as a percentage of TL for type locality *E. macneili* is 40%, and Florida *E. macneili* is 40.9%; whereas the average of *E. bisexus* from the Richlands Quarry is 36%, and *Echinocyamus* cf. *E. parvus* from the Lanier quarry is 38.3%. TH vs TW revealed similar results, with the TH of *E. macneili* from the type locality on average 57.2% TW, and the Florida *E. macneili* is 59.3%, and in Richland Quarry *E. bisexus* the height is only 51.4% TW; specimens of *Echinocyamus* cf. *E. parvus* from the Lanier quarry were closer to *E. macneili* with a TH on average equal to 53.5 % TW.

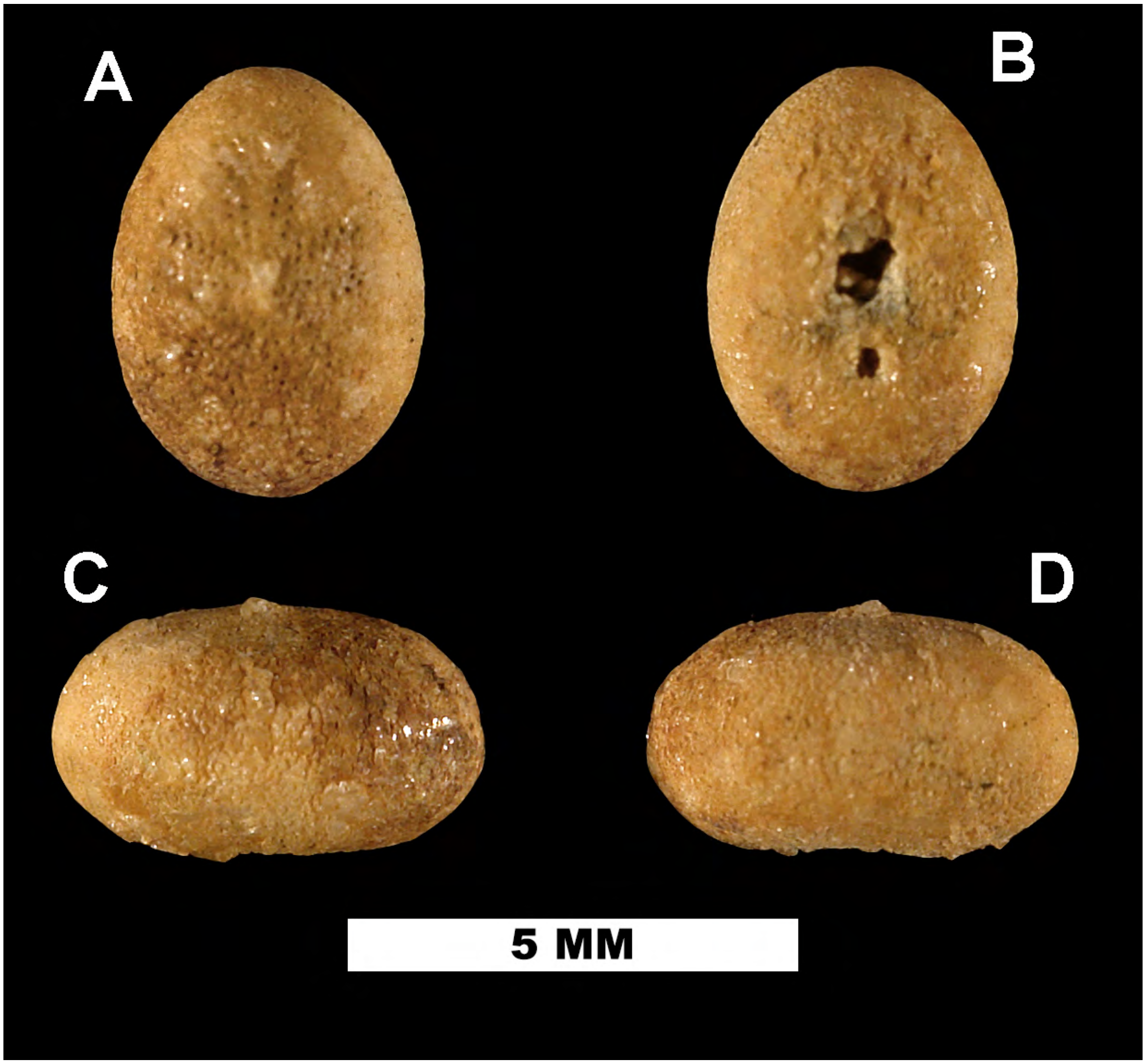


Figure 101: *Fibularia vaughani* (UF 337969), 4.5 mm TL, 3.5 mm TW, 2.5 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

However, a year later Kier erected *Durhamella* Kier, 1968, and placed it in the Neolaganidae without hesitation, although two species of that genus have five genital pores. We recognize both *Durhamella* and *Pentedium* in the Neolaganidae, and further discuss *Durhamella* below.

Without providing a formal statement or reasoning, Kroh and Smith (2010) demoted the Neolaganidae to a subfamily within the Laganidae, subdividing the Laganidae into two subfamilies: the Neolaganinae (with a strong presence in the fossil record of the region), and the Laganinae (with no known representatives in the fossil record of the eastern United States). This designation was apparently adopted by Kroh (2020), as the family Neolaganidae does not appear in that work. Smith and Kroh (2011) followed Durham (1954) in stating that the Neolaganinae have basicoronal plates in the shape of a pentagon, adding that the petals usually have compound plating. The coordinate subfamily Laganinae have basicoronal ambulacral plates in a stellate arrangement with ambulacrals forming points of the star in the aboral direction, and petaloid plating that is usually simple, made entirely of primary plates. We follow Durham (1954) in maintaining the Neolaganidae as a family along with the Laganidae, pending deeper taxon sampling than provided in Kroh and Smith (2010). This is

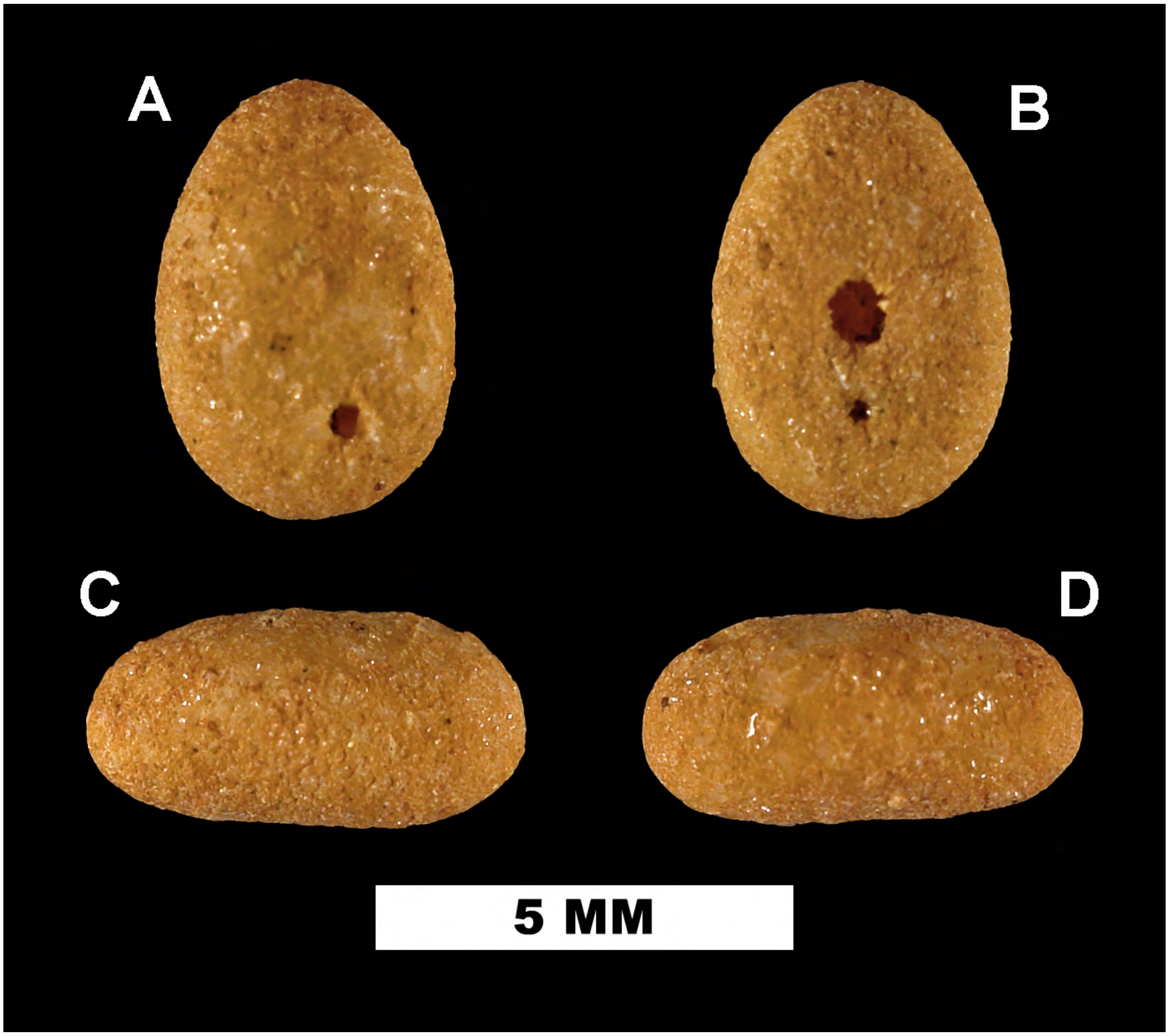


Figure 102: *Fibularia vaughani* (UF 337970), 5 mm TL, 3.5 mm TW, 2.5 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

because their phylogenetic analysis, based on a single laganid and a single neolaganid, provided no evidence for or against placing the Neolaganidae into the Laganidae. Moreover, the latter family is likely not monophyletic (Mooi et al., 2001). In contrast, there is good evidence to suggest that the Neolaganidae is monophyletic.

While determining taxonomic assignment of the new neolaganid species described below, it became apparent that the diagnoses of many neolaganid genera were not, in fact, diagnostic. The greater number of available specimens revealed that many characteristics used by Durham (1954) and Kier (1968) to distinguish the genera are either not consistent or not diagnostic, being present in numerous other genera. Study of oral plate maps for all regional genera (Fig. 105), as well as the plating in the petals (Fig. 106), revealed characteristics that facilitate identification of some of the genera. Genus diagnoses still require comparison of numerous features, such as oral surface plate arrangement, concavity of the oral surface, presence and structure of hydropore grooves, and petaloid structure.

Therefore, revised diagnostic criteria are provided in revisions of *Durhamella, Neolaganum,* and *Weisbordella* below. Even with these revised diagnoses, it seems clear that the Neolaganidae likely contains too many genera, as there remain few diagnostic characteristics to distinguish them. Future revisions will have to take this into account, as well

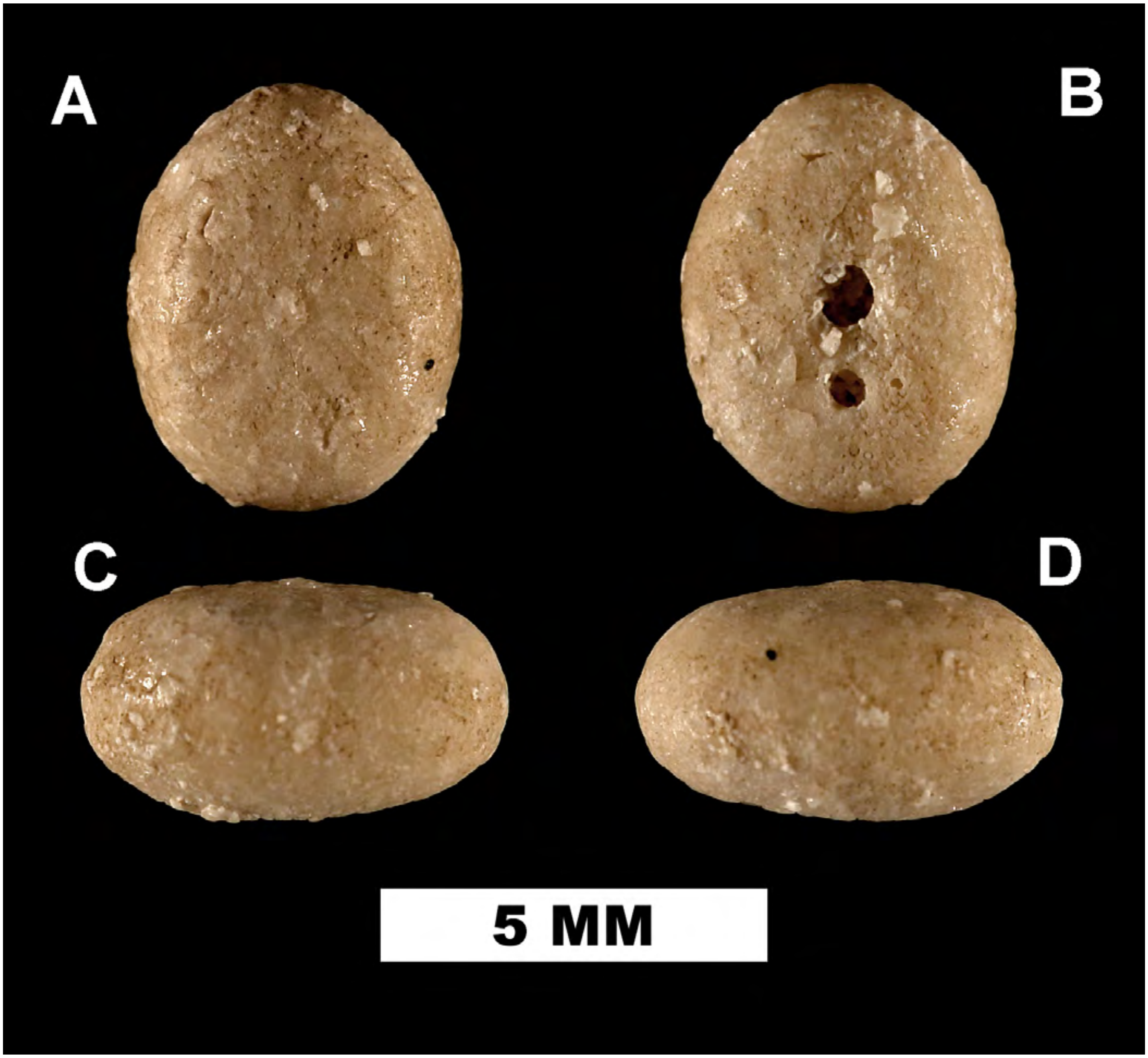


Figure 103: *Fibularia vaughani* (UF 337988), 6.5 mm TL, 5 mm TW, 3.5 mm TH, *Oligopygus phelani* Zone, Upper Eocene lower Ocala Limestone, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: left side. D: right side.

as the many species from the Caribbean that fall well outside the study region.

Genus ***Neolaganum*** Durham, 1954

When Durham (1954) erected *Neolaganum,* he designated it as the type genus of his new family Neolaganidae. He characterized the genus by the moderate number of plates on the oral surface and presence of a hydropore groove, neither of which are diagnostic, either in combination or as unique features. Durham (1954) stated the hydropore groove, the more pentagonal shape, especially posteriorly, and the flat or nearly flat oral surface distinguish this genus from *Weisbordella*. Durham (1954: 681) stressed the importance of the presence of hydropore grooves in this genus but noted: “if these differences should be found to be of lesser value, *Neolaganum* should have priority over *Weisbordella*”. Our analysis indicates the presence of hydropore grooves

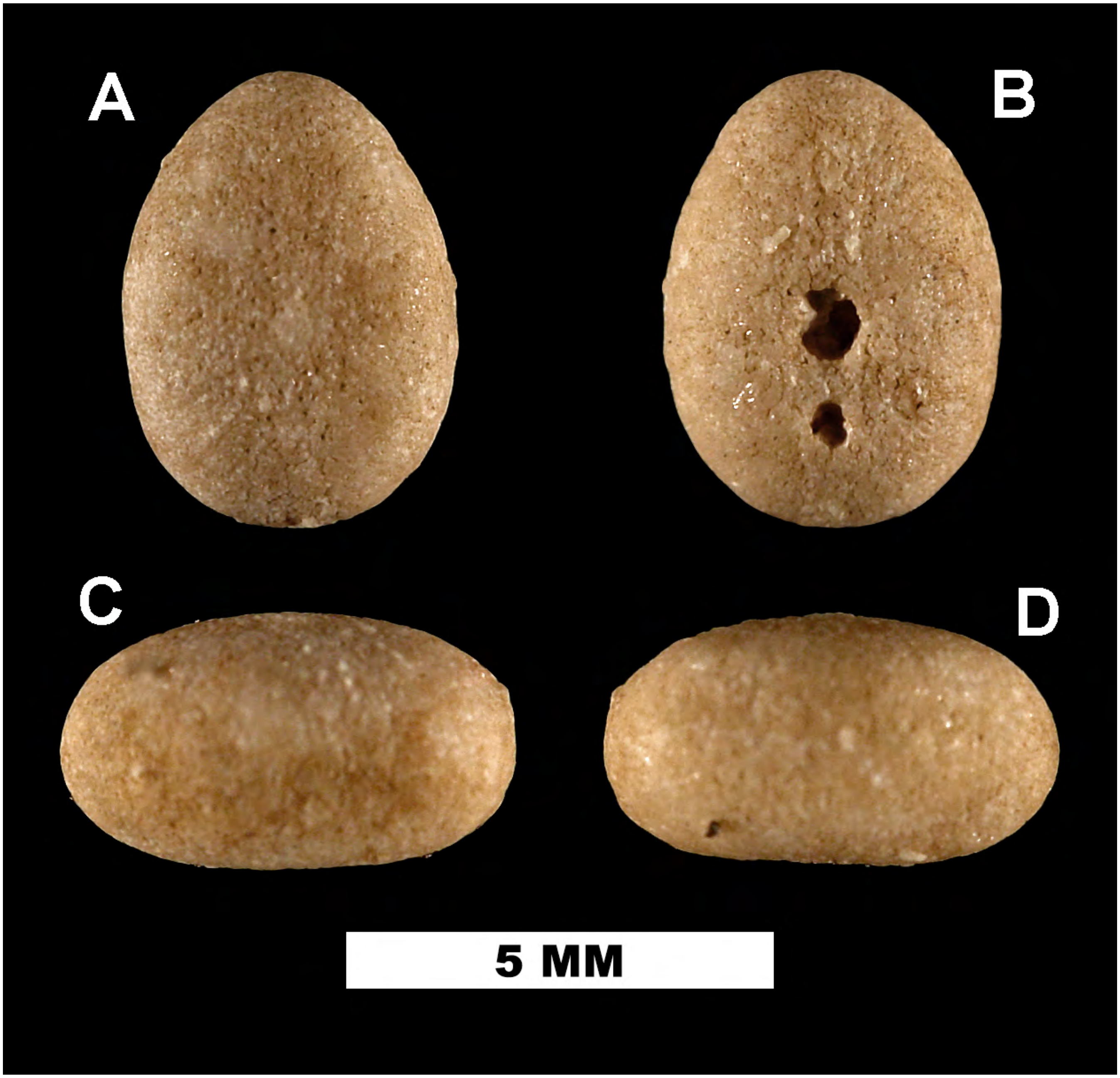
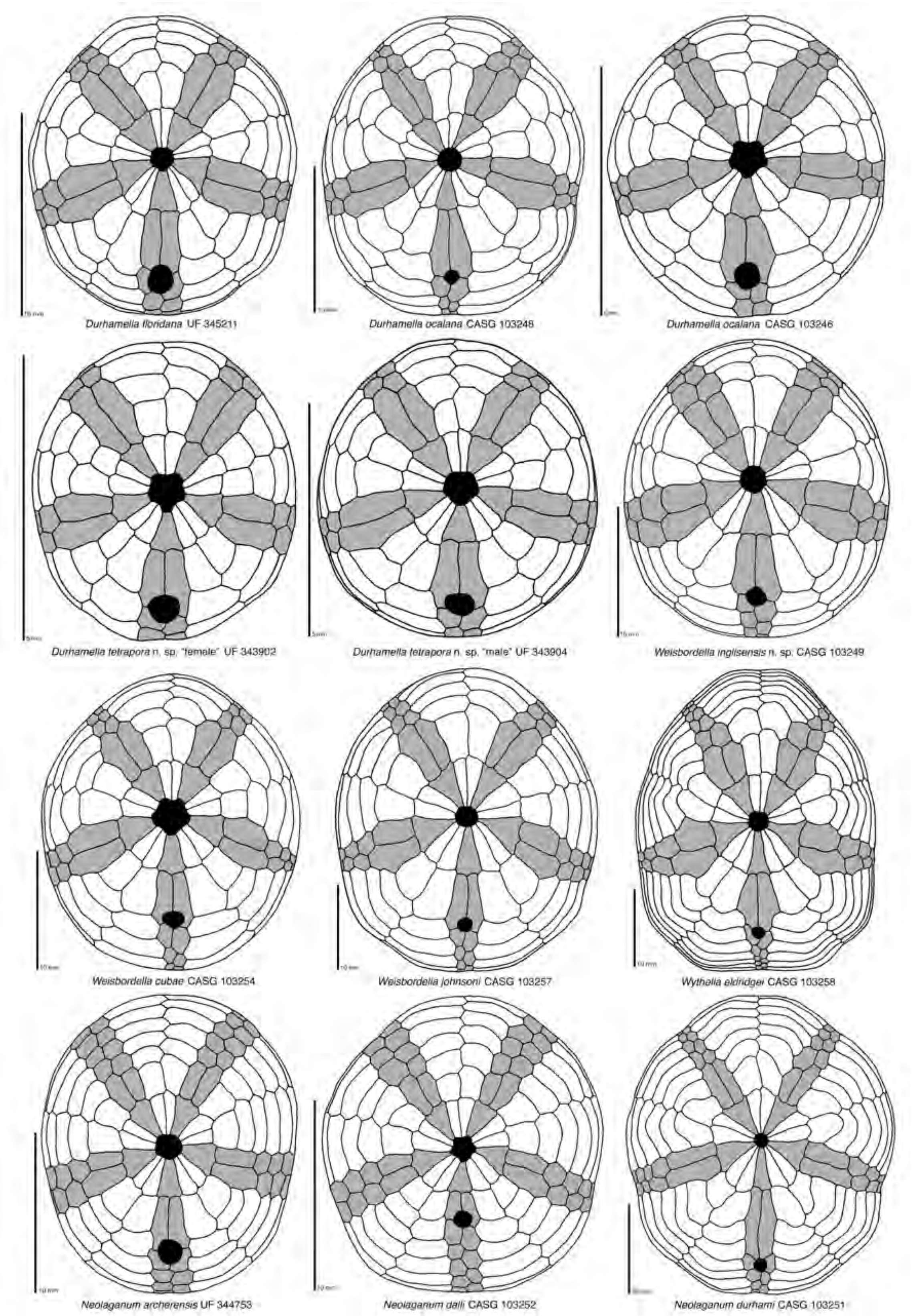


Figure 104: *Fibularia vaughani* (UF 337989), 5 mm TL, 3.5 mm TW, 3 mm TH, *Oligopygus phelani* Zone, Upper Eocene lower Ocala Limestone, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: left side. D: right side.

is widespread in the neolaganids, including *Weisbordella,* and therefore not of great taxonomic significance except in some cases. However, further analysis indicated that we should not consider *Weisbordella* a junior synonym of *Neolaganum* at this time.

Durham (1954) designated *N. archerensis* as the type species for *Neolaganum*. Confusion between *N. archerensis* and *N. durhami*, discussed further in the remarks for *N. archerensis*, indicated that further analysis of the oral plate architecture of *N. archerensis*, not previously considered, needed to be performed. The importance of oral plate architecture in neolaganids was recognized by Durham (1954) when establishing the family, and in describing some of the taxa he placed therein. Therefore, we provide oral plate maps of all three species of *Neolaganum*: *N. archerensis, N. dalli*, and *N. durhami* (Fig. 105).



Durhamella floridana UF 345211

Durhamella ocalana CASG 103248

Durhamella ocalana CASG 103246

Durhamella tetrapora n. sp. "female" UF 343902

Durhamella tetrapora n. sp. "male" UF 343904

Weisbordella inglisensis n. sp. CASG 103249

Weisbordella cubae CASG 103254

Weisbordella johnsoni CASG 103257

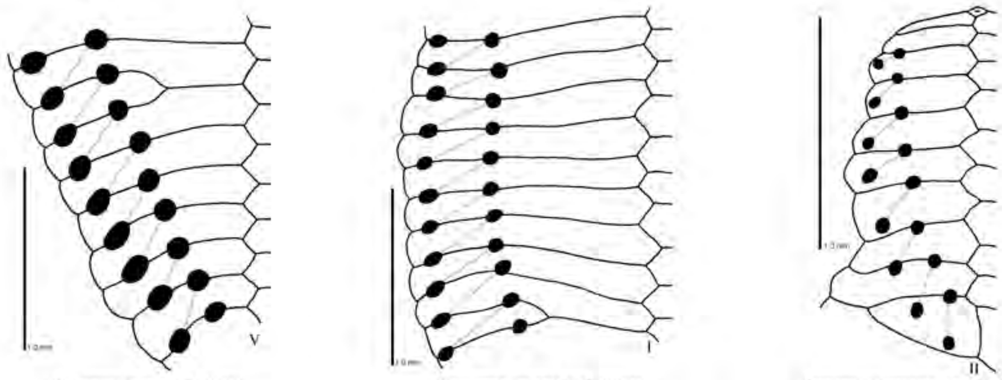
Wythella eldridgei CASG 103258

Neolaganum archerensis UF 344753

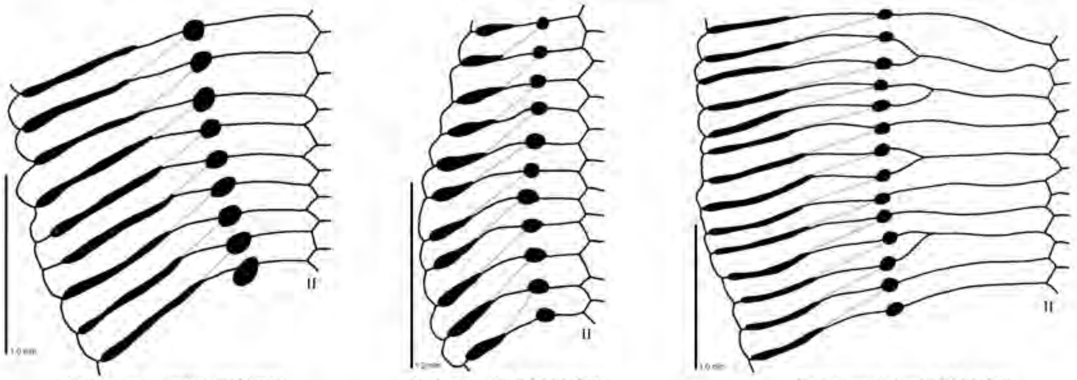
Neolaganum dalli CASG 103252

Neolaganum durhami CASG 103251

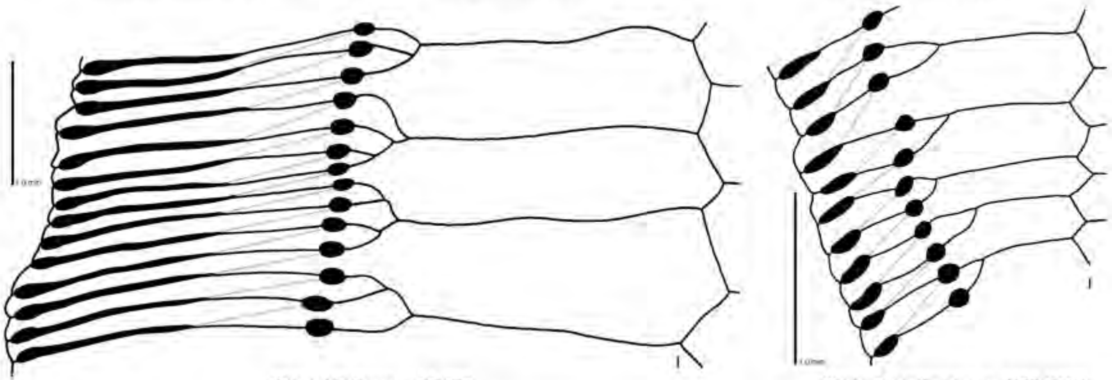
Figure 105: Comparison of oral surface details of Florida neolaganids. Ambulacrum III is towards the top, the interambulacral plates are shaded, and peristome and periproct are solid black (see table 7).



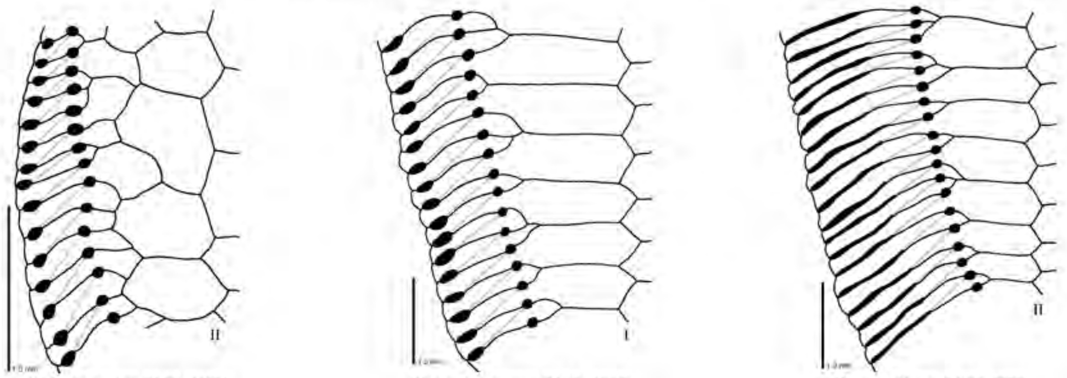
Durhamella floridana UF 345211 *Durhamella ocalana* CASG 103248 *Durhamella tetrapora* n. sp. UF 343904



Neolaganum archerensis UF 344753 *Neolaganum dalli* CASG 103252 *Neolaganum durhami* CASG 103251



Weisbordella libum n. sp. UF 4926 *Weisbordella inglisensis* n. sp. CASG 103249



Weisbordella cubae CASG 103254 *Weisbordella johnsoni* CASG 103257 *Wythella eldridgei* CASG 103258

Figure 106: Plate patterns in petals of Florida neolaganid species. For each, perradius (Lovénian numbering) in which petal is situated is indicated, along with specimen repository. Plating shown for section of b column near approximate midpoint of petal's length (except *D. tetrapora*, for which entire length of b column is depicted, including ocular). Pore pairs indicated by solid black, conjugation of pores by light gray line. Ambitus downward for each image.

Figure 107: *Laganum archerensis* holotype (= *Neolaganum archerensis*) (USNM 164667A), 18 mm TL, 16 mm TW, 3.5 mm TH, Middle Eocene Avon Park Formation, likely from a well, near Archer, Florida. (images from Smithsonian NMNH online database). A: aboral. B: oral.

Neolaganum archerensis, N. dalli, and *N. durhami* all tend to have a greater number of plates on the oral surface, especially in the ambulacra, than *Weisbordella* (Fig. 105; Tables 8, 9). Furthermore, all three *Neolaganum* species have at least one plate more in each of the anterior paired regions (i.e., interambulacral 2 and 3) than in the posterior paired (interambulacral 1 and 4). Therefore, not all the interambulacral regions have the same number of plates in each individual, as in both columns a and b of the anterior pair, there are more oral plates in *Neolaganum* than in *Weisbordella*. This kind of variation suggests that a total number of oral plates among all interambulacra would be helpful to distinguish these taxa. Among all species of *Weisbordella*, the total number or oral interambulacral plates ranges from 41 to 46, whereas in *Neolaganum*, the range is non-overlapping, at 50 to 52. For ambulacral plates, the respective numbers are 54 to 59 in *Weisbordella*, but 66 to 78 in *Neolaganum* (Table 9).

The flat oral surface of *Neolaganum* further distinguishes it from the typically concave oral surface of *Weisbordella*, though in the latter, the concavity can be very shallow.

Emended Diagnosis.—Neolaganids that combine: presence of five gonopores with a branched hydropore groove; almost planar oral surface with between 66 and 78 ambulacral oral plates and 50 to 52 interambulacral plates; poriferous zones equal to or slightly greater than half the width of the poriferous zone as measured from the perradial to abradial suture about two thirds of the length of the petal; at most, one demiplate every third plate in the petal.

Neolaganum archerensis (Twitchell in Clark and Twitchell, 1915)
(Figs. 105-113; Tables 8, 9)

Laganum archerensis Twitchell in Clark and Twitchell, 1915. p. 161. pl. 75, figs. 1a-d.

Echinodiscus archerensis (Twitchell). Lambert and Thiéry, 1925. p. 581.

Laganum archerensis (Twitchell). Cooke and Mossom, 1929. pl. 3, figs. 6a-b.

Rumphia archerensis (Twitchell). Cooke, 1942. p. 26. In part, not pl. 2, figs. 11-13.

Rumphia archerensis (Twitchell). Cooke, 1945. fig. 5, no. 6.

Neolaganum archerensis (Twitchell). Durham, 1954. pp. 680, 681. not txt fig. 28 which is *N.*

Figure 108: *Neolaganum archerensis* (UF 344751), 8.8 mm TL, 8.0 mm TW, 2.7 mm TH, Middle Eocene Avon Park Formation, in a well core at 50 ft. depth (in a 200 ft. deep well) near Lake Wales, Polk County, Florida. A: aboral. B: oral. C: left side. D: right side.

durhami.

Neolaganum archerensis (Twitchell). Durham, 1955. p. 146. not txt figs. 15f, 30b which are *N. durhami*.

not *Neolaganum dalli* (Twitchell). Cooke, 1959. pp. 51-52 (in part). not pl. 21, figs. 1-4, which is *N. dalli*.

Neolaganum archerensis (Twitchell). Durham, 1966. p. 475. (in part) not fig. 365, 1a-1d which are *N. durhami.*

Neolaganum archerensis (Twitchell). Mooi, 1989. p. 37. (in part) not figs. 9b or16c which are *N. durhami*.

Occurrence.—This species has only been recovered from well cuttings in subsurface deposits of the Middle Eocene Avon Park Formation, Florida. It is not known from surface exposures. The type locality is near Archer, Alachua County, where the holotype (USNM 164667A) was presumably obtained from well cuttings at an unknown depth. A few notable lots of this species within the FM-IP collections are UF 12892, from 15.2 m depth in a well near Lake Wales, Polk County, and UF 56401, from 512-518 m depth in a well near Belle Meade, Collier County.

Discussion.—The complicated synonymy, as well as that for *N. durhami,* indicates this species has been misunderstood since its description by Twitchell in Clark and Twitchell (1915). William Healy Dall collected the holotype of *Laganum archerensis* Twitchell in Clark and Twitchell, 1915, as well as the associated holotype of *Laganum dalli* Twitchell in Clark and Twitchell, 1915, from near

Figure 109: *Neolaganum archerensis* (UF 344752), 14.8 mm TL, 12.5 mm TW, 4.1 mm TH, Middle Eocene Avon Park Formation, in a well core at 50 ft. depth (in a 200 ft. deep well) near Lake Wales, Polk County, Florida. A: aboral. B: oral. C: left side. D: right side.

Archer, Alachua County, Florida. It was presumed by Cole and Ponton (1932) and Cooke (1959) that these taxa were both obtained from well cuttings, as no exposures of the Avon Park Formation exist at the surface near Archer.

Twitchell in Clark and Twitchell (1915), described *L. archerensis* from a single specimen collected in strata that were recognized as Oligocene at the time. Twitchell noted its similarity to *L. dalli*, which was collected from the same well cuttings, but distinguished it by a concave ring encircling the petaloid region on the upper surface, narrower petals, less depressed and narrower poriferous zones, and a periproct that was closer to the margin. The holotypes of both species are clearly different from each other (Figs. 107, 114). This is further evidenced by analysis of oral plate architecture.

The oral plate arrangement of *N. archerensis* and *N. dalli* (Fig. 105) demonstrates the first post-basicoronals in interambulacrum 5 (plates 5.b.2 and 5.a.2) of *N. archerensis* are significantly longer

Figure 110: *Neolaganum archerensis* (UF 344753), 18.8 mm TL, 16.7 mm TW, 4.2 mm TH, Middle Eocene Avon Park Formation, in a well core at 50 ft. depth (in a 200 ft. deep well) near Lake Wales, Polk County, Florida. A: aboral. B: oral. C: left side. D: right side.

than those in *N. dalli*. However, even though the periproct of *N. archerensis* is much nearer the posterior margin than in *N. dalli*, the periproct in both species is first in contact with plates 5.b.2 and 5.a.2.

Twitchell assumed that *L. archerensis* and *L. dalli* were associated, as both were collected from the same well. However, there are clear differences in preservation and color of the two holotypes. It is likely they were not obtained from the same depth in the well, as discussed below.

Cole and Ponton (1932) conducted a study of 266 specimens they identified as *Laganum dalli* from numerous deep wells throughout Florida. They noted that no specimens of *L. dalli* had been documented from surface exposures. Their intent was to demonstrate the great variability, especially in periproct placement, found among specimens they ascribed to *L. dalli*. Apparently, their first inclination was to describe a new species for the forms with a more marginal periproct, and an examination of specimens in the FM-IP Collections reveals a few specimens (UF 249008 and UF 249006) with the name "*Laganum polkensis* Ponton" on

UF 249008
FLORIDA GEOLOGICAL SURVEY
No. I-1591 Fm. Eoc. Mid.
Name: Laganum polkensis, Ponton
Description: City of Davenport Well W-11
240' to 250' deep
Identifier see Dr. Cooke letter Date

I-1591. polk- Ponton
Laganum
~~W. 11. Depth 240-250~~
(Look up well)
Eocene (middle) (?)
W. 11- Dep. 240-250
See letter c̄ Dr. Cooke
UF 249008

Figure 111: *Neolaganum archerensis* (UF 249008), 12.8 mm TL, 11.3 mm TW, 3.2 mm TH, Middle Eocene Avon Park Formation, 240-250 ft. depth in the Davenport city well, Polk County, Florida. Specimen was deposited at the Florida Geological Survey (now in the Florida Museum collections) with original labels identifying it as *Laganum polkensis*, attributing the name to Ponton; likely the potential new species indicated by Cole and Ponton (1932). A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: tilted oral viewpoint from posterior. E: peristome. F: left side. G: apical area and petaloid portion of ambulacrum III. H, I: original Florida Geological Survey labels.

the labels (Fig. 111). This was the name Cole and Ponton intended to give to these forms. Interestingly, Cole and Ponton (1932) did not discuss *L. archerensis* and its more posterior periproct, instead concluding that periproct placement of *L. dalli* is highly variable but situated closer to the posterior margin in smaller specimens, even though their data show considerable overlap with periproct position in their "*L. polkensis*" (Cole and Ponton, 1932: table 2). Cole and Ponton (1932) did not distinguish their specimens by population and/or well depth. If specimens of both *L. dalli* and *L. archerensis* exist in these samples (which they likely do), perhaps even from different depths in the well, the finding of variation they ascribed to a single species, *L. dalli*, would be compromised, since there could be two distinct taxa in their samples – whether or not one of these was already named.

Regrettably, Cole and Ponton (1932) did not assign catalog numbers to the specimens they measured or indicate them in some way. However, their specimens were deposited in the collections of the Florida Geological Survey, whose material now resides in the FM-IP Collections at the University of Florida. Specimens from this material are further discussed below.

Cooke (1942) assigned *L. archerensis* to *Rumphia* because of its four genital pores and flat oral surface with ambulacral grooves. He also assigned *L. dalli* to *Peronella* (curiously, a very different genus than the one to which he assigned *L. archerensis*) because of its four genital pores, subpentagonal peristome, buccal pores, and punctate extrapetalous ambulacral regions, which Cooke felt resembled those of *Peronella peronii* (Agassiz, 1841), the type species of *Peronella*. Cooke (1941a) mentioned the great variation in periproct placement among *L. dalli* also noted by Cole and Ponton (1932).

However, Cooke (1942) made an additional decision that would have consequences – confusing species concepts of *L. archerensis* and *L. dalli* for many decades. Cooke (1942) modified the concept of *L. archerensis* by including specimens collected from surface exposures of what would become known as the Inglis Formation, and subsequently lower OLS, at numerous localities in Levy County, Florida. As discussed below, this taxon from the lower OLS would later be described as a member of a new genus, *Neolaganum* Durham, 1954, as *N. durhami* (Cooke, 1959), but misidentification of specimens of *N. durhami* as *N. archerensis* would continue, largely by those following Durham (1954), for example, Durham (1955, 1966), and Mooi (1989).

Durham (1954) erected *Neolaganum* and designated *L. archerensis* as the type species. Making matters worse was that to represent the genus, he figured a specimen, UCMP 33296, that he designated as a hypotype of *N. archerensis*. This specimen was collected from the lower OLS at the mouth of the Withlacoochee River (FM-IP LV024) west of Inglis, in Levy County, Florida. *Neolaganum archerensis* has never been documented at this site, nor are there exposures of the Avon Park Formation in the vicinity, but what is now known as *N. durhami* is very abundant. Cooke (1959) recognized this and postulated a plausible scenario in which Durham (1954) based *Neolaganum* on a misidentified specimen that was *N. durhami*, and not the *L. archerensis* described originally from a well near Archer. Luckily, Durham (1954) indicated that there were no genus-level differences between the taxa, so Durham's description of the genus still applies. However, Durham's (1954) figures of the oral plate arrangement of *N. durhami* (UCMP 33296), erroneously identified as *N. archerensis*, were replicated by Durham, (1955, 1966) and Mooi (1989). As far as we can determine, figures of the oral plating of the holotype of *N. archerensis* (USNM 164667A) have not been published until the present work.

Cooke (1959) recognized *N. archerensis* as a subjective junior synonym of *N. dalli*. He did not provide a rationale for this assertion, but he did refer to the study of Cole and Ponton (1932) while stating that the periproct placement of *L. dalli* is highly variable. As the more posterior periproct of *N. archerensis* is the most reliable characteristic distinguishing it from *N. dalli*, Cooke (1959) likely based his decision on the variability of this feature in *N. dalli* suggested by Cole and Ponton (1932), as

Table 8: Tabular key for genera in the family Neolaganidae Durham, 1954, plus species occurring in study area.

Taxon	Distribution[1]	Test shape	Test length (mm)[2]	Oral surface concavity	Periproct position	Aboral depressions	Petals sunken	Gonopore number	Hydropores	Outer petal pore pair	poriferous zones[4]	Demiplates in petal[5]	Oral ambulacral plate #[6]	Oral interambulacral plate #[7]
Cubanaster Sánchez Roig, 1952	E coast Panama, MX	Elongate oval, thick margin	70	Absent	Closer to peristome than ambitus	None	Slightly	4	In branched groove	Long, slit-like	< 1/2	Rare?	7 – 9	4 – 6
Sanchezella Durham, 1954	Cuba	Very elongate, thick margin	50	Absent	Closer to peristome than ambitus	None	Deeply	4	In branched groove	Long, slit-like	>>> 1/2	Rare	9 – 11	5 – 6
Neolaganum Durham, 1954	FL, CB	Pentagonal, low margin	40	Absent	Near or far from peristome	None	No	5	In branched groove	Slightly elongate to slit-like	= or > 1/2	Absent or every few plates	6 – 8	4 – 6
Neolaganum archerensis (Twitchell, 1915)	FL	Pentagonal, low margin	20	Absent	Closer to ambitus than peristome	None	No	5	In branched groove	Long, slit-like	> 1/2	Absent	6 – 7	5 – 6
Neolaganum dalli (Twitchell, 1915)	FL, CB	Pentagonal, low margin	20	Absent	Closer to peristome than ambitus	None	No	5	In branched groove	Short, only slightly elongate	> 1/2	Absent	6 – 7	4 – 5
Neolaganum durhami Cooke, 1959	FL	Pentagonal, low margin	40	Absent	Closer to ambitus than peristome	None	No	5	In branched groove	Long, slit-like	= 1/2	Every 2nd or 3rd plate	7 – 8	4 – 5
Weisbordella Durham, 1954	AL, FL, GA, CB	Elongate oval, thick or low margin	~80	Variably present	Closer to ambitus than peristome	None	No	4	In long, winding groove	Round to long, slit-like	< *or* <<< 1/2	Always present	5 – 6	3 – 4
Weisbordella cubae (Weisbord, 1934)	FL, GA	Elongate oval, low margin	40	Deep	Closer to ambitus than peristome	None	No	4	In long, winding groove	Round	<<< 1/2	Many, primaries absent	5 – 6	3 – 4
Weisbordella johnsoni (Twitchell, 1915)	AL, FL, GA	Elongate oval, low margin	60	Variable	Closer to ambitus than peristome	None	No	4	In long, winding groove	Almost round	<<< 1/2	Many, primaries rare	~6	~4
Weisbordella inglisensis n. sp.	FL	Elongate oval, low margin	25	Absent	Closer to ambitus than peristome	None	No	4	In long, winding groove	Short, only slightly elongate	<<< 1/2	Every 2nd plate	5	3 – 4
Weisbordella libum n. sp.	FL	Elongate oval, thick margin	~85	Shallow	Closer to ambitus than peristome	None	No	4	In complex branched grooves	Long, slit-like	Slightly < 1/2	Many, primaries rare	~6	~4
Wythella Durham, 1954	FL	Elongate pentagonal, very thin margin	100	Absent	Closer to ambitus than peristome	None	No	4	In short, unbranched groove	Long, slit-like	= 1/2	Many, primaries rare	7 – 8	4 – 6

Table 8 Cont. Tabular key for genera in the family Neolaganidae Durham, 1954, plus species occurring in study area.

Taxon	Distribution[1]	Test shape	Test length (mm)[2]	Oral surface concavity	Periproct position	Aboral depressions	Petals sunken	Gonopore number	Hydropores	Outer petal pore pair	poriferous zones[4]	Demiplates in petal[5]	Oral ambulacral plate #[6]	Oral interambulacral plate #[7]
Wythella eldridgei (Twitchell, 1915)	FL	Elongate pentagonal, very thin margin	100	Absent	Closer to ambitus than peristome	None	No	4	In short, unbranched groove	Long, slit-like	= 1/2	Many, primaries rare	7 – 8	4 – 6
Durhamella Kier, 1968	FL, GA	Oval or pentagonal, low margin	40	Absent	Closer to ambitus than peristome	Present or absent	No	5	In short, unbranched groove	Round	= *or* <<< 1/2	Rare or nearly absent	4 – 6	2 – 4
Durhamella floridana (Twitchell, 1915)	FL, GA	Oval or pentagonal, low margin	25	Absent	Closer to ambitus than peristome	None	No	5	In short, unbranched groove	Round	<<< 1/2	Very rare, every 5 to 10 plates	5 – 6	3 – 4
Durhamella ocalana (Cooke, 1942)	FL	Oval or pentagonal, low margin	40	Strongly developed along sutures	Closer to ambitus than peristome	None	No	5	In short, unbranched groove	Round	<<< 1/2	Virtually absent	5 – 6	3 – 4
Durhamella tetrapora n. sp.	FL	Elongate oval, low margin	10	Present only in some individuals	Closer to ambitus than peristome	None	No	4	In short, unbranched groove	Round	= 1/2	Virtually absent	4 – 6	2 – 3
Pentedium Kier, 1967	GA	Oval, thick margin	5	Absent	Closer to ambitus than peristome	Interambulacral marsupia	No	5	Single, no groove	Round	> 1/2, reduced	?	~4	~3
Tetradiella[3] Liao & Lin, 1981	China	Oval, almost round	5	Absent, slightly convex	Closer to ambitus than peristome	Adapical marsupia	No	4	Scattered, no groove	Round?	> 1/2?, reduced	?	?	?

[1] Standard postal service state abbreviation, plus "CB" = Caribbean and MX = Mexico.

[2] Test length, approximate upper size limit.

[3] Too little is known of this genus to be certain it is a neolaganid.

[4] Measurement is based on the distance across only half the petal (i.e., distance from perradial to abradial suture) at a point about 2/3 the length of the petal from the apical system, as depicted in Fig. 106.

[5] See Fig. 106.

[6] Counted in single column of anterior paired ambulacra II or IV, see Fig. 105.

[7] Post-basicoronals only, counted in single column of anterior paired interambulacra 2 or 4, see Fig. 105.

Table 9: Total oral surface plate counts for typical adult specimens, including basicoronals, of all species of *Neolaganum* and *Weisbordella* except *W. libum*, n. sp.

Plate system	*Neolaganum*			*Weisbordella*		
	archerensis	*dalli*	*durhami*	*cubae*	*johnsoni*	*inglisensis*
Ambulacral	66	69	78	58	59	54
Interambulacral	51	52	50	42	46	41
Ambulacral range for genus	66 – 78			54 – 59		
Interambulacral range for genus	50 – 52			41 – 46		

discussed below.

Cooke (1959: 52) asserted that *N. dalli* should have priority "because *dalli* has been correctly identified and is a well-known species, whereas *archerensis* has been repeatedly confused with the species herein described as *Neolaganum durhami*". Not only is this an inapplicable criterion for nomenclatural decisions, but Cooke did not mention that his own work (Cooke, 1942) was largely the only source of that confusion.

We disagree that *L. dalli* (*N. durhami* as indicated by Cooke [1959]), should be recognized as the type species of *Neolaganum*. Durham (1954) clearly designated *N. archerensis* as the type of his new genus, and as we demonstrate, differentiating it from *N. dalli* is not difficult. Misidentifications after Cooke (1942) notwithstanding, systematists should be able to distinguish among *N. archerensis, N. dalli,* and *N. durhami*.

To verify Cole and Ponton's (1932) assertion of variability in periproct position in *N. dalli*, we sought out the lots they examined in the FM-IP Collections. In addition, we examined numerous specimens of *N. dalli* from *in situ* surface exposures of the Avon Park Formation at the Gulf Hammock Quarry (FM-IP LV004, FM-IP LV039) in Levy County. Specimens from this locality (Figs. 115, 117, 118) clearly do not display the great variation in periproct placement noted by Cole and Ponton (1932). The specimens are indistinguishable from the holotype of *N. dalli* (USNM 164667B) and consistently display a periproct situated further from the margin than that of *N. archerensis*. We measured the periproct position (distance of posterior edge of periproct from posterior margin of the test) in 109 specimens of *N. dalli* from the upper portion of the Avon Park Formation in the Gulf Hammock Quarry. The periproct averages 23.04% TL from the posterior margin (range 17.8-28.3%) (Figs. 114, 115).

Additional specimens of *N. dalli* were obtained from the upper portion of the Avon Park Formation by SCUBA divers in Blue Spring (VO001), Volusia County, Florida, and these specimens are likewise indistinguishable from either the holotype of *N. dalli* or the specimens from Gulf Hammock, again not exhibiting the variation in periproct position suggested by Cole and Ponton (1932) (Fig. 117). At least in these two populations, morphology of *N. dalli* is consistent with characteristics of the holotype.

Specimens with a more posterior periproct are found in certain well cuttings (all within the Avon Park Formation), such as lot UF 296335, from 117 m depth in a well at the Palmetto Phosphate Company near Tiger Bay, Polk County, Florida [site I-1601 of Cole and Ponton, (1932) and FM-IP PO050] and UF 56401 from 1680-1700 ft. depth in a well near Belle Meade, Collier County (FM-IP CR013). The specimens from Tiger Bay were identified as *Laganum dalli* by Cooke on August 30, 1941, and the lot of 193 specimens contains many that are inseparable from *N. archerensis*, as well as some more reminiscent of *N. dalli*. Specimens as large as the holotype of *L. dalli* (16 mm TL, 15 mm TW, 4.5 mm TH) possess periprocts in a position identical to that of *N. archerensis*. Therefore, a more posterior periproct cannot be attributed to ontogenetic effects, contrary to the assertions by Cole and Ponton (1932). This observation alone undermines the conclusions of Cole and Ponton (1932), which were, in turn, the basis for Cooke's (1959) subsequent decision to synonymize *N. archerensis* and *N. dalli*.

In addition, a lot of 66 tests (UF 12892) from 15.2 m depth in a well near Lake Wales, Polk County (FM-IP 3573), also show a more posterior position of the periproct (Figs. 110-112, 115), very similar to that seen in the holotype of *N. archerensis*, but very unlike the situation in the holotype of *N. dalli*. In fact, this lot does not contain any specimens with more anterior periproct positions as seen in *N. dalli*, and all appear to be *N. archerensis*. We measured periproct placement of 34 tests from the Lake Wales well that had preserved oral surfaces (Fig. 113) and the periproct averages 13.52% TL from the posterior test margin. An additional lot of 28 specimens (UF 56401) from 512-518 m depth in a well near Belle Meade, Collier County (FM-IP CR013) show similarly placed periprocts, and again, all appear to be *N. archerensis*. Thirteen specimens from the Belle Meade material had preserved oral surfaces and the periproct of these specimens averaged 15.8% TL from the posterior margin.

When plotted with the holotypes of both *N. dalli* and *N. archerensis*, a clear distinction of the two species is readily apparent (Fig. 113). Taking all the data into account, the periproct of *N. archerensis* averages 14.1% TL from the posterior margin, with a range of 9.5-20.9% TL, but the periproct of *N. dalli* averages 23.04% TL from the posterior margin, with a range of 17.8-28.3%. There is some overlap in these percentage values, but the bivariate plots show that when test size is considered, it is easy to distinguish these two forms based on periproct position alone.

Our data indicate that variation in periproct position of *N. dalli* documented by Cole and Ponton (1932) does not exist in populations of *N. dalli* in the upper portion of the Avon Park Formation exposed in the Gulf Hammock Quarry, Levy County, and Blue Spring, Volusia County. Furthermore, the assertion of Cole and Ponton that the periproct is nearer the posterior margin only in small specimens of *L. dalli* is not evidence that *L. dalli* and *L. archerensis* are the same taxon. The holotype of *L. archerensis* (18 mm TL, 16 mm TW, 3.5 mm TH) is larger than the holotype of *L. dalli* (16 mm TL, 15 mm TW, 4.5 mm TH), yet its periproct is much closer to the margin than that of *L. dalli* (Fig. 107).

That some of the well cuttings contain examples of forms attributable to both *N. archerensis* and *N. dalli* (e.g., UF 56401, UF 296335) is explained by the fact that both species can occur together (as surmised by Clark and Twitchell, 1915), and possibly by mixing of specimens while fossils were collected from the well cuttings. The latter might be verified by more strict sampling of future or existing cores of Avon Park Formation strata.

We therefore conclude that *N. archerensis* is distinct from *N. dalli* as distinguished its more posterior periproct and should remain the type species of *Neolaganum* as designated by Durham (1954).

Emended Diagnosis.—*Neolaganum* with: thick test with almost parallel oral and aboral surfaces, the latter slightly depressed just proximal to the ambitus; long, slit-like outer pores in the petals.

Neolaganum dalli (Twitchell in Clark and Twitchell, 1915)
(Figs. 105, 106, 112-117; Tables 8, 9)

Laganum dalli Twitchell in Clark and Twitchell, 1915. p. 164. pl. 75, figs. 4a-d.

Echinodiscus dalli (Twitchell). Lambert and Thiéry, 1925. p. 581.

Laganum dalli (Twitchell). Cole and Ponton, 1932. p. 23. figs. 1a-12b.

Peronella dalli (Twitchell). Cooke, 1942. p. 26.

Peronella dalli (Twitchell). Cooke, 1948b. p. 91. pl. 22, figs. 5, 6.

Peronella dalli (Twitchell). Fischer, 1951. p. 57.

Neolaganum dalli (Twitchell). Cooke, 1959. pp. 51-52. pl. 21, figs. 1-4.

Neolaganum dalli(Twitchell). Mooi, 1989. fig. 20a.

cf. *Neolaganum dalli* (Twitchell). Donovan, 1993. p. 389. fig. 12.

Neolaganum dalli (Twitchell). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 5.

Occurrence.—*Neolaganum dalli* is very abundant in a soft limestone bed of the Middle Eocene

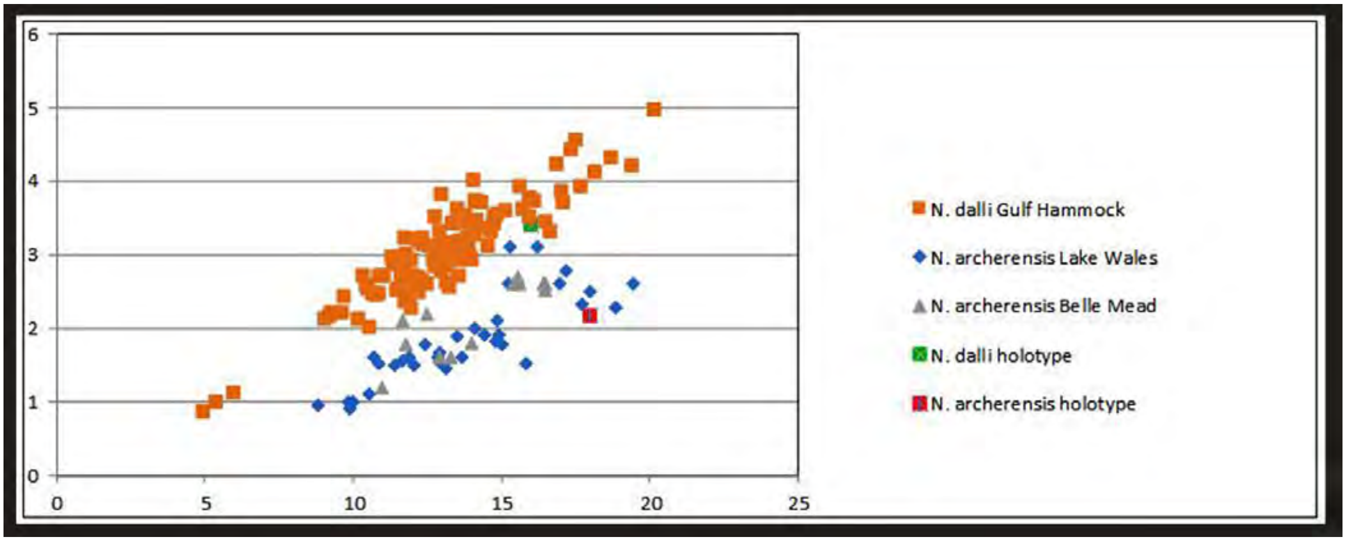


Figure 112: Comparison of periproct placement in *Neolaganum dalli* and *N. archerensis*, including holotypes of each species. Vertical axis is distance, in millimeters, of posterior edge of periproct from posterior margin of test (ambitus). Horizontal axis is test length, in millimeters. *N. dalli* are from the Avon Park Formation in the Gulf Hammock Quarry in Levy County, Florida, and consists of 109 specimens from lots UF 114745, 136349, 156333, 336832, 336853, 336031, and 337030. *N. archerensis* are UF 12892 (50 ft. depth in a well near Lake Wales, Polk County, Florida) and UF 56401 from 1680-1700 ft. depth in a well near Belle Mead, Collier County, Florida.

Avon Park Formation in a now inactive quarry east of Hwy 19/98 in Gulf Hammock (FM-IP LV004, FM-IP LV039), Levy County. Specimens of *N. dalli* have also been obtained from the Avon Park Formation by SCUBA in Blue Spring (FM-IP VO001), Volusia County. Other than these two occurrences, *N. dalli* is documented only from the Avon Park Formation in well cores (e.g., FM-IP PO050). The type locality is a well near Archer in Alachua County.

Donovan (1993) documented *N. dalli* in the Eocene of Jamaica, and Cooke (1948b) noted its occurrence in the Eocene of Panama.

Discussion.—Twitchell in Clark and Twitchell (1915), initially described this species as *Laganum dalli* from a well near Archer, Florida. Twitchell noted that it is most closely related to *Laganum archerensis* from the same well, which Twitchell described a few pages previously in the same work. Twitchell noted that *L. archerensis* is like *L. dalli* but is distinguished from it by the concave ring on its upper surface, narrower petals, less depressed and narrower poriferous zones, and a periproct that is closer to the posterior margin. We figure the holotypes of both species (Figs. 107, 114).

As noted above, Cole and Ponton (1932) reviewed *L. dalli* through study of specimens obtained from wells within Florida. Cole and Ponton discussed variation, especially in periproct position. However, as discussed in the remarks for *N. archerensis*, we believe the specimens Cole and Ponton examined included both *N. dalli* and *N. archerensis*. Specimens of *N. dalli* from the upper portion of the Avon Park Formation in the Gulf Hammock Quarry (FM-IP LV004) and from Blue Springs in Volusia County (FM-IP VO001) show minimal variation in periproct position and are consistent with the holotype of *N. dalli*. Specimens with more posteriorly placed periprocts (*N. archerensis*) are present only in deep well cores, as discussed above in the remarks for *N. archerensis*.

Cooke (1942) reassigned Twitchell's (in Clark and Twitchell, 1915) *L. dalli* to *Peronella*, and *L. archerensis* to *Rumphia*, neither of which are presently regarded as like any neolaganid. Durham (1954) subsequently erected *Neolaganum* and named *N. archerensis* the type species of his new genus.

As noted above, Cooke (1959) considered *N. dalli* and *N. archerensis* to be synonymous (likely informed by the work of Cole and Ponton [1932],

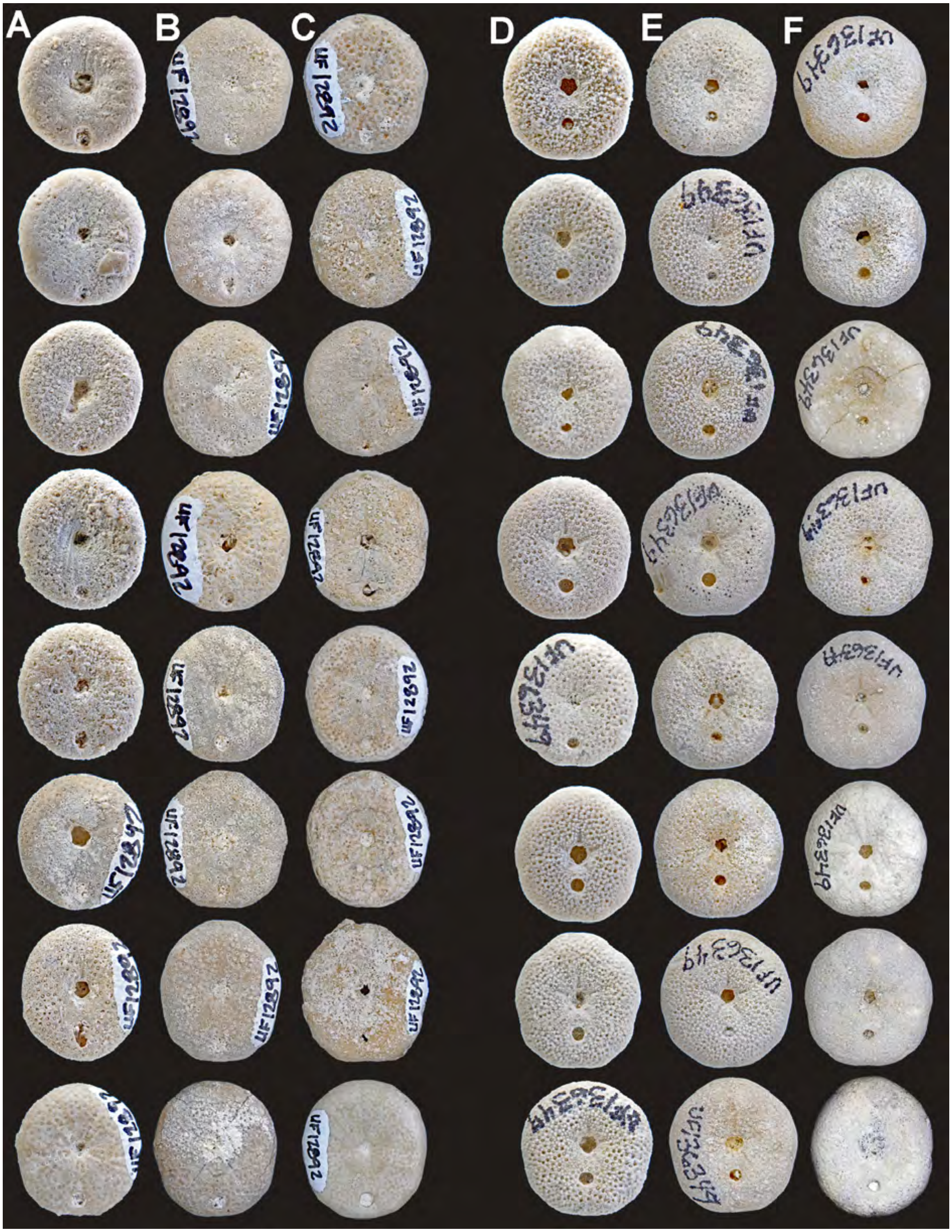


Figure 113: Comparison of oral surfaces showing periproct position in *Neolaganum archerensis* (columns A-C; UF 12892 Avon Park Formation, 50 ft. depth in a well near Lake Wales, Polk County, Florida) and *Neolaganum dalli* (columns D-F; UF 136349 Avon Park Formation, Gulf Hammock Quarry, Levy County, Florida). Test length provided in millimeters from top to bottom of each column: Column A: 8.9, 9.8, 10.1, 10.5, 10.8, 11.4, 11.6, 12.1. Column B: 12.6, 12.8, 12.9, 13.1, 13.5, 14.3, 14.8, 14.8. Column C: 14.9, 15.2, 15.7, 16.9, 17.1, 17.8, 18.4, 18.7. Column D: 9.2, 10.5, 10.7, 10.8, 11.0, 11.3, 11.7, 11.7. Column E: 12.1, 12.2, 12.4, 12.7, 13.5, 13.8, 13.9, 14.0. Column F: 14.1, 14.7, 14.8, 15.2, 15.6, 17.0, 18.6, 20.1.

Figure 114: *Laganum dalli* (= *Neolaganum dalli*) holotype (USNM 164667B), 15.9 mm TL, 15 mm TL, 4.6 mm TH, Middle Eocene Avon Park Formation, likely from a well, near Archer, Alachua County, Florida (images from Smithsonian NMNH online database). A: aboral. B: oral.

all of which they erroneously identified as *N. dalli*). Cooke (1959) asserted, that the species name *dalli* is preferred to *archerensis* because *dalli* had been correctly identified and was a well-known species, whereas *archerensis* has been confused with *Neolaganum durhami* (Cooke, 1942; Durham 1954, 1955). We disagree with Cooke (1942), and recognize both species as distinct. Past confusion is not a criterion for enshrining Cooke's taxonomic error, and in any case, we do not find the "confusion" to be sufficient to suppress *N. archerensis*. Furthermore, we follow the recent stipulation by the IZCN, which states, "... if an author discovers that the type species fixation of a genus-group taxon was based on a misidentification of the type species, the author may, in the interests of stability and without making application to the Commission, fix as type species either the taxonomic species actually involved or the misidentified nominal species fixed previously." In accordance, we follow Durham's (1954) designation of *Laganum archerensis* Twitchell in Clark and Twitchell, 1915 as the type species of the genus-group taxon, *Neolaganum* Durham, 1954.

Neolaganum dalli is characteristic of the Middle Eocene Avon Park Formation and undocumented outside of that unit within the United States. *Neolaganum dalli* is also the only echinoid known from surface exposures of the Avon Park Formation (Fischer, 1951), which is restricted in outcrop to Levy County. However, in the Gulf Hammock Quarry (FM-IP LV004, FM-IP LV039), spoil often contains a mixture of both the Avon Park and lower OLS, so a collection from the locality can create confusion by containing specimens from both units.

The swollen, subpentagonal test of *N. dalli* is very consistent in shape throughout growth, and this readily differentiates it from the thinner, often much larger test of *N. durhami*, which occurs in the lower OLS, immediately overlying the occurrence of *N. dalli* in the Avon Park Formation. The presence of four gonopores in *Neolaganum* readily distinguishes it from members of *Durhamella*, which have five, except for *D. tetrapora* n. sp., which differs in having a much thinner, very small test and, in presumed females, depressions in the aboral surface just proximal to the ambitus.

As stated above, *N. dalli* can readily be distinguished from *N. archerensis*, which also occurs

Figure 115: *Neolaganum dalli* (UF 337953), 16.5 mm TL, 15.5 mm TW, 5.5 mm TH, Middle Eocene Avon Park Formation, Levy County, Florida (FM-IP LV004). A: aboral. B: oral. C: left side. D: right side.

in the Avon Park Formation (but only from well cuttings), because of the more posterior position of the periproct in *N. archerensis* (see treatment of this species, above). *Neolaganum archerensis* also tends to have a few more pore pairs in the petals for any given size. The oral plate arrangements of *N. archerensis, N. dalli*, and *N. durhami* (Tables 7, 8) demonstrate that the first post-basicoronals in interambulacrum 5 (plates 5.b.2 and 5.a.2) of *N. dalli* are significantly shorter than in either *N. archerensis* or *N. durhami*. Nevertheless, even though the periproct of *N. dalli* is much further from the posterior margin than in its congeners, the periproct in all three species is first in contact with plates 5.b.2 and 5.a.2.

Emended Diagnosis.—*Neolaganum* with: thick test with almost parallel oral and aboral surfaces, the latter slightly depressed just proximal to the ambitus; only slightly elongated outer pores in the petals; no demiplates in the petals; periproct closer to peristome than the ambitus.

Neolaganum durhami Cooke, 1959
(Figs. 105, 106, 118; Tables 8, 9)

Rumphia archerensis (Twitchell). Cooke, 1942. p. 27 (in part), pl. 2, figs. 11-13.

Peronella archerensis (Twitchell). Fischer, 1951. p. 58. pl. 2, fig. 3; txt figs. 2, 3.

Neolaganum archerensis (Twitchell). Durham, 1954. txt fig. 28 (in part, figure is *N. durhami*).

Neolaganum archerensis (Twitchell). Durham, 1955. txt figs. 15f, 30b (in part, figures are *N. durhami*).

Neolaganum durhami Cooke, 1959. p. 52. pl. 21. figs. 5-7.

Neolaganum archerensis (Twitchell). Durham, 1966. p. 475. fig. 365, 1a-1d.

Neolaganum durhami (Cooke). Kier, 1970. txt. fig.

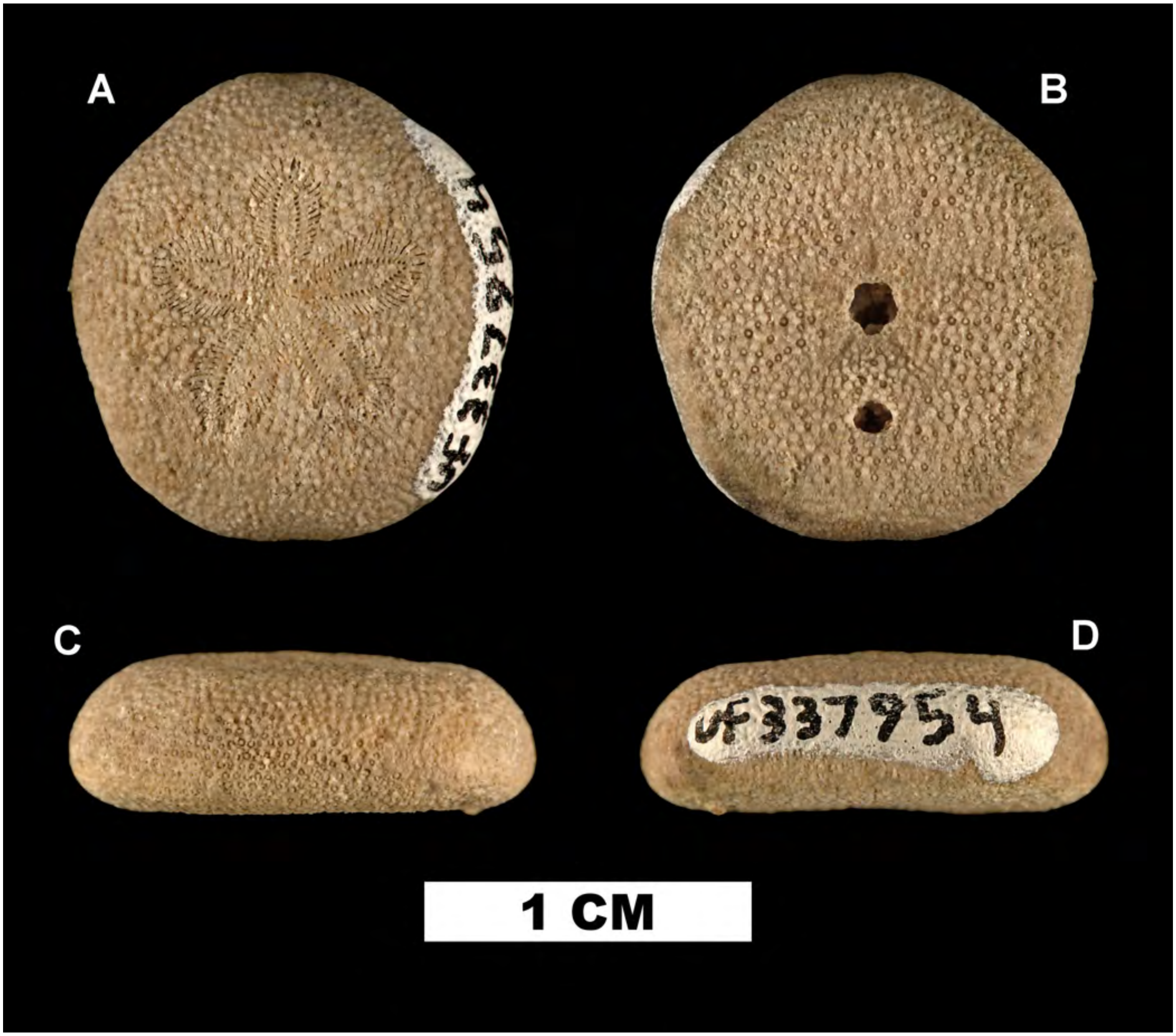


Figure 116: *Neolaganum dalli* (UF 337954), 14.5 mm TL, 13.5 mm TW, 5 mm TH, Middle Eocene Avon Park Formation, Levy County, Florida (FM-IP LV004). A: aboral. B: oral. C: left side. D: right side.

1F.

Neolaganum durhami (Cooke). Toulmin, 1977. p. 343. pl. 67, figs. 1, 2.

Neolaganum durhami (Cooke). Mooi, 1989. fig. 18b. (also 9b and 16c as *N. archerensis*).

Neolaganum durhami (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—This species is abundant in the *Oligopygus phelani* Zone of the lower OLS at numerous localities in Levy County, including the Cross Florida Barge Canal west of Hwy 19/98 south of Inglis (FM-IP CI001), and along the Withlacoochee River near its mouth (FM-IP LV024), west of Yankeetown. The type locality is along the Suwannee River south of Sulphur Spring, 24 km south of Ellaville, Florida.

Discussion.—The taxonomy of this species is entangled with the complicated nomenclatural issues associated with the other two species, *N. archerensis* and *N. dalli.* Cooke (1942) initially discussed specimens of what would eventually be assigned to this species under the name *Rumphia archerensis*, believing the specimens he was exam-

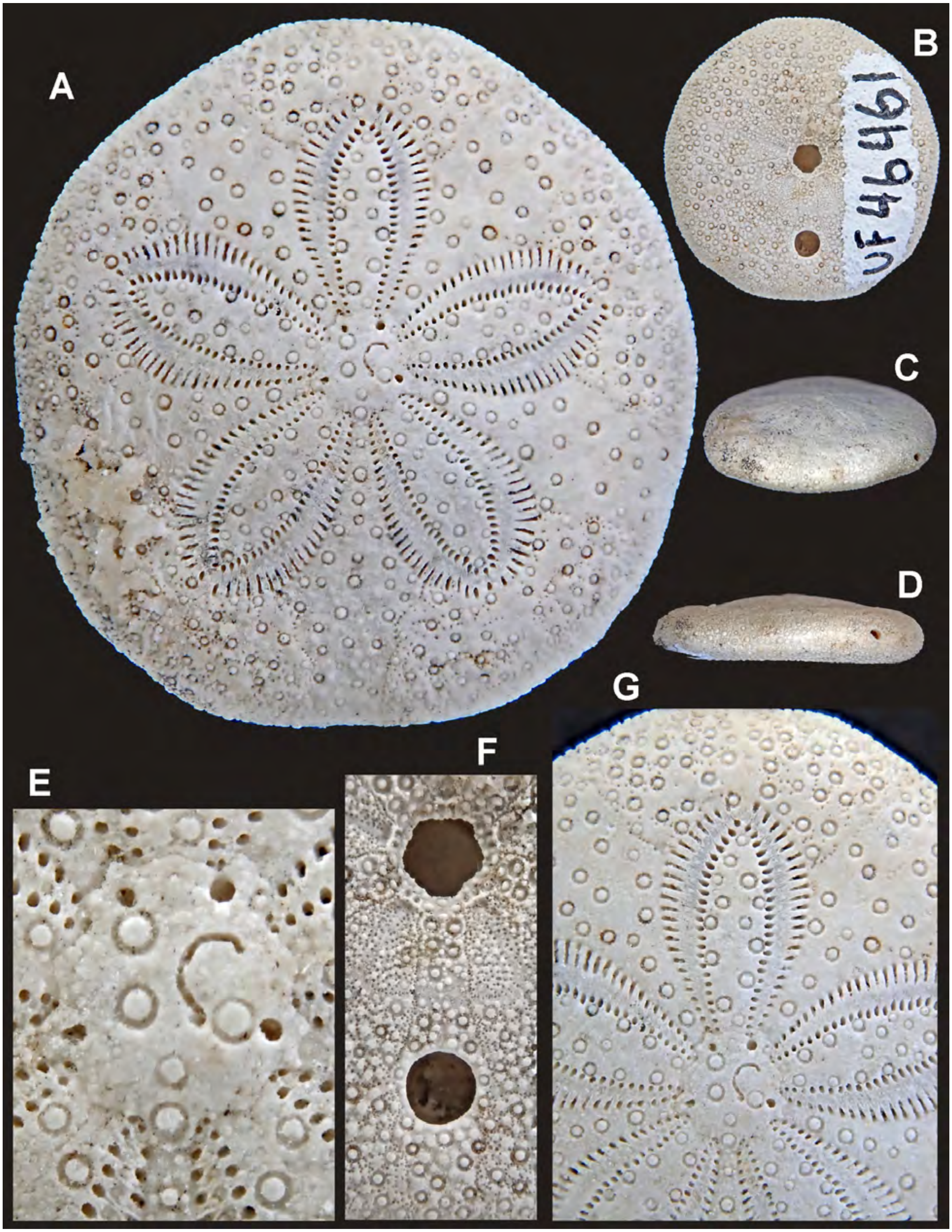


Figure 117: *Neolaganum dalli* (UF 46461), 13.1 mm TL, 12.6 mm TW, 3.2 mm TH, Middle Eocene Avon Park Formation, collected by divers in Blue Springs, Volusia County, Florida (FM-IP VO001). A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: posterior. E: apical area, note very pronounced hydropore groove. F: peristome and periproct. G: petaloid area, note small pores in ambulacrum outside petaloid portion of ambulacrum III. This is what Cooke (1942) described as: punctate extrapetalous ambulacral regions, also seen in the holotype of *L. dalli*.

Figure 118: *Neolaganum durhami* (UF 337984), 33.5 mm TL, 31 mm TW, 5.5 mm TH, *Oligopygus phelani* zone of Upper Eocene lower Ocala Limestone, Citrus County, Florida (FM-IP CI001).

ining were synonymous with Twitchell's (in Clark and Twitchell, 1915) *L. archerensis*. However, the localities Cooke (1942) provided for his specimens of *R. archerensis*, other than the type locality in a well near Archer, Florida, are largely localities in Levy County where *N. durhami* is found in the *Oligopygus phelani* Zone of the lower OLS. The specimen Cooke (1942) figured is from an unknown depth in a well in Polk County, Florida, and this specimen (USNM 498994) has been established to be what would subsequently become recognized as *N. durhami*, not *N. dalli*.

Fischer (1951), following Cooke (1942), discussed the occurrence of *N. durhami* (as *Peronella archerensis*) in the *Oligopygus phelani* Zone in Citrus and Levy Counties, Florida and noted that the type of the species illustrated by Twitchell in Clark and Twitchell (1915) is an unusually flattened specimen. Fischer (1951) was unaware that he was comparing specimens of a different species with Twitchell's form (= *N. archerensis*), but Fischer's figured and referred specimens of *P. archerensis* are also recognizable as *N. durhami*.

Durham (1954) erected *Neolaganum* and described *N. archerensis* as the type species of the genus. However, Cooke (1959) asserted that Durham (1954) mistakenly based the genus on misidentified specimens that he insisted were his *N. durhami*. Although Cooke (1959) didn't provide a rationale for his assertion that Durham misidentified *N. durhami* as *N. archerensis*, it appears he was correct. Durham (1954) considered UCMP 33296 a hypotype of *N. archerensis*. Durham's figures of *N. archerensis* in Durham (1954, 1955, 1966) are of this specimen,

Figure 119: Holotype of *Laganum ocalanum* (= *Durhamella ocalana*) (USNM 372873), 22.3 mm TL, 19.5 mm TW, 3.0 mm TH, Upper Eocene upper Ocala Limestone, two miles NE of Sumterville, Sumter County, Florida. A: aboral. B: oral.

and the specimen is clearly *N. durhami*. In addition, the locality for this specimen is the mouth of the Withlacoochee River west of Yankeetown (FM-IP LV024), which has exposures of the lower OLS containing *N. durhami*, but no trace of exposures of the Avon Park Formation that would contain *N. archerensis*, which has also never been identified in surface exposures. We conclude that Durham (1954) based *Neolaganum* on a specimen (UCMP 33296) he called *N. archerensis* but was actually *N. durhami*. Cooke (1959) later described and named this form as *N. durhami* and included the previous designations in the synonymy of his new species. Nevertheless, as stated above in reference to the ICZN's recommendation concerning misidentified types of a species group, *N. archerensis* is here maintained as the type species of *Neolaganum*.

Neolaganum durhami typically attains a size about twice that of *N. dalli*, is proportionately thinner, and has denser tuberculation (Cooke, 1959). These two species are often found together in mixed spoil of the lowest OLS and underlying Avon Park Formation in the Gulf Hammock Quarry (FM-IP LV004). There remains potential to confuse *N. durhami* with members of *Weisbordella* in mixed spoil of the OLS, but its flattened test, five gonopores, and flat oral surface distinguish *N. durhami* from both species of *Weisbordella* known to occur in the region. *Neolaganum durhami* is more likely to be confused with *Durhamella floridana* (Twitchell in Clark and Twitchell, 1915), from which it can be readily differentiated because *N. durhami* has four gonopores instead of five. *Neolaganum durhami* has much narrower petals than the lanceolate petals of *W. inglisensis* n. sp., with which it occurs within the type area near Inglis, and again, *W. inglisensis* n. sp. has only four gonopores.

Neolaganum durhami is much smaller than the very elongate *W. eldridgei*, which also has a very thin margin and only four gonopores that further distinguish the two species. In addition, these two species are not typically found together. *Wythella eldridgei* occurs in the *Wythella eldridgei* Zone in the uppermost OLS and *N. durhami* appears to be restricted to the *Oligopygus phelani* Zone near the base of the OLS.

Fischer (1951) noted that *N. durhami* (as *Peronella archerensis*) has considerable variation in

Figure 120: *Durhamella ocalana* (UF 337975), 27.5 mm TL, 25 mm TW, 3 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

outline and thickness of the margin. The margin of this species is usually thick, but a collection of specimens will undoubtedly contain some individuals with relatively thin margins. In addition, the ambitus typically has truncations in the posterior ambulacra that are less expressed anteriorly, and this gives the test what Cooke (1959) described as a subdecagonal outline. More rarely, specimens can have a nearly oval or even nearly circular outline. The five gonopores and relatively large number of oral plates (Tables 8, 9) distinguish it from other neolaganids with a similar overall test shape.

Though Fischer (1951: table 1) showed *N. durhami* (as *Peronella archerensis*) to occur throughout the OLS, we have only found *N. durhami* in the *Oligopygus phelani* Zone, where it is commonly found with *D. ocalana*, *E. mooreanus, P. floridanus*, and other, rarer species. *Neolaganum durhami* is not otherwise documented from the upper OLS, and a search of the FM-IP collections revealed no specimens of *N. durhami* from the upper OLS. Therefore, we do not recognize *N. durhami* above the *Oligopygus phelani* Zone of the OLS in Florida.

Emended Diagnosis.—*Neolaganum* with: low test; very elongate, slit-like outer pores in the petals; demiplate every two or three plates in the petals; periproct closer to peristome than the ambitus; large number of plates (usually about 78 in total) in the oral ambulacra.

Genus ***Durhamella*** Kier, 1968

Kier (1968) erected *Durhamella* in honor of J. Wyatt Durham, and designated *D. ocalanum* as the type species, noting the occurrence of what he called "pseudocompound plates" in the petals. Kier

Figure 121: *Durhamella ocalana* (UF 337976), 23.5 mm TL, 21 mm TW, 4 mm TH, *Oligopygus haldemani* Zone Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

stated that the presence of these plates, coupled with basicoronal plates arranged in a pentagon, indicate *Durhamella* should be placed in the Neolaganidae. He did not provide a diagnosis for the genus but did state that it is distinguished from other neolaganid genera by the presence of 5 gonopores, fewer pseudocompound plates in the petals, and the outer pore of the petals not being in a pronounced slit. Like *Durhamella*, *Weisbordella* has a reduced number of oral plates, but differs in that *Durhamella* often has depressions along the sutures in the margins of the aboral regions. In addition, *Weisbordella* has very strongly expressed demiplates in the petals that are very poorly expressed or completely absent in *Durhamella* (Fig. 106). The latter also lacks the long, sinuous, or complexly branched hydropore groove of *Weisbordella*.

Emended diagnosis.—With the inclusion of *Durhamella tetrapora* n. sp., *Durhamella* is now understood to include taxa with both four and five gonopores. *Durhamella* is best characterized by a combination of: depressions in the aboral submarginal region; short, unbranched, hydropore grooves; flat oral surface made up of a reduced number of plates, notably in the interambulacra; very elongate interambulacral first post-basicoronals; and round outer pores in the petal pore pairs.

Durhamella ocalana (Cooke, 1942)
(Figs. 105, 106, 119-123; Table 8)

Laganum ocalanum Cooke, 1942. p. 23. pl. 2, figs. 7-10.

Laganum ocalanum (Cooke). Fischer, 1951. p. 57.

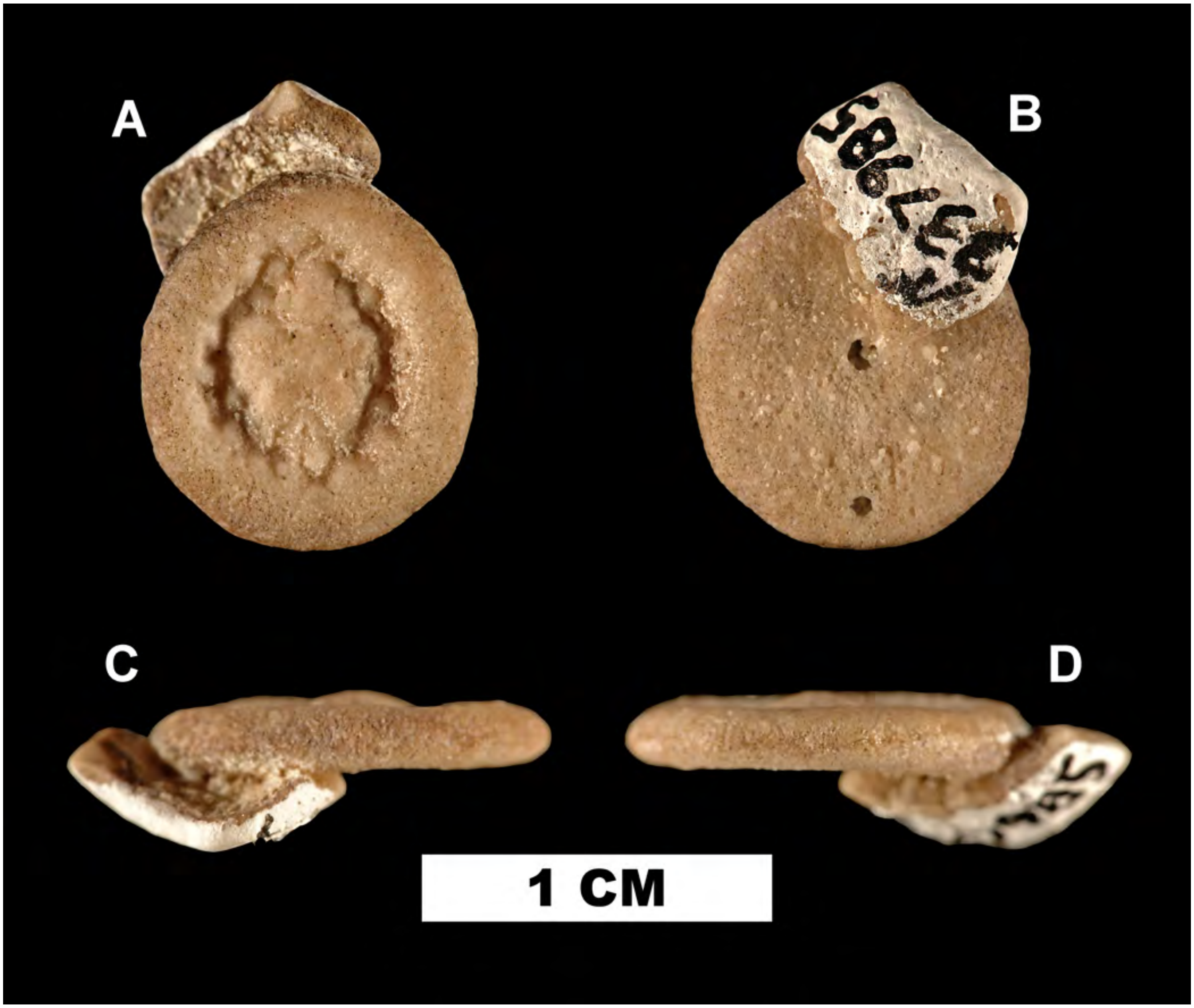


Figure 122: *Durhamella ocalana* (UF 337985), 11 mm TL, 10 mm TW, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: left side. D: right side.

Laganum ocalanum (Cooke). Cooke, 1959. p. 51. pl. 20, figs. 11-15.

Durhamella ocalana (Cooke). Kier, 1968. pl. 6, figs. 1-5; pl. 7, figs. 1-3; pl. 8, figs. 2, 3. figs. 28-30, 32-34.

Laganum ocalanum (Cooke). Toulmin, 1977. p. 342. pl. 64, fig. 6, 7.

Durhamella ocalana (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—Present in both the *Oligopygus phelani* and *Oligopygus haldemani* Zones of the OLS of Florida, and absent only from the uppermost portion of the unit. *Durhamella ocalana* is sporadically common in the *Oligopygus haldemani* Zone of the OLS, especially in quarries near St. Catherine and Center Hill in Sumter County (FM-IP SM010), and northwest of Mayo (FM-IP LF001) in Lafayette County, as well as the type locality of the species in a pit 3.2 km NE of Sumterville.

It is more abundant in the *Oligopygus phelani* Zone in the lower OLS, especially along the banks of the Withlacoochee River, Levy County (FM-IP LV024) and Cross Florida Barge Canal, Citrus County (FM-IP CI001).

Discussion.—Cooke (1942) initially de-

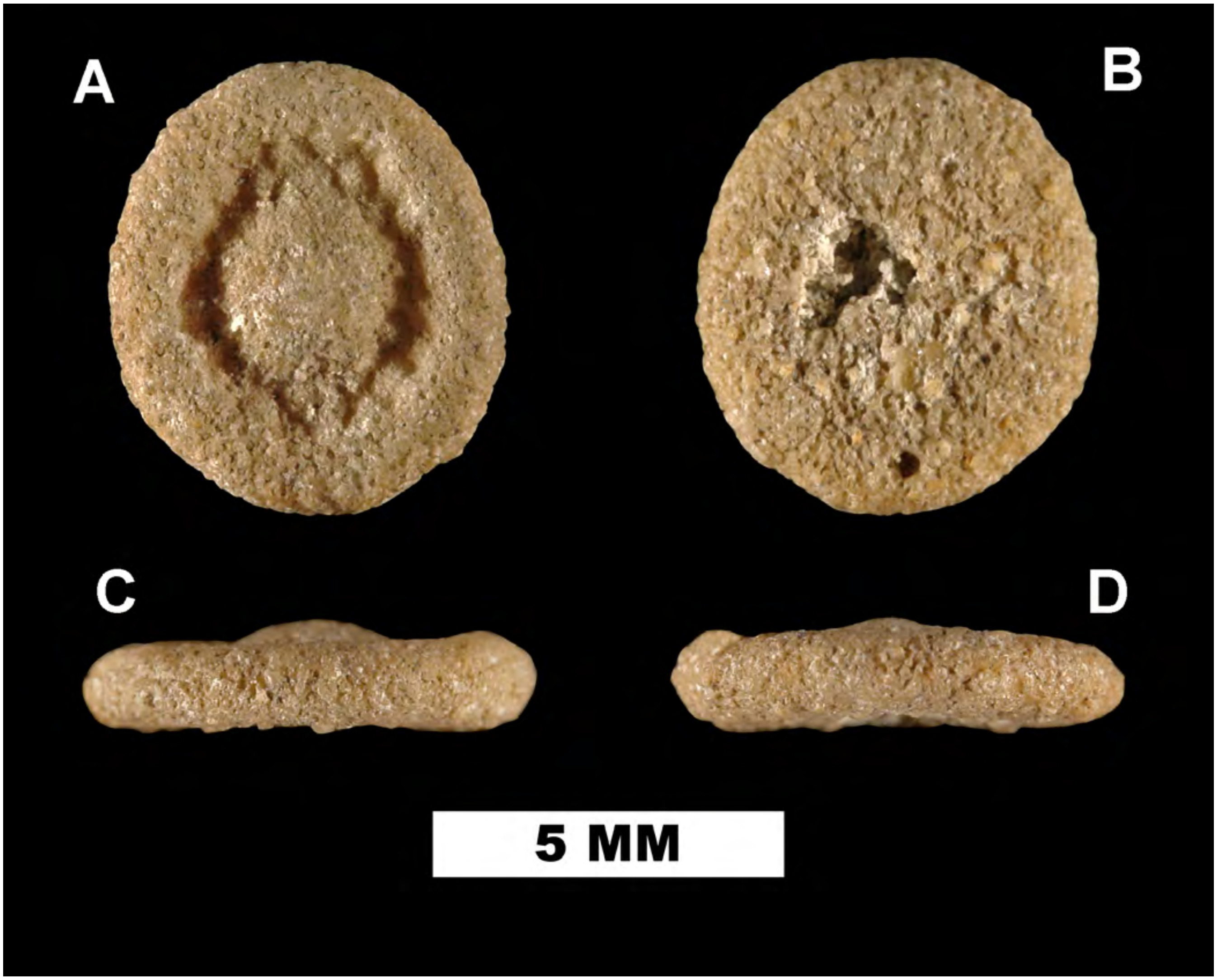


Figure 123: *Durhamella ocalana* (UF 337986), 7.5 mm TL, 6.5 mm TW, 2.0 mm TH, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, Levy County, Florida (FM-IP LV024).

scribed this species as *Laganum ocalanum* from the OLS at numerous localities in Florida. Kier (1968) named *D. ocalanum* the type species of his new genus *Durhamella* and emended the species name from *ocalanum* to *ocalana*. In addition, with over 100 tests available, Kier (1968) redescribed the species in much greater detail than previously.

Durhamella ocalana appears to be restricted to the OLS of Florida and in its adult stages, is a very distinct species that cannot be confused with any other members of the echinoid fauna of the region except for its congener, *D. floridana*. *Durhamella ocalana* is perhaps best characterized by the presence of depressed sutures in the submarginal area on the aboral surface, giving the appearance that the plates surrounded by these sutures are tumid. The depressions, which are absent or only slightly discernable in *D. floridana*, are present in *D. ocalana* in both the adapical interambulacral plates and the ambulacral plates beyond the petals. These two species of *Durhamella* are otherwise very similar, having similar petals, length to width, length to height ratios, similar peristomes, and similar adoral plate arrangement (Kier, 1968). Although, gonopores are found in the smallest identifiable specimens (3.5 mm TL) of *D. ocalana*, depressed sutures in the periphery of the aboral surface are only consistently discernable in specimens greater than 5 mm TL. Therefore, distinguishing small (¡5 mm TL) specimens of *D. floridana* and *D. ocalana* is done with

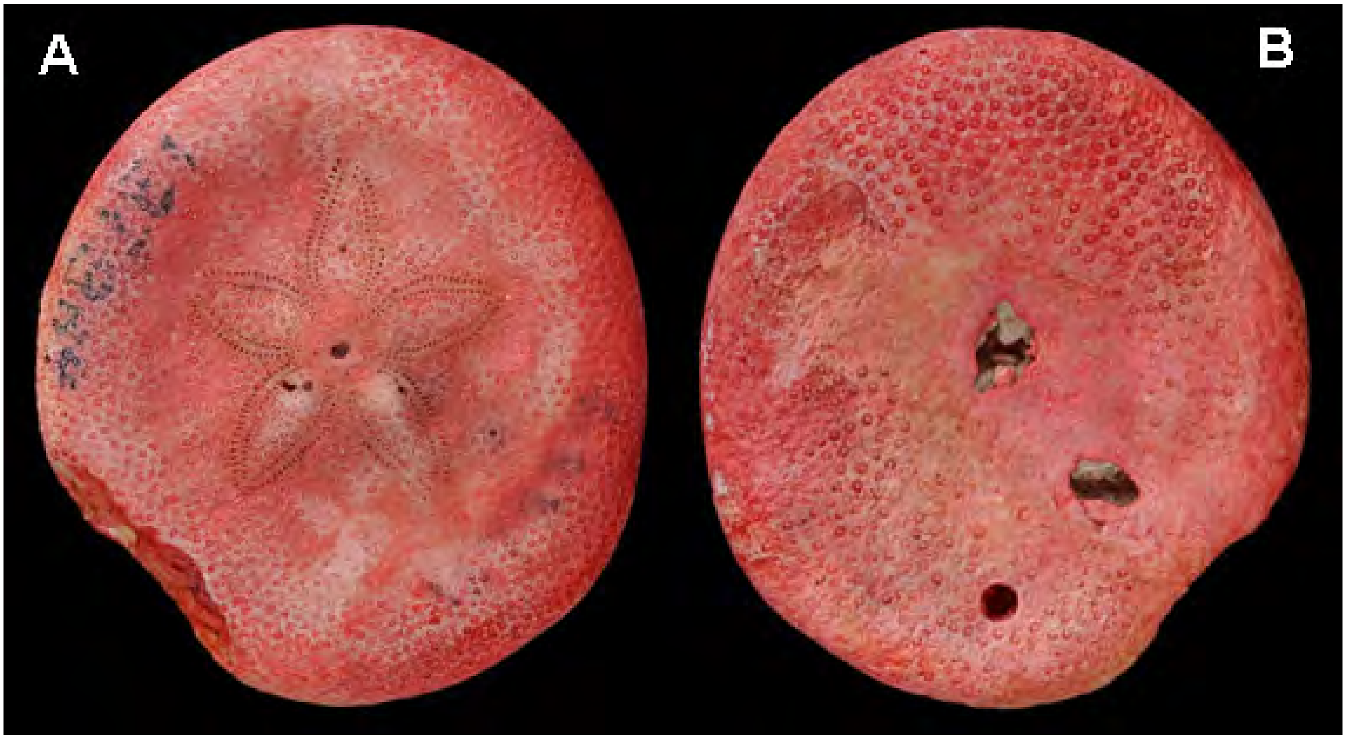


Figure 124: Holotype of *Laganum floridanum* (= *Durhamella floridana*), (USNM 137884), 19.6 mm TL, 17.7 mm TW, 4.2 mm TH, Upper Eocene lower Ocala Limestone, Johnson's Sink, Levy County, Florida. A: aboral. B: oral.

difficulty.

Durhamella ocalana is readily distinguished from *D. tetrapora* n. sp. by the presence of five gonopores and depressed plate sutures near the margins of the aboral surface.

As discussed in the remarks for *D. floridana*, *D. ocalana* and *D. floridana* are often found in association in both the *Oligopygus phelani* and *Oligopygus haldemani* Zones of the OLS of Florida. Specimens of *D. ocalana* and *D. floridana* rarely exceed 10 mm in diameter in the *Oligopygus phelani* Zone where it occurs in abundance with *D. floridana*, *D. tetrapora* n. sp., *E. mooreanus, N. durhami, W. inglisensis* n. sp., and *P. floridanus*. In the *O. haldemani* Zone, *D. ocalana* and *D. floridana* achieve greater sizes, exceeding 35 mm in TL. See the remarks for *D. floridana* for additional comments on the association of these two taxa and possible sexual dimorphism.

Emended Diagnosis.—The only *Durhamella* with a combination of: five gonopores; strongly expressed depressions along the sutures in the peripheral region of the aboral surface; poriferous zones that are much less than half the width of the poriferous zone as measured from the perradial to abradial suture about two thirds of the length of the petal.

Durhamella floridana (Twitchell in Clark and Twitchell, 1915)
(Figs. 105, 106, 124-128; Table 8)

Laganum floridanum Twitchell in Clark and Twitchell, 1915. p. 163. pl. 75, figs. 3a-d.

Echinodiscus floridanus (Twitchell). Lambert and Thiéry, 1925. p. 581.

Laganum floridanum (Twitchell). Cooke, and Mossom, 1929. pl. 3, figs. 5a-b.

Laganum floridanum (Twitchell). Cooke, 1942. p. 23.

Laganum floridanum (Twitchell). Cooke, 1945. fig. 5, no. 5.

Laganum floridanum (Twitchell). Cooke, 1959. pp. 50-51. pl. 20, figs. 8-10.

Durhamella cf. *D. floridana* (Twitchell). Kier, 1968. pp. 29-38. pls. 8.1, 9.1-5, 10.1-3. figs. 27, 31, 34-43.

Laganum floridanum (Twitchell). Toulmin, 1977. pp. 341-342. pl. 67, fig. 3.

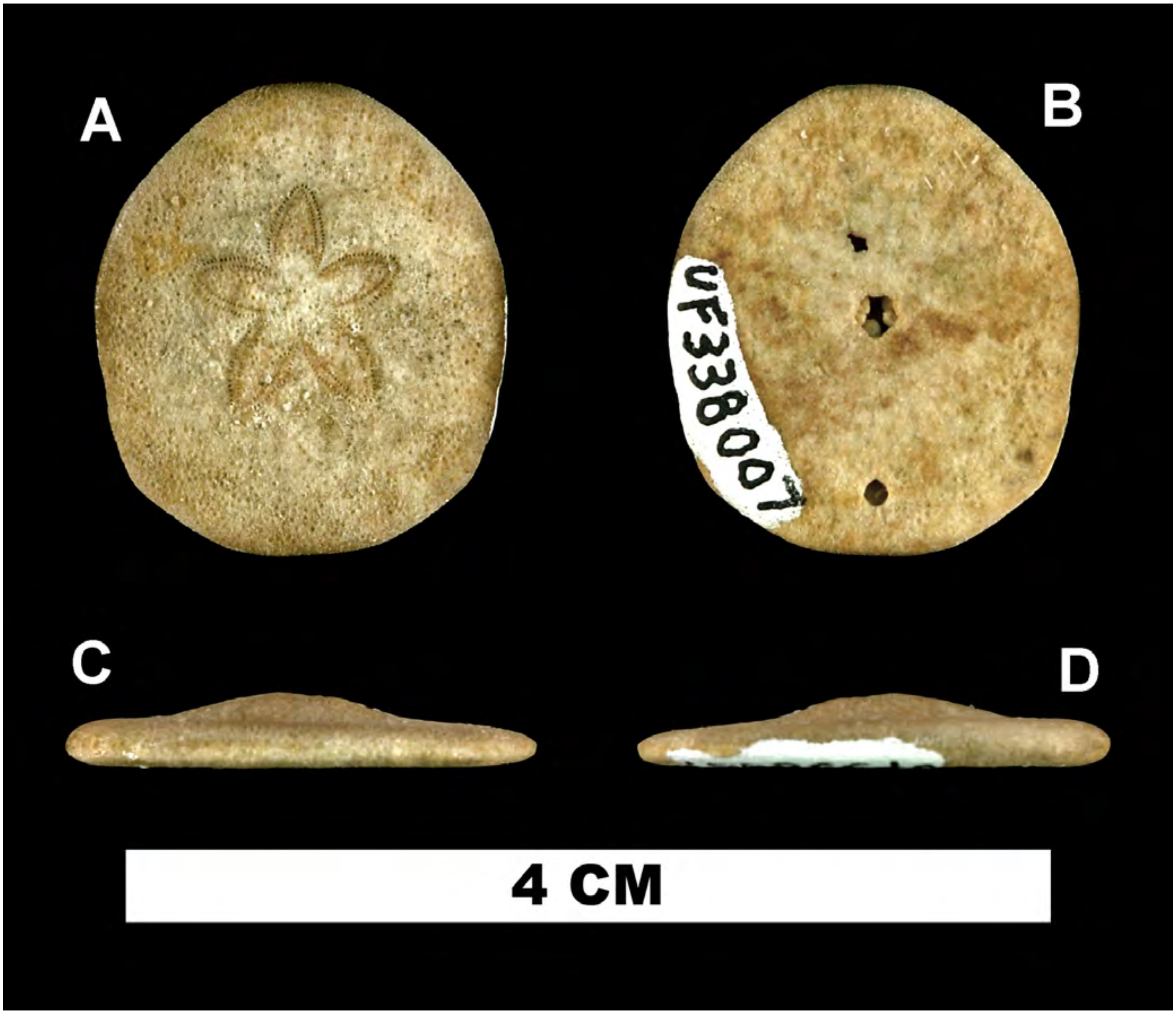


Figure 125: *Durhamella floridana* (UF 338007), 20 mm TL, 17.5 mm TW, 3 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

Durhamella floridanum (Twitchell). Mooi, 1989. fig. 17b.

Durhamella floridana (Twitchell). Osborn et al., 2016. tbl. 2.

Occurrence.—*D. floridana* is present in both the lower and upper divisions of the OLS in Florida. It occurs in the *Oligopygus haldemani* Zone, especially northwest of Mayo (FM-IP LF001), Lafayette County. It is also found in the *Oligopygus phelani* Zone of the lower OLS, occurring along the banks of the Withlacoochee River, Levy County (FM-IP LV024) and Cross Florida Barge Canal, Citrus County (FM-IP CI001). The type locality for the species is Johnson's Sink, (FM-IP 3142), 4 mi. northeast of Williston, Levy County.

Kier (1968) documented the occurrence of *D. floridana* in the Middle Eocene Lake City Formation (now Avon Park Formation) in the subsurface of Georgia.

Discussion.—Twitchell in Clark and Twitchell (1915), initially described this species as *Laganum floridanum* from Johnson's Sink, Levy County, in strata that were at the time considered to

Figure 126: *Durhamella floridana* (UF 337983), 23 mm TL, 19.5 mm TW, 3.5 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side.

be early Oligocene. The stratum at the type locality is now recognized as the Upper Eocene OLS. Twitchell in Clark and Twitchell (1915) initially described this species as having four gonopores, but Cooke (1959) corrected the description to clarify that the species has five gonopores. Kier (1968) subsequently altered the species designation from *floridanum* to *floridana*. Specimens from the type locality, which has since been developed and is no longer accessible, are figured herein (Figs. 127, 128).

Durhamella floridana is usually distinguished from *D. ocalana* by its lack of the characteristic depressed sutures of interambulacral plates on the aboral surface. These depressed sutures give the submarginal area of the aboral surface of *D. ocalana* a "pillowy" appearance. However, it should that noted that weakly depressed sutures may be present in *D. floridana*, as shown in Kier (1968: pl. 9, fig. 1). Therefore, distinguishing between *D. ocalana* and *D. floridana* can be troublesome unless one is able to examine the petal plate architecture (Fig. 106).

The presence of five gonopores readily distinguishes *D. floridana* from *N. durhami, W. inglisensis* n. sp., and *D. tetrapora* n. sp., with which it occurs in the lower OLS. *Durhamella floridana* occurs with *W. cubae* in the *Oligopygus haldemani* Zone of the OLS, from which it is easily distinguished by *D. floridana*'s flat oral surface (the oral surface of *W. cubae* is distinctly concave), its much thinner test, and the presence of five gonopores. It cannot be confused with any other element of the fauna of the OLS, within which it appears to be restricted

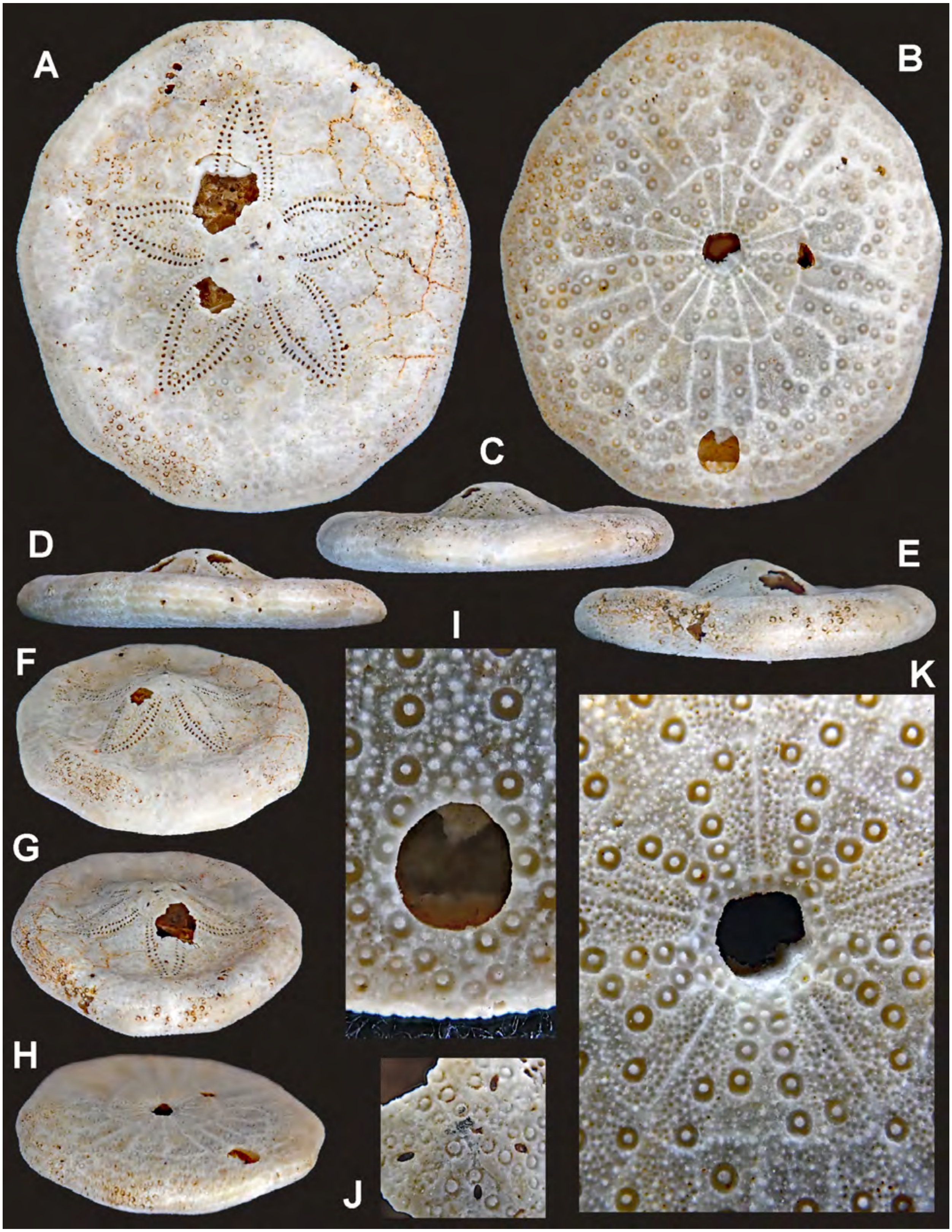


Figure 127: Figure 129: *Durhamella floridana* (UF 345211), 14.7 mm TL, 13.4 mm TW, 3.1 mm TH, Upper Eocene Ocala Limestone from the type locality of the species at Johnson's Sink, Levy County, Florida (FM-IP 3142). A: aboral. B: oral. C: posterior. D: left side. E: anterior. F: tilted aboral viewpoint from posterior. G: tilted aboral viewpoint from anterior. H: oblique oral viewpoint from posterior. I: periproct. J: apical area. K: peristomal area showing oral plating.

Figure 128: *Durhamella floridana* (UF 344747), 11.1 mm TL, 10.7 mm TW, 2.4 mm TH, Upper Eocene Ocala Limestone from the type locality of the species at Johnson's Sink, Levy County, Florida (FM-IP 3142). A: aboral. B: oral. C: right side. D: left side.

other than in the isolated Lake City Formation (now Avon Park Formation) well occurrence in the Glynn County, Georgia (Kier, 1968).

As discussed further in the remarks for *D. ocalana*, it is curious that *D. floridana* and *D. ocalana* are usually found together in the OLS, both in the *Oligopygus haldemani* Zone, where both species are usually larger (Figs. 120, 121), and in the *Oligopygus phelani* Zone, where both species are typically much smaller. In addition, the gonopores of *D. ocalana* are usually, though not always, larger and it is possible that the two species are morphs of the same species: *D. floridana* might represent the males, and *D. ocalana* the females, in which the depressed sutures of the aboral surface of *D. ocalana* facilitate brooding. Such sutures seem to cause a reduction in interambulacra, which in turn could provide more space for the developing young. What spines remain adjacent to the depressions could form a protective screen over the juveniles. However, the fact that *D. ocalana* is typically much more abundant than *D. floridana* at all known exposures casts doubt on this hypothesis, as does the variation in gonopore size of *D. ocalana*, even though it does tend to have larger gonopores. The slightly depressed sutures might also conflict with the interpretation that *D. floridana* is the male of *D. ocalana*, except that as discussed below, Kier (1967) noted that males of *Pentedium curator* can express shallow pits in the anterior paired interambulacra adjacent to the apical system. This illustrates a tendency for males of sexually dimorphic laganids to show some of the secondary sexual features expressed to a much greater degree in the females.

Emended Diagnosis.—The only *Durhamella* with: five gonopores; absence of strong expression of depressions along the sutures in the peripheral region of the aboral surface (if these are present, they are very shallow and nearly indistinguishable); poriferous zones that are much less than half the width of the poriferous zone as measured from the perradial to abradial suture about two thirds of the length of the petal.

Durhamella tetrapora n. sp.

(Figs. 105, 106, 129-132; Table 8)

Diagnosis.—The only *Durhamella* with: four rather than five gonopores; very small test with possible sexual dimorphism.

Description.— Based on three specimens; UF 343902, interpreted as female, two specimens interpreted as male (UF 343903, UF 343904). Small, from 5.4 mm TL to 6.4 mm TL, 4.7 to 6.0 mm TW, slightly subpentagonal, posterior margin truncated, anterior gently rounded, greatest width through peristome; TW averages 93.6% TL in males, 88.4% in female. Test low, TH 24.6 – 26.5% TL, greatest height at apical system. Margin thick, slightly higher anteriorly. Aboral surface depressed between margin and mid-length of petals (sutures of aboral interambulacral plates not depressed as in *D. ocalana*); depression creates shallow indentations marginally adjacent to ambulacra, strongly developed in UF 343902 (female), interpreted as brooding pouches; less depressed ridges radiate from apical area in center of all five interambulacra to margin. Oral surface flat, only slightly depressed near peristome.

Apical system slightly anterior; anterior edge on average 36.9% TL from anterior ambitus, posterior edge on average 39.9% TL from posterior ambitus. Four gonopores well-developed in all three specimens; sexual dimorphism very likely. Gonopores vary in position and size. UF 343902 (female) has large gonopores (avg. 2.3% TW), male gonopores much smaller (avg. 1.4% TW). Gonopores of female more widely separated (anterior pair 14.8% TW apart, posterior pair 23.8 % TW apart), positioned on edge of apical system. Gonopores of males well within apical area, closer together (anterior pair on average 5.4% TW apart, posterior pair on average 9.3% TW apart); males show that separation of posterior pair of gonopores is variable. Shallow, short, unbranched hydropore groove present.

Petals flush, wide apically, nearly closed distally. In smaller specimen (UF 343902: female) petal I and V longest, on average 18.4% TL, petal II and IV shortest, on average 14.5% TL, petal III 16.6% TL. In larger specimens (males) petal III longest, on average 22.2%, petals II and IV shortest, on average 19.3% TL; petals I and V on average 21.0 % TL. Pores round, outer pore not elongate. UF 343902 has one more pore pair per series in petal I and V than other petals, both male specimens have on average one less pore pair per series in petals II and IV than the others. Occluded plates (secondaries that extend from the perradial suture but do not touch an interambulacrum) present distally in most petals (Fig. 132), especially UF 343904 which has one occluded plate in petals I, III, and IV; two in petal II, and three in petal V. Pores more numerous in oral ambulacra; concentrated on adradial sutures; buccal pores present at edge of peristome.

Basicoronal plates form subpentagonal outline with single plate in each interambulacrum, paired plates in each ambulacrum; first post-basicoronal interambulacral plates considerably longer than first post-basicoronal ambulacral plates, extending past second post-basicoronal ambulacral plates. Number of oral interambulacral plates reduced in comparison with other neolaganids except in *Weisbordella* and *Durhamella* (Fig. 105): UF 343904 has six post-basicoronal plates per oral interambulacrum; UF343902 has five post-basicoronal plates in interambulacrum 1-4 and 6 in interambulacrum 5.

Peristome subpentagonal, anterior blunt, posterior pointed; nearly central (posterior edge on average 44.4 % TL from posterior margin, anterior edge on average 43.4% TL from anterior margin), peristome length on average 12.6% TL, slightly

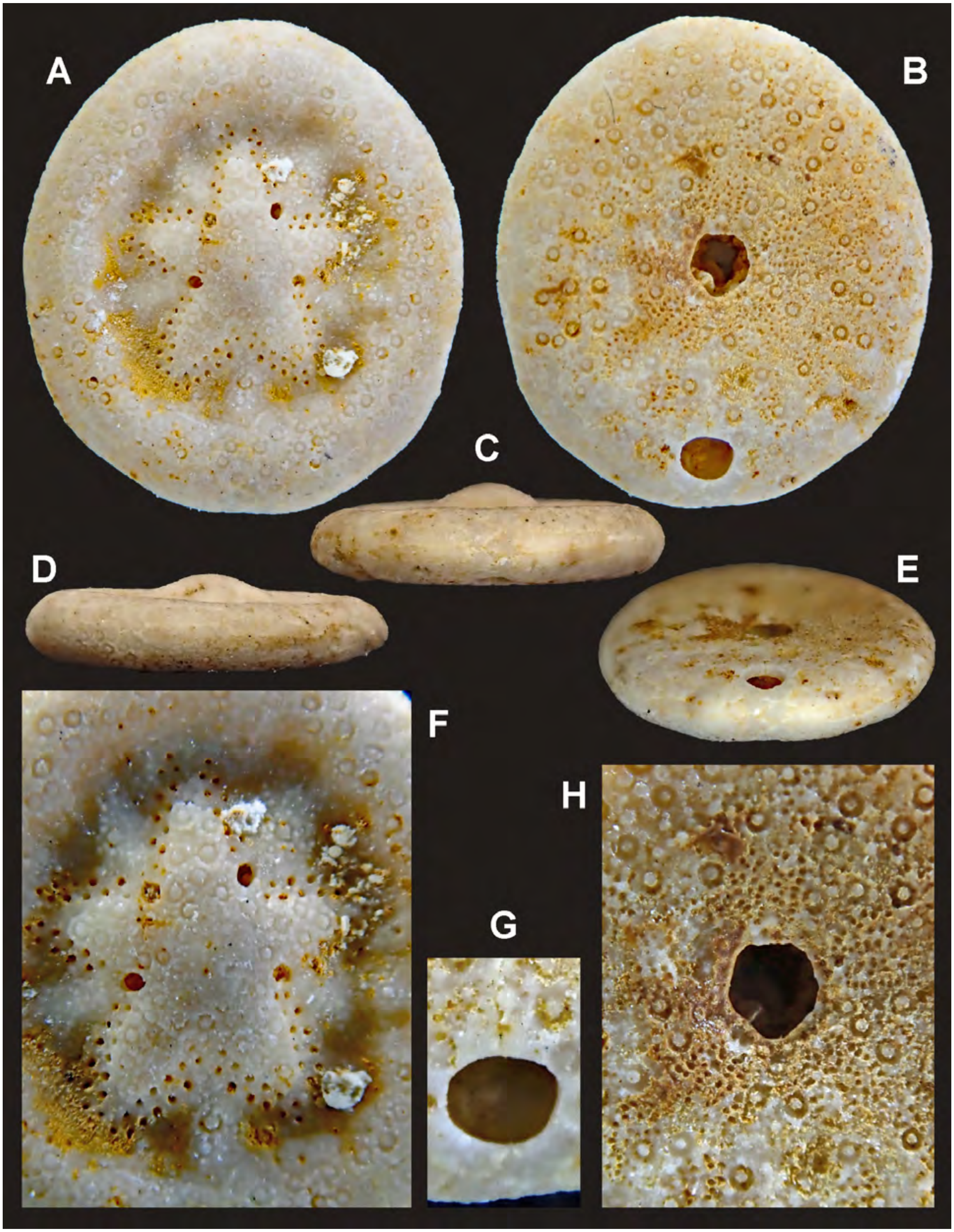


Figure 129: *Durhamella tetrapora* n. sp., holotype, (UF 343902), 5.4 mm TL, 4.7 mm TW, 1.3 mm TH, a female, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, Levy County, Florida (FM-IP LV016). A: aboral. B: oral. C: posterior. D: left side. E: tilted oral viewpoint from posterior. F: petaloid area. G: periproct. H: peristome.

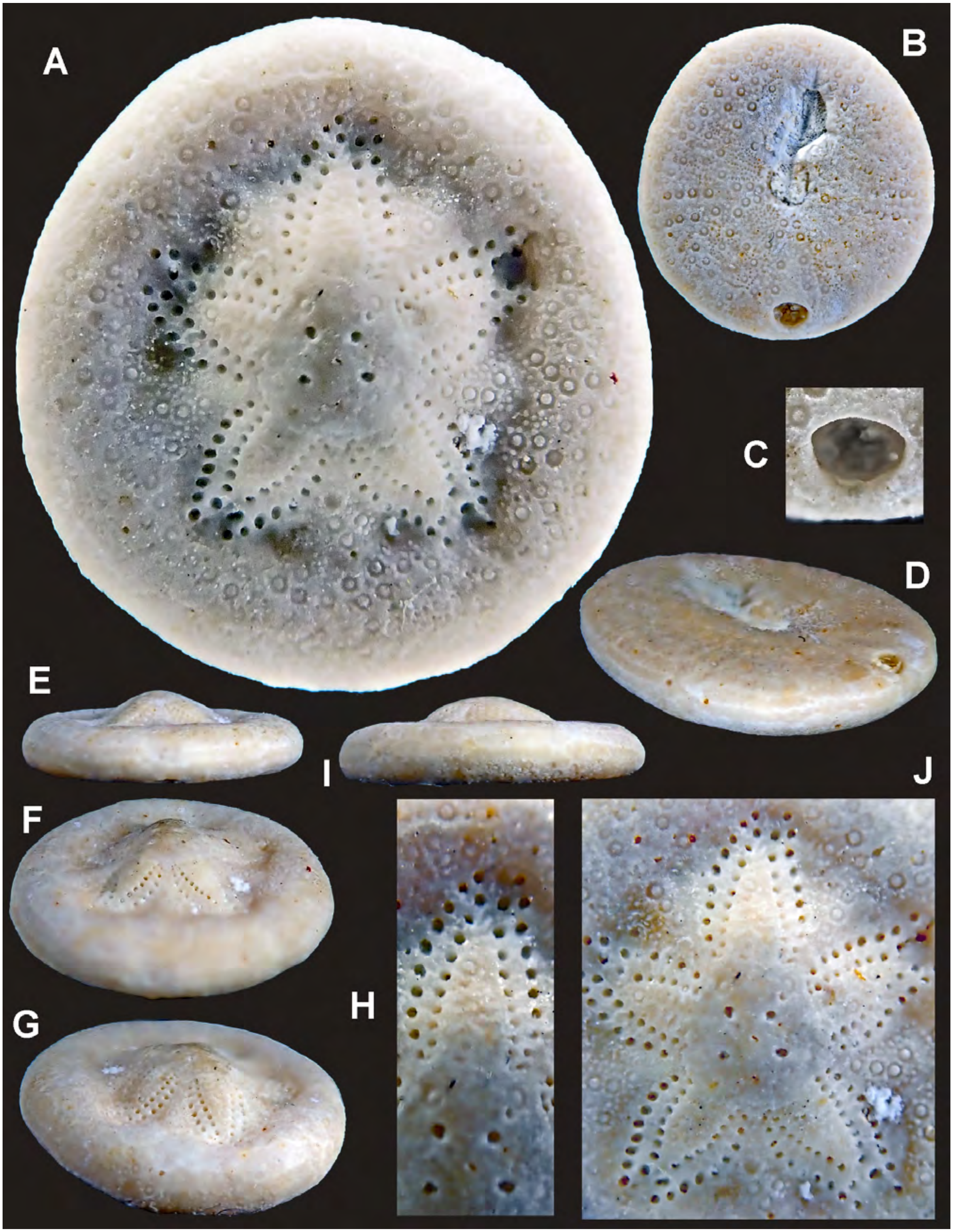


Figure 130: *Durhamella tetrapora* n. sp., paratype, (UF 343903), 6.4 mm TL, 6.0 mm TW, 1.7 mm TH, a male, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, pit north of Hwy 40, west of Hwy 19/98 in Inglis, Levy County, Florida (FM-IP LV016). A: aboral. B: oral. C: periproct. D: oblique oral viewpoint. E: posterior. F: tilted aboral viewpoint from posterior. G: oblique aboral viewpoint from anterior. H: apical area and petaloid portion of ambulacrum III. I: left side. J: petaloid area.

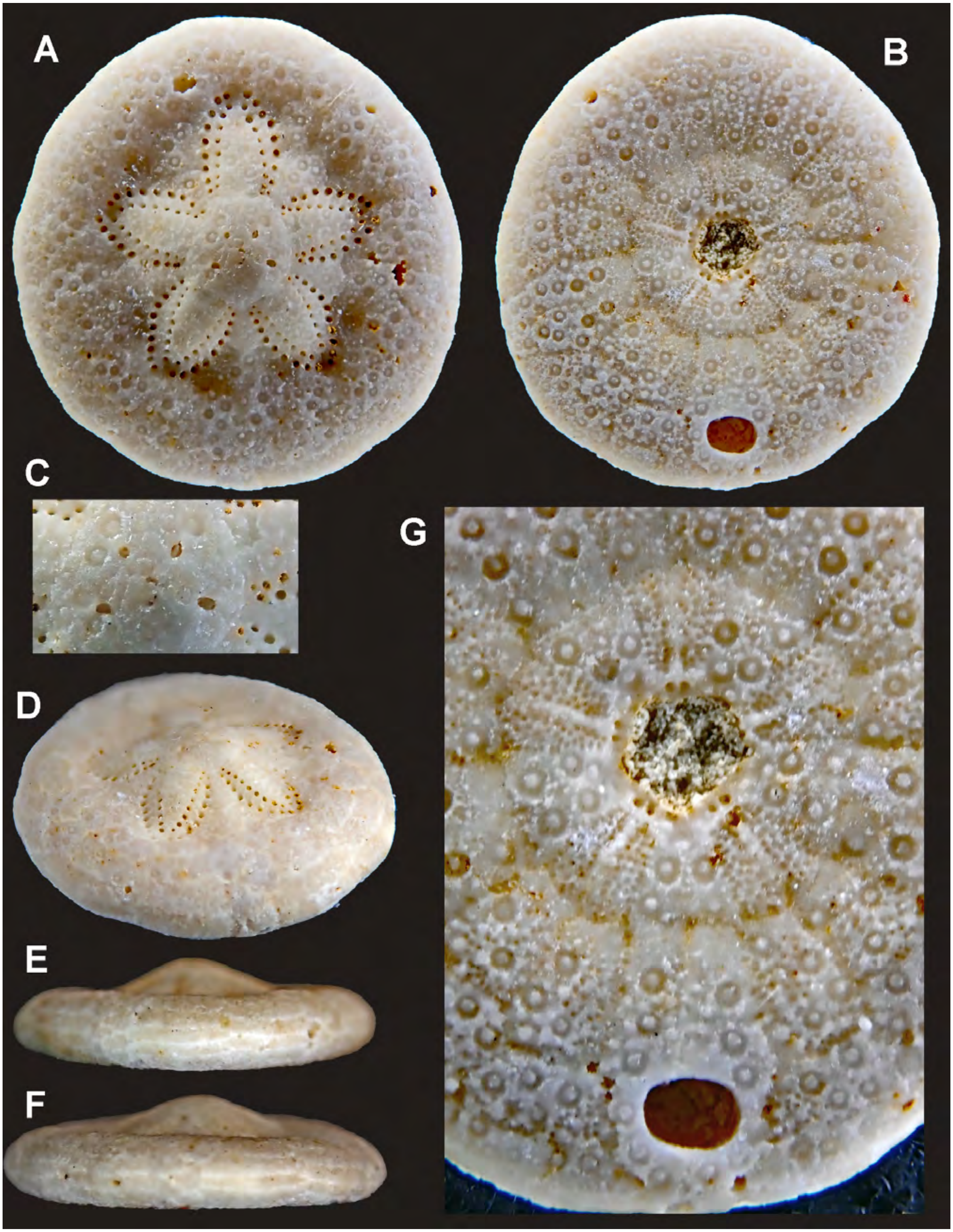


Figure 131: *Durhamella tetrapora* n. sp., paratype, (UF 343904), 6.3 mm TL, 5.9 mm TW, 1.6 mm TH, a male, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, pit north of Hwy 40, west of Hwy 19/98 in Inglis, Levy County, Florida (FM-IP LV016). A: aboral. B: oral. C: apical area. D: oblique aboral viewpoint from posterior. E: anterior. F: left side. G: peristome and periproct with some oral plating exposed.

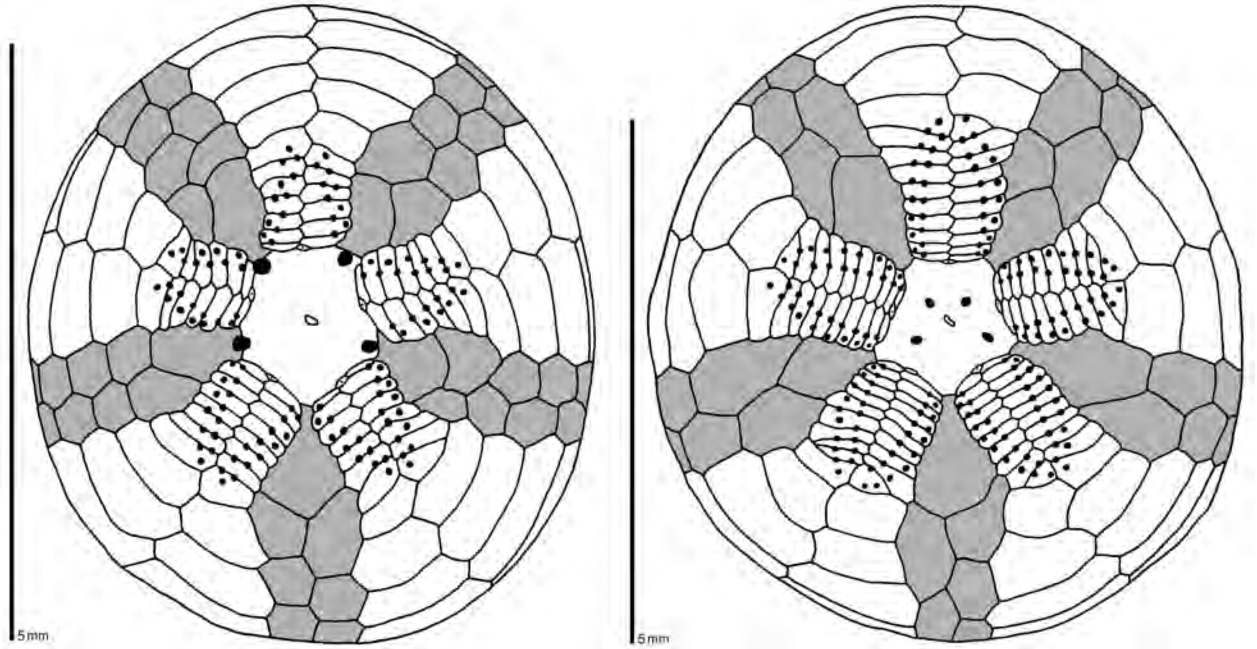


Figure 132: *Durhamella tetrapora* n. sp., comparison of aboral plate arrangement: Left: holotype, (UF 343902), a female. Right: paratype, (UF 343904), a male. Ambulacrum III is towards the top, the interambulacral plates are shaded, and pores are solid black.

longer than wide: peristome width on average 87% length. Periproct ovate, wider than long (height from 74.6 to 83.0% width, average 78.4% width), first in contact with plates 5.a.2 and 5.b.2 (Fig. 105), near the margin: on average 5.8% TL from posterior margin.

Interior structures such as peripheral supports, pillars and lantern not recorded.

Zoobank Nomenclatural Act.—6C5CC4EA-6074-41B1-ADAE-03629917B860

Discussion.—Muriel Hunter collected the holotype (UF 343902) and two paratypes (UF 343903, UF 343904) of *D. tetrapora* n. sp. west of Inglis in Levy County (FM-IP LV016). The specimens are small, from 5.4 to 6.4 mm TL, but likely mature or nearly so, as evidenced by their fully developed gonopores. This species is very similar to the other known species of *Durhamella*; *D. ocalana* and *D. floridana*. However, it is readily differentiated by the presence of four gonopores, instead of the five seen in its two congeners.

Kier (1968) stated the presence of five gonopores, fewer pseudocompound plates in the petals, and the outer petaloid pore not being in a pronounced slit distinguishes *Durhamella* from the other genera of Neolaganidae: as noted in the description, *D. tetrapora* n. sp., shares all these characters. Other than the presence of four rather than five gonopores, the new species shares all characteristics of *Durhamella*, so we place this taxon within *Durhamella* rather than erect yet another new genus. As discussed in the remarks for *Durhamella*, the genus was previously understood only to include taxa with five gonopores. Therefore, assigning *D. tetrapora* n. sp., which has four gonopores, to *Durhamella* required analysis of additional characteristics that diagnose the genus itself.

Durhamella is further characterized by a margin that is usually slightly thickened, but with a depressed aboral submarginal region, and *D. tetrapora* n. sp., also displays this feature. Furthermore, analysis of oral plate structure of *D. floridana*, *D. ocalana*, and *D. tetrapora* n. sp. (Fig. 105), shows they share very similar oral plate arrangement, with a reduced number of plates and greatly elongated first post-basicoronals.

Two of the three specimens of *D. tetrapora* n. sp. (UF 343903, UF 343904) has gonopores situated well within the apical system and are likely males. However, UF 343902 has much larger gonopores

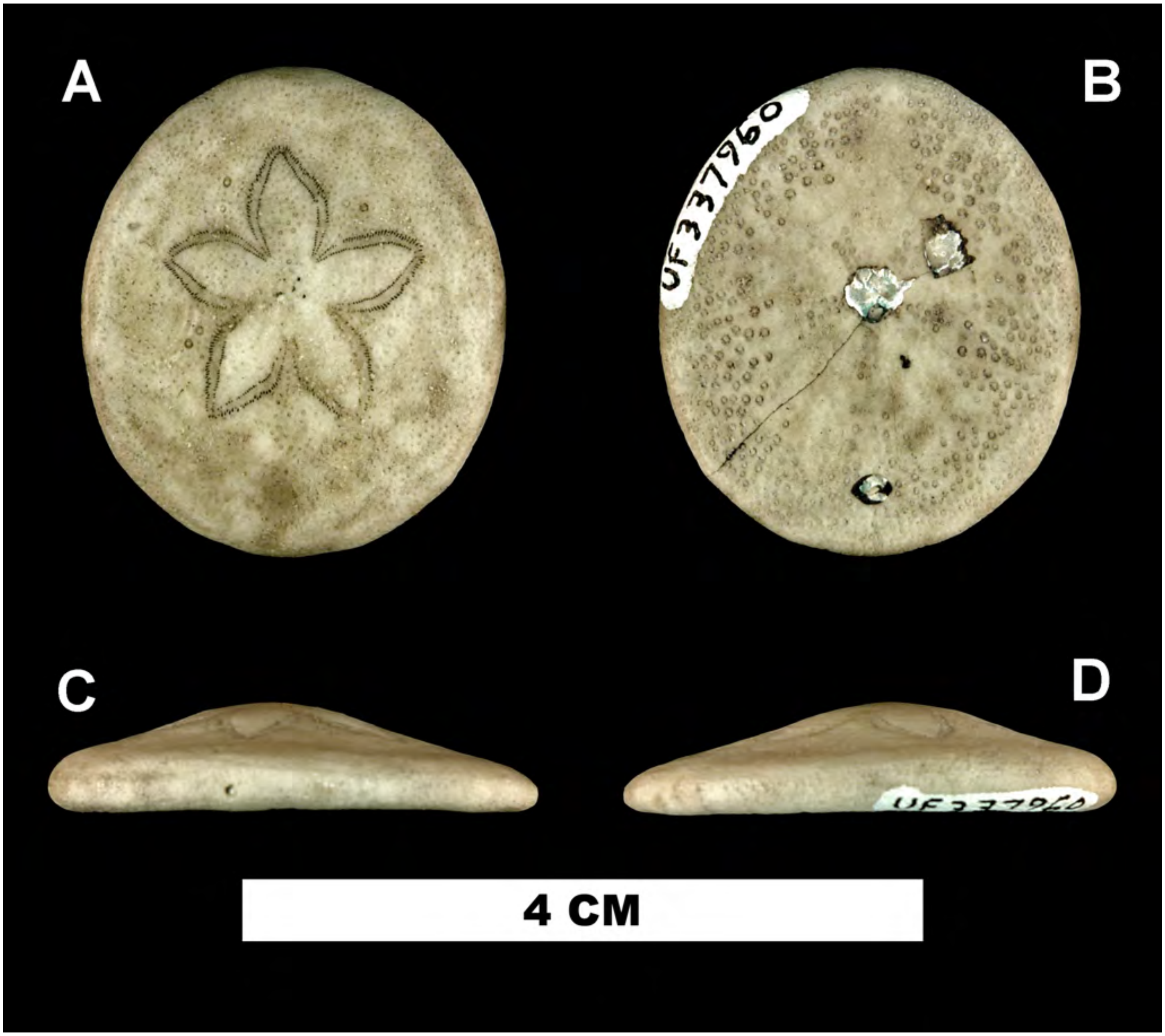


Figure 133: *Weisbordella cubae* (UF 337960), 29 mm TL, 25 mm TW, 6 mm TH, *Oligopygus haldemani* Zone of Upper Eocene Ocala Limestone, Sumter County, Florida (FM-IP SM010). A: aboral. B: oral. C: left side. D: right side.

that are more widely separated and positioned just outside of the apical area, and we interpret this specimen to be a female. The gonopore arrangement is very similar to the sexual dimorphism seen in *Pentedium curator* Kier, 1967. However, as noted by Kier (1967), the males of *P. curator* do not have adapical depressions except for one specimen that has two slight pits in the anterior paired interambulacra adjacent to the apical system, suggesting a tendency for males of some neolaganid taxa to show some of the marsupium-like features seen in the females. Kier (1967) noted that males of *P. curator* did not grow as large as the females, whereas the female *D. tetrapora* n. sp., is 5.4 mm TL, and smaller than the two males which are 6.3 mm and 6.4 mm TL.

Etymology.—The species name highlights the four gonopores, unique to *Durhamella,* seen in each of the known specimens.

Materials and Occurrence.—Holotype (UF 343902) and two paratypes (UF 343903, UF 343904) from the *Oligopygus phelani* Zone of the Upper Eocene OLS, pit on north side of Rt. 40, west of Inglis, Levy County, Florida (FM-IP LV016).

Figure 134: *Weisbordella cubae* (UF 337971), 13.5 mm TL, 12 mm TW, 3 mm TH, *Oligopygus wetherbyi* Zone of Upper Eocene Ocala Limestone, Dixie County, Florida (FM-IP DI001). A: aboral. B: oral. C: left side. D: right side.

Genus ***Weisbordella*** Durham, 1954

Durham (1954) designated *Peronella caribbeana* Weisbord, 1934 as the type species of *Weisbordella*, stating that *Peronella quinquenodulata* Weisbord, 1934; *P. caribbeana*; *Peronella cubae* Weisbord, 1934; *L. dalli*, and *Peronella mirabilis* Jackson, 1922 also likely belong in the genus. We agree with Cooke (1959) and recognize *L. dalli* in *Neolaganum*. Cooke (1942, 1959) also considered *P. quinquenodulata* and *P. caribbeana* to be subjective junior synonyms of *P. cubae*.

Durham (1954) did not recognize *Laganum johnsoni* Twitchell in Clark and Twitchell, 1915 as a *Weisbordella*, leaving it unassigned to genus because he was unable to examine any specimens of the species. Cooke (1959) subsequently placed *L. johnsoni* in *Weisbordella* and we concur. Therefore, our concept of *Weisbordella* follows previous treatments in containing *W. cubae* and *W. johnsoni* from our regional faunas, further adding *W. inglisensis* n. sp. and *W. libum* n. sp. to the genus. The status of *P. mirabilis*, from Trinidad, is uncertain but in any case, this species falls outside the scope of the present work.

Durham (1954) did not publish a viable diagnosis for *Weisbordella* (or any of his new neolaganid genera) as there are no features in his descriptions that we cannot also find in other genera. He distinguished *Weisbordella* from *Neolaganum* by the lack of a hydropore groove, but well-developed hydropore grooves are clearly evident in both *W. cubae*

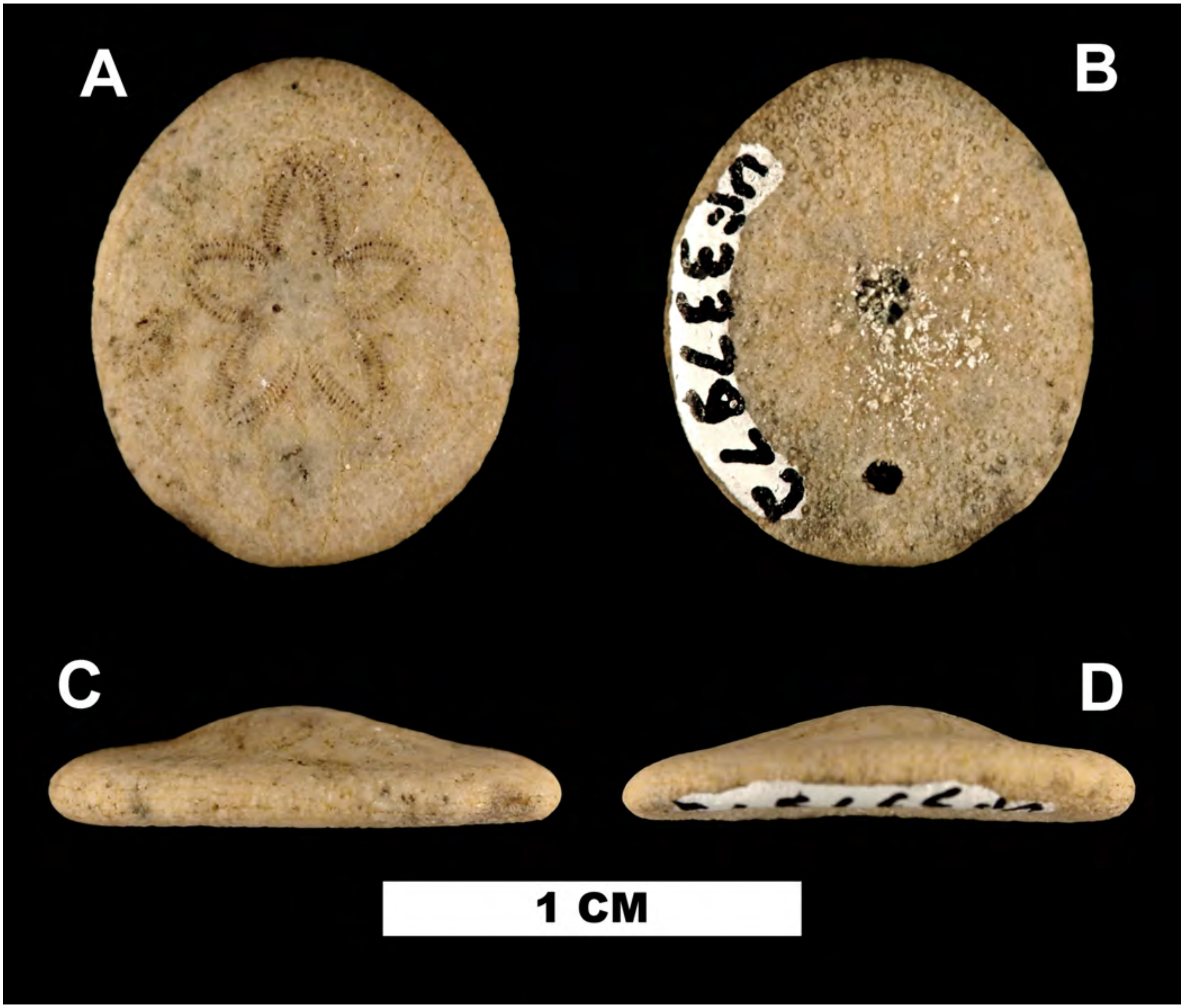


Figure 135: *Weisbordella cubae* (UF 337972), 12 mm TL, 10 mm TW, 2.5 mm TH, *Oligopygus wetherbyi* Zone of Upper Eocene Ocala Limestone, Dixie County, Florida (FM-IP DI001). A: aboral. B: oral. C: left side. D: right side.

and *W. johnsoni*.

Smith and Kroh (2011) acknowledged the presence of hydropore grooves in *Weisbordella*, but stated that the slightly sunken oral surface, short, strongly lanceolate petals, and the sparsity of tubercles surrounding the peristome in *Weisbordella* are more significant in distinguishing it from *Neolaganum*. The relatively dense concentration of tubercles around the peristome used by Smith and Kroh (2011) must be based on examination of *N. durhami*, because in *N. archerensis*, the type species of the genus, there are no more tubercles in the peristomial area than is typical of *W. cubae*, and perhaps even less than is typical for *W. johnsoni*. This feature is not considered reliable to distinguish the two genera.

Cooke (1959) stated that *Weisbordella* can be distinguished from *Neolaganum* by its concave oral surface and absence of food grooves. However, we are unaware of food grooves in any neolaganids. Although some specimens of *W. johnsoni* have almost planar oral surfaces, a concavity is usually expressed to some degree. The concavity is strongly expressed in *W. cubae*, so the concave oral surface, as variable as it is, is a reliable feature of *Weisbordella*. However, a concave oral surface is not

Figure 136: *Weisbordella cubae* (UF 337973), 10.5 mm TL, 9 mm TW, 2.5 mm TH, *Oligopygus wetherbyi* Zone of Upper Eocene Ocala Limestone, Dixie County, Florida (FM-IP DI001). A: aboral. B: oral. C: left side. D: right side.

unique to this genus among laganiforms, and in addition, we herein describe, based on other characters, *W. inglisensis* n. sp., which has a planar oral surface.

Durham (1954: 681) seemed to question the validity of his new genera *Weisbordella* and *Neolaganum* when he stated: "In the present studies the groove in the madreporite seems to be a more significant difference. If these differences should be found to be of lesser value, *Neolaganum* should have priority over *Weisbordella*."

Weisbordella is more reliably distinguished from *Neolaganum* by the fact that it has only four gonopores, and reduced number of post-basicoronal plates (Fig. 105; Tables 8, 9). The oral plate arrangement of *Weisbordella* is much more like that of *Durhamella*. However, *Weisbordella* expresses many more demiplates in the petals, has four gonopores instead of the five seen in all *Durhamella* except *D. tetrapora* n. sp., and lacks the depressed sutures at the aboral margins of *Durhamella*.

Emended Diagnosis.—Neolaganids that com-

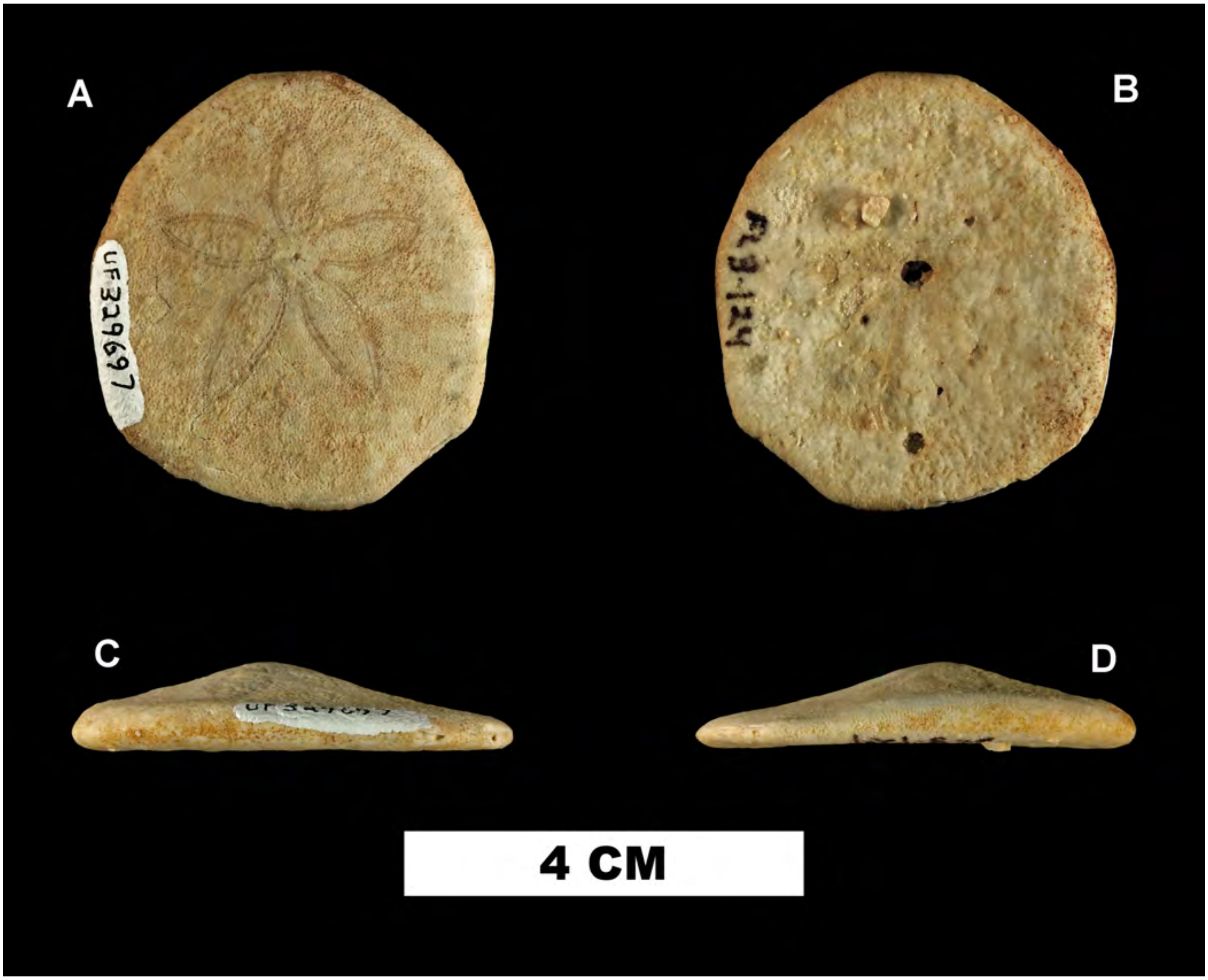


Figure 137: *Weisbordella johnsoni* (UF 329697), 44 mm TL, 41 mm TW, 8 mm TH, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA086). A: aboral. B: oral. C: left side. D: right side.

bine the presence of: four gonopores; a long, sinuous hydropore groove; usually concave oral surface with between 54 and 59 ambulacral oral plates and 41 to 46 interambulacral plates; poriferous zones slightly to much less than half the width of the poriferous zone as measured from the perradial to abradial suture at about two thirds of the length of the petal; and many demiplates in the petals.

Weisbordella cubae (Weisbord, 1934)
(Figs. 105, 106, 133-136; Tables 8, 9)

Peronella cubae Weisbord, 1934. p. 217 (53). pl. 24 (5), figs. 4-6.

Peronella cubae (Weisbord). Cooke, 1942. p. 25. pl. 2, figs. 15-21.

Peronella cubae (Weisbord). Cooke, 1945. fig. 6, no. 6.

Peronella cubae (Weisbord). Cooke, 1948b. p. 91.

Peronella cubae (Weisbord). Sánchez-Roig, 1949. p. 97.

Weisbordella cubae (Weisbord). Durham, 1954. p. 682.

Weisbordella cubae (Weisbord). Cooke, 1959. pp. 53-54. pl. 20. figs. 1-4.

Weisbordella cubae (Weisbord). Scolaro and Ross, 1963. pp. 304-307.

Weisbordella cubae (Weisbord). Toulmin, 1977. p.

Figure 138: *Weisbordella johnsoni* (UF 329698), 52.5 mm TL, 45.5 mm TW, *Oligopygus haldemani* Zone, Upper Eocene upper Ocala Limestone, Jackson County, Florida (FM-IP JA031). A: aboral. B: oral. C: left side. D: right side.

347. pl. 72, fig. 3-4.

Weisbordella cubae (Weisbord). Osborn et al., 2016. tbl. 2.

Occurrence.—*Weisbordella cubae* occurs throughout the OLS, but it is most abundant in the upper part of the unit just below the *Wythella eldridgei* Zone, and the underlying *Oligopygus wetherbyi* Zone. This species is also documented in the Eocene of Georgia (Cooke, 1942). The type locality of *W. cubae* is in Cuba (Weisbord, 1934).

Discussion.—This is the common "sand dollar" of most exposures of the *Oligopygus wetherbyi* Zone of the upper OLS in peninsular Florida. In northern Florida, especially Jackson County, *W. johnsoni* replaces *W. cubae* as the abundant neolaganid in the OLS.

Weisbordella cubae has shorter, broader, and less lanceolate petals than *W. johnsoni*. Its test is also smaller and more ovate, whereas *W. johnsoni* tends towards a more subpentagonal outline, this being more pronounced in larger specimens. The concave oral surface readily differentiates *W. cubae* from *W. inglisensis* n. sp., as well as any species of *Neolaganum* or *Durhamella* with which it may be found.

Although Fischer (1951: table 1) had *W. cubae* in his species list for the Inglis Formation (= lower OLS; *Oligopygus phelani* Zone), it is exceptionally rare in the lowermost OLS.

Emended Diagnosis.—*Weisbordella* with: a deeply concave oral surface; primary plates lacking

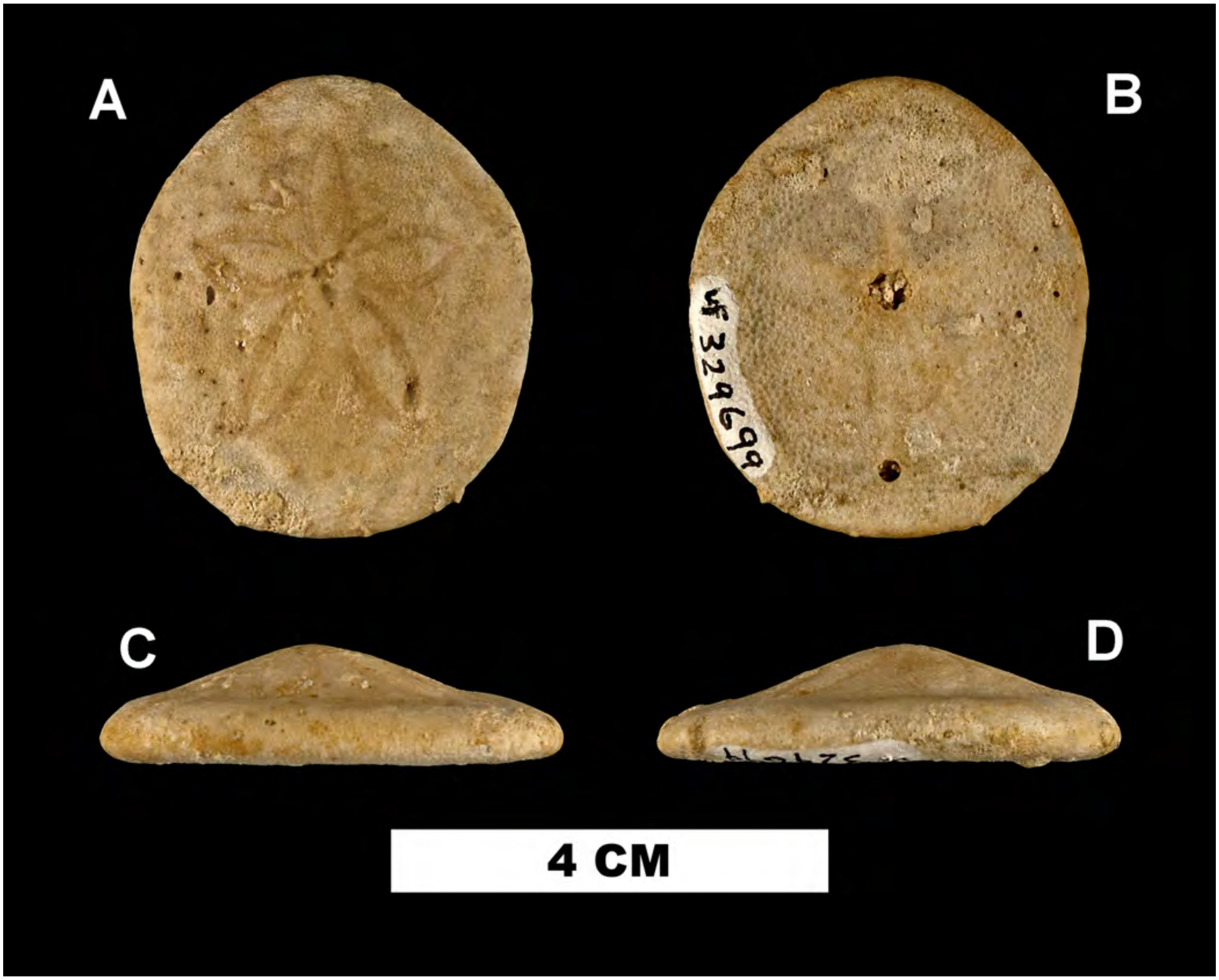


Figure 139: *Weisbordella johnsoni* (UF 329699), 41 mm TL, 35 mm TW, *Oligopygus haldemani* Zone, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA031). A: aboral. B: oral. C: left side. D: right side.

in the petals.

Weisbordella johnsoni (Twitchell in Clark and Twitchell, 1915)
(Figs. 105, 106, 137-139; Tables 8, 9)

Laganum crustuloides (Morton). Clark and Twitchell, 1915. p. 122. figs. 5a-d, 6a-d.
Laganum johnsoni Twitchell, in Clark and Twitchell, 1915. p. 162. pl. 75, figs. 2a-d.
Echinodiscus crustuloides (Morton). Lambert and Thiéry, 1925. p. 581.
Echinodiscus johnsoni (Twitchell). Lambert and Thiéry, 1925. p. 581.
Laganum johnsoni (Twitchell). Cooke, 1926. pl. 96, fig. 2.
Peronella crustuloides (Morton). Cooke, 1942. p. 24.
Weisbordella johnsoni (Twitchell). Cooke, 1959. pp. 54-55. pl. 20, figs. 5-7.
Weisbordella johnsoni (Twitchell). Kier, 1970. txt. fig. 1G.
Weisbordella johnsoni (Twitchell). Toulmin, 1977. p. 347. pl. 71, figs. 7-8.
Weisbordella johnsoni (Twitchell). Osborn et al., 2016. tbl. 2.

Occurrence.—*Weisbordella johnsoni* is very abundant in the OLS in Jackson County, especially in the Sills Pit (FM-IP JA086) and Brooks Quarries

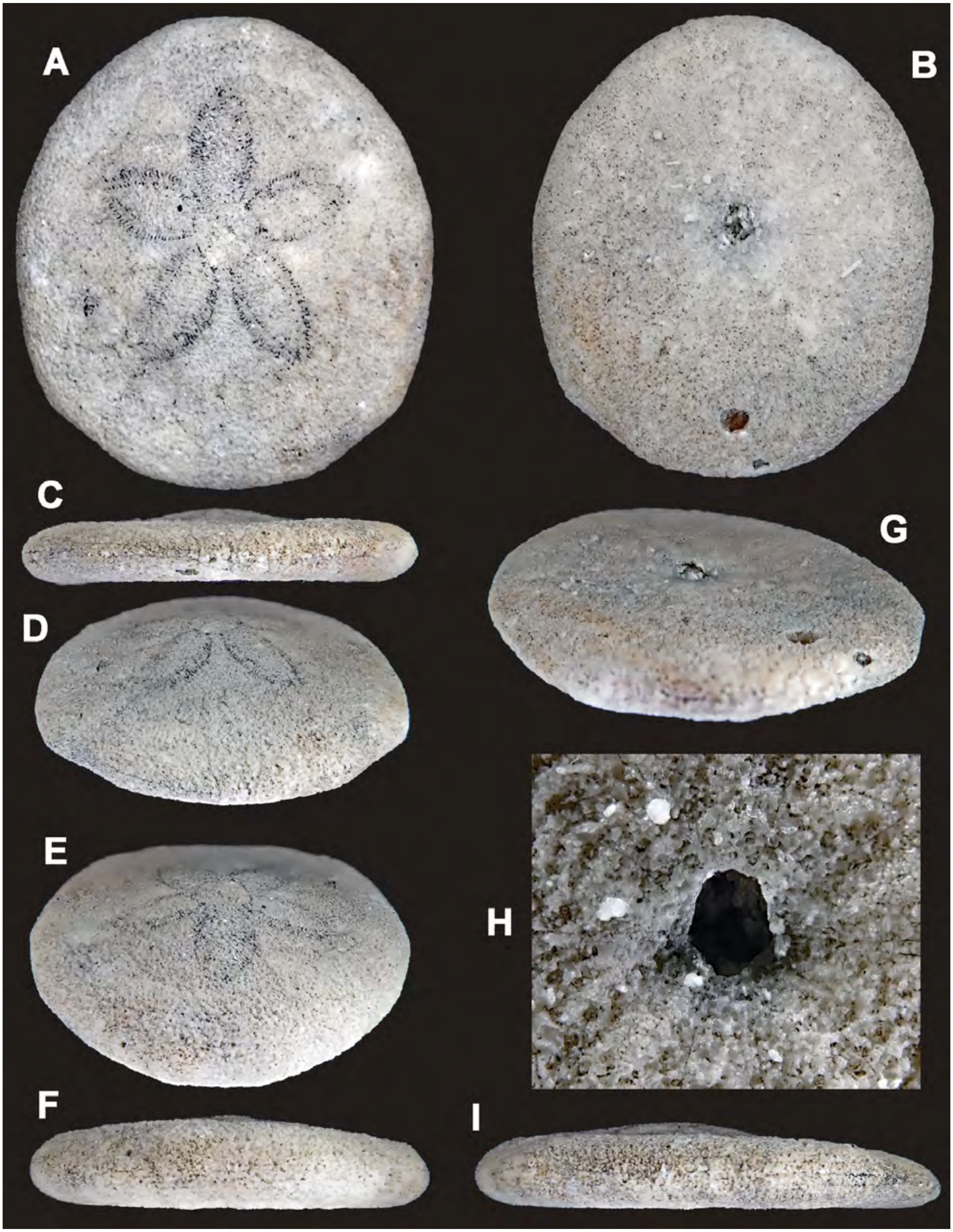


Figure 140: *Weisbordella inglisensis* n. sp., holotype (UF 342099), 21.8 mm TL, 19.1 mm TW, 4.1 mm TH, Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, mouth of Withlacoochee River, west of Yankeetown, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: posterior. D: tilted aboral viewpoint from posterior. E: tilted aboral viewpoint from anterior. F: anterior. G: oblique oral viewpoint from posterior. H: peristome. I: left side.

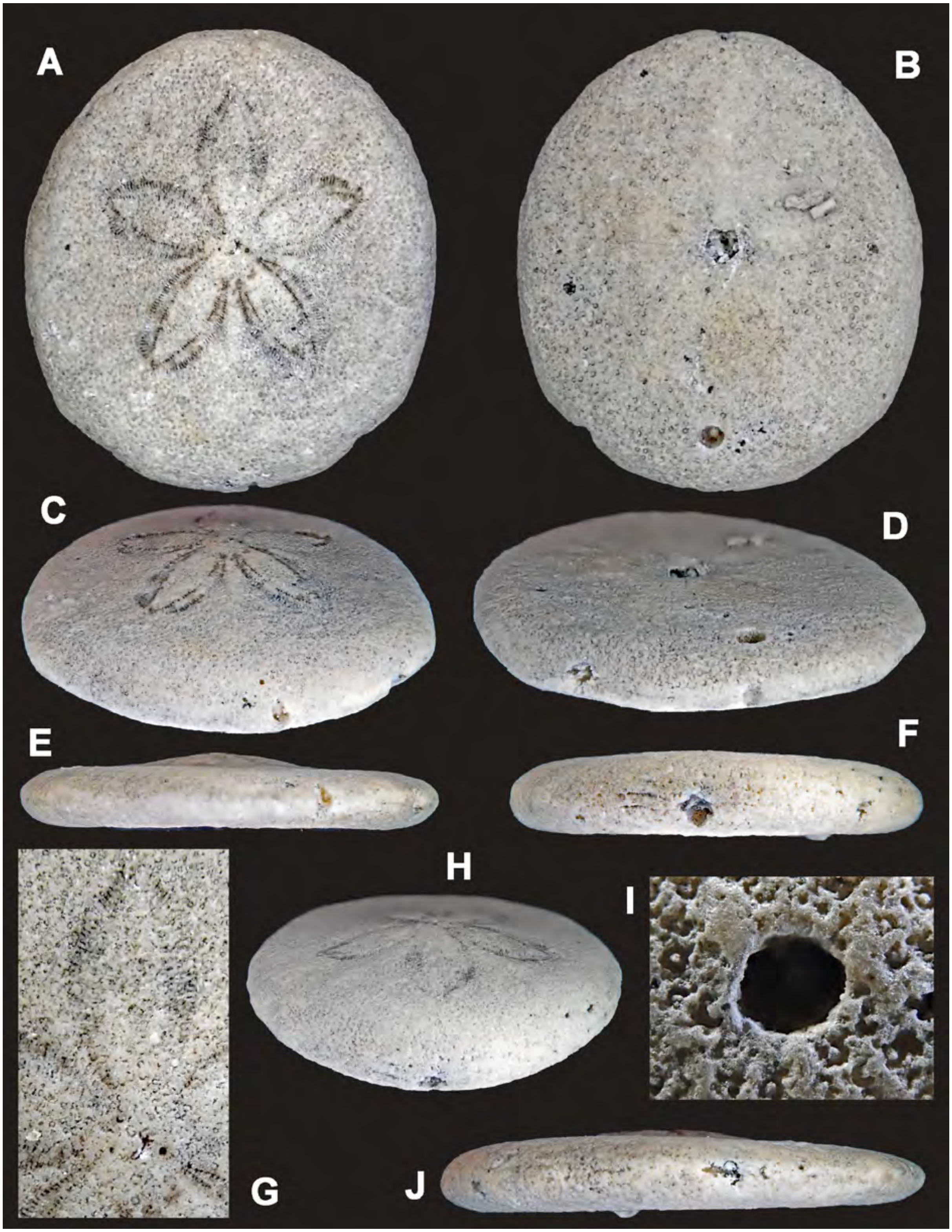


Figure 141: *Weisbordella inglisensis* n. sp., paratype (UF 342100), 23.8 mm TL, 20.9 mm TW, 4.0 mm TH, Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, mouth of Withlacoochee River, west of Yankeetown, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: oblique oral viewpoint from posterior. E: posterior. F: anterior. G: apical area and petaloid portion of ambulacrum III. H: tilted aboral viewpoint from anterior. I: peristome. J: left side.

(FM-IP JA009, (FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039), northwest of Marianna. This species also occurs in the OLS of Alabama (Cooke, 1959; Toulmin, 1977) and Georgia (Cooke, 1959). The type locality is Turks Cave, in Conecuh County, Alabama. Turks Cave is located about 3 mi. west of Brooklyn and is now commonly referred to as Sanders Cave.

Discussion.—Twitchell in Clark and Twitchell (1915), described *Laganum johnsoni* from strata considered to be Lower Oligocene at the time, but now recognized as the Upper Eocene OLS, at Turks (Sanders) Cave in Conecuh County, Alabama. Twitchell in Clark and Twitchell (1915) named the species in honor of Mr. L. C. Johnson, the collector of the holotype, and noted that his new species is very similar to *Laganum crustuloides*, which Morton (1833) described as *Scutella crustuloides* from the Eocene of South Carolina and is now recognized as *Protoscutella plana* (Conrad, 1865). Twitchell in Clark and Twitchell (1915) noted that the specimen he described as *L. johnsoni* from Alabama had a higher test, thicker margin, and significantly concave oral surface.

Cooke (1942) was puzzled by the fact that he was able to document *L. crustuloides* (with *L. johnsoni* as a junior synonym) from the Gulf coastal plain but not from South Carolina (the type area). He therefore suspected that Morton's type of *S. crustuloides* came from Alabama and not from South Carolina.

Cooke (1942) asserted that Morton's (1833) original figure did not match his description of *S. crustuloides*, which Morton described as having a thick margin. Cooke presumed that the specimen Morton illustrated is in fact a specimen of *P. plana*. Therefore, Cooke (1942) asserted that Morton described a Gulf Coast specimen as *S. crustuloides* (the type of this species has been lost), and that Morton (1833) inadvertently figured a different specimen, likely *P. plana*.

To attempt to bring some clarity to this epic of misidentifications, Cooke (1959) asserted that Morton's type material of *S. crustuloides* was lost and that the figure included by Morton (1833) did not match the description of the species. Cooke placed the Gulf Coast form recognized as *L. crustuloides* (Clark and Twitchell, 1915; Cooke, 1942) into synonymy with Twitchell's (in Clark and Twitchell, 1915) *L. johnsoni*. Therefore, the first documentation of what we now refer to as *W. johnsoni* is in Clark and Twitchell (1915) as both *L. crustuloides* and *L. johnsoni*, as recorded in the synonymy above.

When Durham (1954) erected *Weisbordella*, he did not list *W. johnsoni* as a member. He stated that he did not move *L. johnsoni* into any other genus because he was unable to examine material of this species. Cooke (1959), with more material at hand, moved the species to *Weisbordella* and clarified that *W. johnsoni* had not been documented from South Carolina.

Therefore, *W. johnsoni* appears to be restricted to the northern depositional area of the OLS, north of the Suwannee Strait, in Jackson County, Florida, and northward into Georgia and Alabama.

Weisbordella johnsoni, as stated by Cooke (1942, 1959), is highly variable, with great variation in test thickness, outline, and marginal thickness. Some specimens are thick and wafer-like with very swollen margins and a depressed area just inward from the margin. Others are thinner and have a much less swollen margin, with many specimens having intermediate characteristics within the same population. This variation has not helped with clarification of the concept of the species.

Fischer (1951: 57) documented *P. crustuloides* (= *W. johnsoni*) in the lower OLS near Inglis, Florida. As we discussed in the remarks for *W. inglisensis* n. sp., these specimens (UF 317144) are inseparable from *W. inglisensis* n. sp., and we therefore do not recognize *W. johnsoni* as occurring below the *Oligopygus haldemani* Zone of the OLS in the region.

The concave oral surface readily differentiates *W. johnsoni* from any of the species that occur in the lower OLS. However, specimens of *W. johnsoni* from the type area near Brooklyn, Conecuh County, Alabama demonstrate some variation in oral surface concavity, with rare specimens having a nearly flat oral surface. Nevertheless, the typical concave oral surface is a dominant trait in this species.

Weisbordella johnsoni has proportionately longer and more lanceolate petals than *W. cubae*. *Weisbordella cubae* is also smaller and more ovate, whereas *W. johnsoni* tends towards a more subpentagonal outline, especially the posterior portion of the test. This trait is more pronounced in larger specimens. We figure specimens of varying sizes to illustrate this variation (Figs. 137-139). The largest of these (UF 329698) is 52.7 mm in length and 45.4 mm wide.

Emended Diagnosis.—*Weisbordella* with a combination of: proportionately longer, more lanceolate petals than its congeners; a predominance of demiplates in the petals with only rare primary plates; highly variable degree of concavity on the oral surface.

Weisbordella inglisensis n. sp.

(Figs. 105, 106, 140-146; Tables 8, 9)

not *Peronella crustuloides* (Morton). Fischer, 1951. p. 57, tbl.1.

Diagnosis.—*Weisbordella* with a combination of: a planar oral surface; petals with an almost regular pattern of a demiplate for every primary plate.

Description.— Description based on holotype (UF 342099) and eight paratypes (UF 342092, UF 342100-342105, and CASG 103249). Moderately sized neolaganid, largest specimen (UF342100) 23.8 mm TL, 20.9 mm TW, 4.0 mm TH; holotype: 21.8 mm TL, 19.1 mm TW, 4.1 mm TH; small specimens (less than 10 mm TL) nearly circular outline, subovate above 12 mm TL, TW on average 88.5% TL; posterior margin usually truncated at ambulacrum I and V, giving outline subpentagonal aspect; margin at anterior ambulacra less frequently slightly truncated. Test low, largely flattened, apical area slightly raised, highest point anterior of center; TH on average 18.9% TL, slightly wedge-shaped profile, lowest posteriorly; posterior ambitus on average 57.8% height of anterior ambitus; upper surface often very slightly depressed inside margin at end of petals.

Apical area slightly anterior; center of apical system on average 54.1% TL from posterior margin; four gonopores, hydropores in sinuate groove. Petals flush, lanceolate, nearly closed distally, broad; width of widest point of petal I on average 53.4% length of petal; petal II: 57.1%, petal III: 53.4%, petal IV: 58.6%, petal V: 53.7%. Petals extend more than two-thirds of distance from apical system to ambitus; petal III longest, petal II and IV shortest: petal I on average 27.9% TL, petal II: 24% TL, petal III: 26.4% TL, petal IV: 23.7% TL, petal V: 27.3% TL; pore pairs conjugate, outer pore slightly elongate. Petals with one demiplate for each primary plate (Fig. 105).

Oral surface nearly planar. Periproct on average 11.4% TL from posterior margin, first in contact with plates 5a2 and 5b2 (Fig. 105); slightly ovate, wider than long: length on average 83.6% width. Basicoronal plates form subpentagonal outline, with single plate in each interambulacrum, paired plates in each ambulacrum, ambulacral plates about one-half as wide as adjacent interambulacral plates; first pair of postbasicoronal interambulacral plates elongate, usually three shorter plates between them and ambitus. Total of approximately 54 ambulacral and 41 interambulacral plates on oral surface in adult specimens. Peristome subpentagonal to nearly round, nearly central; posterior edge of peristome on average 49.1% TL from posterior margin of test; peristome diameter on average 7.8% TL.

Zoobank Nomenclatural Act.—40BCA279-F8B9-426E-A1F7-3B028C77BE6D

Discussion.—The *Oligopygus phelani* Zone of the lower OLS is rich in neolaganids, with most well-weathered exposures of the limestone portion of the strata formerly known as the Inglis Formation containing *D. ocalana*. *Durhamella ocalana* has unmistakable depressions along the sutures in the area just proximal to margin on the aboral surface. *Neolaganum durhami*, which also occurs in the lower OLS, is distinguished primarily by its much great number of oral ambulacral and interambulacral plates and the fact that it has five gonopores, not four as in all species of *Weisbordella* (including *W. inglisensis* n. sp.). Members of *Neolaganum* also tend to have a branched hydropore groove, whereas *W. inglisensis* n. sp. usually has an unbranched, sinuous groove.

While identification of these two species is relatively simple and straightforward, additional small neolaganids that have previously been misidentified also occur in this horizon. In addition to *D. ocalana* and *N. durhami*, Fischer (1951) documented *Peronella dalli* (= *N. dalli*) from the Inglis Formation (= lower OLS). He admitted that this species had not been found in outcrops of the unit, and we concur. Fischer (1951: table 1) also listed *Peronella cubae* (= *W. cubae*) in the unit, but it is very rare in the lowermost OLS. Fischer (1951) also documented *Peronella crustuloides* (= *W. johnsoni*) in the Inglis Formation. This assertion was based on two poorly preserved specimens measuring 12 mm and 13 mm in length. Fischer did not provide catalog numbers for his specimens of *P. crustuloides* (= *W. johnsoni*). However, we were able to locate them in the UF collections (UF 317144). These two specimens were collected 1 mi. east of the Withlacoochee River bridge at Inglis, south of the river (FM-IP CI053), and are poorly preserved but indistinguishable from *W. inglisensis* n. sp. We are not aware of any occurrence of *W. johnsoni* in the *Oligopygus phelani* Zone (that portion of the lowermost OLS previously referred to as the Inglis Formation). We therefore do not recognize *W. johnsoni* as occurring in Florida below the *Oligopygus haldemani* Zone of the OLS. Fischer's misidentification of the specimens is understandable because, as discussed below, the petals of *W. johnsoni* are very similar to those of *W. inglisensis* n. sp.

The specimens we describe as *W. inglisensis* n. sp. were collected from the limestone portion of the *Oligopygus phelani* Zone of the lower OLS (strata previously included in the Inglis Formation) along the Withlacoochee River at its mouth west of Yankeetown, Levy County (FM-IP LV024), where it occurs with *D. ocalana*, *D. floridana, N. durhami*, *P. floridana*, *E. mooreanus*, *O. phelani*, and other, rarer species. *Weisbordella inglisensis* n. sp. occurs more rarely in the same horizon along the banks of the Cross Florida Barge Canal south of Inglis (e.g., FM-IP CI001) in Citrus County, at the type locality of the Inglis Formation behind the powerplant on the Withlacoochee River east of Inglis, Levy County, and in Briar Cave, Marion County (FM-IP MR018).

Weisbordella inglisensis n. sp. shares characteristics of both *Neolaganum* and *Weisbordella*, further discussed in the remarks on the genus, above. However, the oral plate architecture of *W. inglisensis* n. sp. (Fig. 105; Table 9) clearly shows a significantly reduced number of plates that is not typical for *Neolaganum*. In addition, differs in having four gonopores and a sinuous, rather than branched hydropore groove, and more demiplates in the petal plate pattern. Thus, even though *W. inglisensis* n. sp. lacks the concave oral surface typical of the type species of *Weisbordella*, *W. cubae*, it is clearly more closely related to other taxa in *Weisbordella* than to any member of *Neolaganum*.

Weisbordella inglisensis n. sp. is unlike any of the known *Weisbordella*. In the regional fauna, *W. inglisensis* n. sp. is very similar to *W. johnsoni* from an aboral viewpoint alone (similar petaloid and apical structure). However, the consistently planar oral surface of *W. inglisensis* n. sp. distinguishes it from *W. johnsoni*, as does the more frequent occurrence of demiplates in the petals of the latter. The petals of *W. cubae* have even more demiplates, so along with its very concave oral surface, it is easily distinguished from *W. inglisensis* n. sp.

Etymology.—Named after the community of Inglis, in Levy County, Florida, near the type locality of *W. inglisensis* n. sp.

Material and Occurrence.—Holotype (UF 342099) and paratypes (UF 342100, UF 342101, UF 342102, UF 342103, UF 342104, UF 342105, CASG 103249) from the lower OLS, *Oligopygus phelani* Zone, at the mouth of the Withlacoochee River at the Gulf of Mexico (FM-IP LV024), east of Yankeetown, Levy County, Florida. Also, a paratype UF 342092 from the lower OLS, *Oligopygus phelani* Zone, Cross Florida Barge Canal, south of Inglis, west of Hwy 19/98, Citrus County, Florida. This species has also been found in the *Oligopygus phelani* Zone of the lower OLS in Briar Cave, Marion County (FM-IP MR018).

Weisbordella libum n. sp.
(Figs. 106, 147; Table 8)

not *Clypeaster oxybaphon* (Jackson). Oyen, 2001. pp. 97-98. figs. 3-13 a, b.

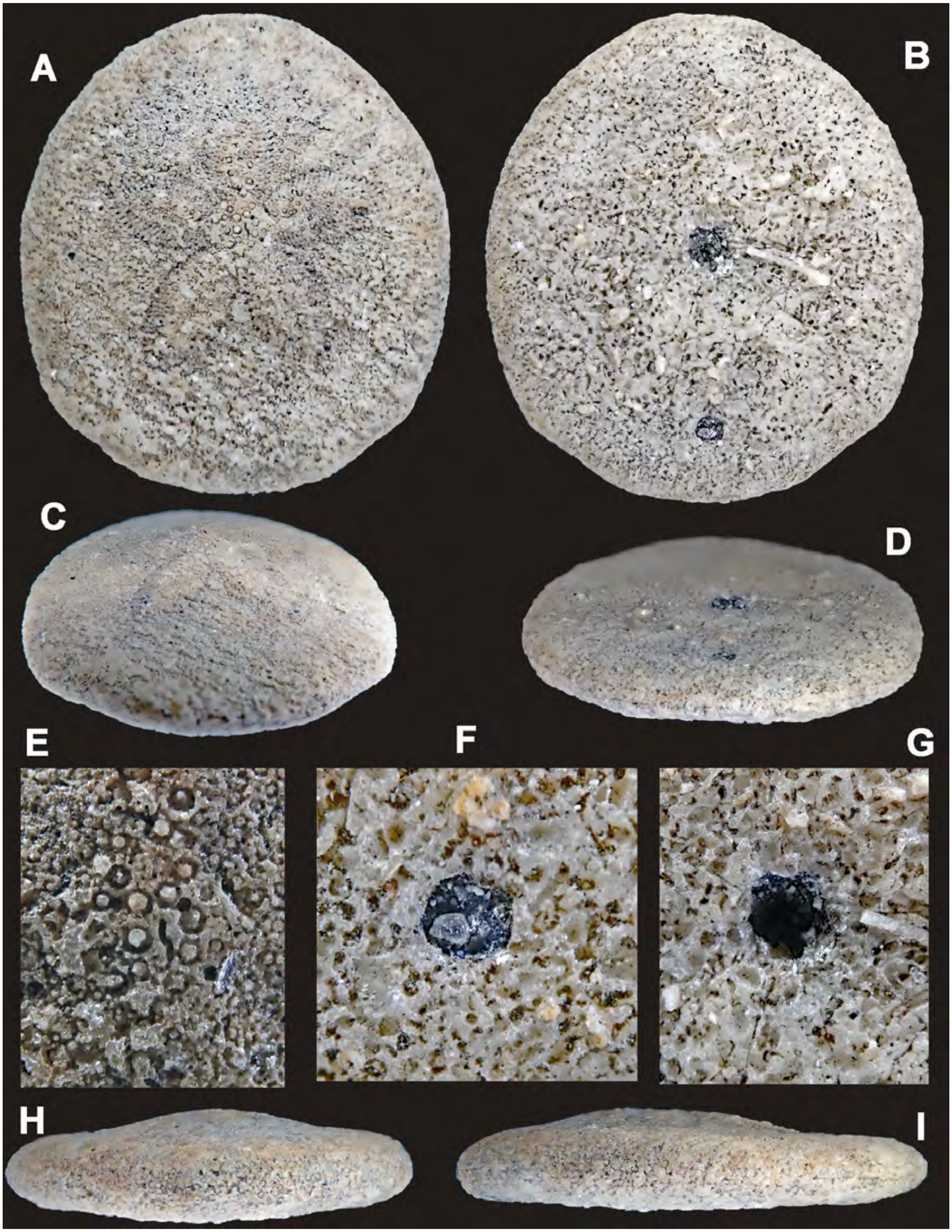


Figure 142: *Weisbordella inglisensis* n. sp., paratype (UF 342103), 12.7 mm TL, 11.4 mm TW, 2.5 mm TH, Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, mouth of Withlacoochee River, west of Yankeetown, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: tilted aboral viewpoint from posterior. D: tilted oral viewpoint from posterior. E: apical area. F: periproct. G: peristome. H: anterior. I: left side.

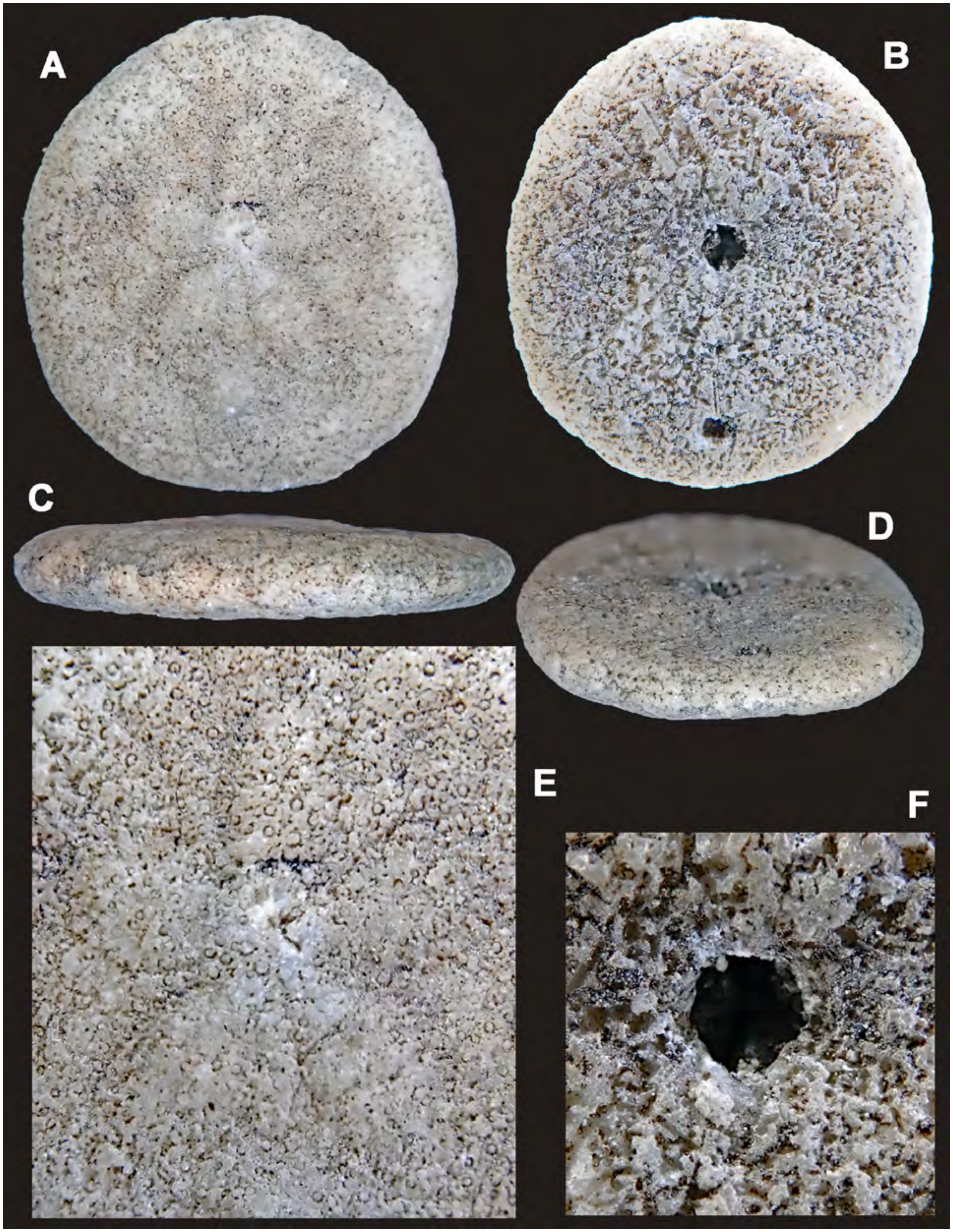


Figure 143: *Weisbordella inglisensis* n. sp., paratype (UF 342104), 11.2 mm TL, 10.2 mm TW, 2.1 mm TH, Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, mouth of Withlacoochee River, west of Yankeetown, Levy County, Florida (FM-IP LV024). A: aboral. B: oral. C: left side. D: tilted oral viewpoint from posterior. E: petaloid area. F: periproct.

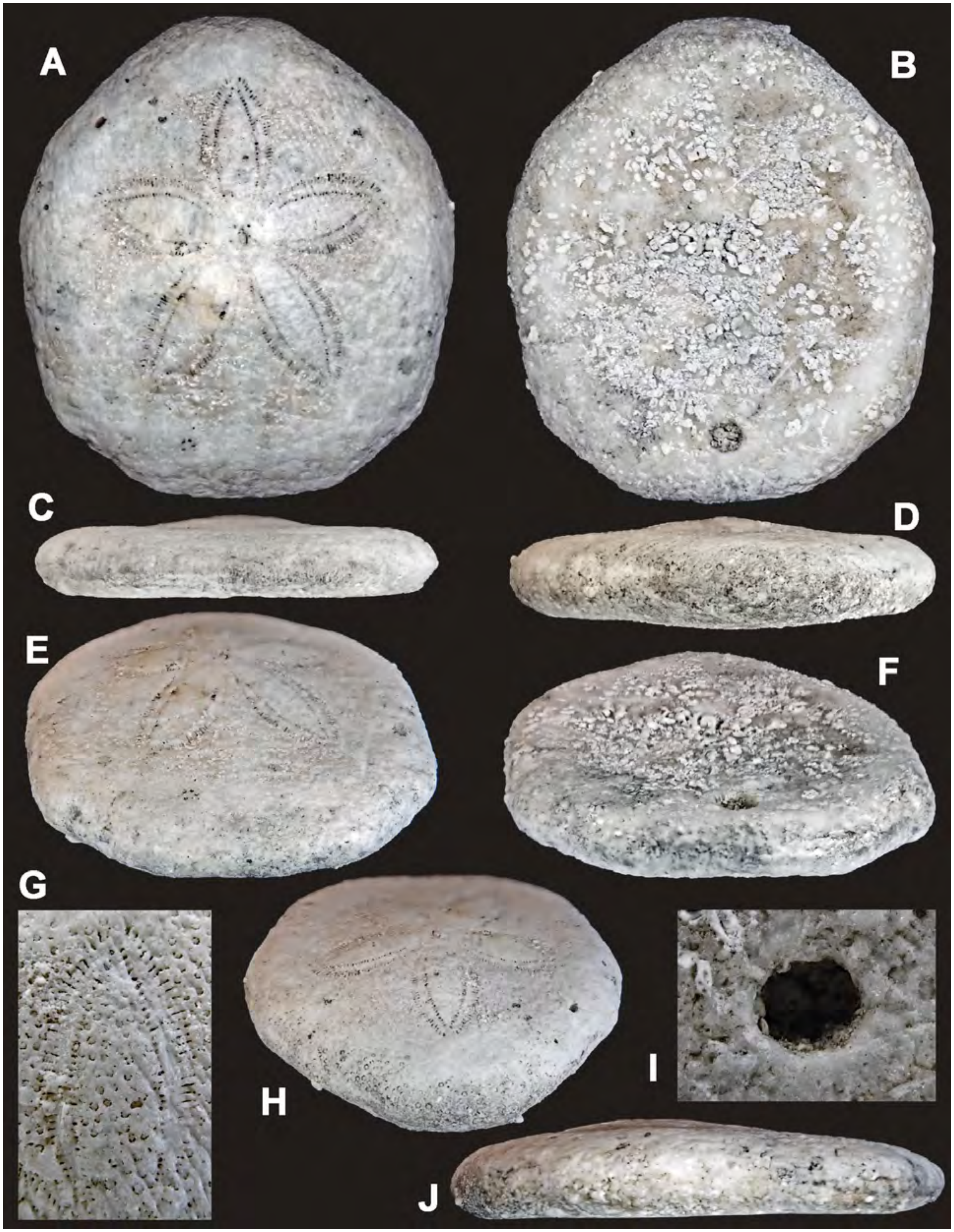


Figure 144: *Weisbordella inglisensis* n. sp., paratype (UF 342092), 24.8 mm TL, 22.2 mm TW, 4.9 mm TH, Upper Eocene, *Oligopygus phelani* Zone of lower Ocala Limestone, Cross Florida Barge Canal south of Inglis, west of Hwy. 19/98, Citrus County, Florida (FM-IP CI001). A: aboral. B: oral. C: posterior. D: anterior. E: tilted aboral viewpoint from posterior. F: tilted oral viewpoint from posterior. G: petaloid portion of ambulacrum III. H: tilted aboral viewpoint from anterior. I: periproct. J: left side.

Figure 145: *Weisbordella inglisensis* n. sp., (UF 343023), 18.1 mm TL, 16.9 mm TW, 3.55 mm TH, *Oligopygus phelani* Zone, Upper Eocene, lower Ocala Limestone, Citrus County, Florida (FM-IP CI012). A: aboral. B: oral. C: left side. D: right side.

Diagnosis.—Very large *Weisbordella* with very thick test, TH estimated to be 20-25% TL; highly complex system of hydropore grooves; petals with very long, slit-like outer pores and two to three demiplates alternating with a single primary.

Description.—Description based on the holotype (UF 4926) and only known specimen of *W. libum* n. sp. Specimen is incomplete (missing posterior portion of test); large, 64.4 mm TL (incomplete) and 69.2 mm TW (estimated dimensions of complete test 85 mm long and 70 mm wide: Fig. 147), estimated ratio of TW to TL 82%; thick, 17.8 mm TH (only measurement that is complete), between 20-25% TL. Test high at the margin and not aborally depressed just proximal to that. Aboral surface with even dispersal of small primary tubercles and fewer, scattered larger tubercles; oral surface evenly covered in tubercles of approximately equal size. Posterior portion of test missing, but test likely elongate; ovate to subpentagonal (Fig. 147).

Anterior edge of apical area 37 mm from anterior margin; four gonopores, average .25 mm in diameter; anterior pair 2.3 mm apart, posterior pair 4 mm apart: nearly twice as far apart as anterior pair. highly complex system of hydropore grooves (Fig. 147).

Petals flush, lanceolate, nearly closed distally, broad; width of widest point of petal II 55% length of petal; petal III: 48%, petal IV: 54. Petals extend more than two-thirds of distance from apical system to ambitus; petal III longest (22.7 mm), petal II (21.8 mm) and IV (21.1 mm) shortest. Poriferous zones wide, but still less than half as wide as distance from perradial suture to abradial suture, pore pairs conjugate, outer pore elongate, slit-like. Petals with two to three demiplates alternating with a single

Figure 146: *Weisbordella inglisensis* n. sp., (UF 344347), 18.5 mm TL, 16.5 mm TW, 4.0 mm TH, *Oligopygus phelani* Zone, Upper Eocene lower portion of Ocala Limestone, Briar Cave, Marion County, Florida (FM-IP MR018). A: aboral. B: oral. C: left side. D: right side.

primary (Fig. 105).

Oral surface with slight concavity that starts from just proximal to ambitus; peristome subpentagonal; width equals 89% peristome height; peristome 39.5 mm from anterior margin. Periproct not preserved. Food grooves absent. Basicoronal plates form subpentagonal outline, with a single plate in each interambulacrum, paired plates in each ambulacrum, ambulacral plates about one-half as wide as adjacent interambulacral plates; first pair of post-basicoronal interambulacral plates elongate, extending to second or third ambulacra post-basicoronals (Fig. 147). Peristome subpentagonal to nearly round, nearly central; posterior edge of peristome on average 49.1% TL from posterior margin of test; peristome diameter on average 7.8% TL.

Internal structure partially visible along broken edge of test; massive peripheral buttress system, extremely thick test, extremely high lantern preserved and in living position within test, spanning the body cavity from aboral to oral interior surfaces of the test, auricle in interambulacrum 5 massive.

Zoobank Nomenclatural Act.—9082B149-35D3-4ED1-890B-8C0CE6D4E6E9

Discussion.—This specimen consists of a large, incomplete test (UF 4926) collected 50 years ago in the upper portion of the Upper Eocene, OLS in the now inactive Mill Creek Quarry (FM-IP LF002), west of Dowling Park in Lafayette County. The precise placement of the specimen within the OLS is not possible, as these data are not indicated on the labels with the specimen, but this quarry exposed both the *Oligopygus wetherbyi* Zone and overlying *Wythella eldridgei* Zone of the upper OLS.

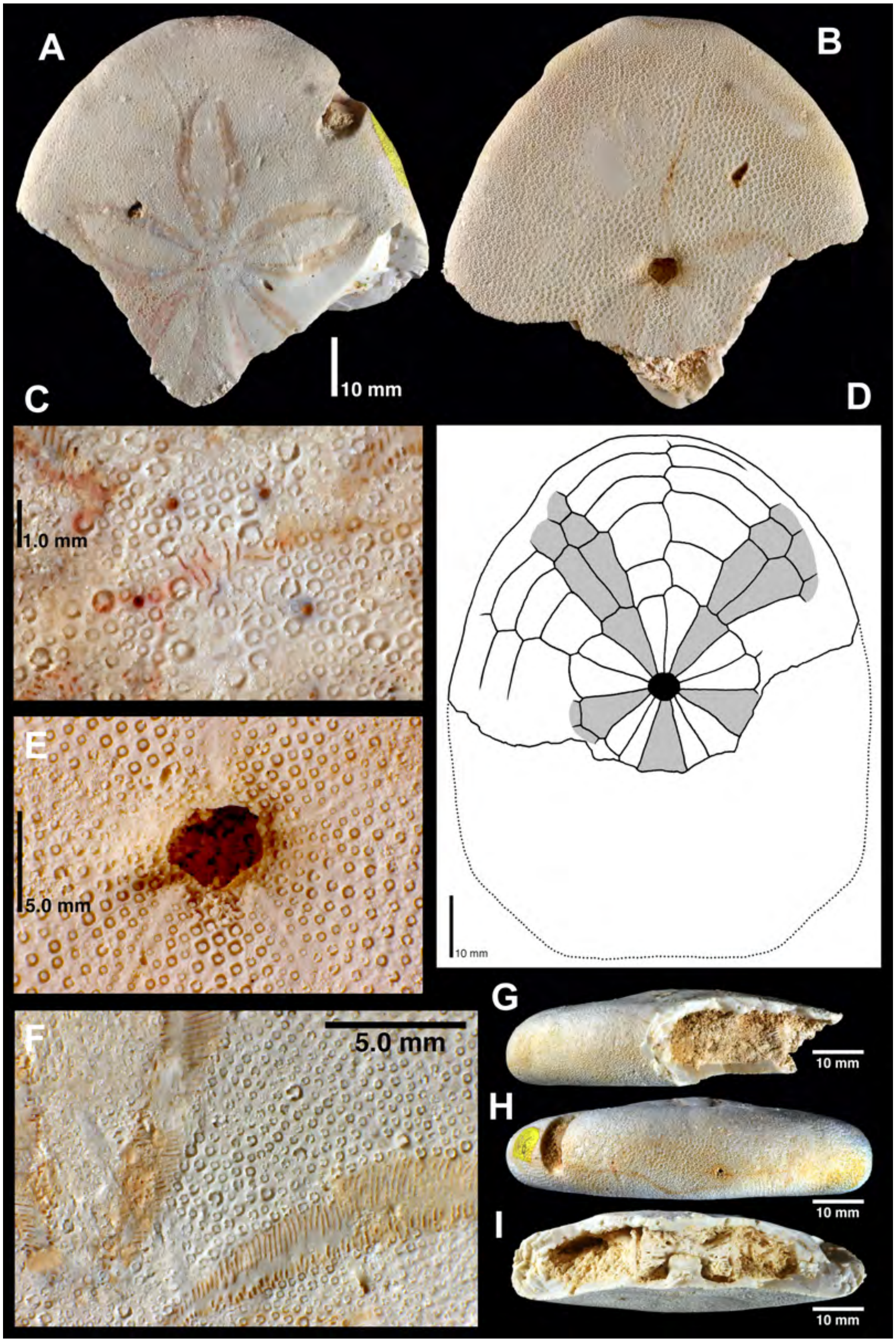


Figure 147: *Weisbordella libum* n. sp., holotype (UF 4926), 64.4 mm TL and 69.2 mm TW (not complete), 17.8 mm TH, Upper Eocene, upper portion of Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: detail of apical system. D: plate detail of oral surface; ambulacrum III towards the top, the interambulacral plates are shaded, and peristome and periproct are solid black. Reconstructed dotted outline is an extrapolation based on the dimensions of other neolaganids. E: detail of peristome. F: detail of aboral interambulacrum 2 showing presence of large and small primary tubercles, as well as portions of the poriferous zones in petals II and III. G: left side. H: anterior (directly ambital view of ambulacrum III). I: slightly upward-tilted posterior view showing the massive peripheral buttress system, extremely thick test, posterior view of the Aristotle's lantern in place, and lantern support (auricle) in interambulacrum 5.

Field notes for this site made by Muriel Hunter during the time the specimen was collected indicate a significant presence of the uppermost OLS (*Wythella eldridgei* Zone) and it is likely the specimen originated from this horizon. However, this taxon is not documented elsewhere, and this cannot be confirmed until additional specimens are found.

The specimen was first recorded by Oyen (2001) as *Clypeaster oxybaphon*. However, the presence of four gonopores, rather than the five typical for *Clypeaster*, and other characters discussed below readily distinguish the specimen from any member of the Clypeasteroida *sensu lato*. As shown in Fig. 147, the broken test shows the interior of the test, revealing a massive peripheral buttress system and a posterior view of an extremely robust Aristotle's lantern in place, with a large, robust auricle visible in interambulacrum 5. This further indicates that this is not a clypeasteroid, but a scutelloid, as clypeasterines do not have interambulacral auricles.

The large test (estimated to have been 85 mm TL and 70 mm TW) with an exceptionally thick test (17.8 mm TH) and highly complex system of hydropore grooves is unique among neolaganids from Florida.

We compared the specimen with neolaganids from elsewhere in the eastern Americas and Caribbean region to ensure it was not synonymous with an already described species, and to support the genus designation. *Cubanaster torrei* (Lambert in Sánchez Roig, 1926) the type species of *Cubanaster*, and *C. acunai* (Lambert in Sánchez Roig, 1926), the two earliest described *Cubanaster* species, differ from *W. libum* n. sp. in having a much lower test, especially at the margin, and depressed just proximal to that, a greater number of plates on the oral surface (even though *Weisbordella libum* n. sp. is much larger), and much narrower interporiferous zones. In addition, *C. torrei* has a more equilateral (i.e., almost circular) test, whereas *C. acunai* appears to have a more elongate test than *Weisbordella libum* n. sp.

Laganum cubensis Lambert, 1925 has been confused in past literature. Lambert (1925: 582) lists the species under the name *Jacksonaster*, stating that it was listed by Egozcue (in Cotteau, 1897: 26, pl. 4) under the name "*Laganum elongatum*". Since that time, it has appeared in works by Sánchez Roig (1924, 1926, 1949) using "*Laganum-elongatum*" in synonymies (which is odd as Egozcue did not use the hyphen in his version of the name), but always unfigured. In Sánchez Roig (1924), the taxon was placed in *Clypeaster* as *C. elongatum*, but subsequently moved to *Jacksonaster* as a new species, *J. cubensis*, in Sánchez Roig (1926), but attributed to Lambert, 1925. It seems that Lambert's coining was a *nomen nudum*, and that Sánchez Roig (1926) should be the author of record. In his entry on *Clypeaster oxybaphon*, Cooke (1942: 13) used the name *Laganum elongatum* (Egozcue in Cotteau, 1897), citing the illustrations in Egozcue's work while stating, "It [meaning *C. oxybaphon*] bears considerable resemblance to *Laganum elongatum* Egozcue (1897, pl. 4), which appears to be a *Clypeaster*." Apparently, Cooke missed Sánchez Roig's (1924) earlier referral to that genus but seemed to be advocating a return to the name "*elongatum*". Jackson (1922: 47) indicated that he had never seen an example of *L. elongatum*, and reiterated Egozcue's description (in Cotteau, 1897). The description, dimensions, and appearance of the specimen in the figures provided by Egozcue (1897: pl. 4) for *L. elongatum* and cited by Lambert (1925: 582) for his *Jacksonaster cubensis*, back up the supposition that the echinoid is most likely a *Clypeaster*.

Laganum elongatum has a deep infundibulum. Although *W. libum* n. sp. has a highly localized depression surrounding the peristome, this is completely unlike what is depicted for *L. elongatum*. The petals, though like those of *W. libum* n. sp., are also consistent in shape with those of other *Clypeaster*. However poorly known, and whatever its correct name might be, "*L. elongatum/cubensis*" does not seem to be related to *W. libum* n. sp.

Jacksonaster depressus [*sic*], as discussed in Sánchez Roig, 1949, is large, but not so large as *W. libum* n. sp., has a distinctly inflated edge, and longer petals with parallel poriferous zones. *Jacksonaster depressus* has a stronger resemblance to *C. torrei* or *C. acunai* than to *W. libum* n. sp. It is presently uncertain what *J. depressus* represents, but it is highly unlikely to be conspecific with *Jacksonaster* *depressum* (L. Agassiz, 1841)

Jacksonaster remediensis Sánchez Roig, 1949 is very much like *Sanchezella sanchezi* except that the petals are not deeply depressed, as Sánchez Roig (1949) himself notes. It is also a small species, and is not comparable to *W. libum* n. sp., which is not only larger, but much wider relative to its TL, and with much narrower interporiferous zones.

Jacksonaster sandiegensis Sánchez Roig, 1949 is a small species relative to others described by Sánchez Roig, and although the specimen illustrated by him seems to be crushed laterally, it still appears to be elongated, much as for other species he later considered to be members of *Cubanaster*, such as *S. sanchezi*. The apical system of *J. sandiegensis* is unknown due to the weathering of the upper surface, but Sánchez Roig (1949) reports that the petals are very large, occupying almost the entire upper surface of the test. It is therefore very unlike *W. libum* n. sp.

Laganum lamberti Sánchez Roig, 1949 is very similar to *L. santanae* (see below, and not to be confused with *Cubanaster santanae* Sánchez Roig, 1952e, also see below), including in petal shape, gonopore number and test shape, and is likely simply a smaller specimen of *L. santanae* Sánchez Roig, 1949), with all the same objections to its identity with *W. libum* n. sp.

Laganum santanae Sánchez Roig, 1949 is a very large species, even larger than the specimen of *W. libum* n. sp., and is relatively thick-edged, and appears, at first glance, to be the closest to *W. libum* n. sp. of all the species considered here. The petals of this species are also remarkably similar to those of *W. libum* n. sp., being somewhat sinuous with wide poriferous zones. However, Sánchez Roig (1949) reports that *L. santanae* has 5 gonopores (presumably part of the reason that he placed it in *Laganum*). In addition, the peristome of *L. santanae* is transversely elongated, and if this is a good character for the species, then it is quite different in shape from the peristome of *W. libum* n. sp.

Cubanaster acunai gigas Sánchez Roig, 1952e is the only form described in Sánchez Roig (1952e) that rivals *W. libum* n. sp. in size, other than *L. santanae*. However, the estimated ratio of TW to TL for *W. libum* is 82%, which is considerably greater than for *C. acunai gigas*. The latter also has a conspicuously sunken aboral region just inside the ambitus (i.e., a very ”inflated” margin), and the petals are also much narrower, with a very narrow interporiferous zone.

Cubanaster camagueyensis Sánchez Roig, 1952e is, like many of the new species described in Sánchez Roig (1952e), elongate and thick edged, but much more like *Sanchezella* than *W. libum* n. sp. in having depressed, long, narrow petals and, if the illustrations can be believed, very distinct food grooves. Gonopore number is not mentioned in the description by Sánchez Roig (1952e), but a specimen of *C. camagueyensis* (UF 216680), clearly shows that there are four.

Cubanaster herrerai Sánchez Roig, 1952e has a conspicuously sunken aboral surface, and long, narrow petals with very narrow interporiferous zones quite unlike those of *W. libum* n. sp. *Cubanaster planipetalum* Sánchez Roig, 1952e seems again to be a more elongate form than *W. libum* n. sp., with short but distinct food grooves which are lacking in the latter, and a slightly depressed aboral surface showing relatively wide petals with narrow poriferous zones.

Cubanaster santanae Sánchez Roig, 1952e is like *W. libum* n. sp. in that it has 4 gonopores and a thickened edge, but it is very elongate, similar in test shape to *Sanchezella*, and has somewhat depressed petals.

Examination of oral plate arrangement (Figs. 105, 147) revealed this taxon is more closely aligned to *Weisbordella* than any other neolaganid. *Neolaganum* and *Cubanaster* have high plate numbers on the oral surface and the plate numbers of *W. libum* n. sp. are fairly low, in spite of its large size. The large, thick test with a highly complex system of hydropore grooves readily distinguishes this species from its congeners. It is hoped that additional collecting will provide more complete specimens of this species to enable a better understanding of its characters (such as true test dimensions, periproct position, and oral surface plate architecture).

Etymology.—The species is named *libum* (Latin, neuter) for its resemblance to a consecrated cake or pancake made in Roman times.

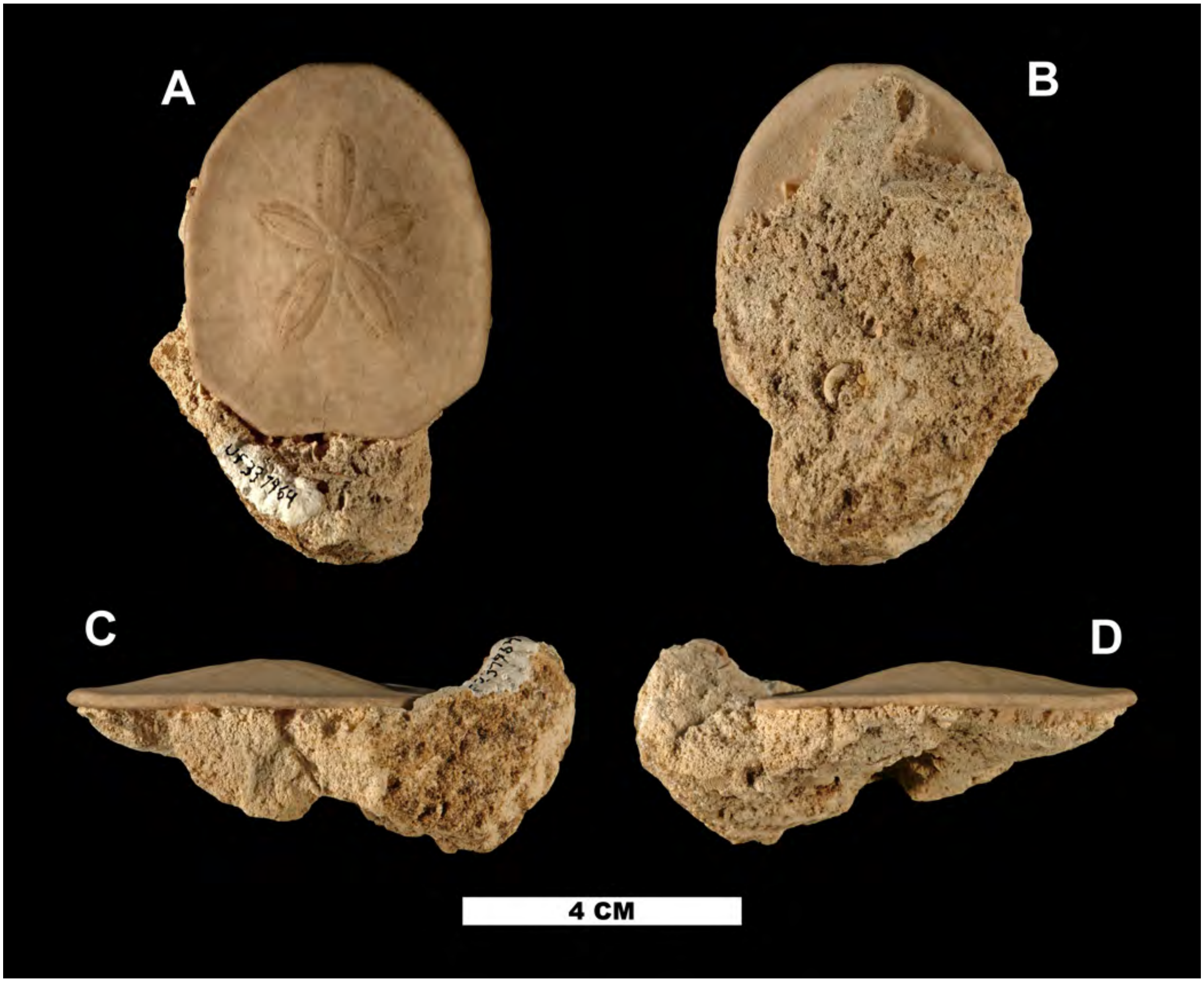


Figure 148: *Wythella eldridgei* (UF 337964), 55 mm TL, 44 mm TW, uppermost portion of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF023). A: aboral. B: oral. C: left side. D: right side.

Material and Occurrence.—This species is known only from the holotype (UF 4926) which was collected in upper portion of the Upper Eocene OLS in the Mill Creek Quarry (FM-IP LF002) west of Dowling Park, Lafayette County, Florida.

Genus ***Wythella*** Durham, 1954

When Durham (1954) described *Wythella* it contained *Wythella eldridgei* as its type and only species. Durham (1954) also designated *Rumphia elegans* Sánchez-Roig, 1949, from the Oligocene of Cuba, as the type species of *Neorumphia*. Durham (1954) distinguished *Wythella* from the very similar *Neorumphia* by noting that the former had fewer plates on the oral surface, a thinner margin, and narrower interambulacral areas at the ambitus. Smith and Kroh (2011) noted that although *Neorumphia* has somewhat wider interambulacral zones at the ambitus, the otherwise very similar plating and appearance render Durham's distinction between the two genera suspect. Smith and Kroh (2011) therefore treated *Neorumphia* as a subjective junior synonym of *Wythella*, with which we agree.

Durham did not provide a diagnosis for the genus, but it is readily distinguished from other neolaganids by its large, very thin test (*W. eldridgei* has the thinnest test relative to TL of all known

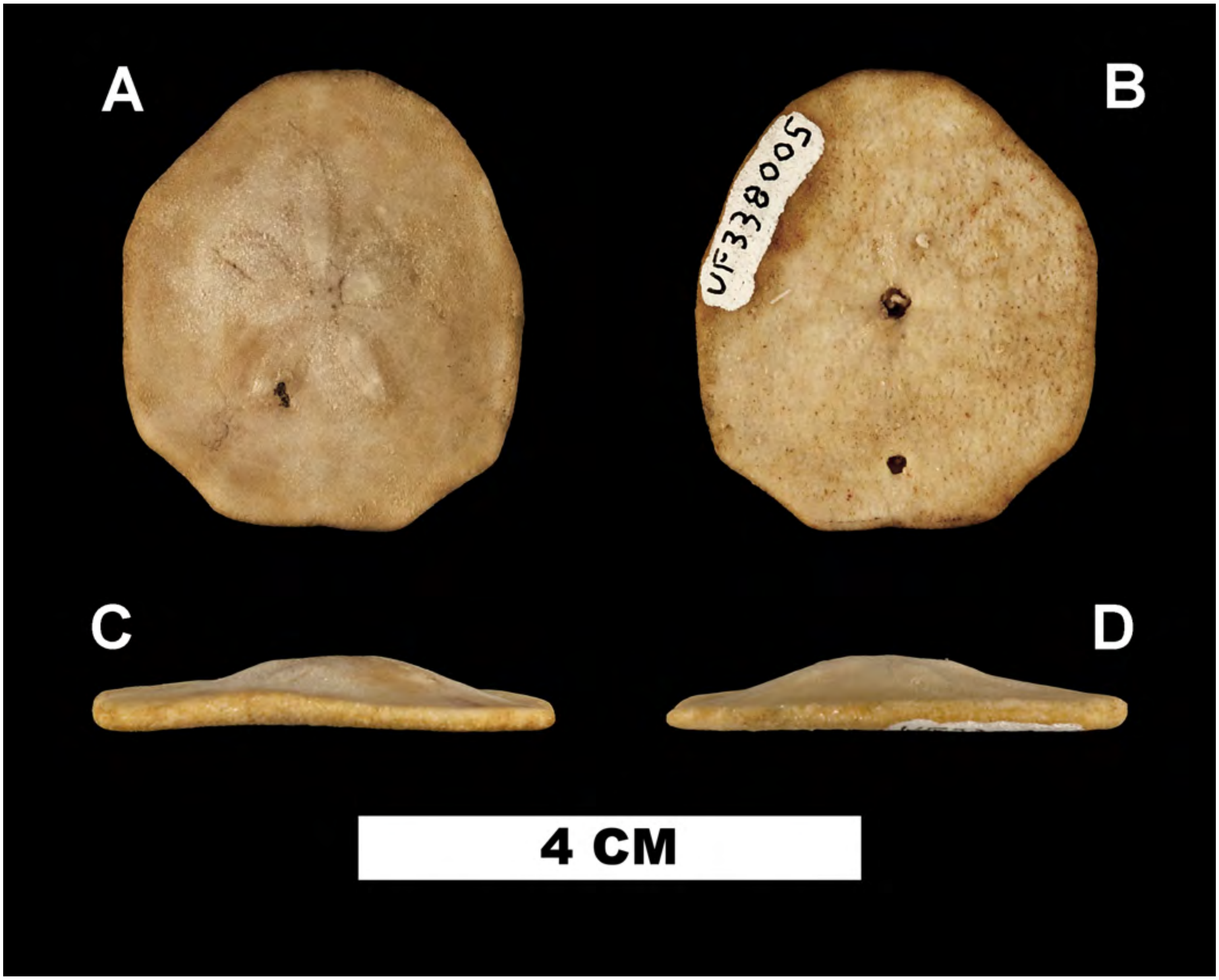


Figure 149: *Wythella eldridgei* (UF 338005), 36 mm TL, 32 mm TW, 5 mm TH, uppermost portion of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF023). A: aboral. B: oral. C: left side. D: right side.

neolaganids), and flat oral surface. In addition, analysis of oral plate architecture of *W. eldridgei* (Fig. 105) reveals that it has a greater number of plates than *Weisbordella* or *Durhamella* and is more similar to *Neolaganum* in this aspect. *Wythella* has at least one plate more in each of the anterior paired interambulacral regions than in the posterior pair. This is also like the condition found in many *Neolaganum*.

Emended Diagnosis.—Large Neolaganidae with a combination of: extremely thin test, especially near the ambitus; short, unbranched hydropore groove; long, slit-like outer pore in petal pore pairs; two or three demiplates alternating with single primary plate; poriferous zone approximately half as wide as the distance from the perradial suture to the abradial suture at a point about 2/3 the length of the petal.

Wythella eldridgei (Twitchell in Clark and Twitchell, 1915)
(Figs. 105, 106, 148, 149; Table 8)

Laganum eldridgei Twitchell in Clark and Twitchell, 1915. p. 160. pl. 74, figs. 2a-d.

Rumphia eldridgei (Twitchell). Stefanini, 1924. pp. 831, 843.

Rumphia eldridgei (Twitchell). Cooke and Mossom,

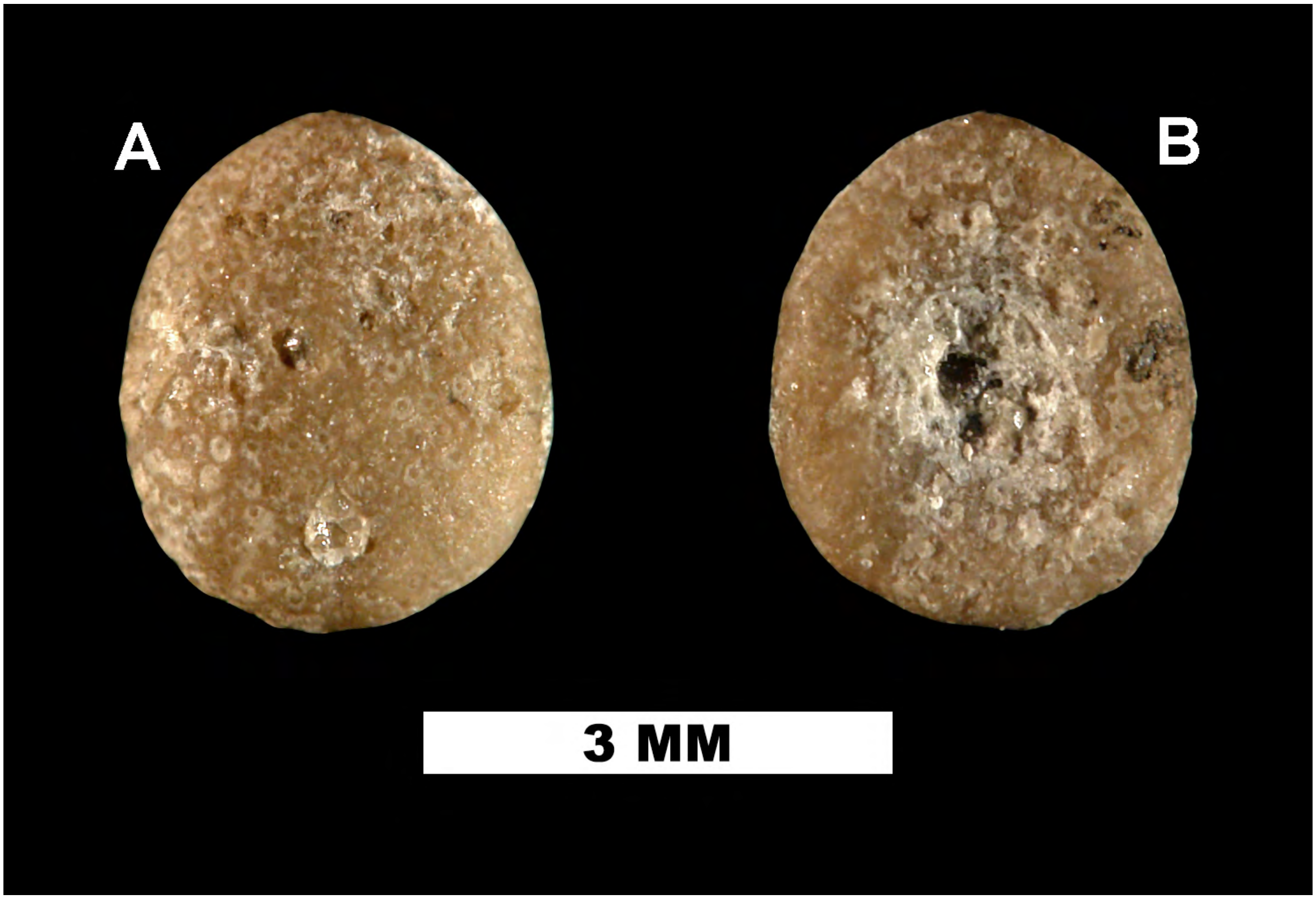


Figure 150: *Porpitella micra* (USNM 462807), Ohio Oil Co Well, 5520-5530 ft depth, Late Cretaceous Atkinson Formation (Applin and Applin, 1965), Hernando County, Florida. A: aboral. B: oral.

1929. pl. 3, fig. 7.

Rumphia eldridgei (Twitchell). Cooke, 1942. p. 27. pl. 2, fig. 14.

Rumphia eldridgei (Twitchell). Cooke, 1945. fig. 5, no. 1.

Wythella eldridgei (Twitchell). Durham, 1954. p. 682. txt fig. 3D.

Wythella eldridgei (Twitchell). Durham, 1955. txt fig. 27d.

Wythella eldridgei (Twitchell). Cooke, 1959. p. 53. pl. 21, figs. 8-10.

Wythella eldridgei (Twitchell). Durham, 1966. p. 475. fig. 365, 5a, 5b.

Wythella eldridgei (Twitchell). Toulmin, 1977. p. 348, pl. 72, figs. 1-2.

Wythella eldridgei (Twitchell). Mooi, 1989. figs. 10a, 16b, 18a.

Wythella eldridgei (Twitchell). Osborn et al., 2016. tbl. 2.

Occurrence.—*Wythella eldridgei* is most commonly found in abundance in a horizon resting just above the *Oligopygus wetherbyi* Zone in the upper OLS; this is the *Wythella eldridgei* Zone, and best exposed in Lafayette, Suwannee, and northern Dixie Counties, Florida, especially west of Dowling Park, Lafayette County (FM-IP LF002), quarries northwest of Mayo, Lafayette County (FM-IP LF001), and O'Brien Quarry (FM-IP SU002) north of Branford, Suwannee County. The type locality of the species is along the Suwannee River, 24 km below Ellaville. Carter and McKinney (1992) documented this species in the OLS of Georgia.

Discussion.—Twitchell in Clark and Twitchell (1915), initially described this very distinctive species as *Laganum eldridgei* from strata referred to the Lower Oligocene from the Suwannee River at Ellaville, Florida. Subsequently, Durham

Figure 151: *Porpitella micra* (USNM 462806), 3 mm TL, 2.5 mm TW, 1 mm TH, Ohio Oil Co Well, 5509-5519 ft. depth, late Cretaceous Atkinson Formation (Applin and Applin, 1965), Hernando County, Florida. A: aboral. B: oral.

(1954) erected *Wythella*, with *W. eldridgei* as the type species.

Wythella eldridgei is thinner, larger, and more elongate than any other sand dollar occurring in the upper OLS. It is found in abundance in a lens of pale soft limestone upwards 1 m thick that rests atop the *Oligopygus wetherbyi* Zone of the upper OLS and below the overlying *Rhyncholampas gouldii*-bearing Oligocene sediments of the Suwannee Limestone in the northern Florida Peninsula. Puri (1957) named this horizon the *Spirolaea* (now *Rotularia*) *vernoni* Zone. Here, *W. eldridgei* occurs with *W. cubae, R. trojana,* and a diverse assemblage of spatangoids that includes *P. dixie, E. ocalanus, P. curvus, S. armiger, B. steinhatchee,* and *O. beckeri.*

Emended Diagnosis.—As for the genus.

Family **SCUTELLINIDAE** Pomel, 1888
Genus ***Porpitella*** Pomel, 1883

Porpitella micra H. L. Clark, 1937
(Figs. 150, 151)

Porpitella micra H. L. Clark, 1937. p. 248.
Porpitella micra (H. L. Clark). Cooke, 1942. p. 30.
Porpitella micra (H. L. Clark). Cooke, 1959. p. 33. pl. 7, figs. 5-7.

Occurrence.—The type locality for this miniscule species is at 3800-4000 ft. depth in the Oakley Estate well 2 in sec. 9, T. 3 N., R. 29 E., Houston County, Alabama. Cooke (1959) stated that the specimens were associated with the oyster *Cubitostrea sellaeformis* (Conrad, 1832), which would indicate the material is from the Middle Eocene Lisbon Formation.

However, this Eocene age was debated by Applin and Applin (1965), who also documented specimens of *P. micra* from a well of the Ohio Oil Company, Hernasco Corp., in sec. 19, T. 23 S., R. 18 E., in Hernando County, Florida. These *P. micra* were from 5509–5519 ft. (1679–1682 m) depth (USNM 462806) and 5520–5530 ft. (1682–1686 m) depth (USNM 462807) in what Applin and Applin assert is the Late Cretaceous Atkinson Formation. If this proves correct, this remarkable finding will make *P. micra* the earliest known of all the scutelloids (see below). *Porpitella micra* is not known from surface exposures in Florida, or anywhere else, being documented only from well cores.

Discussion.—H. L. Clark (1937) described this species from well cuttings in Houston County, Alabama, at a depth of 3800-4000 ft. (1158–1219 m) below the surface, from strata Clark (1937) surmised to be the Middle Eocene Lisbon Formation. As noted above, Cooke (1959) associated the echinoids with *C. sellaeformis*, the characteristic oyster of the upper Lisbon Formation, and reiterated the Eocene age asserted by Clark (1937).

Clark (1937) stated that there were 26 paratypes from the same locality that show great diversity in form and preservation and that few were as well preserved as the holotype, and in most cases, the petals cannot be distinguished. The smallest specimen he recorded is 5 mm TL x 4 mm TW and the largest is 9.5 mm TL x 8.5 mm TW. Clark noted that while most individuals are distinctly longer than wide, with the anterior end narrowed and the posterior margin nearly straight, some are almost circular, one notable example 6 mm TW and less than 7 mm TL. The apical system is nearly central in these more circular specimens, so the anterior position of the apical system is not a constant character. Clark (1937) also mentioned there is great diversity in the concavity of the oral surface. In some cases, the concavity is pronounced and extends from the posterior margin nearly to the anterior end of the test. At the other extreme are individuals in which the entire oral surface is almost flat except for a localized depression around the peristome. Clark (1937) stated there is no American echinoid with which *P. micra* can be confused because the supramarginal periproct and the character of the petals are distinctive.

The Florida specimens (Figs. 150, 151) are very small: 3.2 mm TL, 2.8 mm TW, and 1.1 mm TH; and 3.3 mm TL, 2.9 mm TW, 1.2 mm TH, and not well preserved. Although the aboral surface is well preserved on USNM 462807, and the characteristic aboral periproct is readily discernable, the petals are not.

Applin and Applin (1965) questioned the Middle Eocene age Clark (1937) and Cooke (1942, 1959) attributed to the species at its type locality. The age determination was in part based on the association of the specimens with *Cubitostrea sellaeformis* noted by Cooke (1959). This is a characteristic, saddle-shaped oyster diagnostic for the NP16 zone of the Claibornian Middle Eocene of the Gulf Coast (Baum and Vail, 1988; Toulmin, 1977) and the upper portion of the Lisbon Formation in Alabama. Applin and Applin (1965) reported that Cooke had examined the Florida specimens and identified them as *P. micra*. Our own examination indicated that they are certainly most similar to *P. micra*, but they are not well preserved. As noted by Clark (1937), and discussed above, this is a highly variable species, and the Florida specimens fall within the ranges of variation seen in the type material from Alabama.

As already noted, Applin and Applin (1965) strongly suggested that the Florida specimens were collected in Upper Cretaceous strata within the well core, the exceptionally deep origin of which does imply they come from below the Eocene. Applin and Applin provided the well logs that support this determination. In addition, Applin and Applin (1965) stated that the Hernando County specimens were collected with *Exogyra woolmani* Richards, 1947, (a diagnostic Late Cretaceous species), supporting their claim of a Late Cretaceous age for the specimens. To reconcile this Late Cretaceous occurrence of a previously reported Middle Eocene population of *P. micra*, they studied the cores from the Alabama well (type locality for the species). Applin and Applin (1965: 69) stated the Alabama Geological Survey had also questioned the age of the material from the Alabama well and that their subsurface investigations in the region indicated that the specimens of *Porpitella* from the Houston County well are, like the Florida specimens, of early Atkinson (early Gulf) age (Late Cretaceous).

As mentioned, Clark (1937) and Cooke (1959) based their age determination of *P. micra* on the

Figure 152: *Periarchus floridanus* (UF 12797), 110 mm TL, 110 mm TW, external mold with RTV cast, dolomitic beds of Upper Eocene lowermost Ocala Limestone, Citrus County, Florida (FM-IP CI009). A: external mold. B: RTV cast.

association of *C. sellaeformis* with the type specimens in the Alabama core. *Cubitostrea sellaeformis* is typically a large species of oyster. An example surviving sufficiently intact for full identification in well cuttings would be remarkable, so it is possible this identification was made from incomplete oyster valves.

A Late Cretaceous occurrence of *Porpitella* is remarkable, as the earliest known scutelliforms discussed in recent literature are suggested to appear in the Early Eocene (Smith and Kroh, 2011). However, Mongiardino Koch et al. (2022) provided robust molecular and phylogenetic dating results that strongly suggest an origin of scutelliforms before the Paleocene, making the data concerning the occurrence of *Porpitella* of significance in supporting these findings.

Strictly speaking, a Cretaceous occurrence of a scutelliform does not fit the Paleogene focus of this work. However, the significance of *P. micra* in Upper Cretaceous strata compels us to include the taxon as the earliest documented occurrence of a species of Scutelloida. Accordingly, we have not included this species in the Eocene distribution table of Florida taxa (Table 1).

Infraorder **SCUTELLIFORMES** Haeckel, 1896
Family **PROTOSCUTELLIDAE** Durham, 1955
Genus ***Periarchus*** Conrad, 1866

Periarchus floridanus Fischer, 1951
(Figs. 152, 153)

Periarchus lyelli (Conrad). Cooke, 1942. p. 14. (in part, references to this species in Florida are *P. floridanus*).

Periarchus lyelli floridanus Fischer, 1951. p. 60. pl. 1, figs. 1-4; txt figs. 4, 5.

Periarchus lyelli floridanus (Fischer). Cooke, 1959. p. 42. pl. 13, fig. 4.

Periarchus lyelli floridanus (Fischer). Toulmin, 1977. p. 344. pl. 70, fig.4.

Figure 153: *Periarchus floridanus* (UF 12882), 64.5 mm TL, 65 mm TW, external mold with RTV cast, dolomitic beds of Upper Eocene lowermost Ocala Limestone, Citrus County, Florida (FM-IP CI009). A: external mold. B: RTV cast.

Periarchus floridanus (Fischer). Oyen and Portell, 2001. pp. 193-218. pl. I, fig. 1.

Periarchus lyelli floridanus (Fischer). Osborn et al., 2016. tbl. 2.

Occurrence.—This is the common large sand dollar of the *Oligopygus phelani* Zone of the lower OLS (formerly Inglis Formation) of Citrus and Levy Counties and is present in varying concentrations (usually as test fragments) at nearly all exposures of the unit. A few localities include: Cross Florida Barge Canal (e.g., FM-IP CI001) south of Inglis, Citrus and Levy Counties; mouth of Withlacoochee River west of Yankeetown, Levy County (type locality: FM-IP LV024); and Cemex (formerly Independent Aggregates) Quarry, southwest of Inglis, Citrus County (FM-IP CI017).

Toulmin (1977) documented the occurrence of *P. floridanus* in the Moodys Branch Formation along the east bank of the Chattahoochee River at mile 36.4 above the confluence with the Flint River in Early County, Georgia.

Discussion.—Although Cooke (1942) documented the presence of *Periarchus lyelli* within the Eocene strata of Florida, Fischer (1951) was first to recognize the differences between this west central Florida population and typical *P. lyelli* when he described the form as *P. lyelli floridanus*. Fischer (1951) documented his new subspecies at numerous localities near Inglis in Citrus and Levy Counties in strata that were at the time recognized as the Moodys Branch Formation. This Upper Eocene deposit would subsequently be designated as the Inglis Member of the Moodys Branch Formation, Inglis Formation, and later as the lower OLS; it is the *Oligopygus phelani* Zone of the lower OLS. Although this species would later be documented from strata outside the Inglis area, the type area is its area of greatest concentration.

Like Carter et al. (1989: tables 1, 4) and Oyen

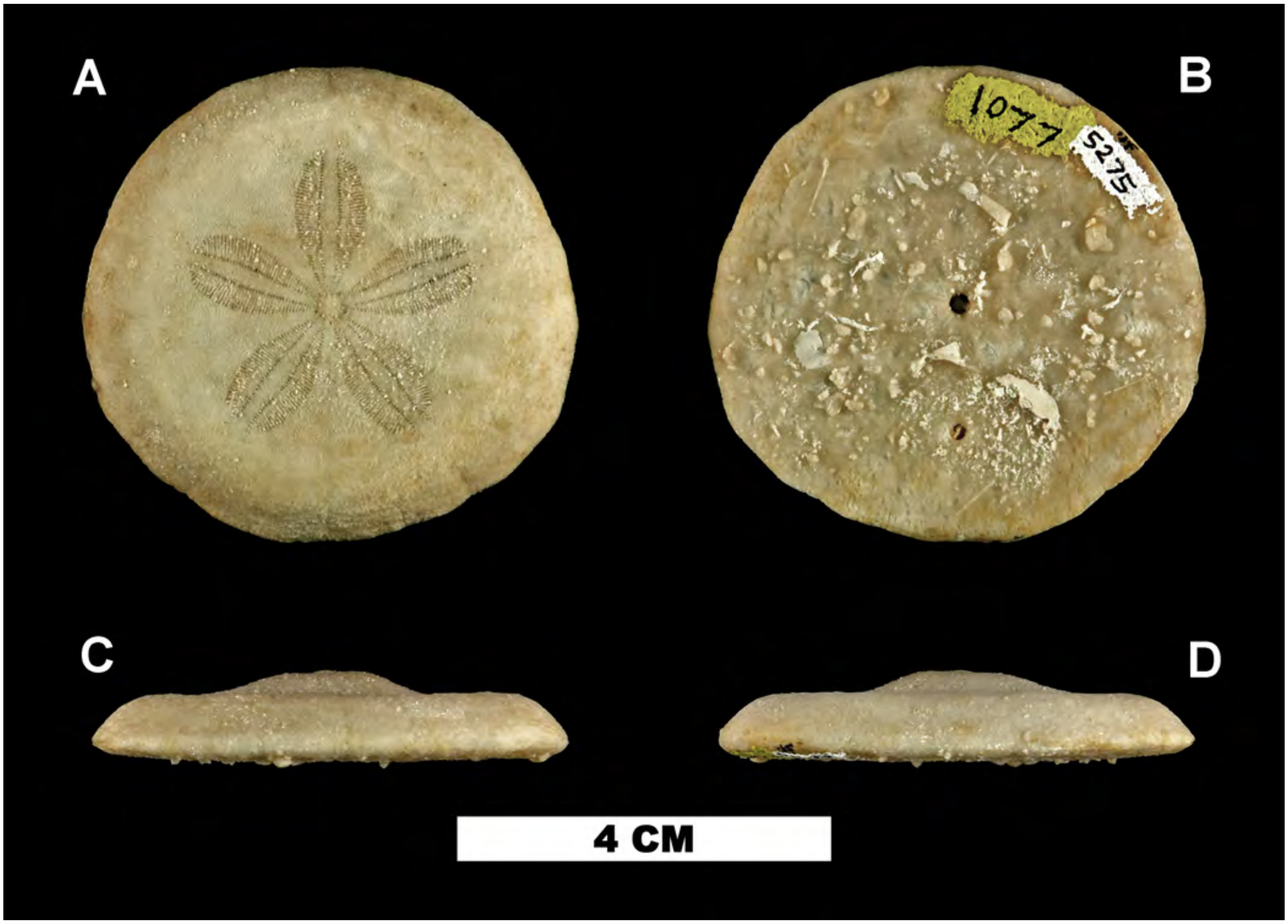


Figure 154: *Periarchus quinquefarius* (UF 5275), 49 mm TL, 51 mm TW, 9.5 mm TH, upper portion of Upper Eocene Ocala Limestone, Suwannee County, Florida (FM-IP SU004). A: aboral. B: oral. C: left side. D: right side.

and Portell (2001), we consider the very thin margin, flat test with a gentle bevel leading adapically from the margin, and proportionately shorter petals distinct enough to warrant considering *P. floridanus* at the species level, rather than as a subspecies of *P. lyelli*. These features are very stable and consistent in mature specimens.

Though *P. floridanus* is exceptionally abundant in the lower OLS, it is typically represented as a dense accumulation of fragments. Complete individuals are rare, due to the very large, thin, and fragile test of the species. In this horizon, *P. floridanus* occurs with an assemblage of much smaller scutelloids represented by the neolaganids *W. inglisensis* n. sp., *D. ocalana, N. durhami*, *E. mooreanus, O. phelani*, and many other, rarer species. *Periarchus floridanus* also occurs in the dolomite beds of the basal OLS, which form the lowest beds of the OLS and are well exposed along the Cross Florida Barge Canal south of Inglis. Here, *P. floridanus* is preserved as internal and external molds along with *E. clevei*. We figure a few of these molds (Figs. 152, 153)

Periarchus quinquefarius (Say, 1825)
(Figs. 154, 155)

Scutella 5-*faria* Say, 1825. p. 228 (read to the academy in 1825, published in 1827).
not *Scutella rogersi* (Morton). Agassiz, 1841. p. 85. pl. 19a, figs. 1-4.
Mortonia rogersi (Morton). Desor, 1858. p. 231.
Mortonia quinquefaria (Say). Conrad, 1866. p. 32.
not *Mortonella rogersi* (Morton). Pomel, 1883. p. 70.
not *Scutella* (*Mortonia*) *rogersi* (Morton). Gregorio, 1890. p. 250. pl. 43, figs. 18-19 (not fig. 16).

Figure 155: *Periarchus quinquefarius* (UF 338250), 53 mm TL, 54 mm TW, 8 mm TH, upper portion of Upper Eocene Ocala Limestone, Suwannee County, Florida (FM-IP SU003). A: aboral. B: oral. C: left side. D: right side.

Mortonia quinquefaria (Say). Grabau and Shimer, 1910. p. 593.

not *Mortonella rogersi* (Agassiz not Morton). Stefanini, 1911. p. 685. pl. 22, figs. 2, 3.

Mortonella quinquefaria (Say). Clark and Twitchell, 1915. p. 128. pl. 60, figs. 2a-f; pl. 61, figs. la-b (includes additional synonymy).

Periarchus quinquefarius (Say). Cooke, 1942. p. 15.

Periarchus kewi Cooke, 1942. p. 16. pl. 1, figs. 12-14.

Mortonella quinquefaria (Say). Mortensen, 1948. p. 391, txt figs. 228a-c.

Mortonella quinquefaria (Say). Durham, 1955. p. 155. txt figs. 1L, 18c.

Periarchus quinquefarius (Say). Cooke, 1959. pp. 43-44. pl. 14, figs. 6-8.

Periarchus quinquefarius kewi (Cooke). Cooke, 1959. p. 44. pl. 14, figs. 4-5.

Mortonella quinquefaria (Say). Durham, 1966. p. U477. figs. 368, 4.

Periarchus quinquefarius kewi (Cooke). Pickering, 1970. p. 20. p. 28, p. 62.

Periarchus quinquefarius (Say). Pickering, 1970. pp. 20, 33, 61.

Periarchus quinquefarius (Say). Huddlestun and Hetrick, 1986. p. 15.

Mortonella quinquefaria (Say). Mooi, 1989. fig. 27a.

Mortonella quinquefarius kewi (Cooke). Oyen, 2001. pp. 41, 41. figs. 3-5, c-d.

Mortonella quinquefarius (Say). Osborn et al., 2016. tbl. 2.

Occurrence.—This species is the characteristic sand dollar of the Sandersville Limestone Member of the Tobacco Road Sand (*sensu* Huddlestun and Hetrick, 1986) in Georgia, especially near Sandersville, Washington County. The species is exceptionally rare in Florida. Carter (1987a) and Oyen (2001) documented this species in the upper OLS of Suwannee County. We confirmed this after examining two specimens in the FM-IP collections, UF 5275 from the Watermelon Pit (FM-IP SU004) and UF 338250 from the greatly enlarged quarry operation currently known as the Branford 01A Quarry (FM-IP SU003), north of Branford, Suwannee County. Both specimens were collected *ex situ*, but the strata exposed in this quarry represent the *Oligopygus wetherbyi* Zone and overlying *Wythella eldridgei* Zone. Therefore, the specimens came from no lower than the *Oligopygus wetherbyi* Zone of the upper OLS. These are the only documented occurrences of this species in Florida.

Discussion.—This species has the distinction of being the first echinoid described from North America. Thomas Say described the species in 1825 but did not figure it. Clark and Twitchell (1915) and Cooke (1959) attributed the species to Say's date of reading (November 8, 1825) at the Academy of Natural Sciences in Philadelphia. However, Say's paper: "*On the species of the Linnaean genus* Echinus*, inhabiting the coast of the United States*", within which he described *P. quinquefarius*, was published in 1827 as clearly indicated on the title page. This led to some confusion and caused difficulty researching the initial description of *P. quinquefarius.*

Agassiz (1841) was the first to figure and describe what was Say's *Scutella quinquefarius,* although he called it *Scutella rogersi* Morton, 1834. Subsequently, Desor (1858) founded his genus *Mortonia* using the thick margin for this species as diagnostic, but he replicated the error of Agassiz, and placed the species under the name *Mortonia rogersi*.

The confusion between *M. quinquefarius* and *C. rogersi* was first noted by Gregory (1892) but it persisted until Clark and Twitchell (1915) clarified the synonymies of both species, which are very distinct. These latter authors properly apportioned which species were being referred to by which name in the previous literature. These corrections are provided in our synonymies for each species.

Pomel (1883) changed the genus for this species from *Mortonia* to *Mortonella* because Gray (1851) had already used the name *Mortonia* for a subgenus of *Echinocyamus* (now considered a genus). Durham (1955) appealed to the International Commission on Zoological Nomenclature to formalize this designation and asserted that Desor (1858) intended to designate the form recognized as *Scutella quinquefarius* Say, 1825, as the type species of his new genus *Mortonia*, and not *Scutella rogersi* Morton, 1834, and that misidentification of the two species created the confusion. The ICZN approved Durham's requests in opinion 358 (1955).

Although this species was the type of *Mortonella* Pomel (1883: 70), the differences between *Mortonella* and *Periarchus* were too insignificant for Cooke (1959) to justify the retention of *Mortonella*. The most conspicuous difference between the genera is in the thickness of the margin, but margin thickness is variable in both genera, and as clarified by Cooke, some individuals of *P. quinquefarius* are as thin as some of *P. lyelli.* Cooke (1959) asserted that if *Mortonella* is to be retained, it should not rank higher than subgenus.

Durham (1966) retained *Mortonella* without commenting on Cooke's (1959) assertion. Some subsequent workers have continued usage of *Mortonella* (Mooi, 1989; Carter, 1987a). Like Cooke (1959), we do not see sufficient differences between *Mortonella* and *Periarchus* to warrant retaining *Mortonella* as a distinct genus.

Periarchus quinquefarius can be distinguished from the other species of *Periarchus* by its proportionately longer petals, its usually thicker margin, and by its deeper and more conspicuous food grooves (Cooke, 1959).

Carter (1987a) was the first to document the occurrence of this species outside of Georgia when he listed it as occurring near Suwannee, Florida. Oyen (2001) subsequently documented numerous specimens in the Florida Museum collections from Florida [UF 2202, UF 2203, and UF 2204 (each lot consists of numerous specimens)]. However, associated data attributes them to Georgia. Oyen (2001) also figured and described a specimen he referred to *Mortonella quinquefarius kewi* (UF 5275) from Florida, and this specimen is attributed to the upper OLS of Suwannee County. We have examined this specimen in the FM-IP collections, and it is indeed *P. quinquefarius* from the Watermelon Pit (FM-IP SU004), expanded and now known as the Branford 01A Quarry, (FM-IP SU003) north of Branford, Suwannee County. A second specimen attributable to this species was found recently in the Denali Quarry. These are the only confirmed occurrences of the species in Florida or anywhere south of the Suwannee Strait. The specimens (Figs. 154, 155) have a distinctly beveled margin characteristic of Cooke's (1942) *P. kewi*.

Cooke (1942) described *Periarchus kewi* as a distinct species. However, in 1959 he changed that opinion and reassigned it as a subspecies of *P. quinquefarius*, mostly because it is associated with the typical form, whose margin often shows a tendency to become beveled. The distinguishing features of the variety are the strongly tumid central region, the swollen submargin, and the plainly beveled edge (Cooke, 1959). Cooke (1959) described his subspecies *P. quinquefarius kewi* as follows: horizontal outline circular; upper surface tumid medially, swollen beyond the petals, sloping steeply to the margin; margin thin; oral side flat; other features as in the typical variety. Because the typical form also shows a tendency for a beveled margin, as stated by Cooke (1959), and both forms occur together in Georgia, we cannot justify differentiating them at either the species or subspecies level.

Genus ***Protoscutella*** Stefanini, 1924

Protoscutella pentagonium Cooke, 1942

(Fig. 156)

Protoscutella pentagonium Cooke, 1942. p. 18, pl. 2, figs. 4-6.

Protoscutella pentagonium (Cooke). Mortensen, 1948. p. 390.

Protoscutella pentagonium (Cooke). Cooke, 1959. p. 39. pl. 15, figs. 6-8.

not *Protoscutella tuomeyi* (Twitchell). Zachos and Molineux, 2003. pp. 495, 497. figs. 3.10-3.12, 3.14, 3.15 (in part, they referred specimens of *P. pentagonium* from the Weches Formation to *P. tuomeyi*).

Protoscutella sp. (Cooke). Osborn et al., 2013. fig. 2.

Occurrence.—The type locality of this species is a well of the Chipley Oil Company at Falling Waters, about 6.4 km south of Chipley, Washington County: depth unknown; Cooke (1942) stated that it was probably about 183 m (about 600 ft.), embedded in white sand (USGS 13145). It is not otherwise known from Florida.

Cooke (1959) documented *P. pentagonium* in the Eocene of Texas, but Zachos and Molineux (2003) did not. They provided localities for *P. tuomeyi* in the Middle Eocene Weches Formation near Nacogdoches and San Augustine Texas, which we believe are likely *P. pentagonium*. As stated in Osborn et al. (2013), they are not *P. tuomeyi*.

Discussion.—The type locality of *P. pentagonium* is inconveniently located approximately 183 m below the surface from a well core in Washington County in the panhandle of Florida (Cooke, 1942; 1959). Cooke (1942) stated that the holotype was collected in strata likely attributable to the Lisbon Formation (Middle Eocene), though he was not certain of this.

Bryan (2018) provided an updated log of the Chipley Oil Company Well (FGS W-1) with updated stratigraphic nomenclature that states strata at the 183 m level (about 600 ft.: depth of *P. pentagonium* provided by Cooke) is Claibornian and notes the presence of a small scutellid at 650 ft. They also note the presence of another scutellid fragment at ~975 ft. in a clay bed, likely of the Lisbon Formation.

This species has not otherwise been documented from the fossil record of Florida.

Subterclass **ATELOSTOMATA** von Zittel, 1879

Order **SPATANGOIDA** L. Agassiz, 1840

Suborder **MICRASTERINA** Fischer, 1966

incertae sedis

Genus ***Gillechinus*** Fell, 1964

Gillechinus alabamensis (Cooke, 1942)

(Fig. 157)

Figure 156: *Protoscutella pentagonium* holotype (USNM 498992), 30.0 mm TL, 31.4 mm TW, 6.1 mm TH, well of the Chipley Oil Company at Falling Water, 4 miles south of Chipley, Washington County, Florida. A: aboral. B: oral. C: left side. D: right side.

Eupatagus (*Brissopatagus*) *alabamensis* Cooke, 1942. p. 58. pl. 4, figs. 7, 8.

Eupatagus (*Brissopatagus*) *georgianus* Cooke, 1942. p. 58. pl. 7, figs. 8-11.

Eupatagus (*Brissopatagus*) *alabamensis* (Cooke). Cooke, 1959. p. 92. pl. 43, figs. 5-11.

Gillechinus alabamensis (Cooke). Henderson and Fell, 1969. pp. 2-29.

Brissopatagus alabamensis (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—Within Florida, this species is known from one documented specimen (UF 337963), from the uppermost portion of the OLS exposed in Brooks Quarry, near Marianna (FM-IP JA009), Jackson County. The species is more widespread in the Upper Eocene Shubuta Clay of Alabama and OLS of Georgia. The type locality of the species is St. Stephens Bluff, Washington County, Alabama.

Discussion.—Cooke (1942) described *Eupatagus* (*Brissopatagus*) *georgianus* from the OLS of Georgia and *Eupatagus* (*Brissopatagus*) *alabamensis* from the Shubuta Clay of Alabama. Cooke (1959) later placed *E. georgianus* in synonymy with *E. alabamensis*. We agree with his assessment. Henderson and Fell (1969) referred this species to *Gillechinus*.

This species is rare throughout its distribution, and prior to Osborn et al. (2016), was undocumented in Florida deposits. Within Brooks Quarry (FM-IP JA009), a single, small (32 mm TL, 29 mm TW) specimen (UF 337963) of *G. alabamensis* was found with *M. mortoni, O. haldemani,* and *W.*

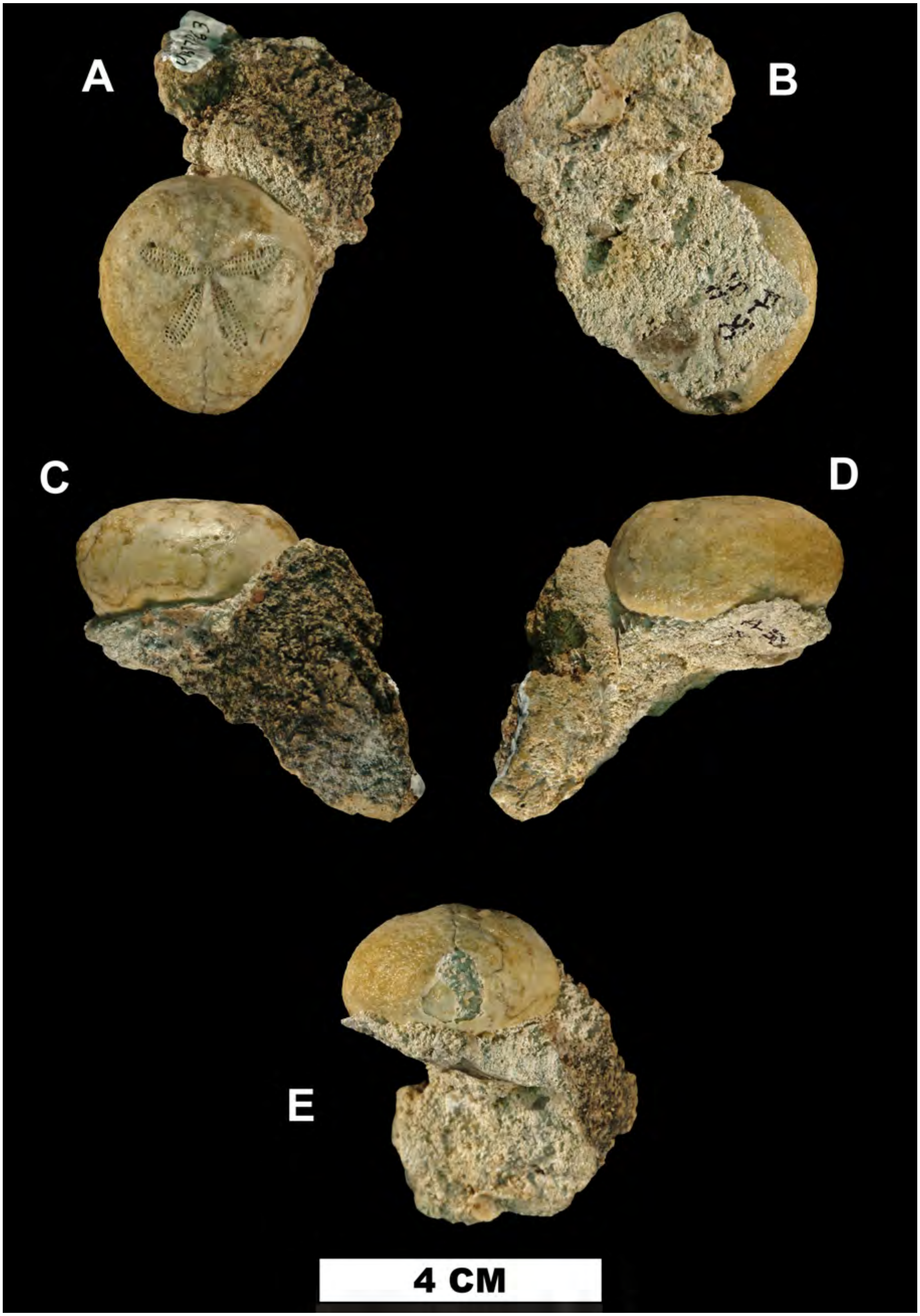


Figure 157: *Gillechinus alabamensis* (UF 337963), 32 mm TL, 29.5 mm TW, uppermost portion of Upper Ocala Limestone in the Marianna Lime Quarry, Jackson County, Florida (FM-IP JA009). A: aboral. B: oral. C: left side. D: right side. E: posterior.

johnsoni, in the upper portion of the OLS. The reduced number of very large tubercles confined to the region aboral to the peripetalous fasciole in the paired interambulacra readily distinguishes this species from any other spatangoid echinoid in the Cenozoic fauna of the region.

Suborder **PALEOPLEUSTINA** Markov and Solovjev, 2001
Family **SCHIZASTERIDAE** Lambert, 1905
Genus ***Ova*** Gray, 1825

Ova beckeri (Cooke, 1942)
(Figs. 158-160)

Schizaster beckeri Cooke, 1942. p. 40. pl. 3, figs. 5-8.
Ditremaster beckeri (Cooke). Cooke, 1959. p. 77. pl. 30, figs. 9-12.
Ditremaster beckeri (Cooke). Toulmin, 1977. pp. 339-340. pl. 65, figs. 11-13.
Schizaster beckeri (Cooke). Kier, 1984. p. 57.
Ditremaster beckeri (Cooke). Neraudeau, 1994. tbl 3.
Schizaster beckeri (Cooke). Osborn et al., 2016. tbl 2.

Occurrence.—*Ova beckeri* is most commonly found in the *Wythella eldridgei* Zone near the top of the upper OLS, especially south of Tennille (FM-IP DI001), west of Dowling Park (FM-IP LF002), and west of Center Hill in Sumter County (FM-IP SM010). The holotype (USNM 499008) was collected in the Gainesville Rock Pit near Arredondo, and the paratype (USNM 499009) is from the Suwannee River west of Dowling Park, Lafayette County. This species was documented in the Eocene of Alabama by Toulmin (1977).

Discussion.— Cooke (1942) described *Schizaster beckeri* from the OLS in Florida. Cooke (1942) stated that it differs from the other members of *Schizaster* in the region by its higher, more rotund test, and presence of only two gonopores. In this same work, he described *Schizaster* (*Linthia*) *ocalanus*, which also has only two gonopores, but he referred it to the subgenus *Linthia*. The traits Cooke (1942) listed do not serve to distinguish between *O. ocalanus* and *O. beckeri*. However, they are distinct, with *O. beckeri* being proportionately longer, with a shallower anterior sulcus, more posterior apical system, and anterior paired petals that are angled more anteriorly

Cooke (1959) placed *S. beckeri* in *Ditremaster*, stating that *Ditremaster* differs from *Schizaster* by its lack of a deep, continuous, anterior sulcus and its apparent lack of lateral fascioles. Kier (1984: 57) subsequently stated that *Ditremaster beckeri* should be referred to *Schizaster*, as its latero-anal fasciole is distinct, whereas no latero-anal fasciole is present in *Ditremaster*.

The two gonopores of *Ova beckeri* presently exclude it from placement in *Schizaster* (Smith and Kroh, 2011), as the membership in the latter is restricted to those forms with four gonopores. Therefore, we place *S. beckeri* Cooke, 1942 in *Ova*. Smith and Kroh (2011) list the very similar *Schizaster subcylindricus* (Cotteau, 1875) from the Eocene of St. Bartholomew, Cuba, and Jamaica as belonging to *Ova* but do not discuss *O. beckeri*. Cooke (1959) noted the latter's similarity with *Ova subcylindricus*, indicating that it is very closely related but has somewhat shorter anterior petals.

This affinity with *O. subcylindricus* is undeniable and the two species are obviously closely related. Kier (1984) stated that these two species differ only in that the anterior petals in *O. subcylindricus* are slightly shorter and the apical system is more anterior. Kier indicated the anterior petals in *O. beckeri* have a length 48% TL as opposed to 34-41% in *O. subcylindricus*. *Ova beckeri* is likewise similar in general form to *Schizaster camagueyensis* (Weisbord, 1934), from the Late Eocene of Cuba. However, the number of gonopores of this species is not provided in the original description of Weisbord (1934) or Kier (1984).

In Florida, *O. beckeri* most commonly occurs near the top of the OLS with *W. eldridgei, R. trojana, S. armiger,* and many other, rarer species. The presence of two gonopores and ovate, proportionately elongate test that lacks an anterior sulcus distinguishes *O. beckeri* from any species with which it occurs.

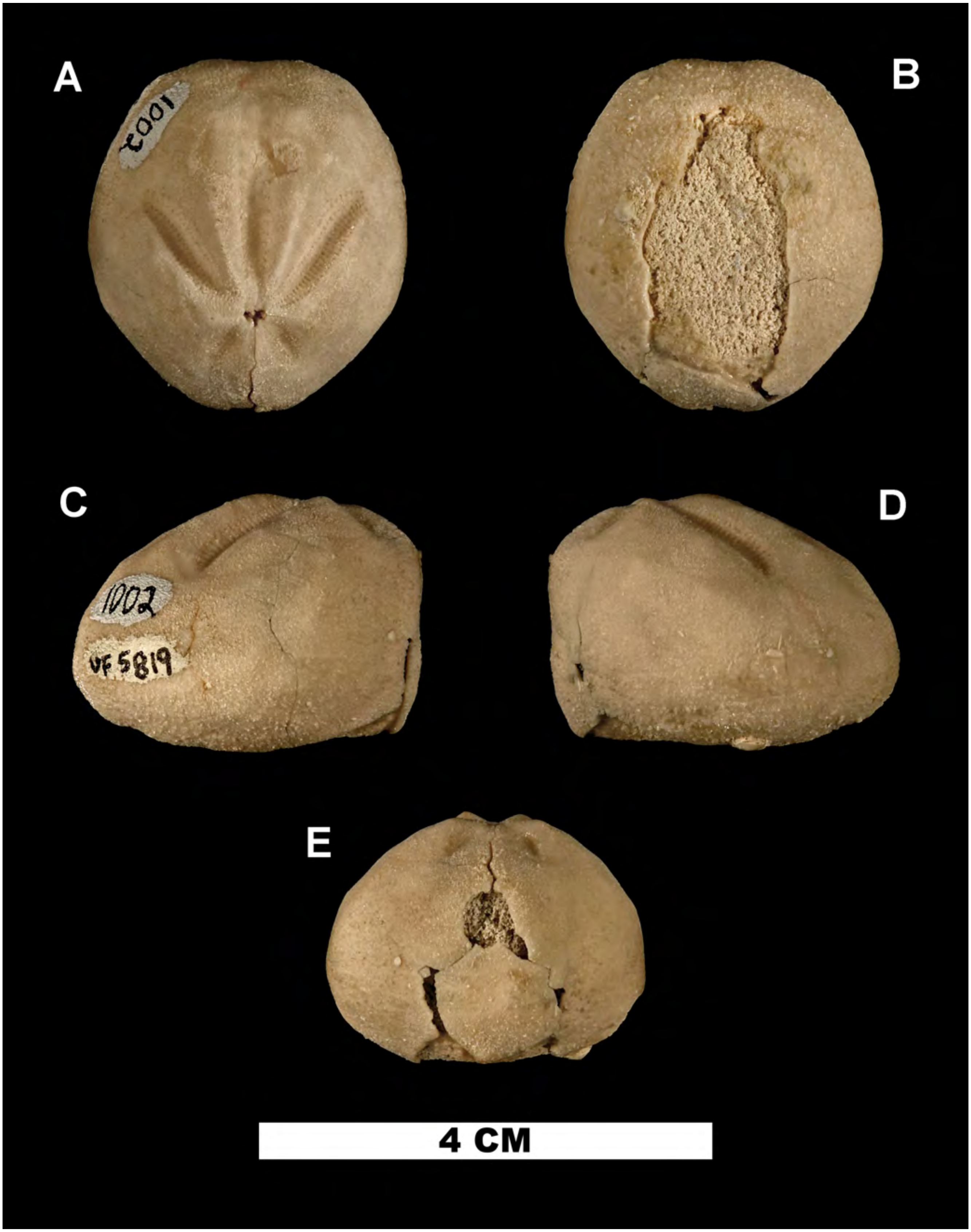


Figure 158: *Ova beckeri* (UF 5819), 33 mm TL, 31 mm TW, 24 mm TH, upper beds of Ocala Limestone, Lafayette County, Florida (FM-IP LF001). A: aboral. B: oral. C: left side. D: right side. E: posterior.

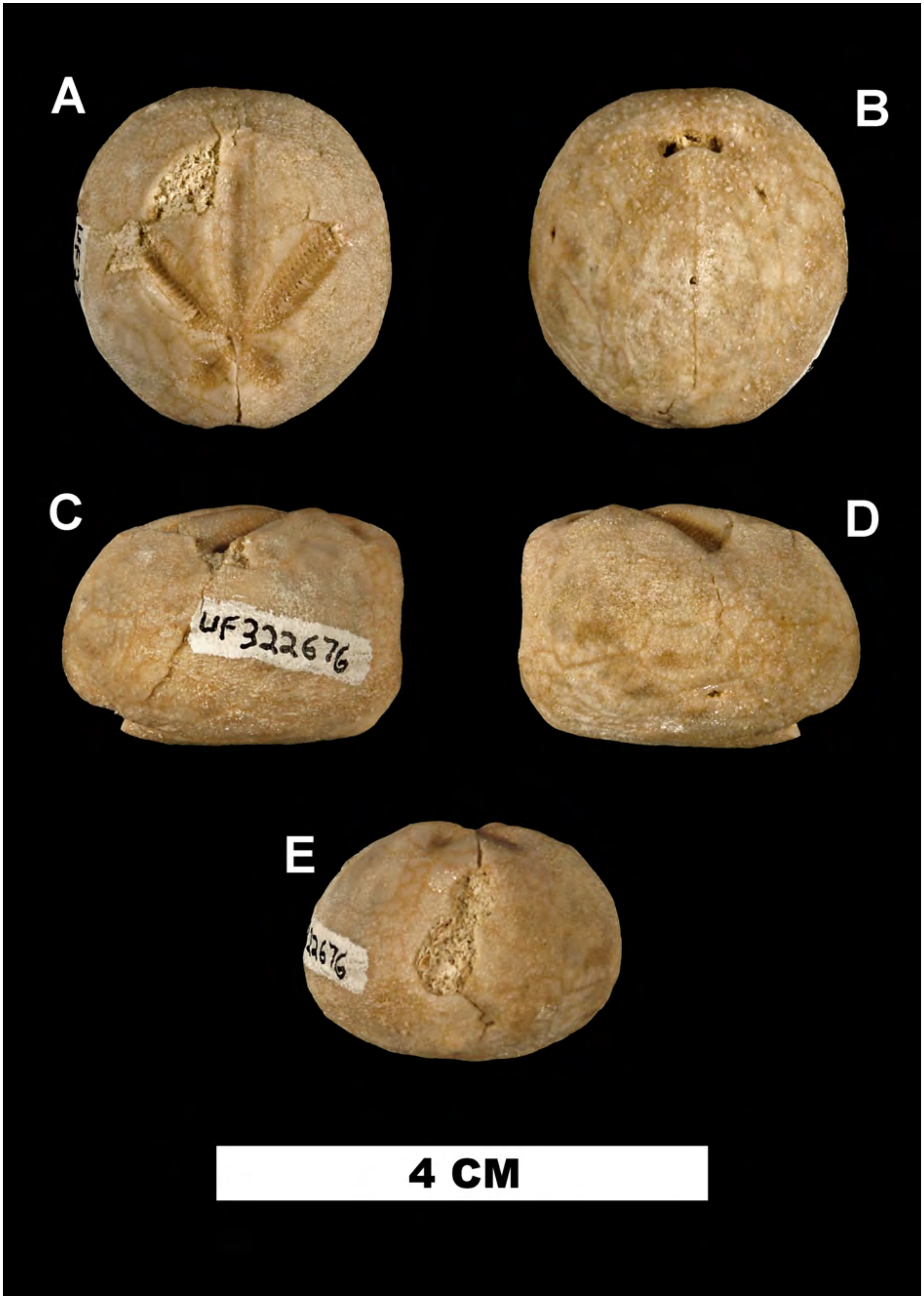


Figure 159: *Ova beckeri* (UF 322676), 27 mm TL, 25 mm TW, 19 mm TH, Upper Eocene upper Ocala Limestone, Taylor County, Florida (FM-IP 5649). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 160: *Ova beckeri* (UF 341764), 19 mm TL, 17 mm TW, 13 mm TH, upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA033). A: aboral. B: oral. C: left side. D: right side. E: anterior. F: posterior.

Ova ocalanus (Cooke, 1942)
(Fig. 161)

Schizaster (*Linthia*) *ocalanus* Cooke, 1942. p. 42. pl. 5, figs. 18-22.
Schizaster (*Brachybrissus*) *ocalanus* (Cooke). Cooke, 1959. p. 73. pl. 29, figs. 13-17.
Schizaster ocalanus (Cooke). Toulmin, 1977. p. 347. pl. 71, figs. 4-6.
Schizaster ocalanus (Cooke). Osborn et al., 2016. tbl 2.

Occurrence.—This species is most commonly found in the *Oligopygus wetherbyi* Zone of the OLS, where it is especially abundant near Kendrick, Marion County (type locality), in the Cemex Quarry (FM-IP SM010) west of Center Hill, Sumter County, and the O'Brien Quarry in Suwannee County (FM-IP SU002); see Cooke (1959) for additional localities.

Discussion.—This species is more rotund than other American species of schizasterid, and although it has historically been referred to *Schizaster* (Cooke, 1942; 1959), clarification of the characters of the genus by Smith and Kroh (2011) indicate that this assignment is incorrect in the present concepts of these schizasterid genera. Cooke (1959) referred it to the subgenus *Brachybrissus*. However, Smith and Kroh (2011) considered *Brachybrissus* a synonym of *Schizaster* and referred schizasterids with a well-developed latero-anal portion of the marginal fasciole and two gonopores to *Ova*. We concur, placing *S. ocalanus* in *Ova*. The presence of two gonopores readily distinguishes this species from other schizasterids of the region except for *O. beckeri*, which is proportionately longer, with a shallower anterior sulcus, more posterior apical system, and anterior paired petals that are angled more anteriorly.

Genus ***Schizaster*** L. Agassiz, 1836
Schizaster americanus Clark in Clark and Twitchell, 1915
(Figs. 162-168)

Schizaster americanus Clark in Clark and Twitchell, 1915. p. 176. pl. 82, figs. 2a-d.
Schizaster americanus (Clark). Lambert and Thiéry, 1925. p. 526.
Schizaster americanus (Clark). Cooke, 1942. p. 40.
Paraster americanus (Clark). Cooke, 1959. p. 72. pl. 30, figs. 5-8.
Paraster americanus (Clark). Pickering, 1970. pp. 20, 28, 34.
Schizaster (*Paraster*) *americanus* (Clark). Dockery, 1980. p. 193. pl. 82, fig. 1.
Schizaster americanus (Clark). Oyen and Portell, 2001. p. 202.
Schizaster americanus (Clark). Osborn and Ciampaglio 2014. p. 142.
Schizaster sp. cf. *S. americanus* (Clark). Donovan et al., 2015. pp. 5-6. fig. 3 (not *S. americanus*).

Occurrence.—Within Florida, this species is most abundant in the Lower Oligocene Marianna Limestone where it occurs in the Brooks Quarries (FM-IP JA013, FM-IP JA019, FM-IP JA026, FM-IP JA029) near Marianna, Jackson County; Dry Creek (FM-IP JA010), south of Marianna, Jackson County; and in a dolomite quarry north of Altha, Jackson County (FM-IP JA014). *Schizaster americanus* is much more rarely found in the Suwannee Limestone in the Terramar Quarry (FM-IP PO017) in Polk County, and the Bridgeboro Limestone in the Duncan Church Quarry (FM-IP WG002) in Washington County.

Schizaster americanus also occurs in Oligocene strata of Alabama, Georgia, and Mississippi. The type locality is the Marianna Limestone near Brandon, in Rankin County, Mississippi.

Discussion.—*Schizaster americanus* is the only spatangoid present in the typical Marianna Limestone in Jackson County, Florida. However, in the dolomitic facies of the Marianna Limestone, exposed along the banks of Dry Creek (FM-IP JA010) south of Marianna, *S. americanus* occurs with *P. cassadyi* n. sp. and *C. rogersi*. A few kilometers eastward in quarries north of Altha (FM-IP JA014), also in the dolomitic facies, *S. americanus* occurs with *E. aldrichi* and *C. rogersi*. See the discussion for the Marianna Limestone in the stratigraphic overview section for more on these dolomitic facies

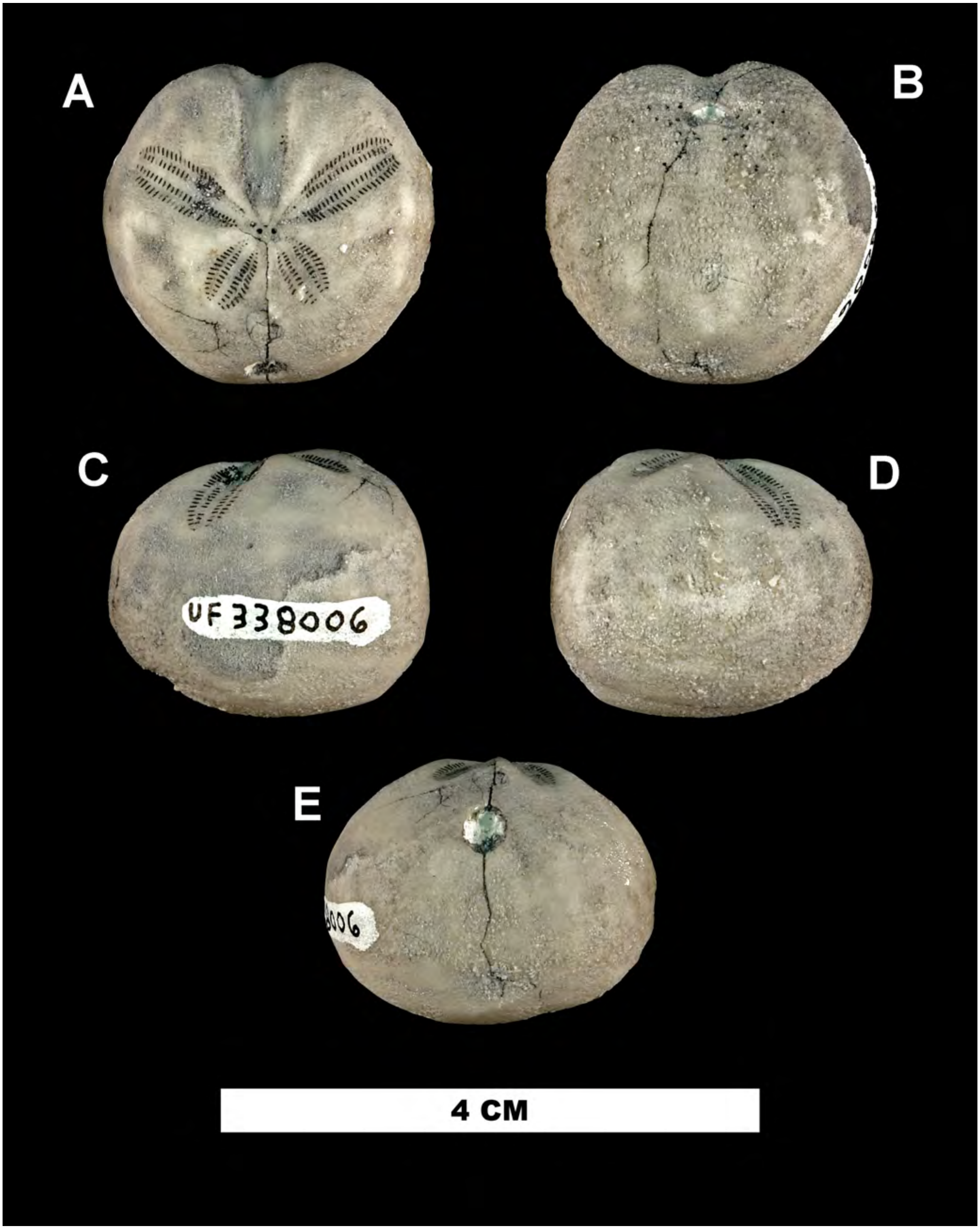


Figure 161: *Ova ocalanus* (UF 338006), 23 mm TL, 24 mm TW, 19 mm TH, *Oligopygus wetherbyi* zone of Upper Eocene upper Ocala Limestone, Sumter County, Florida (FM-IP SM010). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 162: *Schizaster americanus* (UF 337961), 35.5 mm TL, 33.5 mm TW, 24.5 mm TH, Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA029). A: aboral. B: oral. C: left side. D: right side. E: posterior.

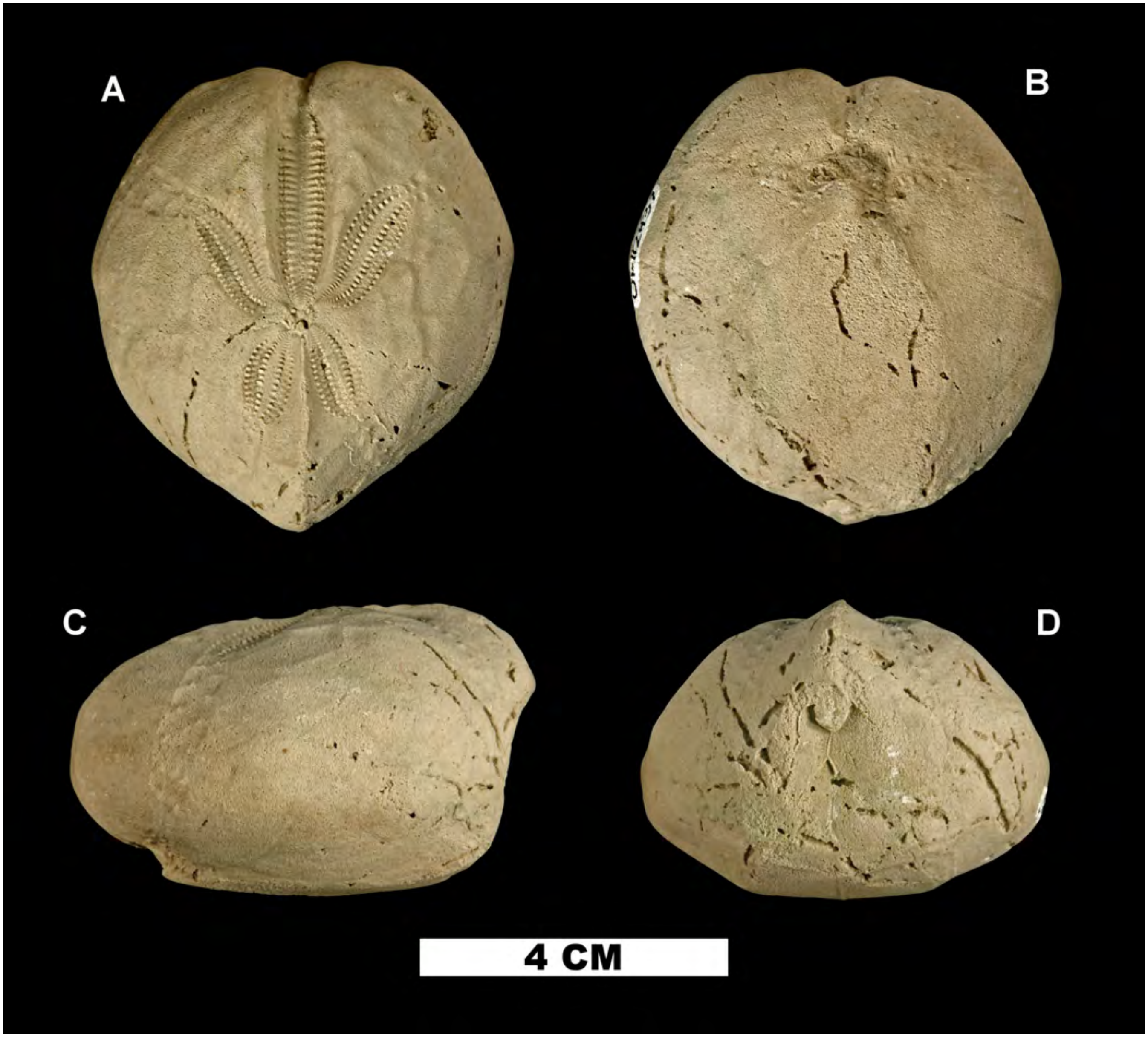


Figure 163: *Schizaster* cf. *S. americanus* (UF 112437), 57 mm TL, 52.5 mm TW, 36.5 mm TH, dolomitic portion of Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA014). A: aboral. B: oral. C: left side. D: posterior.

in southern Jackson County.

Schizaster americanus is much more rarely found in the Suwannee Limestone and is represented by one specimen (UF 27345) from the Terramar Quarry (FM-IP PO017) in Polk County. It is also rarely found in the Bridgeboro Limestone and is represented by three specimens [UF 55006 (2 specimens), UF 61440] from the Duncan Church Quarry in Washington County (FM-IP WG002).

Cooke (1959) noted that *S. americanus* is proportionately shorter than *S. armiger,* and that its posterior petals are somewhat shorter. However, *S. americanus* demonstrates considerable variability in the degree of divergence of the anterior petals and position of its apical system (often more posterior in specimens from the Chickasawhay Limestone of Alabama). A series of specimens preserved as molds from the dolomitic facies of the Marianna Limestone north of Altha (FM-IP JA014) show significant variation in apical system placement (more posterior in some specimens), degree of divergence of ambu-

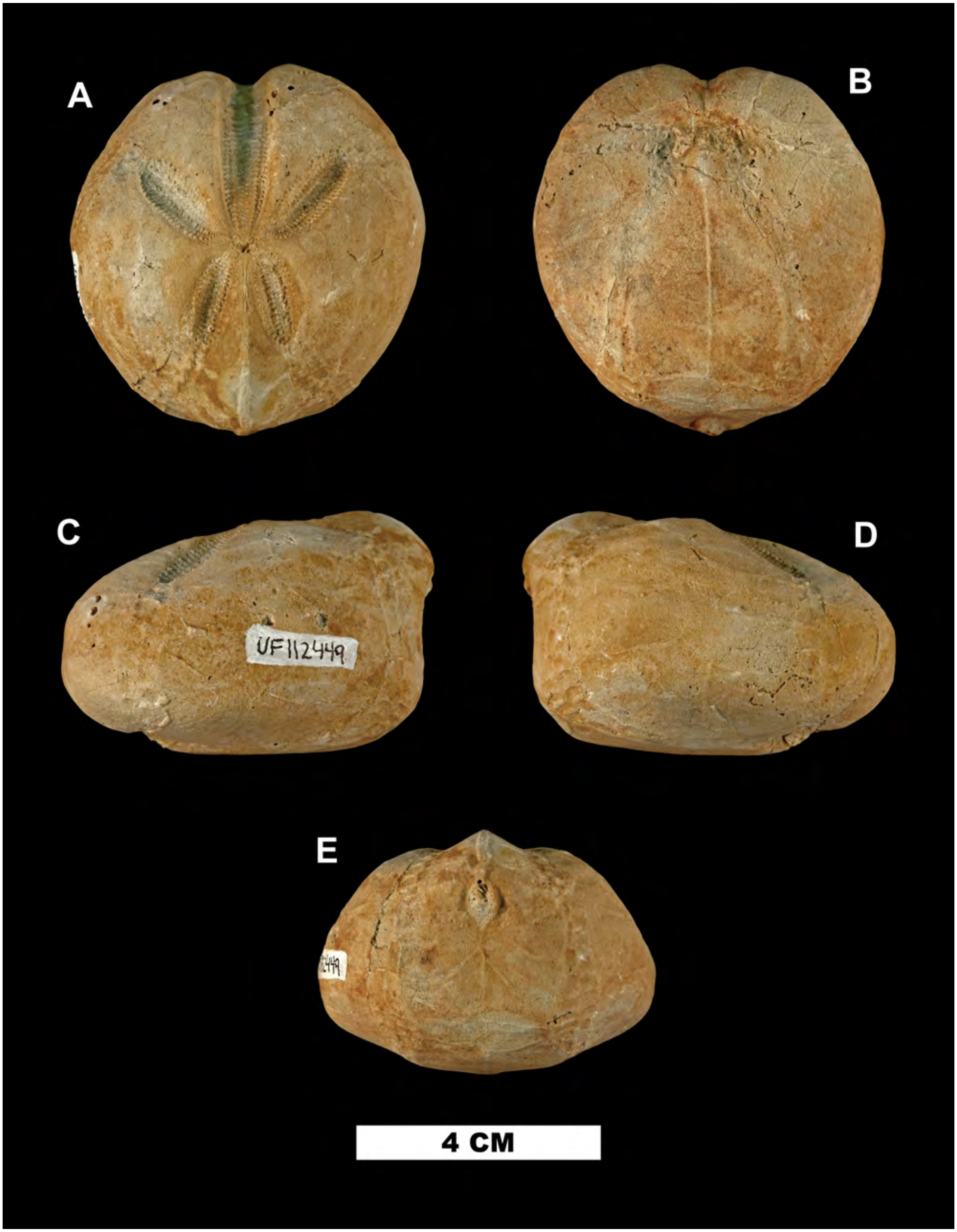


Figure 164: *Schizaster* cf. *S. americanus* (UF 112449), 58 mm TL, 56 mm TW, 37 mm TH, dolomitic portion of Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA014). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 165: *Schizaster* cf. *S. americanus* (UF 112348), 52.5 mm TL, 49.5 mm TW, 33.5 mm TH, dolomitic portion of Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA014). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 166: *Schizaster* cf. *S. americanus* (UF 112344), 34.5 mm TL, 33 mm TW, 22.5 mm TH, dolomitic portion of Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA014). A: aboral. B: oral. C: left side. D: right side. E: posterior.

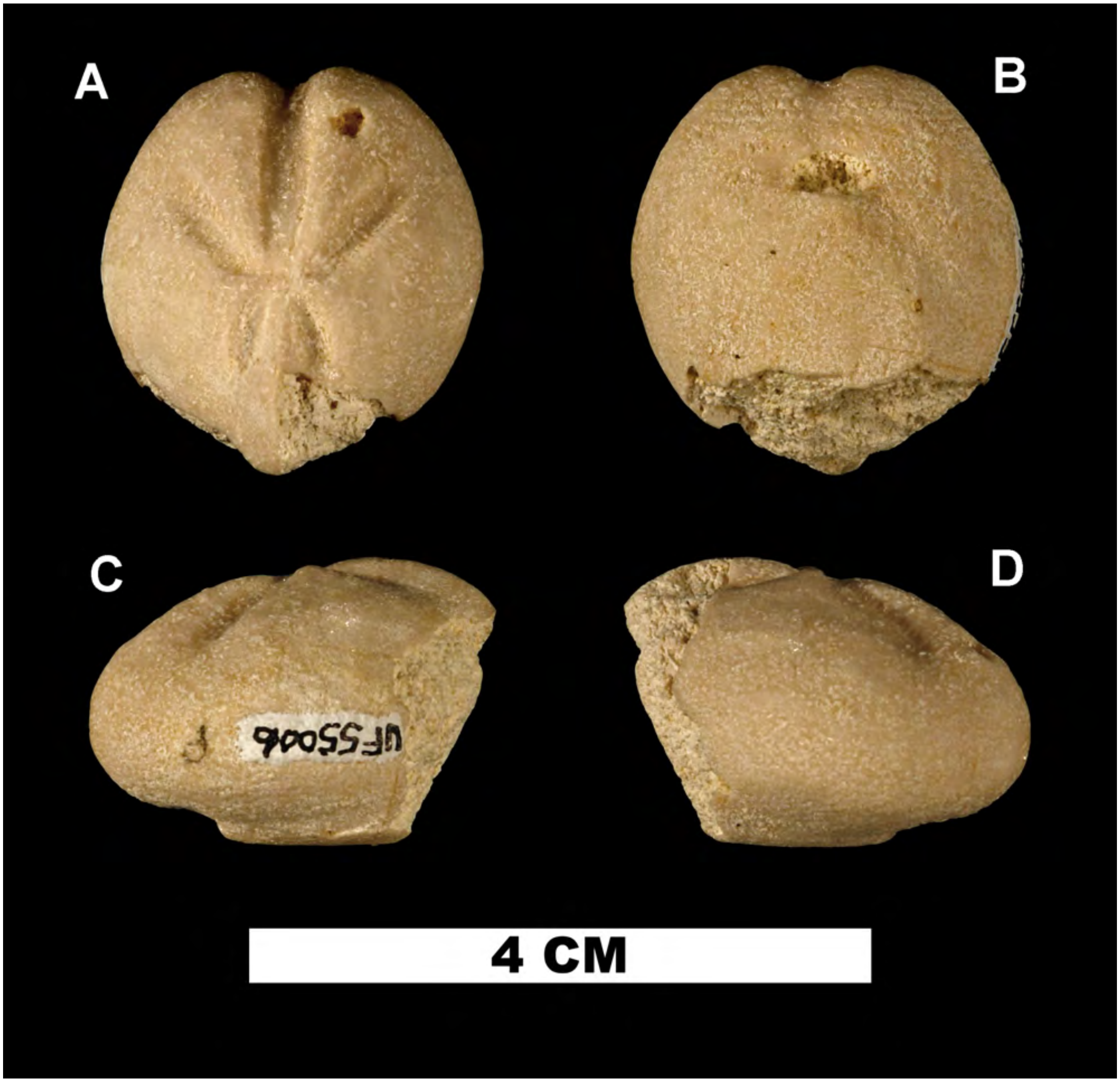


Figure 167: *Schizaster americanus* (UF 55006), 31 mm TL, 29.5 mm TW, 23.5 mm TH, Oligocene Bridgeboro Limestone, Washington County, Florida (FM-IP WG002). A: aboral. B: oral. C: left side. D: right side.

lacra II and IV, and height of the anterior portion of the test, with some being much more wedge-shaped in profile than is typical for the species (Fig. 165).

Schizaster armiger Clark in Clark and Twitchell, 1915
(Figs. 169, 170)

A sea urchin, Harris, 1894. p. 172. pl. 6, fig. 11.

Schizaster armiger Clark in Clark and Twitchell, 1915. p. 152. pl. 70, figs. 1a-d.

Schizaster floridanus Clark in Clark and Twitchell, 1915. p. 175. pl. 82, figs. 1a-c.

Schizaster armiger (Clark). Lambert and Thiéry, 1925. p. 524.

Schizaster armiger (Clark). Cooke, 1942. p. 39.

Schizaster armiger (Clark). Cooke, 1948b. p. 92. pl. 22, figs. 1-4.

Paraster armiger (Clark). Cooke, 1959. pp. 71-72. pl. 30, figs. 13-15.

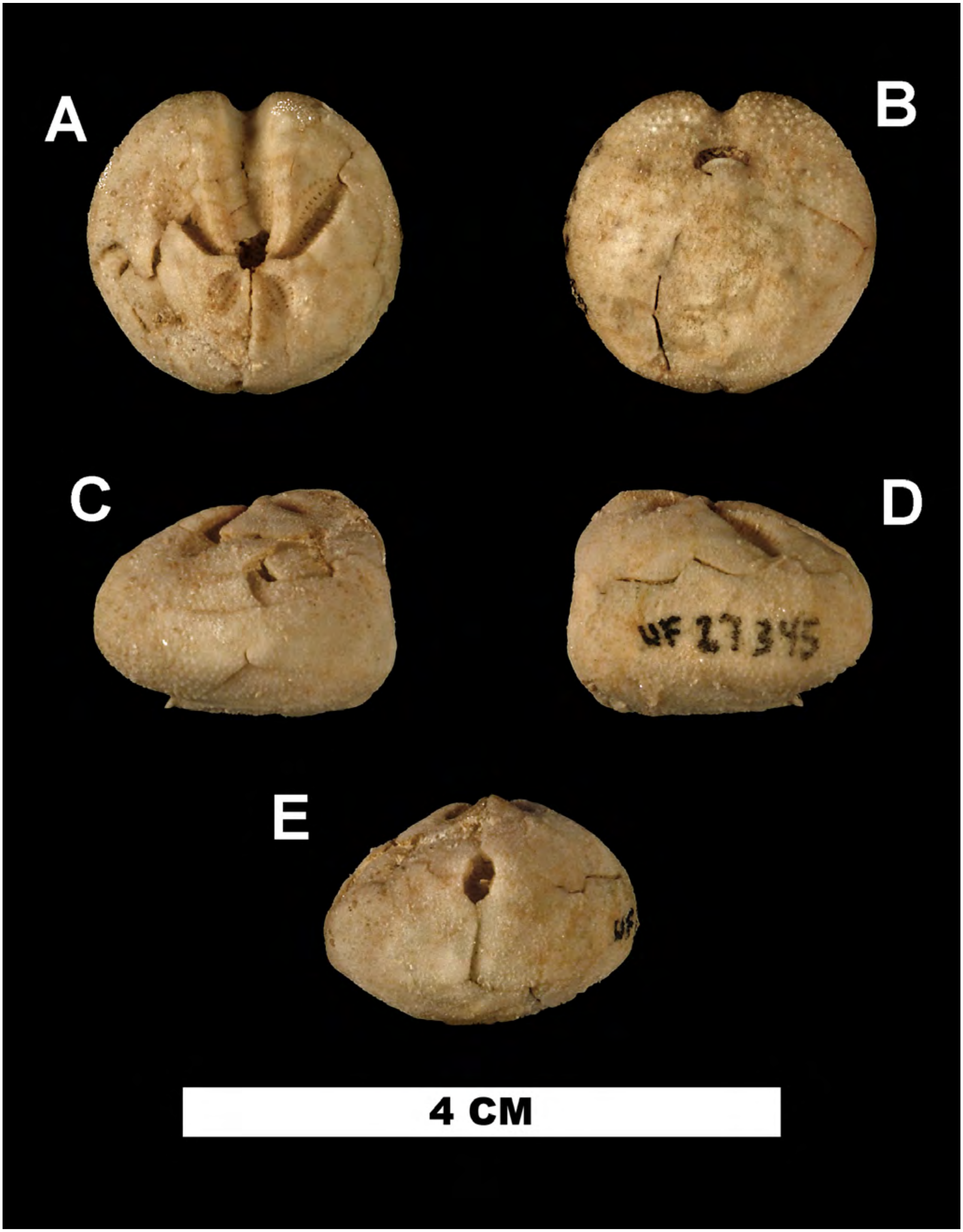


Figure 168: *Schizaster americanus* (UF 27345), 20 mm TL, 21 mm TW, 15 mm TH, Lower Oligocene Suwannee Limestone, Polk County, Florida (FM-IP PO017). A: aboral. B: oral. C: left side. D: right side. E: posterior.

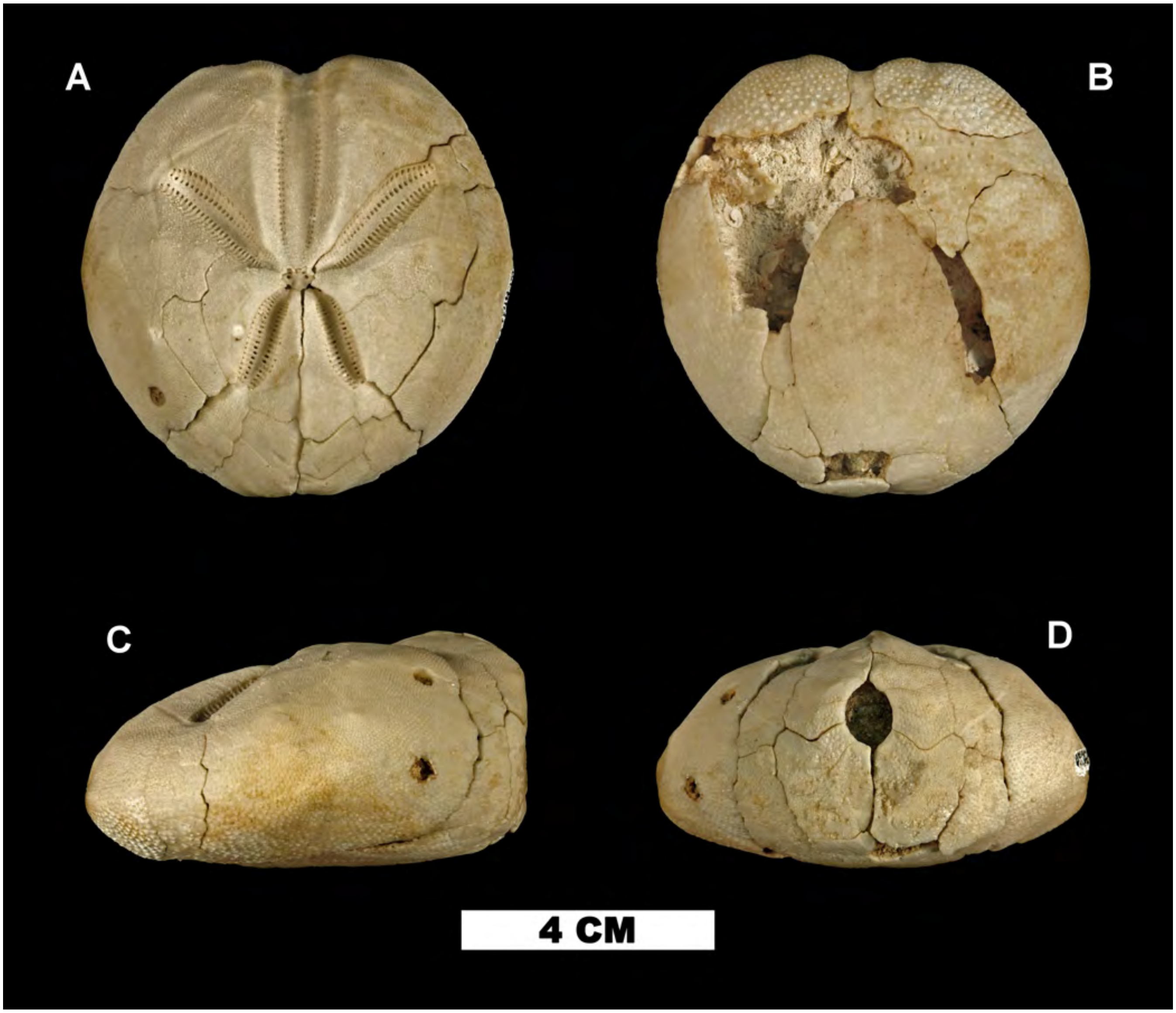


Figure 169: *Schizaster armiger* (UF 114429), 74.5 mm TL, 72 mm TW, 37.5 mm TH (specimen is slightly compressed), upper portion of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF002). A: aboral. B: oral. C: left side. D: posterior.

Schizaster (*Paraster*) *armiger* (Clark). Toulmin, 1977. p. 346. pl. 70, figs. 5-7.

Schizaster armiger (Clark). Osborn et al., 2016. tbl 2.

Occurrence.—This species is present in the upper OLS where it is most commonly encountered in association with *W. eldridgei* in the uppermost portion of the unit. A few localities include: Johnson's Sink, Levy County (type of *Schizaster floridanus* Clark in Clark and Twitchell, 1915); northwest of Mayo (FM-IP LF001), Lafayette County; north of Branford (FM-IP SU002), Suwannee County; and south of Tennille (FM-IP DI001), Dixie County.

Schizaster armiger is also found in Upper Eocene strata of Alabama, Arkansas, Georgia, Mississippi, and Panama (Cooke, 1948b; 1959). The holotype of *S. armiger* (USNM 141104) was collected in the Upper Eocene Yazoo Formation near the Cocoa Post Office, Choctaw County, Alabama.

Discussion.—Gilbert Harris first documented this species in the *Annual Report of the Geological Survey of Arkansas for 1892* (1894: 172), in which he identified it as "A Sea Urchin" from Cornish Ferry on the Sabine River. The figure he provided was good enough to permit its identifi-

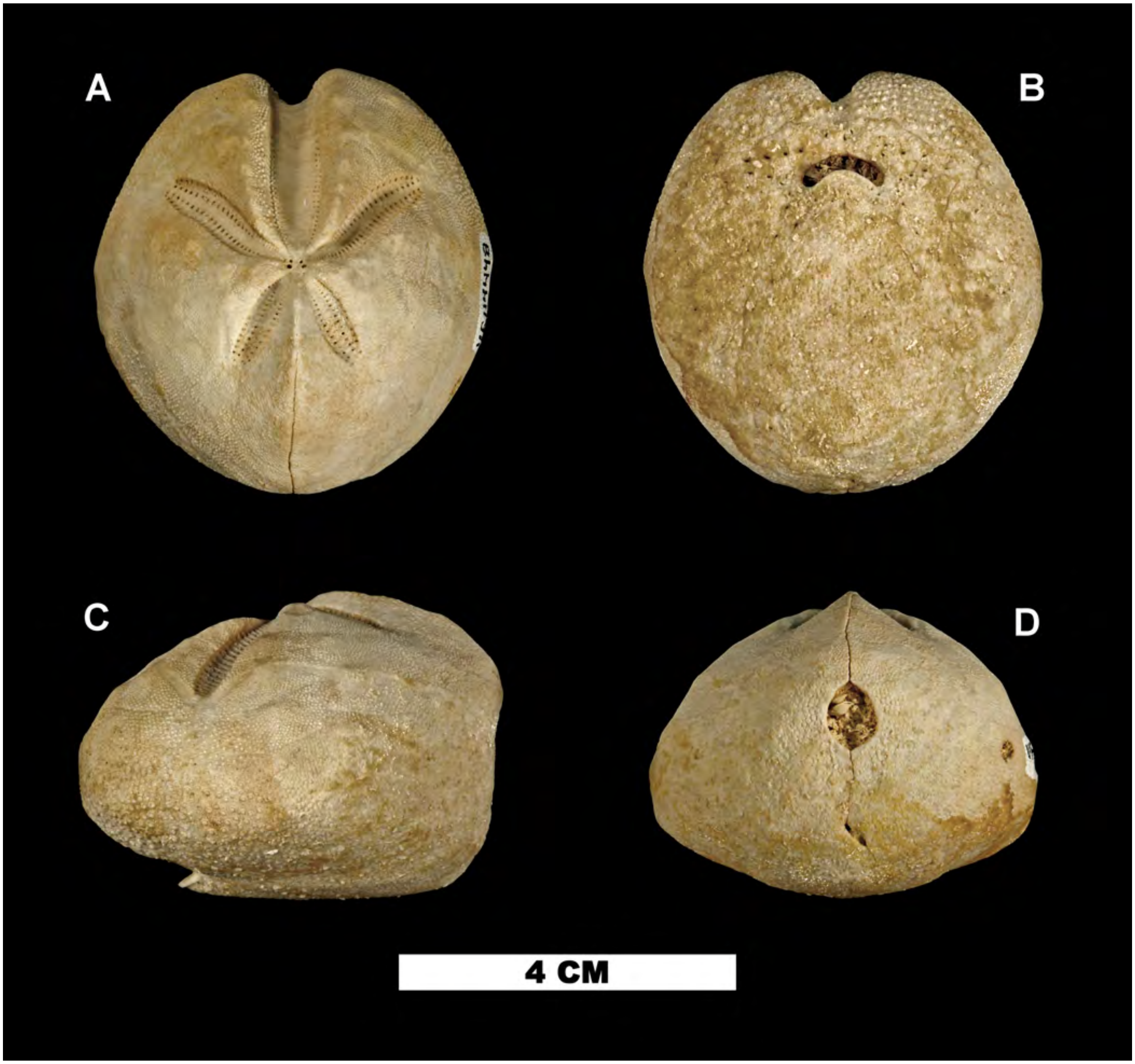


Figure 170: *Schizaster armiger* (UF 114448), 50 mm TL, 47 mm TW, 36.5 mm TH, Upper Eocene Ocala Limestone, Alachua County, Florida (FM-IP AL004). A: aboral. B: oral. C: left side. D: posterior.

cation as *S. armiger*, which Clark, in Clark and Twitchell (1915), subsequently described from a specimen collected in the Upper Eocene strata of Choctaw County, Alabama. Cooke (1942) acknowledged the identification of Harris' specimen when he documented the occurrence of *S. armiger* at the east bank of the Sabine River at Cornish Ferry (Caveness Landing) about 8 km east-northwest of Warren, Bradley County, Arkansas, and listed G. B. Harris as the collector of the specimen.

Clark in Clark and Twitchell (1915), described *S. floridanus* from Johnson's Sink in Levy County, Florida, in the same work in which he described *S. armiger*, though Cooke (1942) considered *S. floridanus* a synonym of *S. armiger*. Subsequent authors have followed this synonymy, as do we.

Cooke (1959) stated that *S. armiger* is proportionately longer, and its posterior petals are somewhat longer than in *S. americanus*. Cooke (1959) also stated that the type and other specimens from western Alabama have wider petals than those from Florida and that there is some variation in the relative length of the posterior petals, an observation we have also made.

Schizaster armiger is commonly encountered in the *Wythella eldridgei* Zone in the upper OLS of the northern Florida peninsula where it occurs with *W. eldridgei* and a diverse assemblage of spatangoids, including *P. dixie, E. ocalanus, P. curvus, B. steinhatchee,* and *O. beckeri.*

Schizaster carlsoni n. sp.

(Figs. 171-173)

Diagnosis.— *Schizaster* with high (TH on average 70% TL), narrow test (TW on average 90.8% TL) that is not sharply wedge-shaped in lateral view, with a nearly central apical system (center of apical system on average 47.3% TL from posterior margin), petals of ambulacra I and V short (length on average 21.9% TL) and diverging on average at 47° from each other, petals of ambulacra II and IV long, extending nearly to margin (length on average 40.4% TL), slightly sinuous, and divergent on average 95° from each other, curving towards the anterior until their ends, at which point they curve slightly posteriorly.

Description.—Description based on the holotype (UF 342111), three paratypes (UF 342112, UF 342113, UF 342114), and non-type material, all from the type locality (FM-IP HE038).

Moderately sized *Schizaster*, largest complete specimen (UF 342114) 50.2 mm TL, smallest (UF 342111) 38.0 mm TL; test ovate, narrow, narrowing posteriorly, TW on average 90.8% TL; test high, TH on average 70% TL, greatest height posterior, test slopes gently anteriorly from apical; only slightly wedge-shaped in lateral viewpoint; greatest width nearly central, adjacent to apical area; test narrows laterally above ambitus towards aboral highest point of test. Apical system ethmolytic; nearly central, center of apical system on average 47.3% TL from posterior margin; four gonopores, posterior pair slightly larger and further apart than anterior pair. Ambulacrum III not petaloid, in very deep, steep-sided depression extending from apical system to anterior notch, and continuing to the peristome, depression deepest and widest midway between apical system and anterior margin; furrow on average 12% TW at widest point, sides of furrow nearly vertical, often overhung, enlarged pore pairs present from apical system to about two-thirds distance to margin. Pore-pairs of paired petals strongly conjugate; interporiferous zones slightly wider than single poriferous zone. Petals of ambulacra I and V short, extending less than halfway from apical system to margin (length on average 21.9% TL); narrow (width on average 34% petal length); bent sharply posteriorly, in deep, ditch-like depression; on average divergent from each other by 47°, range 37-55°; widest point medially; tapered but open distally. Petals of ambulacra II and IV slightly sinuous, divergent from each other on average 95°; curved towards anterior until end where they often curve slightly posteriorly; long, extending more than two-thirds distance from apical system to margin; length on average 40.4% TL; widest point medially, tapered but open distally.

Periproct small (periproct height on average 26.5% TH), ovate, taller than wide (width on average 49.7% periproct height), high on near-vertical, slightly overhung truncate face, lower edge of periproct on average 39.6% TH above posterior margin. Peristome anterior, posterior edge on average 63% TL from posterior margin, kidney shaped, open towards anterior; wider than high, height on average 43.4% peristome width. Labrum short and wide, plastron wide posteriorly, widest point on average 14.5% TW, tapers anteriorly.

Tubercles on aboral surface minute, uniform, evenly and densely distributed. Oral tuberculation fine, dense and uniform. Well-developed peripetalous and lateral fascioles present, but not completely discernable on any specimen (largely due to air abrasive preparation required to remove specimens from stubborn matrix).

Zoobank Nomenclatural Act.—451038E1-8AED-4A66-9C4A-0699500242E9

Discussion.— *Schizaster carlsoni* n. sp. has not been documented outside of the basal portion of the Lower Oligocene Suwannee Limestone in

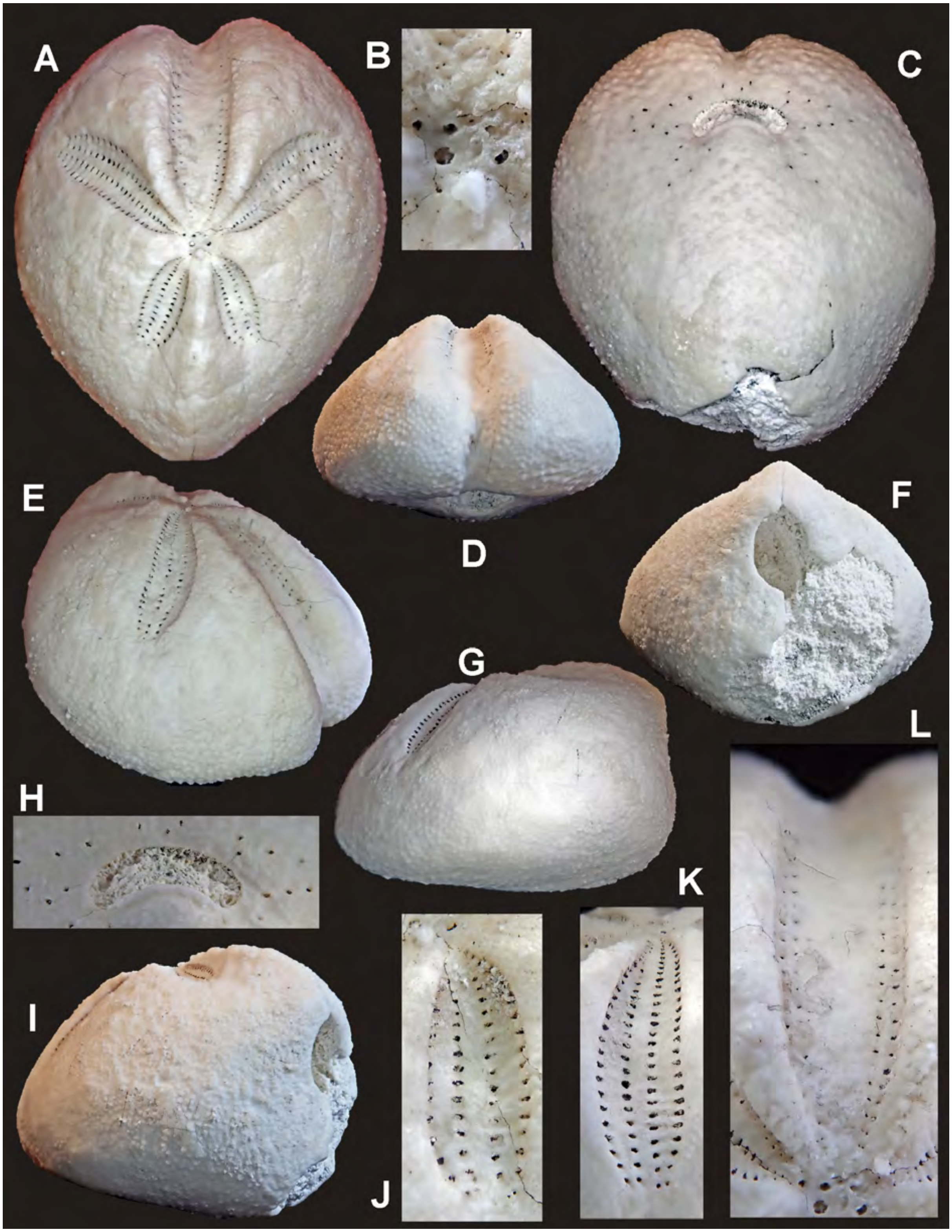


Figure 171: *Schizaster carlsoni* n. sp., holotype (UF 342111), 38.0 mm TL, 34.1 mm TW, 25.2 mm TH, lower bed of the Lower Oligocene Suwannee Limestone, Vulcan Quarry northwest of Brooksville, Hernando County, Florida (FM-IP HE038). A: aboral. B: apical area. C: oral. D: anterior. E: oblique lateral viewpoint from anterior. F: posterior. G: left side. H: peristome. I: oblique lateral viewpoint from posterior. J: petaloid portion of ambulacrum I. K: petaloid portion of ambulacrum IV. L: ambulacrum III and apical area.

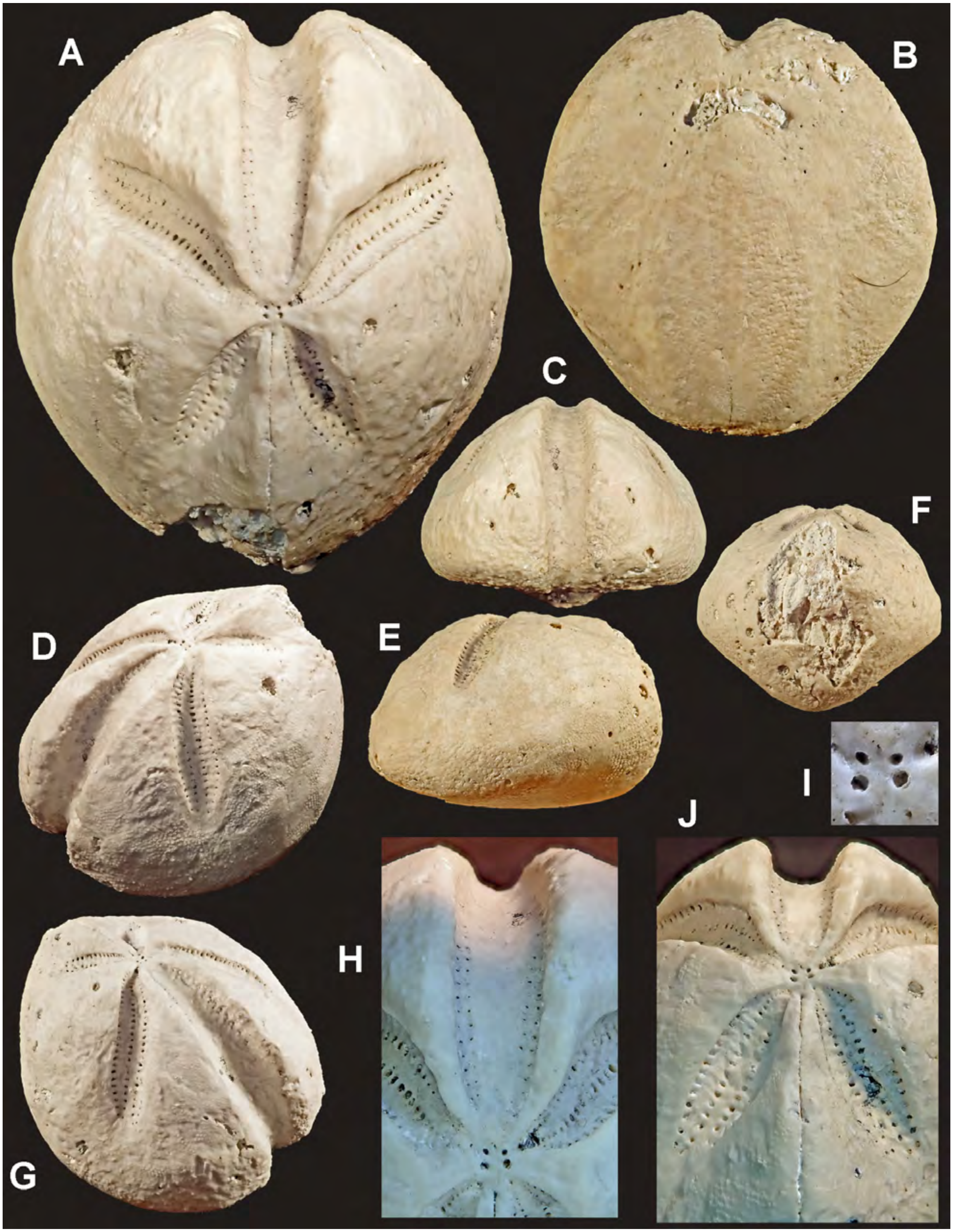


Figure 172: *Schizaster carlsoni* n. sp., paratype (UF 342112), 50.9 mm TL (TL not complete due to damaged posterior), 46.8 mm TW, 34.0 mm TH, lower bed of the Lower Oligocene Suwannee Limestone, Vulcan Quarry northwest of Brooksville, Hernando County, Florida (FM-IP HE038). A: aboral. B: oral. C: anterior. D, G: oblique aboral viewpoints from anterior. E: left side. F: posterior. H: apical and ambulacrum III. I: apical area. J: tilted viewpoint of petaloid area from posterior.

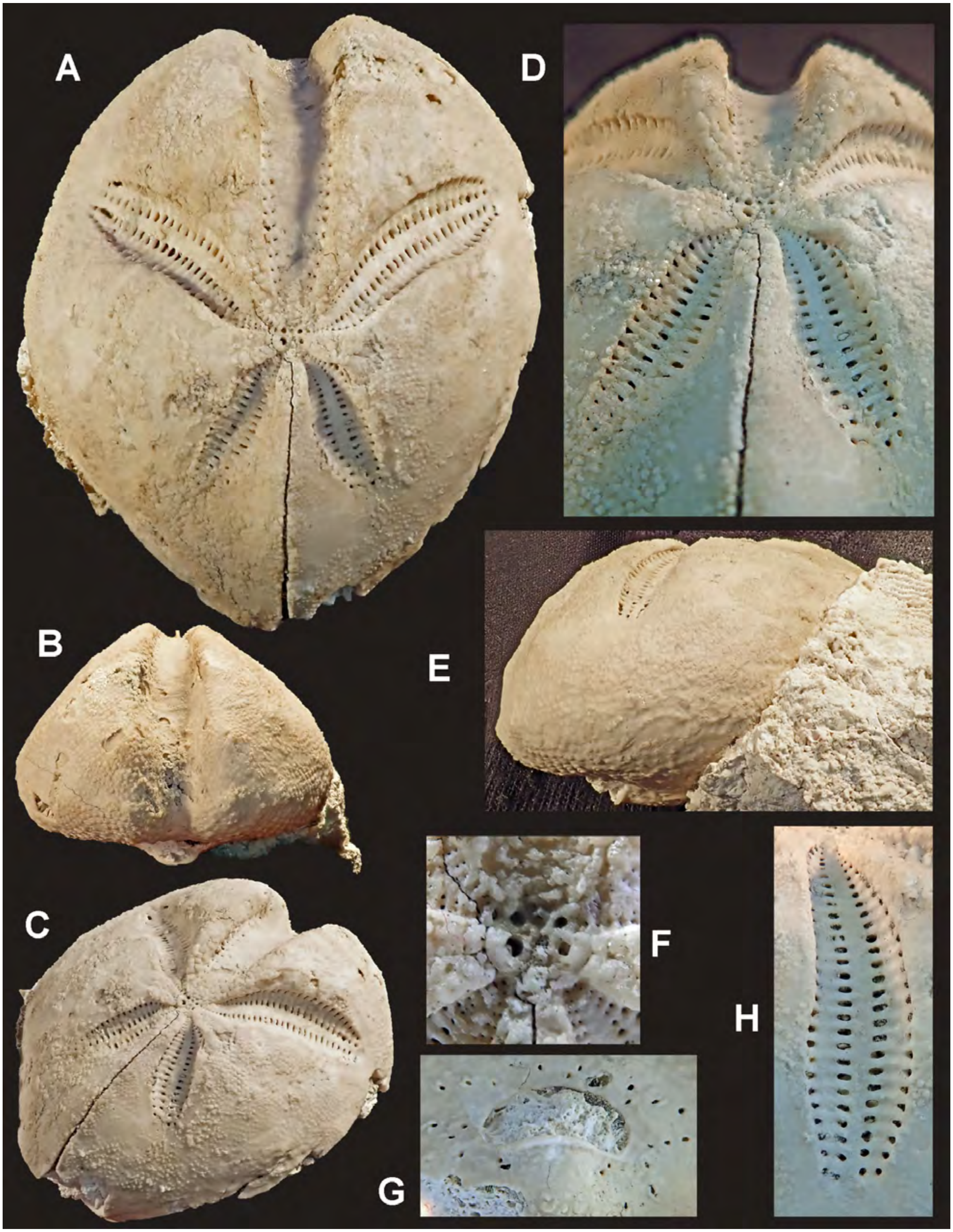


Figure 173: *Schizaster carlsoni* n. sp., paratype (UF 342113), 41.0 mm TL, 36.9 mm TW, 27.0 mm TH (complete TW and TH obscured by matrix), lower bed of the Lower Oligocene Suwannee Limestone, Vulcan Quarry northwest of Brooksville, Hernando County, Florida (FM-IP HE038). A: aboral. B: anterior. C: oblique aboral viewpoint. D: tilted viewpoint of petaloid area from posterior. E: left side. F: apical area. G: peristome. H: petaloid portion of ambulacrum II.

the Vulcan Quarry, roughly 5 mi. northwest of Brooksville, Hernando County, Florida (FM-IP HE038). The horizon bearing *S. carlsoni* n. sp. is below the general floor of the quarry and usually only exposed during the excavation of drainage basins and canals. *Schizaster carlsoni* n. sp. is rarely found with more abundant *Clypeaster* sp. B, *R. gouldii*, which are typically larger in this horizon than in the overlying beds of the Suwannee Limestone, *E. dumonti* n. sp., and rare specimens of *Phyllacanthus* cf. *P. mortoni*.

Schizaster carlsoni n. sp. joins *S. americanus*, from which it is readily distinguished by its narrower test and longer and more sinuous ambulacra II and IV, as the only other *Schizaster* documented from the Oligocene of North America.

Schizaster carlsoni n. sp. is not similar to the other five species of *Schizaster* that occur in the Cenozoic deposits of the extended region, which includes: *S. alabamensis* Clark in Clark and Twitchell, 1915 (Lower Paleocene of the Gulf Coast), *S. caddoensis* Zachos in Zachos and Molineux, 2003 (Middle Eocene of Texas), *S. armiger* (Upper Eocene of Florida and the Gulf Coast), *S. susana* Zachos in Zachos and Molineux, 2003 (Upper Eocene of Texas and Louisiana), and *S. kieri* (Pliocene of Florida); not *S. ocalanus, S. beckeri*, or *S. stenzeli* Zachos in Zachos and Molineux, 2003, which have only two gonopores and are placed in *Ova*.

The modern *Schizaster* of the region includes *S. doederleini* (Chesher, 1972) and *S. floridiensis* (Kier and Grant, 1965), but not *S. orbignyanus* Agassiz, 1880, which only has two gonopores and therefore belongs in *Ova*.

Schizaster is abundantly represented in the fossil faunas of the remainder of the eastern Americas and the Caribbean region. We compare *S. carlsoni* n. sp. to all of them, below.

Kier (1984) recognized 16 distinct species of *Schizaster* in Eocene to Miocene strata of Cuba. These 16 species are reduced from 37 species previously documented in the Cuban faunas, largely in the works of Sánchez-Roig. Of the 21 species Kier (1984) did not recognize, he noted the types of ten are lost or too poorly preserved to permit recognition of distinguishing characters, one is transferred to a different genus, and the remainder are considered subjective junior synonyms of the 16 species he retained.

Among the Cuban species, 13 of the 16 species recognized by Kier (1984) are: *S. bathypetalus* Clark, in Arnold and Clark, 1927, Eocene (this species was initially described from Jamaica); *S. cartagensis* (Sánchez-Roig, 1949), Oligocene-Miocene; *S. delgadoi* (Sánchez-Roig, 1953b), Late Oligocene; *S. egozcuei* Lambert, 1925, Oligocene-Miocene; *S. fernandezi* Sánchez-Roig, 1952c, Miocene; *S. formelli* Kier, 1984, Eocene; *S. gerthi* Pijpers, 1933, Eocene, initially described from Bonaire; *S. llagunoi* Lambert and Sánchez-Roig in Sánchez-Roig, 1949, Eocene-Oligocene; *S. munozi* Sánchez-Roig, 1949, Oligocene-Miocene; *S. neuvitasensis* (Weisbord, 1934), Late Eocene; *S. rojasi* Sánchez-Roig, 1952c, Oligocene-Miocene; *S. sanctamariae* Sánchez-Roig, 1949, Oligocene, and *S. santanae* Sánchez-Roig, 1949, Late Eocene.

Agassiz (1872) placed *S. cubensis* in *Meoma*. Kier (1984) omitted *Schizaster cubensis* D'Orbigny, 1847 from his catalog of Cuban *Schizaster* because he considered the form unrecognizable beyond the genus level. However, the taxon is notable because it seems to be the member of the genus attributed to the Pliocene of Cuba.

The remaining three species Kier (1984) recognized are *S. subcylindricus* Cotteau, 1875, initially described from the Eocene of St. Bartholomew, which has two gonopores and therefore belongs in *Ova*, and two species which are very similar to it: *Schizaster cubitabellae* (Weisbord, 1934) and *S. camagueyensis* (Weisbord, 1934), both from the Late Eocene of Cuba. These two species are very similar to *O. subcylindricus* as well as *O. beckeri*. However, the apical systems appear to be damaged in the types, thus the number of gonopores is not apparent in their figures and is also not provided in the descriptions of Weisbord (1934) and Kier (1984). Both both species could be conspecific with *O. subcylindricus* and therefore a member of *Ova* (having two gonopores). In addition, the type and only known specimen of *S. cubitabellae* is only 50% complete, making determination of its features difficult. Specimens with better preserved apical systems would be required to establish their genus placement with certainty.

Of these Cuban taxa, *S. carlsoni* n. sp. is most like *S. bathypetalus* Clark, 1927, and the similarities of these two taxa are discussed below. However, *S. carlsoni* n. sp. is also like *S. cartagensis*. The holotype of this species is well-figured by Kier (1984: pl. 16, figs. 4-6), and has a similar globose form that lacks a sharply wedge-shaped profile, a more anterior apical system, and long petals. However, ambulacrum II and IV of *S. cartagensis* are more divergent and less sinuous than *S. carlsoni* n. sp.

The fossil record of Jamaica shares *S. bathypetalus* and *O. subcylindricus* with Cuba, and also includes the following species: *S. altissimus* Clark, in Arnold and Clark, 1927, from the Eocene; *S. dumblei* Israelsky, 1924, which was initially described from Mexico; however, Kier (1984) thought the specimens Arnold and Clark (1927) documented from Jamaica are likely *O. subcylindricus*, though Donovan (2003) did not entirely agree, and *S. hexagonalis* Clark, 1927, from the Eocene. Specimens described from Jamaica, but no longer recognized in *Schizaster*, are *S. dyscritus* Clark, in Arnold and Clark, 1927, which was moved to *Caribbaster* by Kier (1984), and *S. brachypetalus* Clark, in Arnold and Clark, 1927, which Kier (1984) demonstrated is a synonym of *O. subcylindricus*. Of these taxa, *S. carlsoni* n. sp. can only be confused with *S. bathypetalus*, which as mentioned above, also occurs in the Eocene of Cuba.

Schizaster bathypetalus is figured by Arnold and Clark (1927: pl. 12, figs. 1-4), and Kier (1984: pl. 15, fig. 2) persuasively figured the holotype (MCZ 3294). Kier (1984) reasonably placed *Schizaster gigas* Sánchez-Roig, 1953c and *Schizaster pentagonalis* Sánchez-Roig, 1953c in synonymy with *S. bathypetalus*. *Schizaster carlsoni* n. sp. can be distinguished from the type of *S. bathypetalus* by its proportionately shorter posterior petals. Kier noted the holotype of *S. bathypetalus* has posterior petals 34% TL, whereas in *S. carlsoni* n. sp., they range from 20-25% TL (21.9 % TL average). Furthermore, Clark (in Arnold and Clark, 1927), stated TW is practically equal to TL on *S. bathypetalus*, but in *S. carlsoni* n. sp., TW is on average 90% TL.

Cotteau (1875) described the previously discussed *O. subcylindricus* from the Eocene of St. Bartholomew, but he also named *S. antillarum* Cotteau, 1875, from St. Barts, as well as *S. clevei* Cotteau, 1875, from the Oligocene of Antigua and Anguilla, and *S. loveni* Cotteau, 1875, from Anguilla, which was also documented in Puerto Rico (Jackson, 1922; Gordon, 1963). *Schizaster carlsoni* n. sp. cannot be confused with any of Cotteau's species.

The fossil faunas of eastern Mexico contain the previously mentioned *S. dumblei*, which also questionably occurs in Jamaica; *S. cristatus* Jackson, 1917, from the Oligocene (*S. cristatus* was initially described from the Miocene of Panama; see below); *S. tampicoensis* Israelsky, 1924, from the Miocene, and *S. scherzeri* Gabb, 1881, originally described from the Miocene of Costa Rica (see also Dickerson and Kew, 1917). *Schizaster carlsoni* n. sp. cannot be confused with any of these Mexican species.

In addition, *S. eustatii* Engle, 1961 was described from the Pleistocene of St. Eustatius, based on a poorly preserved specimen that clearly has shorter posterior ambulacra than *S. carlsoni* n. sp., among other distinguishing features. Jackson (1917) described *S. panamensis* and *S. cristatus* from the Miocene of Panama. However, Kier (1984: 10) stated both Panamanian species are too poorly preserved for comparisons. Durham (1961) described *S. costaricensis* Durham, 1961, from the Miocene of Costa Rica. However, as well documented by Durham (1961) and Fischer (1985) this species has only two gonopores and should be reassigned to *Ova*.

Therefore, with the addition of *S. carlsoni* n. sp., *Schizaster* includes no fewer than 34 species in the Cenozoic fossil faunas of the eastern Americas and Caribbean region. However, as discussed above, many of these species are inadequately described and figured, but all readily distinguished from *S. carlsoni* n. sp.

Etymology.—Named in honor of Robert Carlson of St. Petersburg Florida, collector of the type material.

Material and Occurrence.—Holotype (UF 342111) and paratypes (UF 342112, UF 342113, UF 342114) from the lower beds of the Suwannee Limestone in the Vulcan Quarry, northwest of Brooksville, Hernando County (FM-IP HE038).

Family **PRENASTERIDAE** Lambert, 1905
Genus ***Agassizia*** Valenciennes, 1846

Agassizia clevei Cotteau, 1875
(Figs. 174, 175)

Agassizia clevei Cotteau, 1875. p. 33. pl. 6, figs. 2-8 (in part, not figs. 9, 10).

Agassizia floridana de Loriol, 1887. p. 398. pl. 17, figs. 9-9f.

Agassizia conradi (Bouvé). Clark and Twitchell, 1915. p. 174. pl. 81, figs. 3a-d.

Agassizia clevei (Cotteau). Jackson, 1922. p. 71. pl. 12, figs. 5-7.

Agassizia inflata Jackson. Arnold and Clark, 1927. p. 56.

Agassizia caribbeana Weisbord, 1934. p. 238. pl. 27, figs. 1-6.

Agassizia camagueyana Weisbord, 1934. p. 247. pl. 9, figs. 5,6.

Agassizia floridana (de Loriol). Cooke, 1942. p. 44. pl. 3, figs. 1-4.

Agassizia clevei (Cotteau). Sánchez-Roig, 1949. p. 256.

Agassizia avilensis Sánchez-Roig, 1949. p. 260. pl. 8, figs. 1-6.

Agassizia camagueyana (Weisbord). Sánchez-Roig, 1949. p. 253.

Agassizia floridana (de Loriol). Fischer, 1951. p. 73. pl. 6, figs. 3, 4.

Agassizia floridana (de Loriol). Cooke, 1959. p. 75. pl. 32, figs. 1-4.

Agassizia clevei (Cotteau). Gordon, 1963. p. 640. fig. 1. pl. 80, figs. 1-3.

Agassizia floridana (de Loriol). Toulmin, 1977. p. 338. pl. 64, fig. 1-3.

Agassizia clevei (Cotteau). Kier, 1984. pp. 62-65. fig. 23. pls. 29-31.

Agassizia clevei (Cotteau). Osborn et al., 2016. tbl 2.

Occurrence.—*Agassizia clevei* occurs throughout the OLS. It is commonly encountered in the upper OLS in the Brooks Quarries (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031), northwest of Marianna, Jackson County; quarry northwest of Mayo (FM-IP LF001), Lafayette County; and numerous other localities. This species is also widespread in the *Oligopygus phelani* Zone of the lower OLS, especially along the Withlacoochee River west of Yankeetown (FM-IP LV024), Levy County and along the Cross Florida Barge Canal (FM-IP CI001), south of Inglis, Citrus County. The type locality of *A. floridana* is near Gainesville (de Loriol, 1887).

This species is also found in the OLS of Georgia (Cooke, 1959), and throughout the Caribbean region. In Cuba [(type of *A. caribbeana,* Late Eocene; type of *A. camagueyana*, Oligo-Miocene; and type of *A. avilensis*, Oligo-Miocene (Kier, 1984)]. In Anguilla [(type of *A. clevei,* Miocene Anguilla Formation (Cotteau, 1875; Kier, 1984)]; Puerto Rico (Gordon, 1963); and Trinidad [Eocene (Jeannet, 1928)].

Discussion.—Bouvé (1851) described *Hemiaster conradi* from Paleogene strata of Georgia. However, his brief description and sketched outlines of the specimen are not diagnostic. The test is most likely an *Agassizia* and, as it was found with *E. patelliformis* (the other species Bouvé described from the deposit), it is perhaps what is now referred to *A. clevei*. However, this cannot be determined with certainty.

De Loriol (1887) described *Agassizia floridana* from the Eocene of Florida. However, Clark and Twitchell (1915) believed *A. floridana* was a subjective junior synonym of Bouvé's *H. conradi*, which they placed in *Agassizia.* Cooke (1942: 45) invited H. L. Clark to examine Bouvé's type of *H. conradi* in the Museum of Comparative Zoology, and he notes Clark stated that specimen is "absolutely unidentifiable even to the family, let alone genus or species." Therefore, Cooke (1942) recognized de Loriol's *A. floridana* for the specimens from Florida and Georgia that he discussed. However, if Bouvé's *H. conradi* were recognizable, and verified as conspecific, it would have precedence over *A. clevei*, as well as de Loriol's (1887) *A. floridana*.

Figure 174: *Agassizia clevei* (UF 329693), 24.5 mm TL, 23 mm TW, 19 mm TH, *Oligopygus haldemani* Zone of Upper Eocene upper Ocala Limestone, Jackson County, Florida (FM-IP JA009). A: aboral. B: oral. C: left side. D: right side. E: posterior.

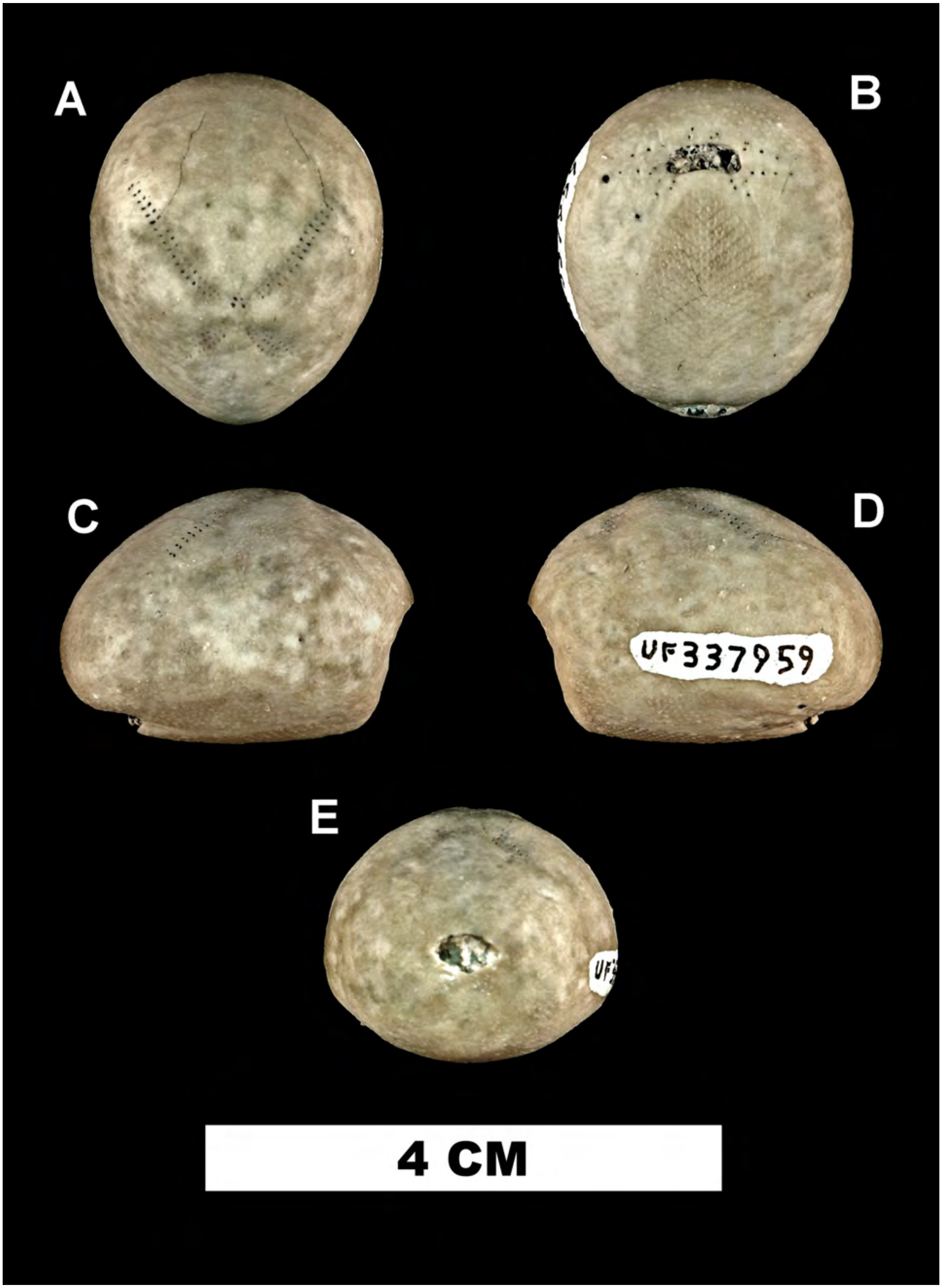


Figure 175: *Agassizia clevei* (UF 337959), 25.5 mm TL, 21.5 mm TW, 19 mm TH, *Oligopygus haldemani* Zone Upper Eocene Ocala Limestone, Sumter County, Florida (FM-IP SM010). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Kier (1984) compared the Cuban species of *Agassizia* with their North American and Caribbean region counterparts. Kier (1984) studied many specimens of *A. floridana* from the Late Eocene of Florida and could not distinguish them from the types of *A. clevei* from Anguilla. He searched for differences with particular care because the Florida specimens are Eocene and those from Anguilla are Miocene, and he acknowledged that echinoids do not commonly have such a wide stratigraphic range. However, he could find no substantive differences. He therefore considered *A. floridana* a subjective junior synonym of *A. clevei*.

Cooke (1942, 1959) considered *A. inflata* Jackson, 1922 and *A. egozcuei* Lambert, 1925, from the Eocene of St. Bartholomew, to be synonyms of *A. floridana*. Kier (1984) asserted that *A. egozcuei* is a synonym of *A. inflata*, also stating that *A. inflata* can be distinguished from *A. clevei* by its more anterior apical system and possession of a few enlarged pore pairs in the anterior poriferous zone. He stated that in none of the 17 specimens of *A. floridana* (= *A. clevei*) he examined were large pore pairs present in the anterior poriferous zones.

Within the eastern United States, *A. clevei* is most found in the Upper Eocene OLS of Florida where it is a consistent presence in the *Oligopygus haldemani* Zone, but also occurs more rarely in the overlying *Oligopygus wetherbyi* Zone, as well as in the underlying *Oligopygus phelani* Zone in Citrus and Levy Counties. It is much more rarely represented in the equivalent strata in southwestern Georgia. The species is typically small but can reach significant size, the largest specimen in the USNM, from the Steinhatchee River in Florida, being 36 mm TL, 34 mm TW, and 28 mm TH (Cooke, 1942).

Agassizia mossomi Cooke, 1942
(Figs. 176, 177)

Agassizia (*Anisaster*) *mossomi* Cooke, 1942. p. 46. pl. 5, figs. 14-17.

Agassizia (*Anisaster*) *mossomi* (Cooke). Cooke, 1959. p. 76. pl. 32, figs. 5-9.

Agassizia mossomi (Cooke). Kier, 1997. pp. 10, 11. fig. 5. pl. 7, figs. 1-8; pl. 8, figs. 1-8.

Agassizia mossomi (Cooke). Zachos and Molineux, 2007. pp. 79-91. fig. 5e.

Agassizia mossomi (Cooke). Osborn and Ciampaglio, 2014. p. 142.

Occurrence.—Within Florida, *A. mossomi* occurs in the Lower Oligocene Suwannee Limestone at numerous localities, including quarries west of Brooksville (FM-IP HE019), Hernando County and in the Bridgeboro Limestone south of Chipley (FM-IP WG002), Washington County. The type locality is in the Suwannee Limestone at the Florida Rock Products Quarry southwest of Brooksville, Hernando County. It is perhaps most abundant in the Suwannee Limestone at the Terramar Quarry in Polk County (FM-IP PO017).

This species is more commonly found in the Oligocene of Alabama (Cooke, 1959; Osborn and Ciampaglio, 2014), Georgia (Cooke, 1959), Mississippi (Cooke, 1959), North Carolina (Kier, 1997), and Texas (Zachos and Molineux, 2007).

Discussion.—Although Cooke (1942) documented this species from the Lower Oligocene Suwannee Limestone of Florida, it has since been proven to be more widely distributed in the region. *Agassizia mossomi* occurs throughout nearly the entire extent (both geographically and stratigraphically) of the Oligocene strata of the region, from the Lower Oligocene Marianna Limestone of the Gulf Coast to the Upper Oligocene Chickasawhay Limestone of Alabama and River Bend Formation of North Carolina.

Cooke (1959) stated that *A. mossomi* is higher and more nearly spherical, its apex is farther forward, its petals are more deeply sunken, and the anterior pores of the front pair of ambulacra are more fully developed than in *A. floridana* (= *A. clevei*) or *A. wilmingtonica* (= *A. inflata*). The presence of these pore pairs in the distal half of the anterior column of ambulacra II and IV has caused this species to be placed in the subgenus *Anisaster* by some authors (e.g., Cooke, 1959). This species cannot be confused with any echinoid documented from Oligocene deposits in the region.

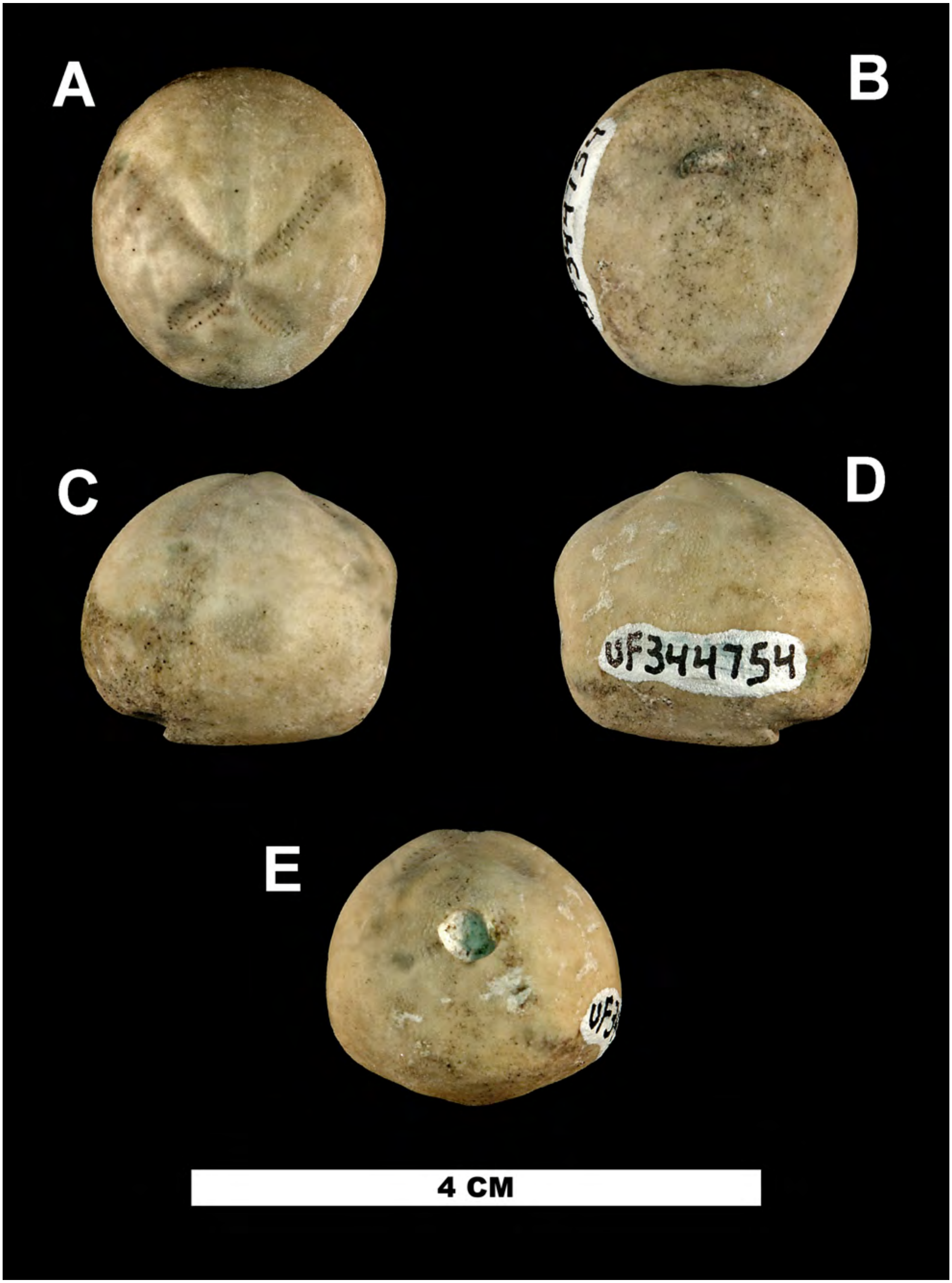


Figure 176: *Agassizia mossomi* (UF 344754), 21 mm TL, 20 mm TW, 19 mm TH, Lower Oligocene Suwannee Limestone, Polk County, Florida (FM-IP PO017). A: aboral. B: oral. C: left side. D: right side. E: posterior.

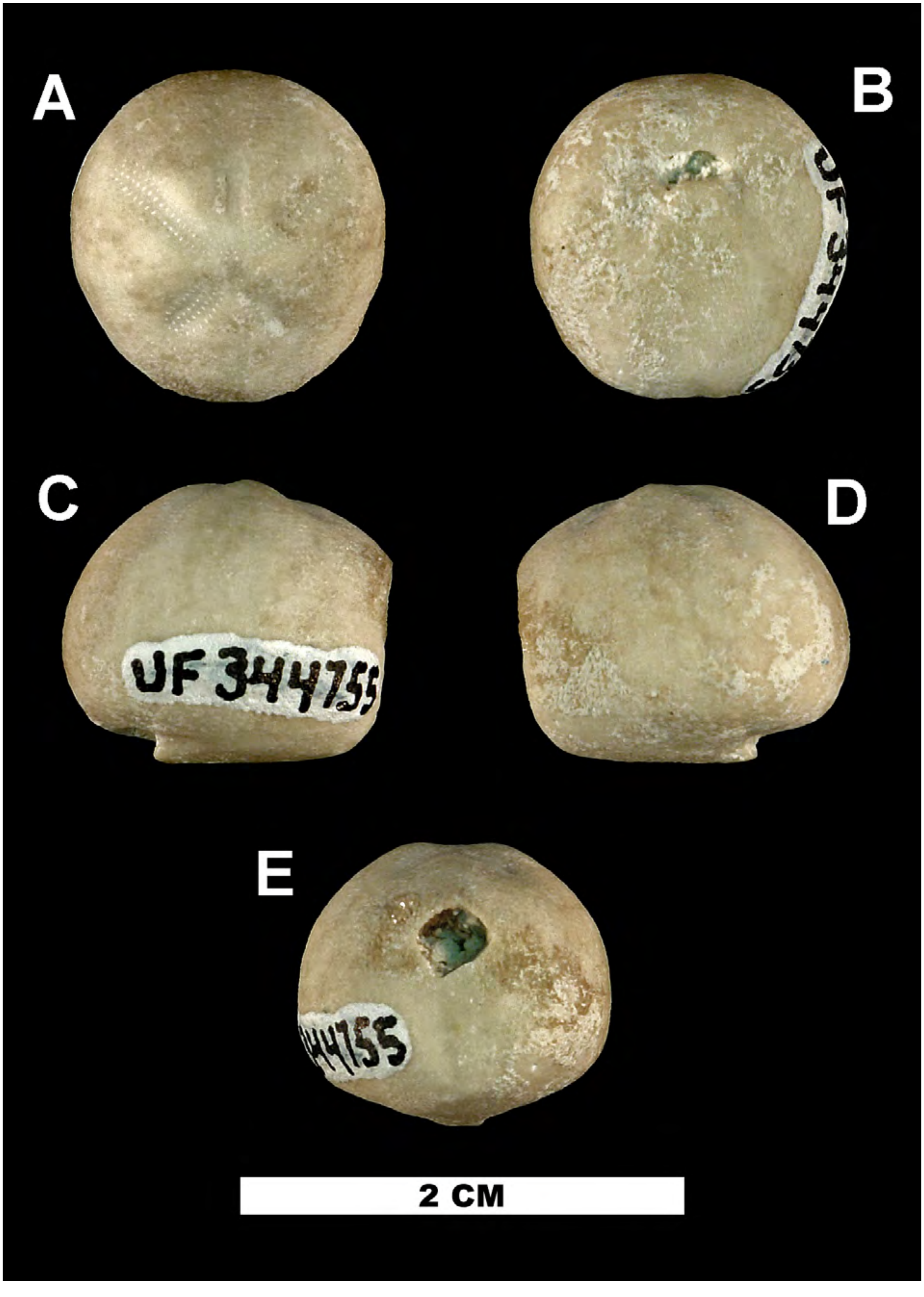


Figure 177: *Agassizia mossomi* (UF 344755), 15 mm TL, 14 mm TW, 13 mm TH, Lower Oligocene Suwannee Limestone, Polk County, Florida (FM-IP PO017). A: aboral. B: oral. C: left side. D: right side. E: posterior.

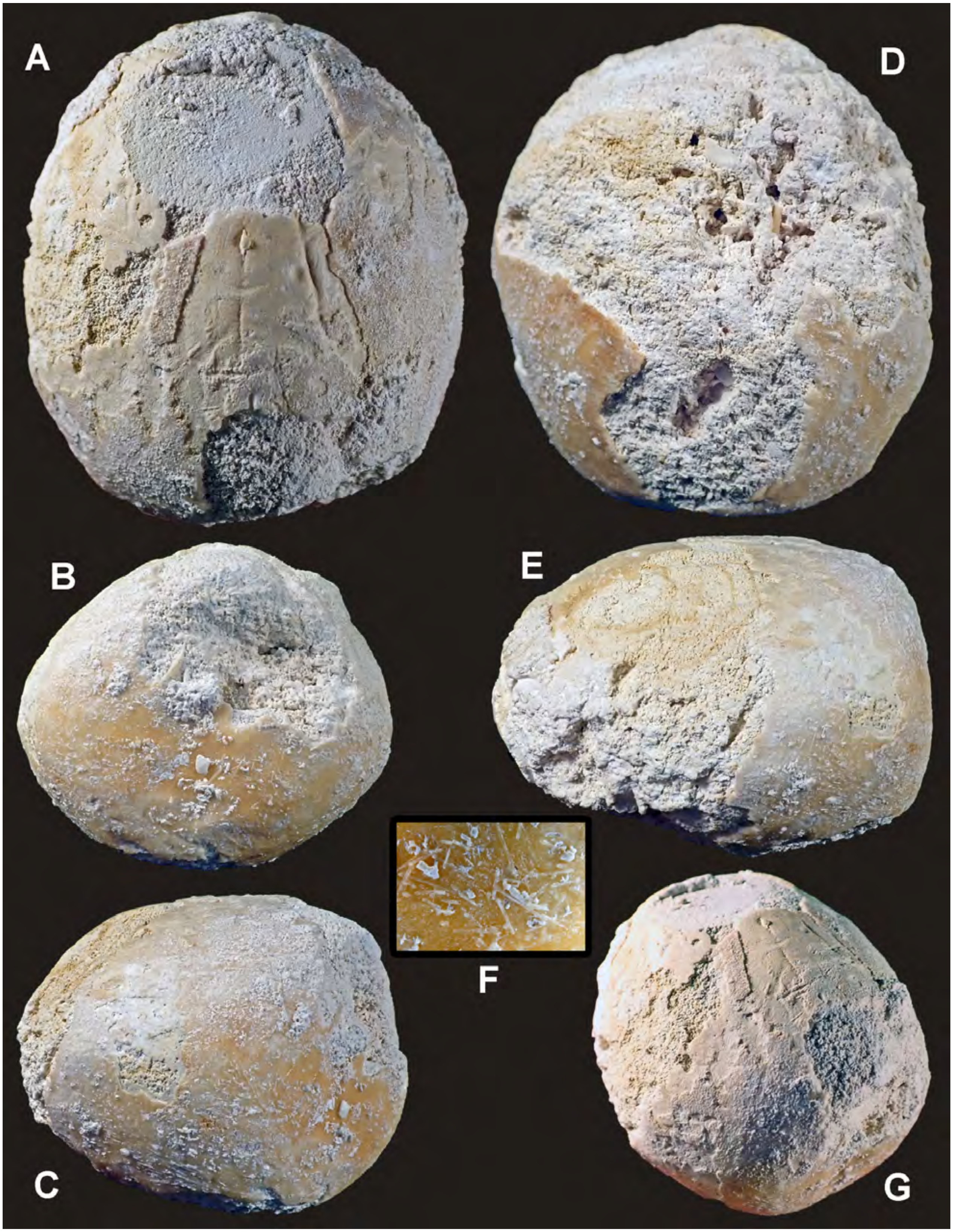


Figure 178: cf. *Prenaster* sp. (UF 337992), 64.2 mm TL, 57.4 mm TW, 49.5 mm TH, collected from the *Haimea brooksi* Zone, Upper Eocene Ocala Limestone, dredged ~80 ft. below top of unit and overlying Bumpnose Limestone, Brooks Quarry, northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: posterior. C: oblique lateral viewpoint from posterior. D: oral. E: left side. F: spines near lateral ambitus near posterior. G: oblique aboral viewpoint from posterior.

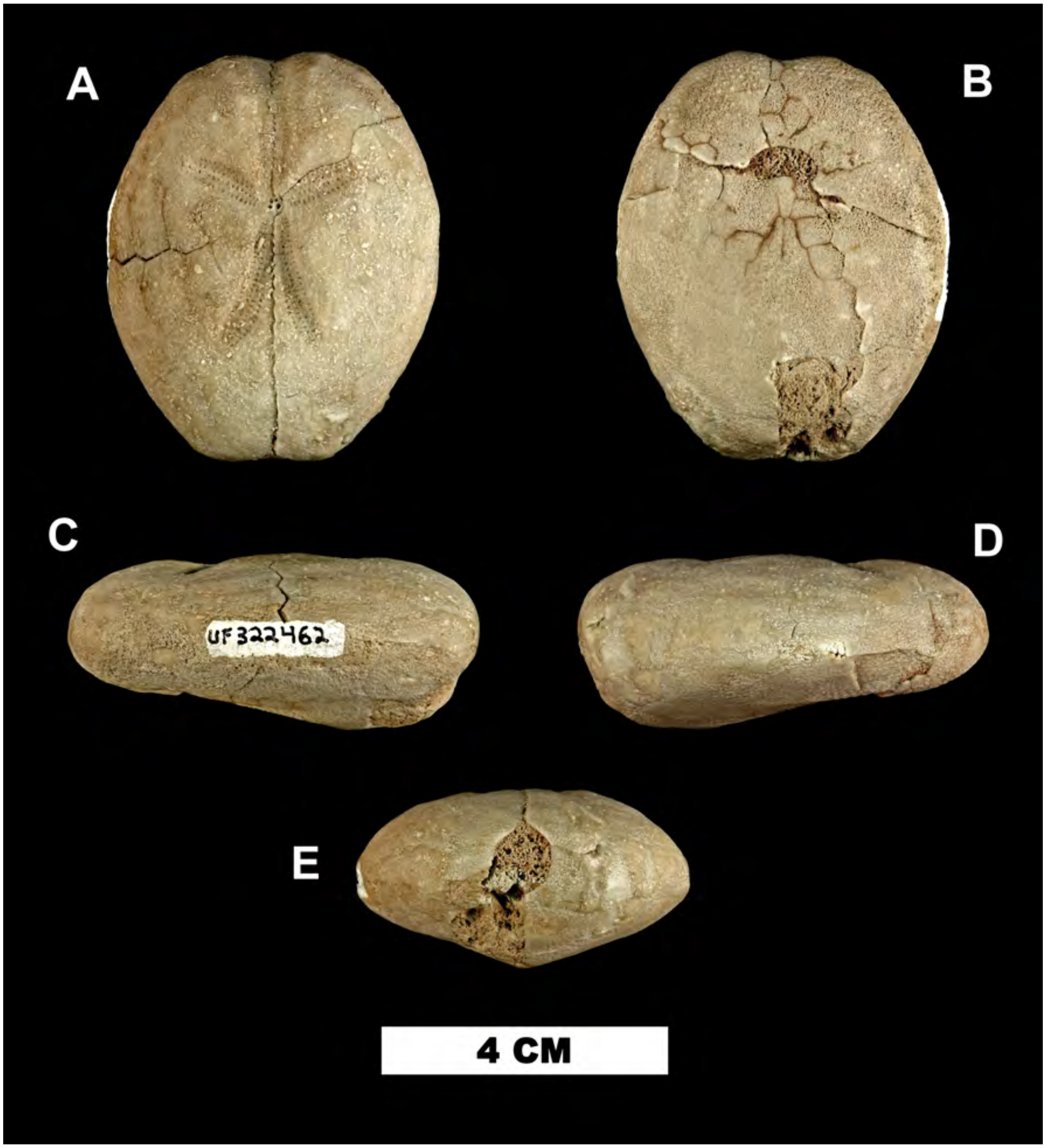


Figure 179: *Brissopsis steinhatchee* (UF 322462), 52 mm TL, 42.5 mm TW, 24 mm TH, Uppermost portion of Upper Eocene Ocala Limestone, Suwannee County, Florida (FM-IP SU002). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Genus ***Prenaster*** Desor, 1853
cf. ***Prenaster*** sp.
(Fig. 178)

Discussion.—This specimen in unlike any species currently documented from the North American echinoid faunas. It was collected in the OLS, in the *Haimea brooksi* Zone, dredged 29-30 m below the top of the Eocene exposures within the Brooks Quarry northwest of Marianna, Jackson County (FM-IP JA039). Some test is preserved, but the specimen largely consists of an internal mold of a rather large echinoid. The specimen is 64 mm TL, 57 mm TW, and 49 mm TH, although none of these measurements indicate actual dimensions of the complete test.

The specimen is rotund, with a nearly completely preserved flat posterior surface with the periproct situated high on the posterior face. The apical system is missing, but based on the pre-

Figure 180: *Brissopsis* cf. *B. steinhatchee* (UF 2122), 96.5 mm TL, 72 mm TW, 34.5 mm TH, an exceptionally large specimen, *Oligopygus phelani* Zone of Upper Eocene lower Ocala Limestone, Levy County, Florida (FM-IP 2409). A: aboral. B: oral. C: left side. D: posterior.

served portions of the ambulacra, would have been positioned far anteriorly on the aboral surface. A few spines are preserved on the posterior and oral surfaces. Faint traces of a lateroanal fasciole are discernable low on the posterior margin. We are reluctant to do any additional preparation to further expose any fascioles given the incompleteness of the test, particularly considering that even if fascioles were further exposed, they would not be sufficient to determine either genus or species of the specimen. We likewise prefer not to risk removal of any of the preserved spines.

What is preserved of the specimen is not distinguishable from *Prenaster*, especially the general test shape and very anterior apical system. The specimen is most like *Prenaster jeanneti* Pijpers, 1933, from the Eocene of Bonaire, which was well figured by Kier (1984: pl. 41, figs. 6-8). The Florida specimen is slightly larger than the maximum size of 52 mm TL, 45 mm TW of *P. jeanneti*.

If additional material is collected that enables the genus identification of *Prenaster* to be confirmed, this is the first documentation of *Prenaster* on mainland North America. However, it is represented in the Eocene of Bonaire, as discussed above, and by five species in the Cuban Eocene faunas: *P. clarcki* Sánchez Roig, 1949 [which Kier (1984) corrected to *P. clarki*], *P. elongatus* Sánchez Roig, 1949, and *P. sanchezi* Lambert, in Sánchez Roig, 1949 [Kier (1984) asserted these three species were unrecognizable]; *P. nuevitasensis* Sánchez Roig, 1949 (which was transferred to *Aguayoaster* by Zitt, 1981), and *P. parvus* Palmer, in Sánchez Roig, 1949, which Kier (1984) redescribed and is readily distinguishable from this specimen. Given the presence of *Prenaster* in the Cuban faunas, its presence in the Florida Eocene would not be surprising.

Carolinaster varnami Osborn et al., 2016 is comparable in general prenasterid features to the Florida specimen. However, without further information concerning genus features of cf. *Prenaster* sp., notably the number of gonopores, it is not certain that the two forms are congeneric, let alone conspecific.

Chesher (1968) described *Saviniaster enodatus*, which has subsequently been placed in *Prenaster*, from the modern faunas off the Bahama Islands. Thus, the genus is known from regional waters today.

Suborder **BRISSIDINA** Kroh and Smith, 2010
Family **BRISSIDAE** Gray, 1855
Genus ***Brissopsis*** L. Agassiz, 1840

Brissopsis steinhatchee Cooke, 1942
(Figs. 179, 180)

Brissopsis steinhatchee Cooke, 1942. p. 49. pl. 5, figs. 29-32.

Brissopsis steinhatchee (Cooke) Cooke, 1945. p. 61, fig. 6, no. 4 (after Cooke, 1942).

not *Brissopsis biarritzensis* (Cotteau). Cooke, 1959. p. 85. pl. 38, figs. 14-18 (in part, specimen figured is *B. steinhatchee*).

Brissopsis steinhatchee (Cooke). Cooke, 1959. p. 85. pl. 38, figs. 9-13.

Brissopsis steinhatchee (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—This species occurs throughout the OLS of Florida but is most commonly found in the upper portion of the unit in association with *W. eldridgei*. Localities include that of the type, in a pit near the Steinhatchee River east of Clara, Dixie County; north of Branford, Suwannee County (FM-IP SU002); northwest of Mayo (FM-IP LF001), Lafayette County; and south of Tennille (FM-IP DI001), Dixie County. *Brissopsis steinhatchee* is much rarer in the lower OLS where it occurs along the Cross Florida Barge Canal south of Inglis (FM-IP CI001), Levy County.

This species rarely occurs in the OLS of Alabama (Cooke, 1959).

Discussion.—*Brissopsis steinhatchee* is most abundant near the top of the OLS, where it occurs in the *Wythella eldridgei* Zone with *S. armiger, P. dixie, O. beckeri, R. trojana,* and other, rarer species. In Jackson County, the species rarely occurs in the *Oligopygus haldemani* Zone, and it is even rarer near the base of the OLS in the *Oligopygus phelani* Zone.

Cooke (1959) discussed and figured a specimen of *Brissopsis* from the "OLS", likely strata now referred to the Shubuta Member of the Yazoo Clay of Monroe County, Alabama that he referred to *Brissopsis biarritzensis* Cotteau, 1884. The latter was described from the Eocene Lou Cout, Villa Eugenie near Biarritz, France. The specimens Cooke (1959) described (USNM 562454a, b) have anterior petals that were less divergent than in the two specimens of *B. steinhatchee* he had available for study (the holotype and paratype). Carter et al. (1989) stated that the figures of the specimen provided by Cooke (1959) display a specimen no less similar to *B. steinhatchee* than to the figures of *B. biarritzensis* in Cahuzac and Roman (1984) and that the specimen may simply be a variant of *B. steinhatchee*. We agree, as additional specimens of *B. steinhatchee* reveal that the specimen figured by Cooke (1959: pl. 38, figs. 14-18) falls within the variability of *B. steinhatchee* displayed in specimens from the type area of Dixie County, Florida. The species is now known to show a greater degree of variability in divergence of ambulacra I and V, as well as ambulacra II and IV than was understood from the two specimens Cooke had available for study.

The largest specimen available (UF 2122) is from the *Oligopygus phelani* Zone at the Cross Florida Barge Canal (FM-IP 2409) and measures 96.5 mm TL, 72.1 mm TW, 34.4 mm TH (Fig. 180).

cf. ***Brissopsis*** sp.
(Fig. 181)

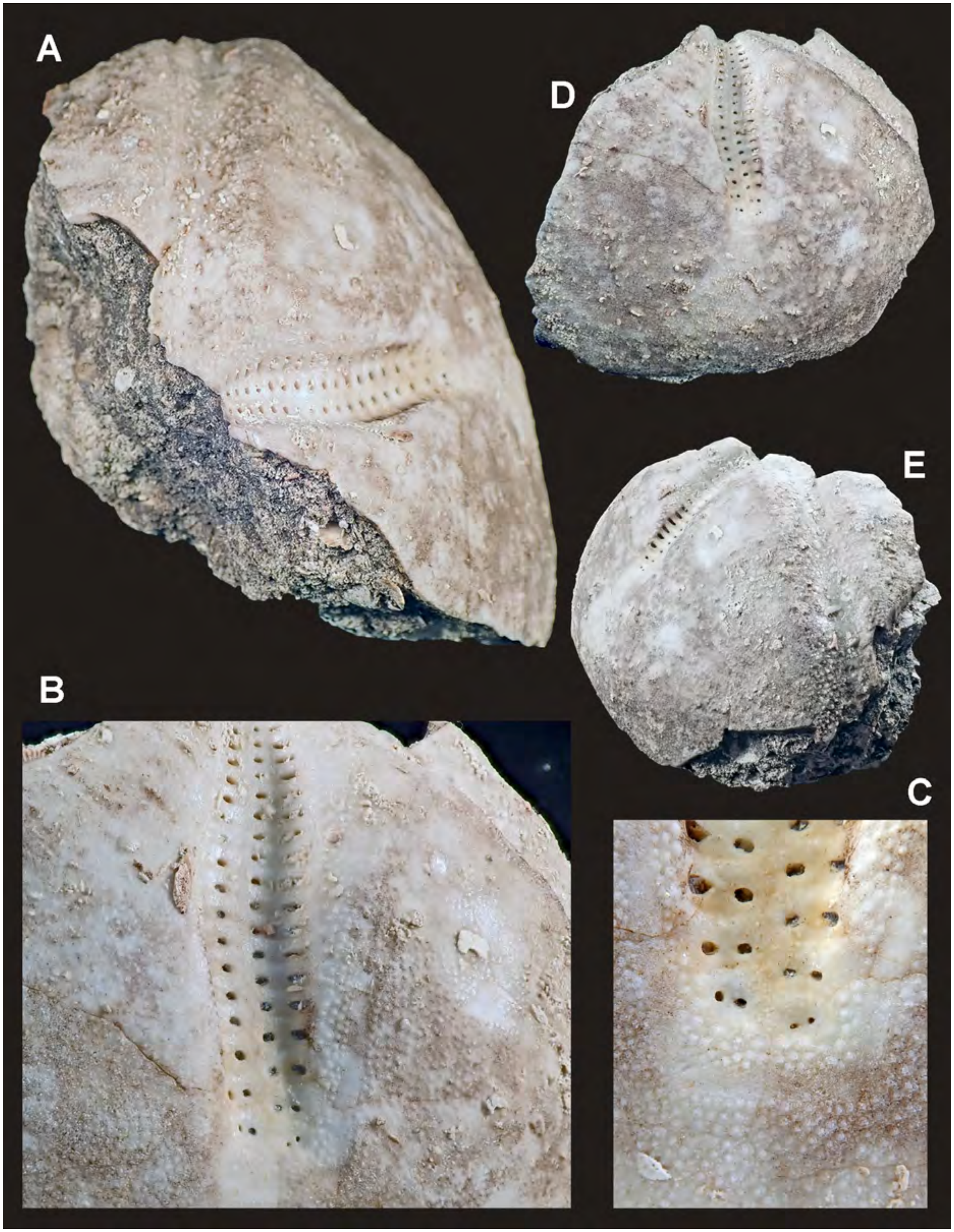


Figure 181: cf. *Brissopsis* sp. (UF 337993) portion of ambulacra II and III of a large spatangoid that cannot be attributed to any known taxa from the region. The specimen has a peripetalous fasciole that very closely follows the ambulacra and is very similar to the genus *Brissopsis*; thus, the generic attribution questionably assigned herein. Specimen measures: 72.9 mm TL, 52.2 mm TW, 46.4 mm TH, though none of the measurements are complete, *Wythella eldridgei* Zone at the top of the Upper Eocene, upper Ocala Limestone, quarry west of Dowling Park, Lafayette County, Florida (FM-IP LF002) A: aboral. B, C: petaloid portion of ambulacrum II, note how tightly the peripetalous fasciole follows the ambulacrum. D: oblique lateral viewpoint. E: oblique posterior viewpoint.

Discussion.—This specimen consists of approximately a posterior quarter of the test, with portions of ambulacra II and III, of what would have been a very large spatangoid, measuring 73 mm TL, 52 mm TW, and 46 mm TH. Given its incompleteness, none of these measurements reflects its true dimensions. The specimen was collected with *W. eldridgei* from the uppermost bed of the OLS (*Rotularia vernoni* Zone) west of Dowling Park, Lafayette County (FM-IP LF002). Although the specimen is incomplete, enough is preserved to determine that it does not belong to any species currently known from the Paleogene faunas of the region. However, it remains impossible to attribute it to any named species from the fossil faunas of the remainder of the eastern Americas.

The specimen is very similar to *Brissopsis* in that it has a peripetalous fasciole that closely follows the ambulacra. Therefore, it is conditionally assigned to *Brissopsis*. If this is a *Brissopsis*, it is significantly larger than any documented specimens of *B. steinhatchee*, the only Eocene representative of the genus in the eastern United States. The largest specimen of *B. steinhatchee* (UF 2122: Fig. 180) is 96 mm in length. Given similar proportions, and conservatively estimating that this specimen shows less than 50% of its TL, it would have exceeded 145 mm in length.

Genus ***Brissus*** Gray, 1825

Brissus bridgeboroensis Carter, 1987b
(Fig. 182)

Brissus bridgeboroensis Carter, 1987b. pp. 1043-1046.

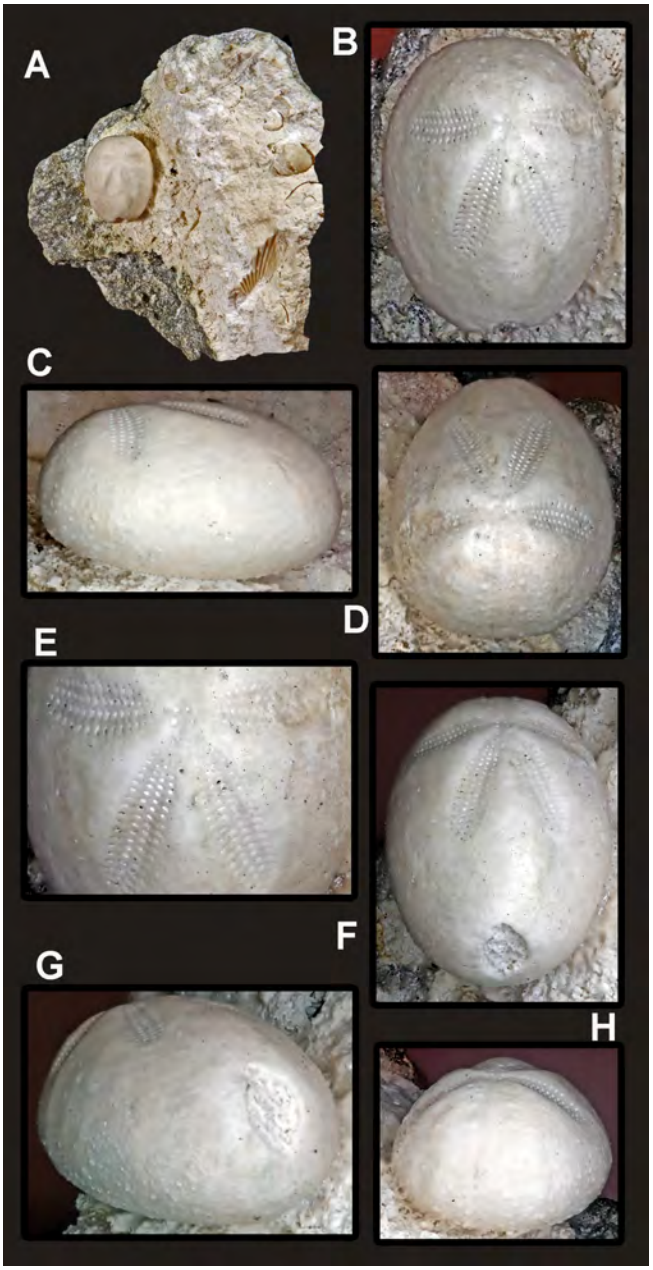


Figure 182: *Brissus* cf. *B. bridgeboroensis* (UF 342093), 19.9 mm TL, Lower Oligocene Suwannee Limestone, Sunwest Mine, west of Aripeka, Florida (FM-IP PA010). A: specimen in matrix. B: aboral. C: left side. D: tilted aboral viewpoint from anterior. E: petaloid area with apical system. F: tilted aboral viewpoint from posterior. G: posterior. H: anterior.

Occurrence.—Suwannee Limestone, Sunwest Mine, southwest of Aripeka, Pasco County. This species is also documented from the Bridgeboro Limestone near Florala, Covington County, Alabama, and southwest of Bridgeboro, Mitchell County, Georgia (the type locality).

Discussion.—Carter (1987b) described *B. bridgeboroensis* from a single specimen collected in the Lower Oligocene Bridgeboro Limestone of Mitchell County, Georgia. He differentiated it from the extant *B. unicolor* by its longer posterior petals, fewer pore pairs in the paired petals, its apical system closer to the anterior margin, and complete lack of a dorsal keel in interambulacrum 5 (Carter, 1987b).

Heller and Bryan (1992) subsequently documented the occurrence of *B. bridgeboroensis* at Huddlestun's (1993) type locality for the Florala Member of the Bridgeboro Limestone in Covington County, Alabama.

This is the first record of the species both outside of the Bridgeboro Limestone, and within Florida. The occurrence of this single, small (20 mm TL) specimen from Aripeka expands the distribution of the species geographically southward and stratigraphically upward into the Suwannee Limestone.

Zachos and Molineux (2007) documented imperfect specimens of a *Brissus* from Oligocene strata at Damon Mound, Brazoria County, Texas which they attributed to *Brissus exiguus* Cotteau, 1875 [which Cooke (1961) synonymized with *B. unicolor*]. They stated that *B. bridgeboroensis* differed from the specimens from Damon Mound in having a much more anteriorly eccentric apical system and a greater divergence of the anterior paired ambulacra (these differences are not evident in the specimens figured). However, they did not further describe, provide measurements of, or further discuss the specimens and conspecificity cannot be ruled out. Until additional specimens of *B. bridgeboroensis* are available for comparison, the variability within the species remains largely unknown.

Brissus jonesi n. sp.

(Figs. 183-187)

Diagnosis.—*Brissus* with large ovate periproct; periproct width on average 60.8% periproct height; periproct height on average 35.1% TL and 54.5% TH and center of apical system on average 70.2 % TL from posterior margin; 77.1% TL in holotype.

Description.—Description based on the holotype (UF 342106) and four paratypes (UF 342107, UF 341761, UF 341762, UF 341765). Test small to moderately sized, largest complete specimen designated the holotype (37.7 mm TL, 30.7 mm TW, 24.1 mm TH); largest specimen is paratype UF 341765: approximately 45 mm TL (posterior missing so the specimen could be much larger), 43.3 mm TW, 33.7 mm TH; smallest is paratype UF 341761 (12.0 mm TL, 9.6 mm TW, 7.8 mm TH); TW 81.4% TL in holotype, average 82.3%; TH 63.9% TL in holotype, average 66.2%; greatest TW posterior of apical system, greatest TH posterior. Test ovate, narrows posteriorly in holotype, less so in smaller specimens. Anterior abrupt and nearly vertical in holotype, more gently rounded in smaller specimens. Posterior ambitus above periproct in holotype, angles sharply anteriorly towards oral surface, less angled in smaller specimens. Aboral surface gently rounded in smaller specimens, raised medially in holotype. Test covered with relatively evenly dispersed, small tubercles, more pronounced in smaller specimens.

Apical system anterior, center of apical system 77.1% TL from posterior margin in holotype, more posterior in smaller specimens: 69.8 % TL in specimen 20.9 mm TL, 63.7% TL in specimen 12.0 mm TL; center of apical system on average 70.2 % TL from posterior margin; apical system ethmolytic; 4 gonopores.

Ambulacrum III not petaloid, in very shallow depression from apical system to peristome, pores minute; ambulacra II and IV transverse, nearly forming 180° angle to each other; ambulacra I, II, IV, and V in deep grooves in holotype, shallower depressions in smaller paratypes; petals of ambulacrum I and V longest: on average 43.7% TL in holotype, proportionately shorter in smaller specimens: average 37.3% TL, extending two-thirds distance to ambitus; petals of ambulacrum II and IV on average 29.3% TL in holotype, average 25.3% TL; extending nearly to ambitus. Petals narrow, ambulacrals I and V width on average 20% petal length; petal II and IV width on average 25.7% petal length; interporiferous zones moderately narrow; inner pore circular, outer pore elongate, pores conjugate; petals closed distally.

Periproct very large, inframarginal, high on overhanging posterior truncation; higher than wide; periproct height on average 35.1% TL and 54.5% TH; periproct width on average 60.8% periproct height. Peristome anterior, posterior edge of peristome on average 66.9% TL from posterior margin; peristome large, wider than high; peristome height on average 42% peristome width; labrum very short;

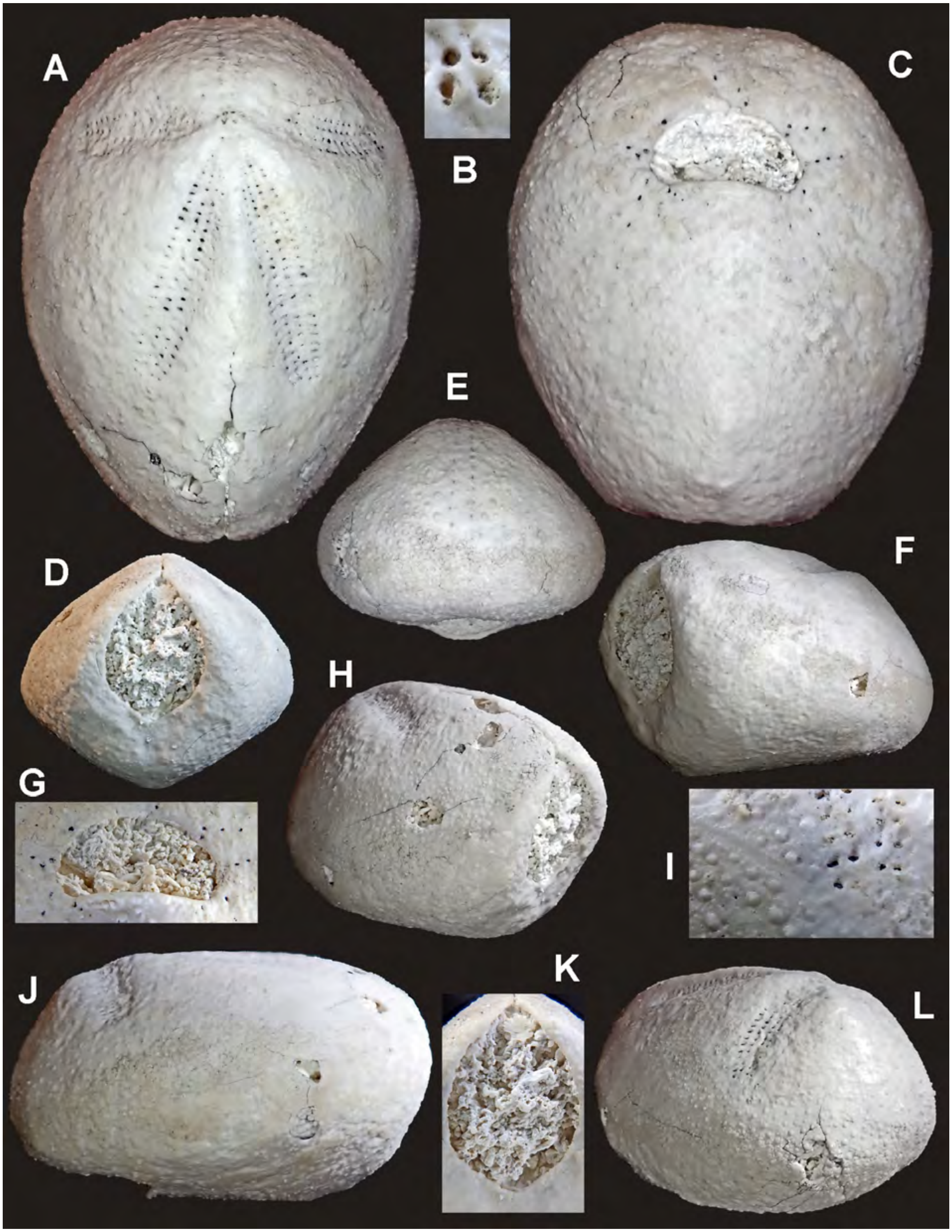


Figure 183: *Brissus jonesi* n. sp., holotype (UF 342106), 37.7 mm TL, 30.7 mm TW, 24.1 mm TH, Upper Eocene, *Haimea brooksi* Zone of the Ocala Limestone, Brooks Quarry northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: apical area. C: oral. D: posterior. E: anterior. F: oblique lateral viewpoint from posterior. G: peristome. H: oblique lateral viewpoint from posterior. I: peripetalous fasciole and distal end of petal of ambulacrum II. J: left side. K: periproct. L: oblique lateral viewpoint from anterior.

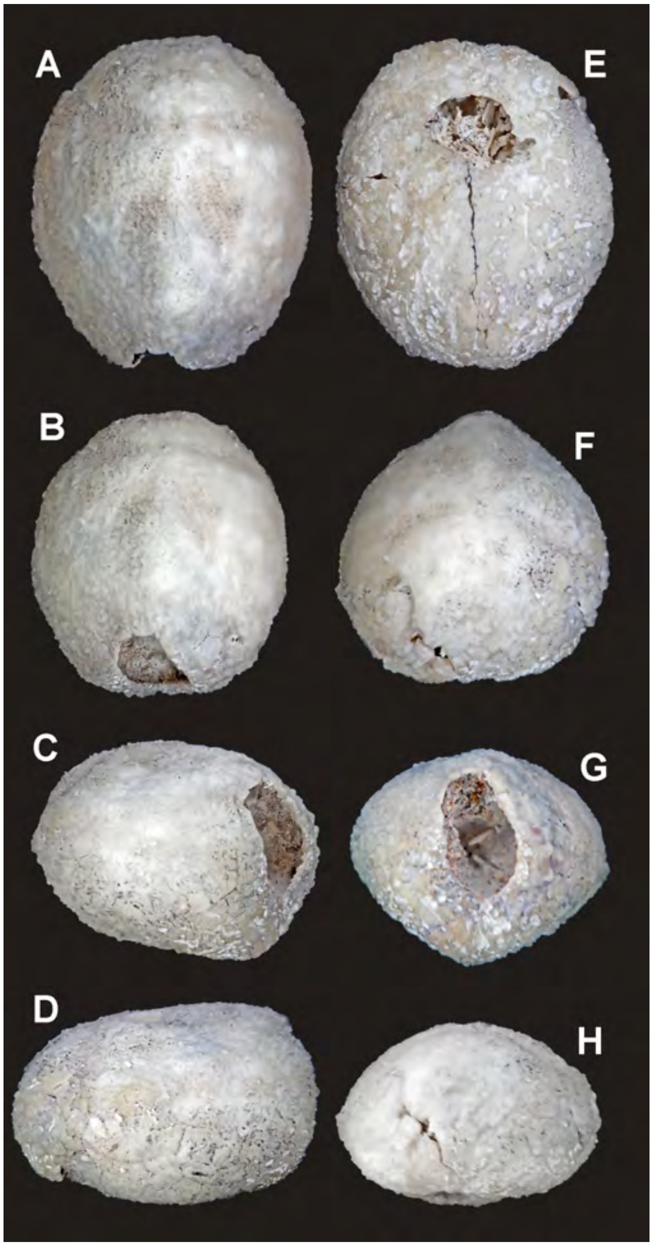


Figure 184: *Brissus jonesi* n. sp., paratype (UF 342107), 20.9 mm TL, 17.9 mm TW, 14.6 mm TH, a very corroded specimen lacking most surface details, Upper Eocene, *Haimea brooksi* Zone of the Ocala Limestone, Brooks Quarry northwest of Marianna, Jackson County, Florida (FM-IP JA039). A: aboral. B: tilted aboral viewpoint from posterior. C: oblique lateral viewpoint from posterior. D: left side. E: oral. F: tilted aboral viewpoint from anterior. G: posterior. H: anterior.

plastron long and wide, bowed outward medially.

Due to weathering, only short traces of fascioles preserved; peripetalous and subanal fascioles present. Peripetalous fasciole moderately indented in interambulacrum 5; not otherwise preserved but presumably indented in all 5 interambulacra. Subanal fasciole not completely preserved; consistent with being bilobed.

Zoobank Nomenclatural Act.—BDC07B8D-897C-45DD-B552-371BA875A472

Discussion.—*Brissus jonesi* n. sp. is the first species of *Brissus* described from the Eocene of the eastern United States. It is unknown outside of Jackson County, Florida, where it occurs in the OLS dredged from 24 m below the top of the Eocene in the Brooks Quarry (FM-IP JA039) west of Marianna, in a horizon of *Asterocyclina*-rich limestone with a diverse echinoid assemblage that includes *H. brooksi, O. haldemani, O. rotundus, W. johnsoni, R. georgiensis, R. mariannaensis* n. sp., and other, rarer species (Table 1; Fig. 6). Brooks Quarry is the type locality of the species. However, paratypes were also obtained from the same horizon (with *H. brooksi*) in Jackson Blue Spring east of Marianna, at a depth of 26-27 m (FM-IP JA033).

The holotype (UF 342106) and paratype (UF 342107) from Brooks Quarry (FM-IP JA039) are complete. However, only one (UF 341761) of the three paratypes from Jackson Blue Spring (FM-IP JA039) retains the posterior portion of the test. The posterior portion of the two complete paratypes is hollow and exceptionally fragile because the sediment that infilled, and provided support for, the test has weathered out through the periproct. This is problematic because the holotype (37.7 mm TL) has a much more tapered posterior outline, has a steeper anterior, less rounded (steeper laterally) aboral surface, and more anterior apical area than the two smaller paratypes, which are 12.0 and 20.9 mm TL. Lacking additional complete, larger specimens, it is not possible to verify if this represents typical ontogenetic narrowing of the posterior end of the test, movement of the apical area anteriorly, and development of a steeper anterior end or if these features are unique to the holotype.

Though *Brissus* is well documented in the global fossil record from the Eocene to Pleistocene strata, it is relatively rare in both the fossil record and modern fauna in the eastern United States, being represented only by the Oligocene *B. bridgeboroensis*, Pliocene *B. glenni,* and extant *B. unicolor*.

The fossil faunas of the Caribbean region also include *B. exiguus*, from the Miocene of Anguilla,

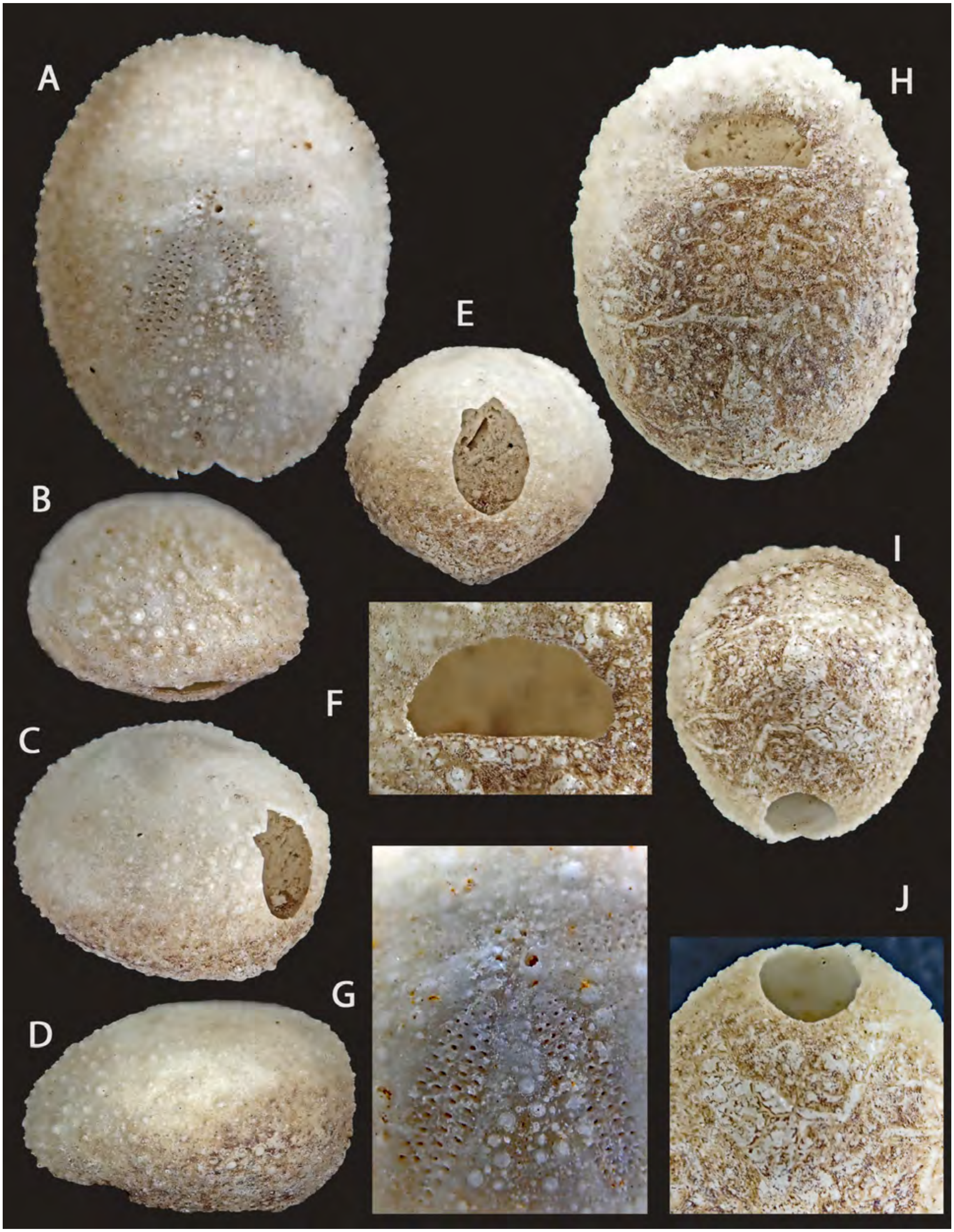


Figure 185: *Brissus jonesi* n. sp., paratype (UF 341761), 12.0 mm TL, 9.6 mm TW, 7.8 mm TH, Upper Eocene, *Haimea brooksi* Zone of the Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033). A: aboral. B: anterior. C: oblique lateral viewpoint from posterior. D: left side. E: posterior. F: peristome. G: apical area and petaloid portion of ambulacra I and V. H: oral. I: oblique oral viewpoint from posterior. J: oblique posterior viewpoint from oral surface; no trace of subanal fasciole is preserved in this corroded and very weathered specimen.

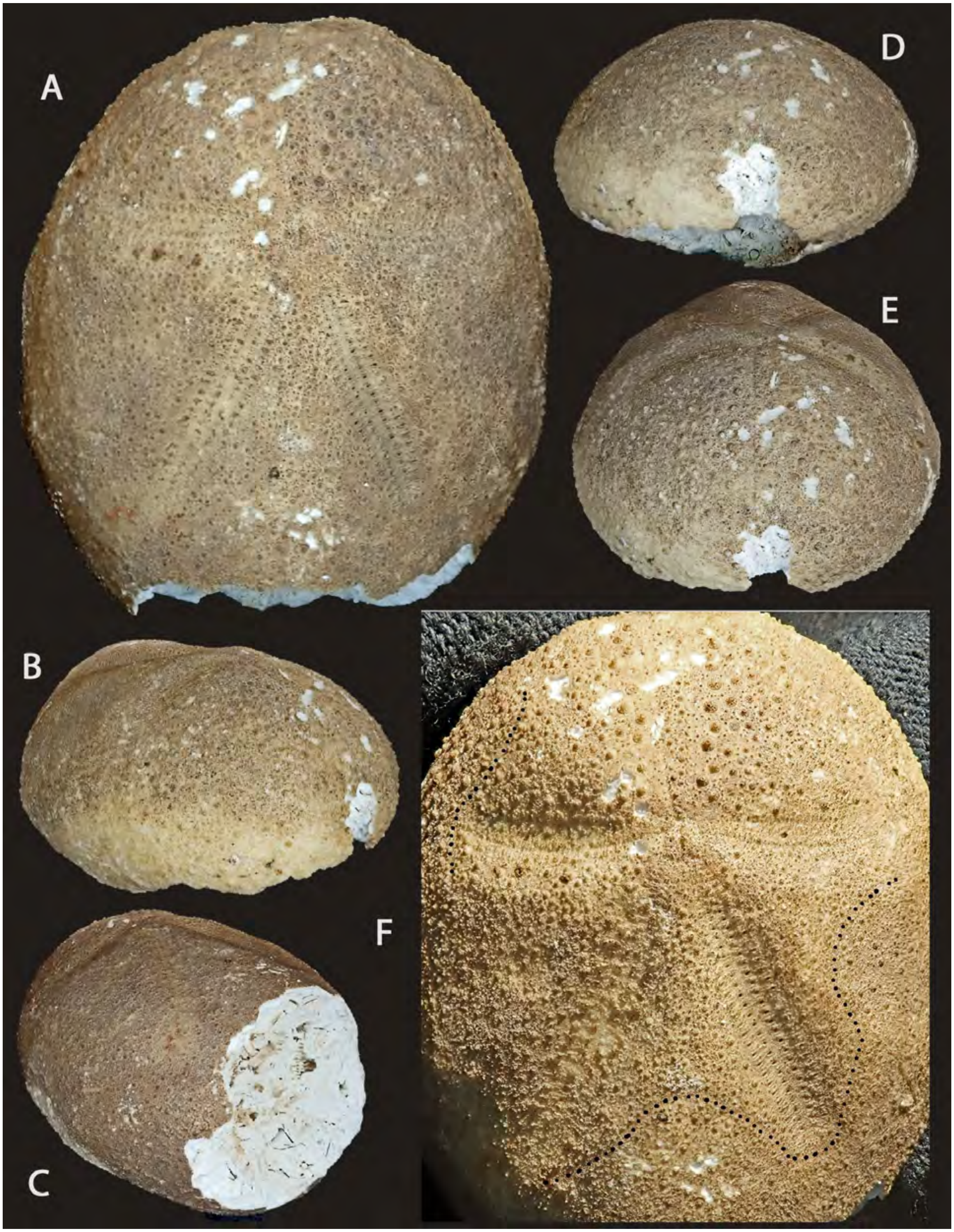


Figure 186: *Brissus jonesi* n. sp., paratype (UF 341762), 34 mm TL (incomplete), 29.3 mm TW, 21,4 mm TH, Upper Eocene, *Haimea brooksi* Zone of the Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033). A: aboral. B: oblique lateral viewpoint from anterior. C: oblique lateral viewpoint from posterior. D: anterior. E: tilted aboral viewpoint from anterior. F: aboral surface with strong cross lighting to enhance peripetalous fasciole detail; indicated with stippled line where discernable.

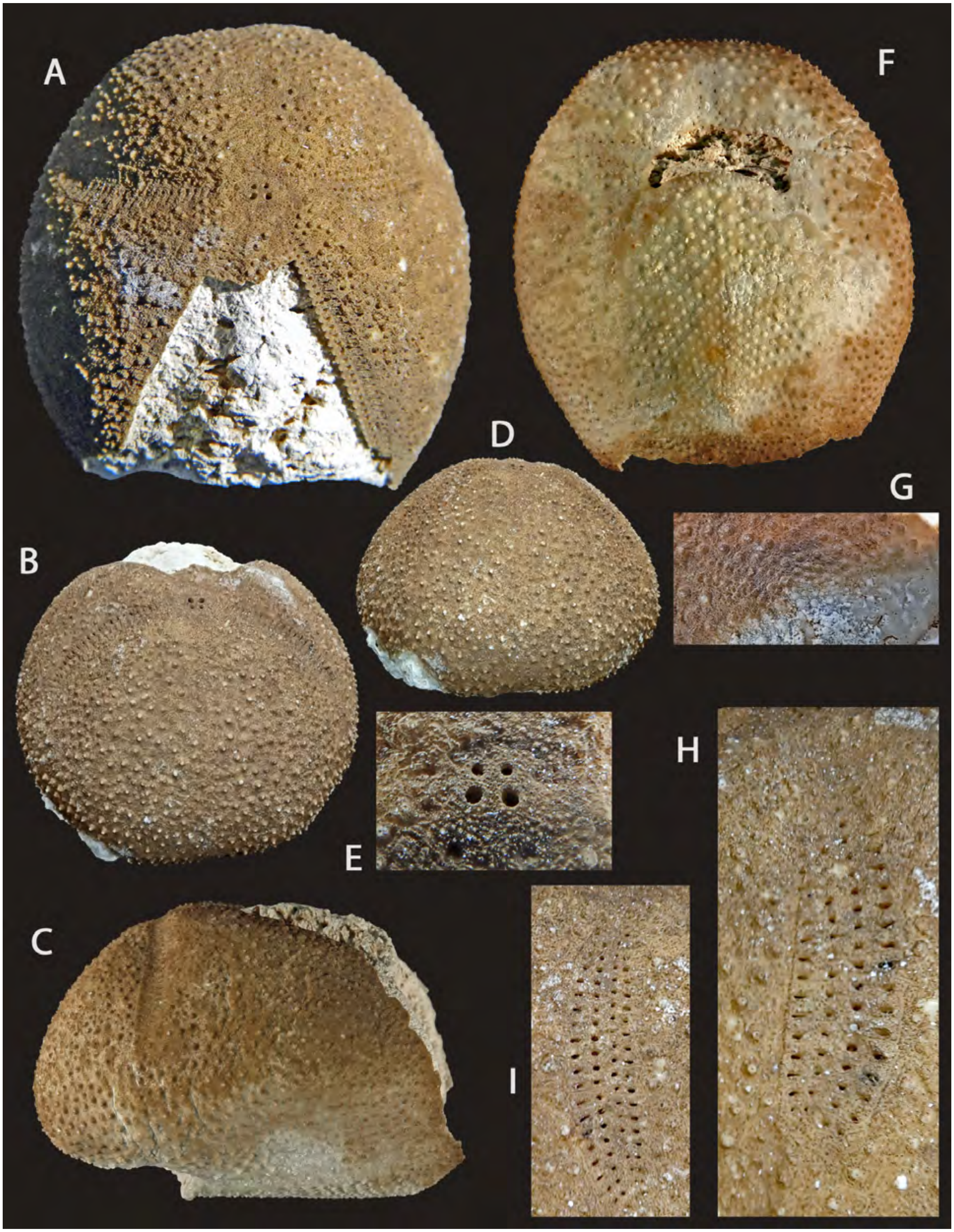


Figure 187: *Brissus jonesi* n. sp., paratype (UF 341765), 45.5 mm TL (incomplete), 43.3 mm TW, 33.7 mm TH (incomplete), Upper Eocene *Haimea brooksi* Zone of the Ocala Limestone, Jackson Blue Spring, Jackson County, Florida (FM-IP JA033. A: aboral. B: tilted aboral viewpoint from anterior. C: left side. D: posterior. E: apical area. F, G: oral; posterior end is largely missing but anterior portion of subanal fasciole is preserved, indicated by stippling. H: petaloid portion of ambulacrum IV. I: petaloid portion of ambulacrum II.

which, as noted by Kier (1984: 81), is based on two deformed specimens that make it difficult to be certain of diagnostic characters. Cooke (1961) considered *B. exiguus* a subjective junior synonym of *B. unicolor*. *Brissus jonesi* n. sp. cannot be confused with *B. exiguus*.

Kier (1984) recognized, redescribed, and figured five species of *Brissus* in the Cuban Cenozoic faunas: *B. cabrerai* (Sánchez-Roig, 1953c); *B. camagueyensis* Weisbord, 1934; *B. caobaense* Sánchez-Roig, 1953b; *B. durhami* (Sánchez-Roig, 1952a), and *B. minutus* Sánchez-Roig, 1949. In addition, Kier (1984) noted that Sánchez-Roig (1949) reported a specimen of *B. unicolor* from the Pleistocene of Cuba, but the specimen is no longer available for study. Of these, *Brissus jonesi* n. sp. is most similar to *B. caobaense* from the Cuban Eocene, but the two species are readily distinguished by the greater height of *B. jonesi* n. sp. (63.9-69.8% TL vs 49% TL in *B. caobaense*), and the much larger and proportionately narrower periproct of *B. jonesi* n. sp. (periproct height on average 35.1% TL in *B. jonesi* n. sp. and 20% in *B. caobaense*; periproct width 60% periproct height in *B. jonesi* n. sp. and 50% in *B. caobaense*).

Donovan et al. (2015) documented an assemblage of internal molds that are readily identifiable as belonging to *Brissus* from the Miocene of the Cayman Islands. They recognized the form as *Brissus* cf. *B. oblongus* Wright, 1855, noting its similarities with the form from Malta. The specimens may represent a new species, but Donovan et al. (2015) considered it best not to erect a new species based on internal molds. These specimens are not comparable to *B. jonesi* n. sp.

Etymology.—Named in honor of Douglas S. Jones, Florida Museum of Natural History Director and Invertebrate Paleontology Curator, for his many years of contributions and service.

Material and Occurrence.—Holotype UF 342106 and paratype UF 342107 from the type locality in the OLS, where it occurs with *H. brooksi* and *O. haldemani* in material dredged from 24 m below the top of the Eocene stratum in the northwesternmost pit in the quarry complex of Leon Brooks, northwest of Marianna, Jackson County, Florida (FM-IP JA039). Additional paratypes (UF 341761, UF 341762, UF 341765) are from Jackson Blue Spring east of Marianna at a depth of 26-27 m (FM-IP JA033).

Genus ***Plagiobrissus*** Pomel, 1883

Plagiobrissus curvus (Cooke, 1942)
(Fig. 188)

Eupatagus (*Plagiobrissus*) *curvus* Cooke, 1942. p. 56. pl. 7, figs. 5-7.
Eupatagus sp. Fischer, 1951. pp. 84, 85. pl. 5, fig. 5.
Plagiobrissus curvus (Cooke). Cooke, 1959. pp. 87-88. pl. 39, figs. 3-6.
Plagiobrissus curvus (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—This species is rarely encountered in the OLS of Florida. The type locality is along the Chipola River above the bridge at Marianna, Jackson County. *Plagiobrissus curvus* is also found at the nearby Brooks Quarries (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039) northwest of Marianna, Jackson County, in the *Wythella eldridgei* Zone west of Dowling Park, Lafayette County (FM-IP LF002), and northwest of Mayo (FM-IP LF001), Lafayette County, among other localities. The species is more rarely encountered in the *Oligopygus phelani* Zone of the lower OLS where Fischer (1951) documented it along the Withlacoochee River west of Yankeetown, Levy County (FM-IP LV024). It also occurs in the OLS of Georgia (Cooke, 1959; Carter and McKinney, 1992).

Discussion.—*Plagiobrissus curvus* is typically rare but widespread in the OLS. Near Marianna in Jackson County Florida, it occurs in the *Oligopygus haldemani* Zone, and in Lafayette County it occurs in the *Oligopygus wetherbyi* Zone of the upper OLS. The species is much rarer in the *Oligopygus phelani* Zone of the lower OLS (Fischer, 1951). The prominent large tubercles and curving ambulacra readily distinguish this species from other members of the genus in the region, as well as from *E. ocalanus*, with which it often occurs.

Figure 188: *Plagiobrissus curvus* (UF 322381), 93.5 mm TL, 76 mm TW, uppermost portion of Upper Eocene Ocala Limestone, Lafayette County, Florida (FM-IP LF015) A: aboral. B: oral. C: left side. D: right side.

Plagiobrissus dixie (Cooke, 1942)
(Fig. 189)

?Brissoides (*Koilospatangus*) *floridanus* (Clark). Lambert and Thiéry, 1924. p. 454.

Eupatagus (*Plagiobrissus*) *dixie* Cooke, 1942. p. 55. pl. 6, figs. 1-3.

Plagiobrissus? dixie (Cooke). Cooke, 1959. p. 87. pl. 40, figs. 1-5.

Plagiobrissus? dixie (Cooke). Toulmin, 1977. p. 345. pl.70, figs. 1-3.

Plagiobrissus dixie (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—Within Florida, *P. dixie* occurs in the upper portion of the OLS, especially the uppermost portion of the unit where it occurs in the *Wythella eldridgei* Zone. The type locality is north of Mayo, Lafayette County. The species also occurs north of Branford (FM-IP SU002), Suwannee County; northwest of Mayo (FM-IP LF001), Lafayette County; the Brooks Quarries near Marianna (FM-IP JA009, (FM-IP JA018, FM-IP JA027, FM-IP JA031), and in the Shubuta Clay of Alabama (Toulmin, 1977) and OLS of Georgia (Cooke, 1959).

Discussion.—*Plagiobrissus dixie* commonly can be found at the very top of the OLS, in the *Wythella eldridgei* Zone where it occurs with *R. trojana* and an assemblage of spatangoids that are otherwise rare in the unit, including *B. steinhatchee,*

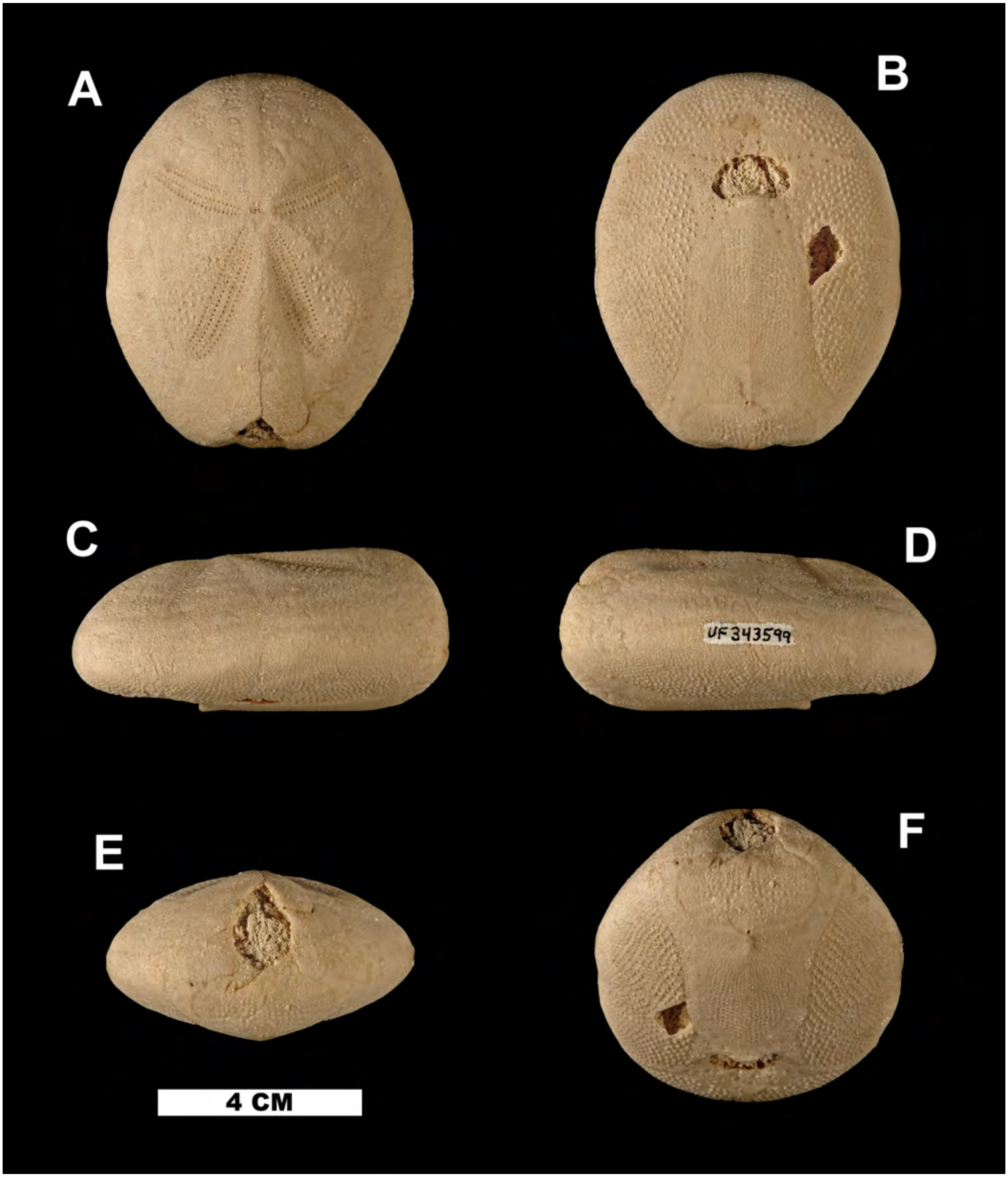


Figure 189: *Plagiobrissus dixie* (UF 343599), 75 mm TL, 62 mm TW, 32 mm TH, uppermost portion of Upper Eocene Ocala Limestone, Dixie County, Florida (FM-IP DI013). A: aboral. B: oral. C: left side. D: right side. E: posterior. F: tilted oral viewpoint from posterior.

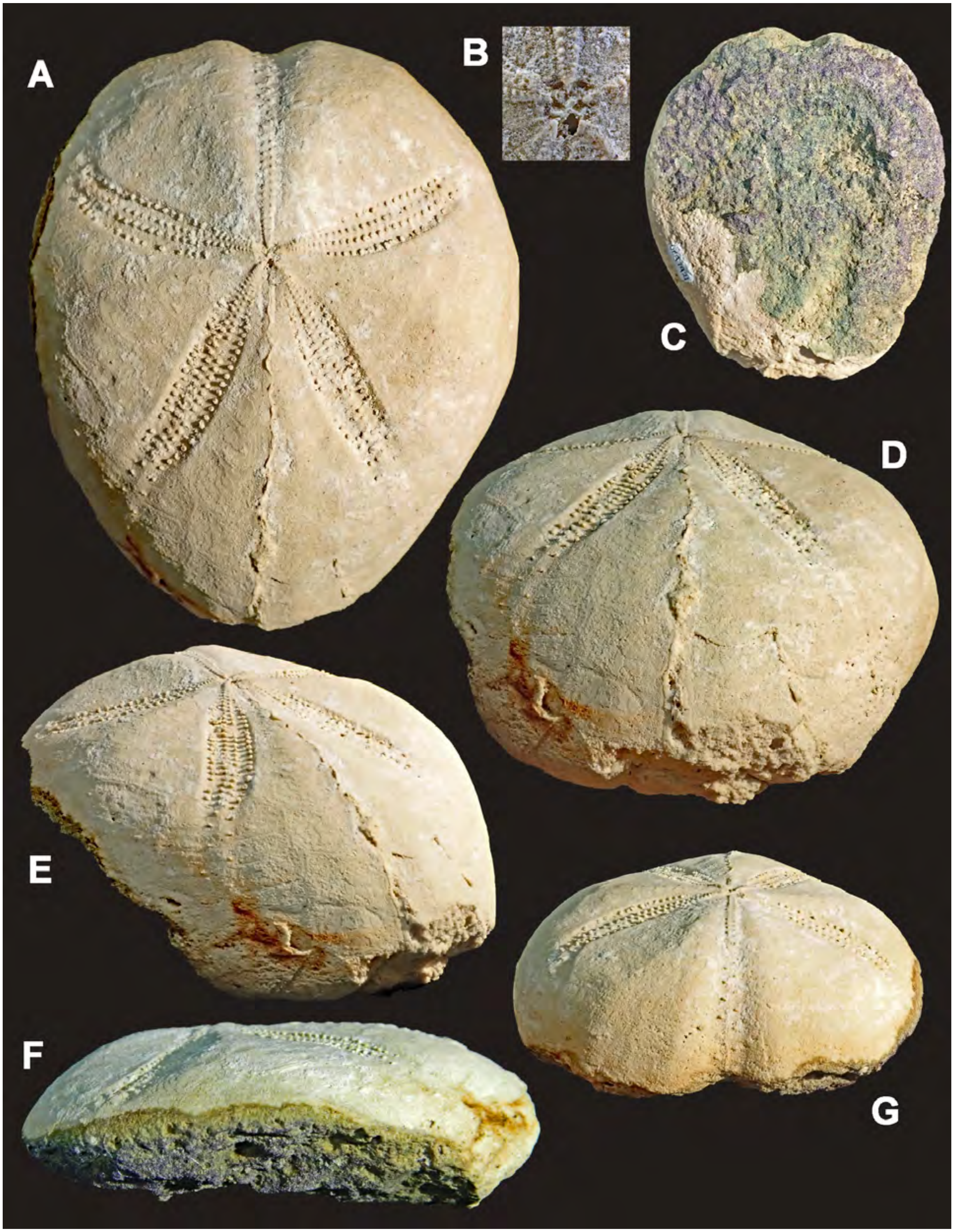


Figure 190: *Plagiobrissus cassadyi* n. sp., holotype (UF 97921), 82 mm TL, 70.5 mm TW, 30.5 mm TH (TW and TH incomplete), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: aboral. B: apical area. C: oral. D: tilted aboral viewpoint from posterior. E: oblique aboral viewpoint from posterior. F: left side. G: tilted aboral viewpoint from anterior.

Figure 191: *Plagiobrissus cassadyi* n. sp., paratype (UF 105223), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). External mold of specimen showing large tubercles confined within peripetalous fasciole, which is stippled where visible.

E. ocalanus, O. beckeri, S. armiger, and other uncommon taxa. The species is more rarely encountered in the *Oligopygus haldemani* Zone in Jackson County, Florida where it is found with *W. johnsoni* and other, rarer species.

Cooke (1959) reassigned *Eupatagus dixie* to *Plagiobrissus* because of the narrowness of the ambulacra and the length of the plastron. However, he only tentatively placed this species in that genus, because of the lack of evidence of an anal fasciole in specimens he had available for study. Examination of additional well-preserved specimens (e.g., UF 343599) does reveal traces of anal branches on the subanal fasciole (Fig. 189), so assignment to *Pla-*

giobrissus is confirmed. In addition, *P. dixie* shares other traits of that distinguish it from *Eupatagus*, such as the long, narrow, somewhat curving ambulacra, rather than straight, lanceolate ambulacra as in typical *Eupatagus*. Cooke (1959) also indicated that *Plagiobrissus* has a long plastron connected with a short labrum, and this contrasts with the V-shaped plastron and long, narrow labrum of *Eupatagus*. In addition to the presence of the anal fascioles, the narrow, slightly curved petals readily differentiate *P. dixie* from *E. ocalanus*, which is the only species that it could possibly be confused with in the OLS.

Plagiobrissus cassadyi n. sp.
(Figs. 190-195)

Brissopatagus sp. Oyen 2001. pp. 136-138. figs. 3-18, A, B.

Diagnosis.—*Plagiobrissus* with broad test (TW on average 89.7% TL); ambulacra II and IV divergent from each other at 148° (on average), flexed distally towards anterior; distinct sulcus where ambulacrum III crosses anterior margin; large tubercles confined aboral to peripetalous fasciole of interambulacra 1, 2, 3 and 4 only, tubercles in interambulacra 1 and 4 arranged in rows, tubercles in anterior interambulacra haphazardly distributed.

Description.—Based on the holotype (UF 97921), five paratypes (UF 40441, UF 105223, UF 105225, UF 105226, UF 105227), and non-type material in the FM-IP collections. Specimens consist of both internal and external molds. Therefore, measurements of TL, TW, and TH are slightly less than if specimens still had test preserved.

Test subovate, broad anteriorly, tapering posteriorly, with shallow anterior sulcus; moderately sized, largest specimen 83.9 mm TL; holotype 82 mm TL, 70.5 mm TW, 30.5 mm TH (TW and TH incomplete), TW on average 89.7% TL; test depressed overall, TH on average 36.9% TL; highest point posterior, widest point just posterior of apical system. Apical system anterior, on average 67% TL from posterior margin; four gonopores, no further details discernable, but appears to be ethmolytic. Petals narrow, weakly sunken, flexed outward distally; ambulacrum III not petaloid, in shallow notch at anterior margin. Petals of ambulacra I and V longest; petal I on average 37% TL, petal V on average 38.6% TL; on average divergent from each other by 51°, narrow (width on average 20.2 petal length); petals II and IV shortest, with petal II on average 33.4% TL, petal IV on average 33.6 TL; narrow (width on average 22.3% petal length), on average divergent from each other by 148°; distally curved towards anterior.

Large tubercles confined aboral to peripetalous fasciole in interambulacra 1, 2, 3, and 4, but absent in interambulacrum 5. Tubercles in interambulacra 1 and 4 arranged in slightly crooked rows, tubercles in anterior paired interambulacra haphazardly arranged, not in distinct rows. Peripetalous fasciole prominent, running close to tips of paired petals, not indented between them. Subanal fasciole present, wide (width on average 44.1% TW); anal branches not discernable. Periproct on truncate, overhanging posterior; ovate, height on average 94% periproct width; height on average 38% TH. Peristome anterior, posterior edge on average 82% TL from posterior margin; wider than high, kidney-shaped, with short, wide labrum. Plastron broad, medially convex. Oral plating and tuberculation unknown.

Zoobank Nomenclatural Act.—20D5AF6C-6090-408F-837F-8E1BA04992F7

Discussion.— All known specimens of this taxon are preserved as molds (both external and internal) from a dolomitic bed in the upper portion of the Lower Oligocene Marianna Limestone in the bed and banks of Dry Creek, a tributary of the Chipola River, south of Marianna in southern Jackson County (FM-IP JA010). Here, *P. cassadyi* n. sp. occurs with moldic *C. rogersi* and rarer *S. americanus* and *Phyllacanthus* cf. *P. mortoni*. Although the moldic preservation is not optimal, sufficient detail is preserved, especially on the external molds, to describe the species and recognize it as a new taxon. Although measurements of TL, TW, and TH are slightly less than what the specimens would be with preserved test, ratios recorded above remain useful for comparison with other taxa.

This is the first known occurrence of *Plagio-*

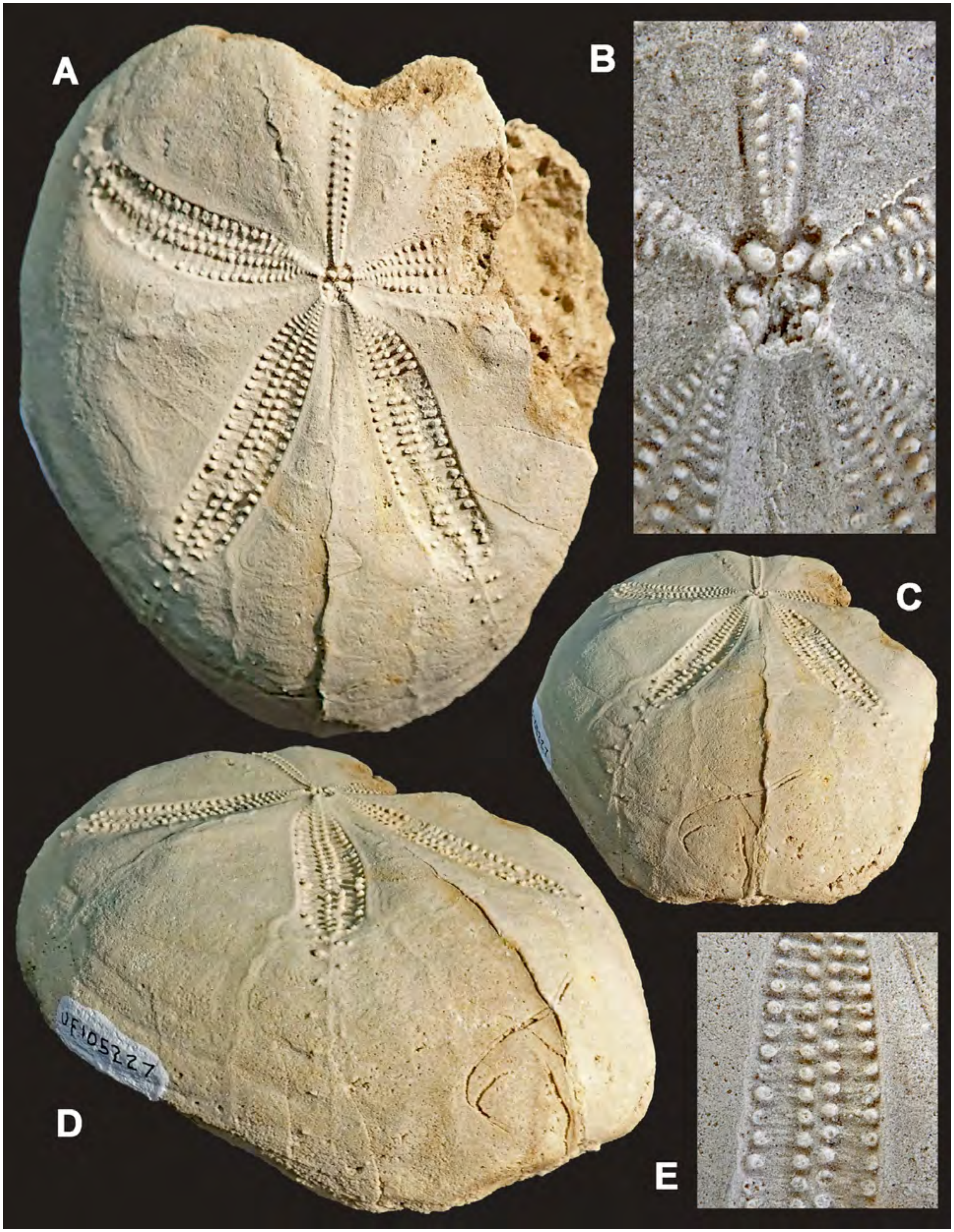


Figure 192: *Plagiobrissus cassadyi* n. sp., paratype (UF 105227), 76.7 mm TL, 65.8 mm TW, 25.9 mm TH (no dimensions are complete), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: aboral. B: apical area. C: tilted aboral viewpoint from posterior. D: oblique aboral viewpoint from posterior. E: close-up of pore-pairs at widest point of petal in ambulacrum V.

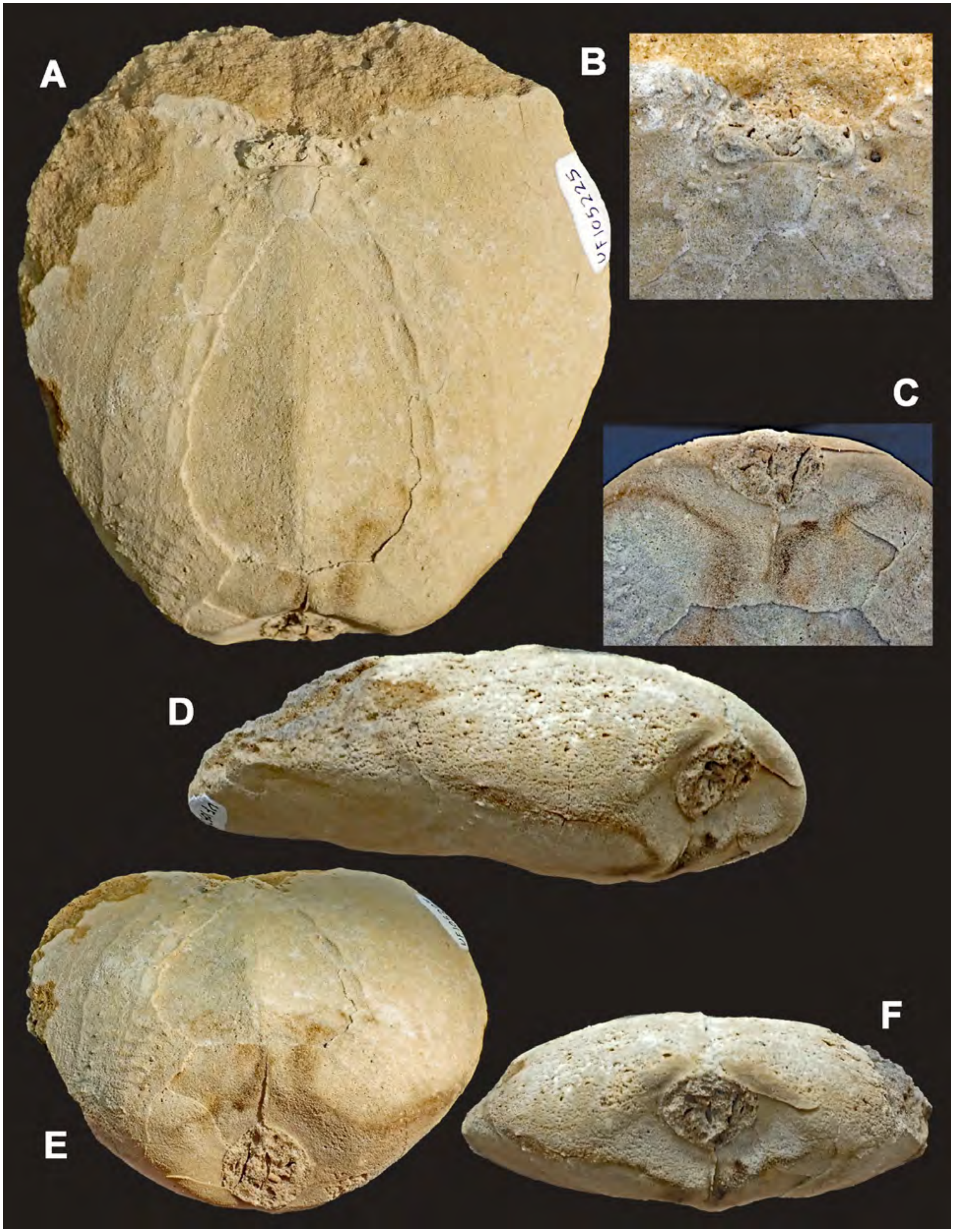


Figure 193: *Plagiobrissus cassadyi* n. sp., paratype (UF105225), 77.5 mm TL, 73.6 mm TW, 28.0 mm TH (no dimensions are complete), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: oral. B: peristome. C: periproct and indications of subanal fasciole. D: oblique lateral viewpoint from posterior. E: tilted oral viewpoint from posterior. F: posterior.

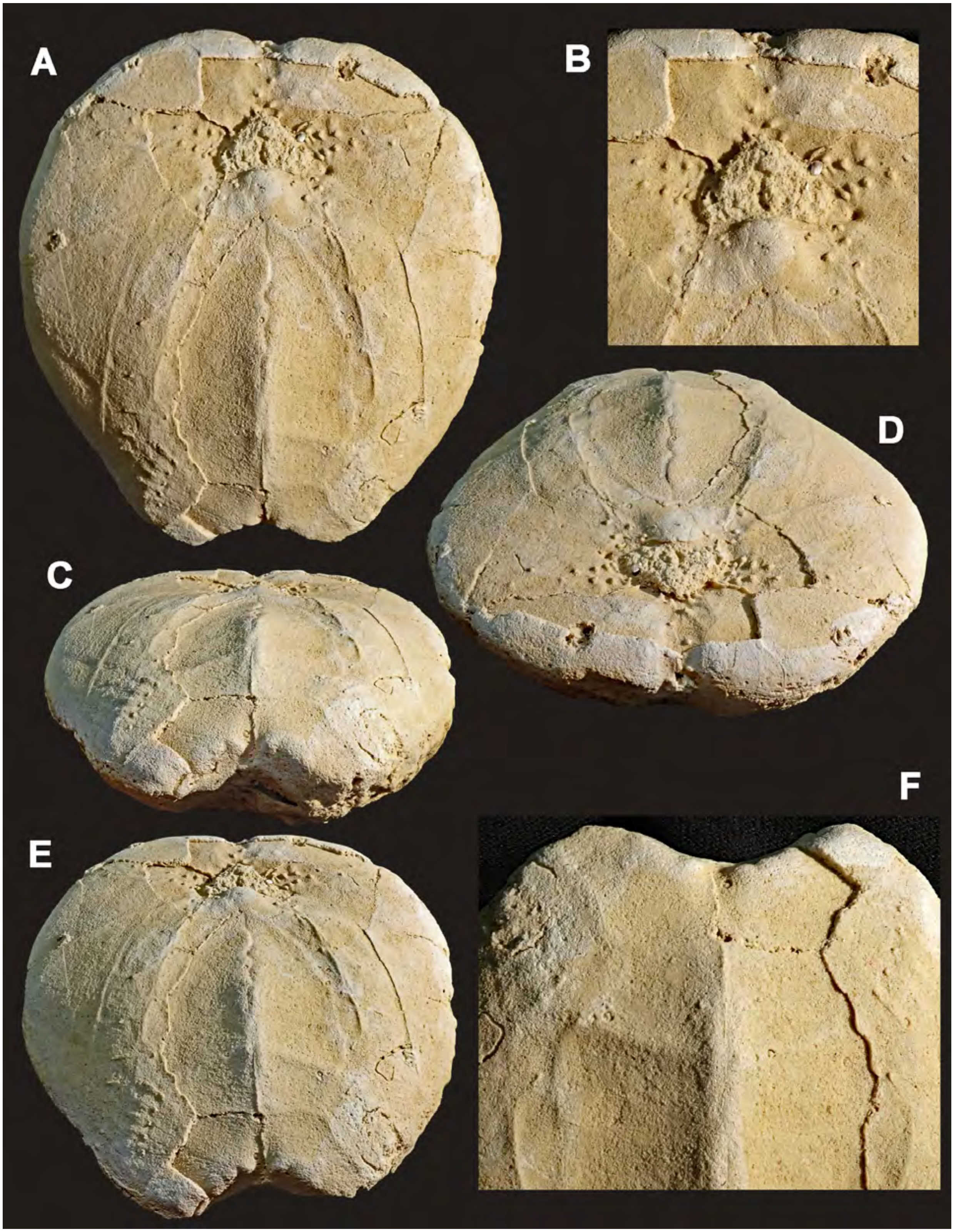


Figure 194: *Plagiobrissus cassadyi* n. sp., paratype (UF40441), 83.9 mm TL, 76.6 mm TW (TH incomplete; aboral surface is completely corroded), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: oral. B: peristome. C: tilted oral viewpoint from posterior. D: tilted oral viewpoint from anterior. E: tilted aboral viewpoint from posterior. F: posterior end of oral surface showing indications of subanal fasciole.

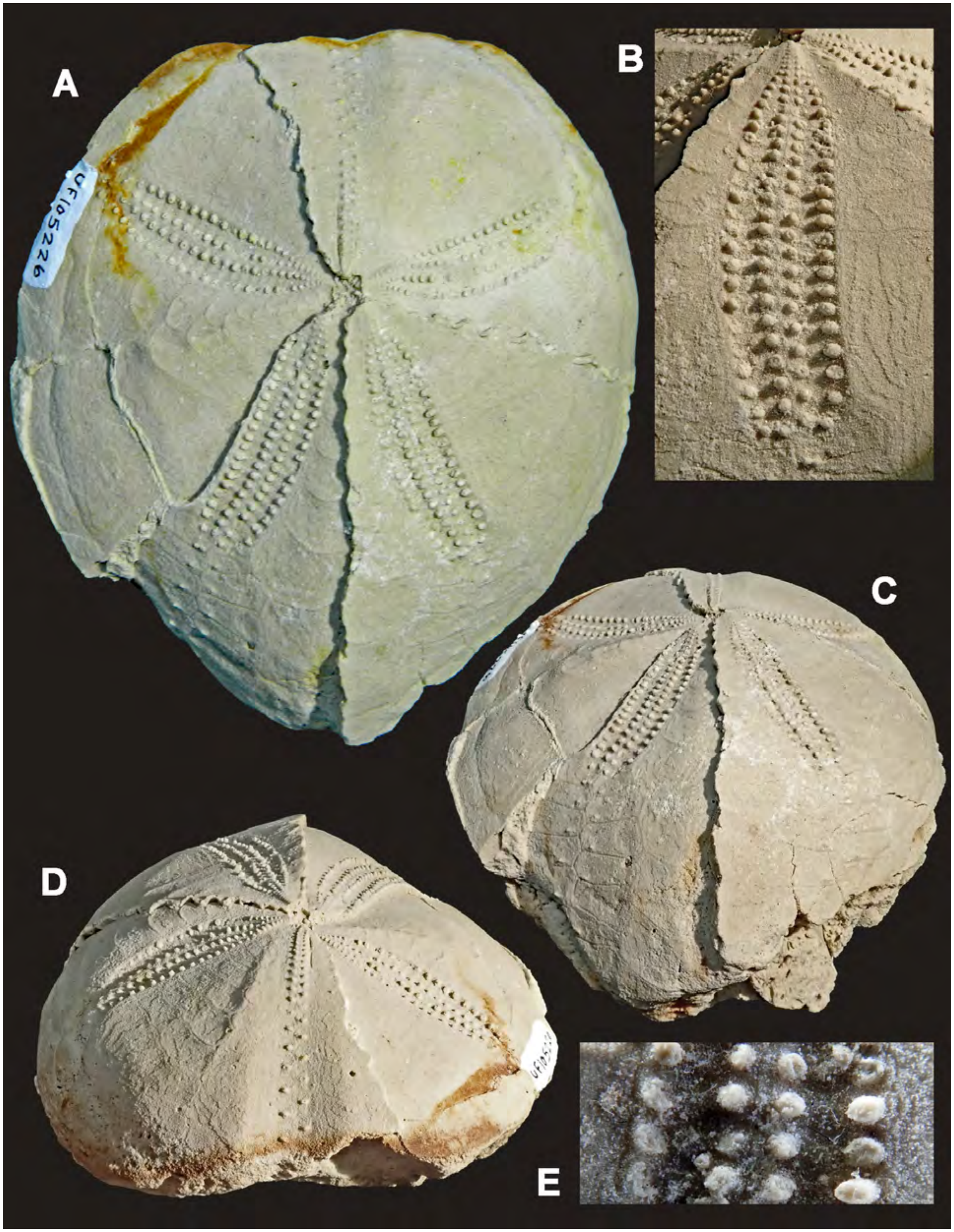


Figure 195: *Plagiobrissus cassadyi* n. sp., paratype (UF105226), 73.4 mm TL, 67.7 mm TW (TH incomplete), dolomitic facies in upper part of the Lower Oligocene Marianna Limestone, Jackson County, Florida (FM-IP JA010). A: aboral. B: ambulacrum I. C: tilted aboral viewpoint from posterior. D: tilted aboral viewpoint from anterior. E: pore-pairs at widest point of petal in ambulacrum I.

brissus in the Oligocene of North America, which, together with *E. dumonti* n. sp., adds data to an otherwise relatively depauperate regional Oligocene spatangoid fauna (Table 4).

Oyen (2001) first documented this species and placed it in *Brissopatagus*. However, he recognized that it likely represented a new species, but did not name it. *Brissopatagus* was reviewed by Henderson and Fell (1969), and *P. cassadyi* n. sp. is readily separated from members of *Brissopatagus* since the anterior interambulacra are not depressed. In *Brissopatagus*, the paired interambulacral regions immediately posterior to the paired anterior petals is distinctly concave, forming a depression that is confluent with the petals.

This species cannot be assigned to *Eupatagus* due to the presence of slightly depressed petals and distinct anterior notch in *P. cassadyi* n. sp. Although details of the apical system are largely lacking, *P. cassadyi* n. sp. has a distinct subanal and peripetalous fasciole, and narrow, slightly sunken petals, all features suggesting the family Brissidae. The low test, large aboral, interambulacral primary tubercles that are confined to the region aboral to the peripetalous fasciole, and narrow petals with the posterior pair flexed laterally at their tips suggests *Plagiobrissus*. Although the currently available specimens do not provide sufficient detail of the posterior region to detect anal branches on the subanal fasciole, the specimens are otherwise more like *Plagiobrissus* than any other genus.

Plagiobrissus occurs as old as the Eocene, where it is represented in eastern North American faunas by *P. curvus* and *P. dixie* in the Upper Eocene deposits of the southeastern United States. Prior to the recognition of *P. cassadyi* n. sp., the genus appeared to have a lengthy regional gap in the fossil record between Late Eocene occurrences noted in this paper, and Late Pliocene occurrence of *Plagiobrissus sarae* Ciampaglio et al., 2009, and the Recent *P. grandis* (Gmelin, 1791). The latter is only tentatively documented in the fossil record of the region (Osborn et al., 2020). *Plagiobrissus cassadyi* n. sp. cannot be confused with any of these species. It is perhaps nearest in overall morphology to *P. dixie*, from which it is readily distinguished by its possession of more numerous large primary tubercles within the peripetalous fasciole, broader, more cordate test, and deeper anterior notch. The tuberculation of *P. cassadyi* n. sp. is more like that of *P. curvus*, but the petals of these two species are very different.

Although there are other occurrences of *Plagiobrissus* in the fossil record of the eastern Americas, it is relatively rare. We compare *P. cassadyi* n. sp. to all the known taxa below.

Kier (1980: 11) documented *Plagiobrissus* sp. from the Castle Hayne Limestone of North Carolina but did not figure or describe the material. *Plagiobrissus* is present in sporadic concentrations in the fossil record of the Caribbean region, largely concentrated in Eocene deposits. Kier (1984) did not find the genus in Cuban faunas.

Plagiobrissus loveni (Cotteau, 1875) is common in the Eocene of Jamaica (Arnold and Clark, 1927; Donovan, 1993) as well as at its type locality in St. Bartholomew (Cotteau, 1875; Jackson, 1922). The abundant large tubercles on the aboral surface of this species are unique. Arnold and Clark (1927) stated that the plastron of *P. loveni* is distinctly different than that of *P. grandis* and suggested the species may not be a *Plagiobrissus*. However, subsequent authors have not reassigned the species, and we consider *P. loveni* to be correctly assigned. The aboral tuberculation of *P. loveni* readily distinguishes it from *P. cassadyi* n. sp. In addition, *P. cassadyi* n. sp. has a much more tapered posterior region than *P. loveni*, and its peripetalous fasciole does not closely follow the ambitus, as it does in *P. loveni*.

Arnold and Clark (1927) also described *P. abruptus, P. elevatus, P. latus, P. perplexus*, and *P. robustus* from Eocene deposits of Jamaica. These five species, most of which were described from incomplete holotypes, were further discussed by Donovan (1993) and *P. cassadyi* n. sp. is not conspecific with any of them.

Jeannet (1928) described *Plagiobrissus lamberti* using a very incomplete test from Venezuela, which Cooke (1961) did not figure in his review of the fauna, perhaps due to the poor quality of the fossil. Anisgard (1954) figured an unnamed Eocene species of *Plagiobrissus* from a deep well in

Venezuela, but the specimen consists of the anterior portion of the test and lacks features that would allow comparison to other heart urchins.

Sánchez-Roig (1949) described *Brissolampas santanae*, which he subsequently assigned into his new genus *Moronaster* (Sánchez-Roig, 1952a). This species shares similar gross morphology to *P. cassadyi* n. sp. However, as noted by Kier (1984), no types of this species or the other species Sánchez-Roig placed in *Moronaster* can be located for comparison. The existing figures are poor and show badly weathered specimens, making assignment even to genus uncertain. Kier (1984) presumed the species belong to either *Pericosmus* or *Antillaster*.

Cooke (1961) documented fragmentary material from the Miocene? of Venezuela that he attributed to *P. grandis*. The fragment he discussed and figured (Cooke, 1961: pl. 13, fig. 1) likely belongs to *Plagiobrissus*, but its assignment to *P. grandis* is questionable due to the lack of diagnostic features on the incomplete specimen. Conspecificity with *P. sarae*, a stratigraphically more logical comparison, could not be ruled out.

Kew, in Dickerson and Kew, 1917 described *Metalia cumminsi* from the Cenozoic of Mexico, but this was referred to *Plagiobrissus* by Israelsky (1924). However, Durham (1961) clarified that this species belongs to *Lajanaster* Lambert and Sánchez Roig in Sánchez Roig, 1926.

Durham (1961) described the very elongate *Plagiobrissus costaricensis* as well as *P. malavassii*, which occur together in the Miocene of Costa Rica. Neither of these species could be confused with *P. cassadyi* n. sp. The narrow test of *P. costaricensis* readily differentiates it from *P. cassadyi* n. sp., and petals II and IV of *P. malavassii* are not flexed distally towards the anterior as in *P. cassadyi* n. sp.

Macropneustes mexicanus Kew, in Dickerson and Kew, 1917, was described from the Oligocene to Miocene strata of Topila, Mexico, and seems to be the most similar taxon to *P. cassadyi* n. sp. in the Americas. *Macropneustes mexicanus* was subsequently transferred to *Brissopatagus* by Israelsky (1924) and later to *Gillechinus* by Henderson and Fell (1969). Although *G. mexicanus* and *P. cassadyi* n. sp. are very similar in petaloid structure and test shape, the primary tubercles are arranged differently. In *Gillechinus*, the primary tubercles are arranged in rows expressed within the peripetalous fasciole only on the posterior columns of plates in the paired interambulacra. In external molds of *P. cassadyi* n. sp. (Fig. 191), primary tubercles are arranged within the peripetalous fasciole throughout the paired interambulacra.

With the addition of *P. cassadyi* n. sp., *Plagiobrissus* now includes 18 species from the eastern Americas. However, as mentioned above, several of these species remain poorly known.

Etymology.—Named for Tim Cassady, who not only brought the locality to the attention of RWP, but donated most of the specimens collected from the site, including the holotype and paratypes.

Material and Occurrence.—This species is represented by the holotype (UF 97921) and paratypes (UF 40441, UF 105223, UF 105225, UF 105226, UF 105227), all internal and external molds, from the dolomitic facies of the Lower Oligocene Marianna Limestone along Dry Creek, south of Marianna, in southern Jackson County (FM-IP JA010).

Superfamily **SPATANGOIDEA** Gray, 1825
Family **MACROPNEUSTIDAE** Lambert, 1905
Genus ***Macropneustes*** L. Agassiz in Agassiz and Desor, 1847

Macropneustes mortoni (Conrad, 1850)
(Fig. 196)

Holaster mortoni Conrad, 1850. p. 40. pl. 1, fig. 10.

Holaster mortoni (Conrad). Boyle, 1893. p. 150.

Macropneustes mortoni (Conrad). Stefanini, 1911. p. 700.

Macropneustes mortoni (Conrad). Clark and Twitchell, 1915. p. 155. pl. 72, figs. 1a-d.

Macropneustes mortoni (Conrad). Cooke, 1926. pl. 96, figs. 1a-b.

Macropneustes mortoni (Conrad). Cooke, 1942. p. 51.

Macropneustes mortoni (Conrad). Cooke, 1959. p. 82. pl. 37, figs. 5-9.

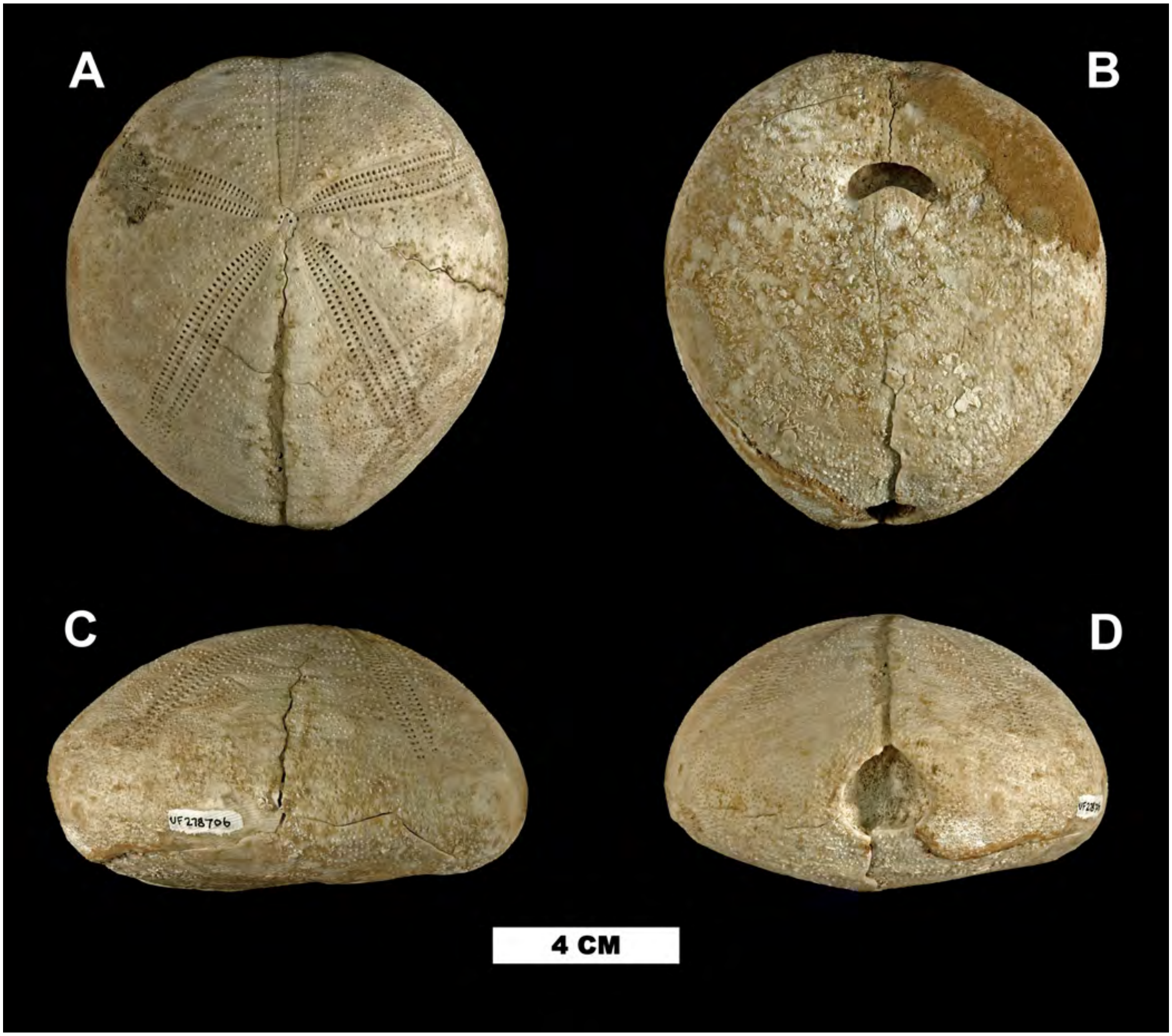


Figure 196: *Macropneustes mortoni* (UF 278706), 106 mm TL, 97.5 mm TW, 61.5 mm TH, Upper Eocene Ocala Limestone, Jackson County, Florida (FM-IP JA085). A: aboral. B: oral. C: right side. D: posterior.

Macropneustes mortoni (Conrad). Pickering, 1970. pp. 20, 27, 64.

Macropneustes mortoni (Conrad). Toulmin, 1977. p. 342. pl. 67, figs.7, 8.

Macropneustes mortoni (Conrad). Heller and Bryan, 1992. pp. 345-346.

Macropneustes mortoni (Conrad). Osborn et al., 2016. tbl. 2.

Occurrence.—Within Florida, this species appears to be restricted to the OLS of Jackson County (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031) where it occurs with *Oligopygus haldemani*. It is also found in the Upper Eocene of Alabama (Toulmin, 1977) and Georgia (Cooke, 1959). The type locality is near Palmyra in Lee County, Georgia (Conrad, 1850).

Discussion.—*Macropneustes mortoni* has not been documented south of the Suwannee Strait in peninsular Florida. In Jackson County, especially in the Brooks Quarries (FM-IP JA009, (FM-IP JA018, (FM-IP JA027, FM-IP JA031, FM-IP JA039), it occurs with *O. haldemani, W. johnsoni, R. conradi,* and numerous other, less common species in the

Figure 197: *Eupatagus clevei* (UF 12808), 101.5 mm TL, 82.5 mm TW, 40.5 mm TH, internal mold from dolomitic beds of lowermost portion of the Upper Eocene Ocala Limestone, Citrus County, Florida (FM-IP CI009). A: aboral. B: oral. C: left side. D: posterior.

Asterocyclina Zone just below the contact with the Bumpnose Limestone.

Heller and Bryan (1992) documented the presence of a large echinoid they identified as *M. mortoni* in the Lower Oligocene (Vicksburgian) Florala Member of the Bridgeboro Limestone near Florala, Covington County Alabama. They discussed the significance of the species occurring in Oligocene strata, as *M. mortoni* had previously been only documented from the Upper Eocene. We have collected specimens of *M. mortoni* from the OLS in this quarry, with other, typically Upper Eocene species such as *R. conradi* and *W. johnsoni*. Unless the Heller and Bryan (1992) specimen was extracted *in situ* from the Bridgeboro limestone, it is possible it came from Eocene strata in the quarry. We do not consider the species to occur in the Oligocene (Fig. 4). The specimen is incomplete with damage on the posterior margin. If additional specimens are collected from the definitive Bridgeboro Limestone strata in the Florala Quarry, they should be compared with *Eupatagus dumonti* n. sp. The low test, flush petals and very large periproct of *E. dumonti* n. sp. would be distinctive.

The large test with thin walls of *M. mortoni* cannot be confused with that of any other member of the Eocene echinoid fauna of the region.

Family **EUPATAGIDAE** Lambert, 1905

Genus ***Eupatagus*** L. Agassiz in Agassiz and Desor, 1847

Eupatagus clevei (Cotteau, 1875)

(Figs. 197-200)

Euspatangus clevei Cotteau, 1875. p. 44. pl. 8, figs. 1-4.

Euspatangus grandiflorus Cotteau, 1875. p. 45. pl. 8, figs. 5, 6.

Eupatagus clevei (Cotteau). Guppy, 1882. p. 199.

Eupatagus grandiflorus (Cotteau). Jackson, 1922. p. 89. pl. 15, figs. 5, 6.

Eupatagus clevei (Cotteau). Jackson, 1922. p. 90. pl. 16, figs. 1, 2.

Eupatagus hildae Hawkins, in Arnold and Clark, 1927. p. 81-82. pl. 22, figs. 9, 10. txt. fig. 1.

Eupatagus grandiflorus (Cotteau). Molengraaff, 1929. p. 72. pl. 24, figs. 1, 2; pl. 25, fig. 1.

Eupatagus grandiflorus (Cotteau). Arnold and Clark, 1934. p. 156.

Eupatagus clevei (Cotteau). Cooke, 1948b. p. 92. pl. 22, fig. 9.

Brissoides grandiflorus (Cotteau). Sánchez-Roig,

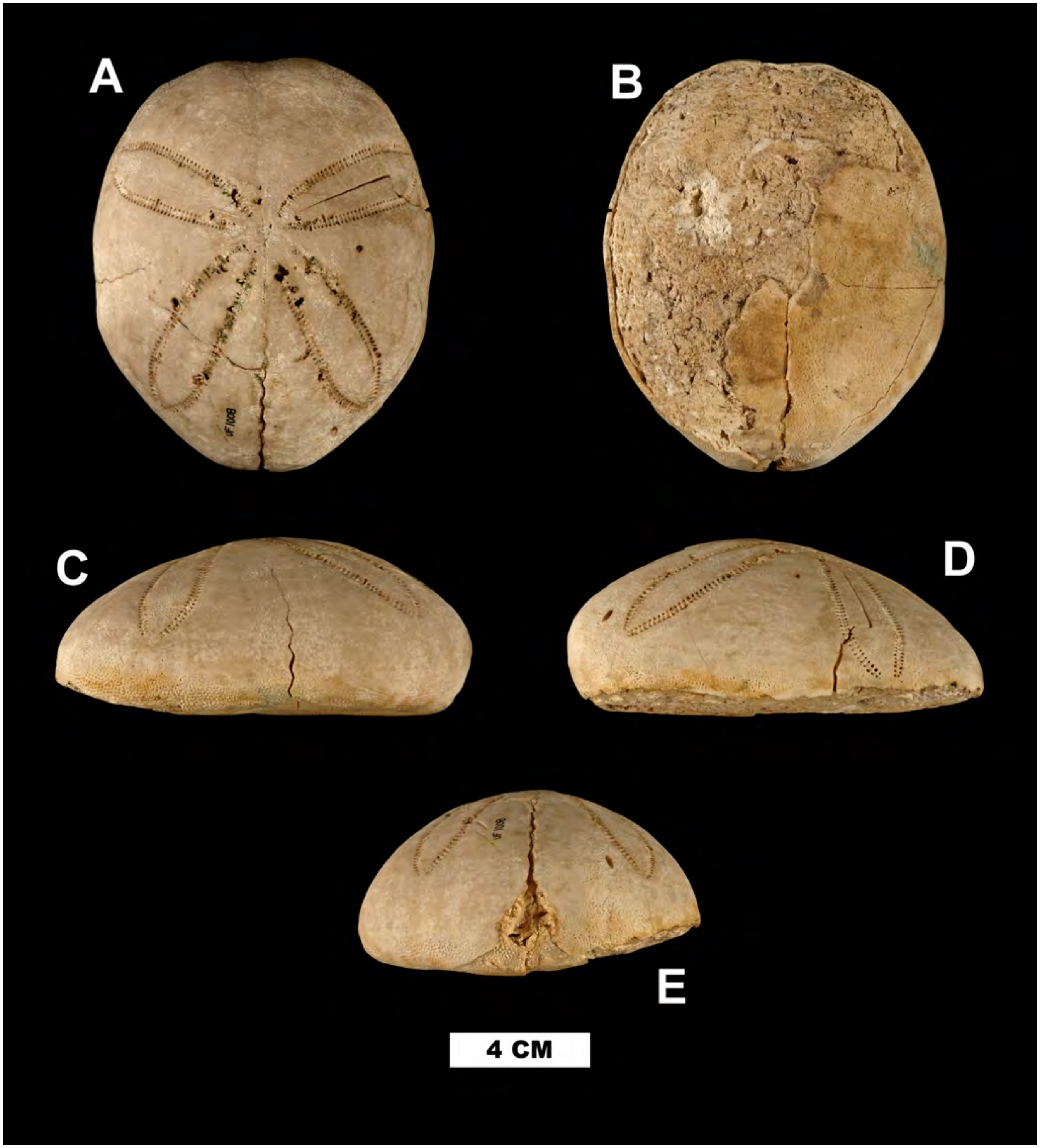


Figure 198: Holotype of *Eupatagus ingens* (= *E. clevei*), (UF 1008), 128 mm TL, 105 mm TW, 54 mm TH (test height is obscured by squishing of the test and missing portion of oral surface), Upper Eocene lower Ocala Limestone, Citrus County, Florida (FM-IP CI010). A: aboral. B: oral. C: left side. D: right side. E: posterior.

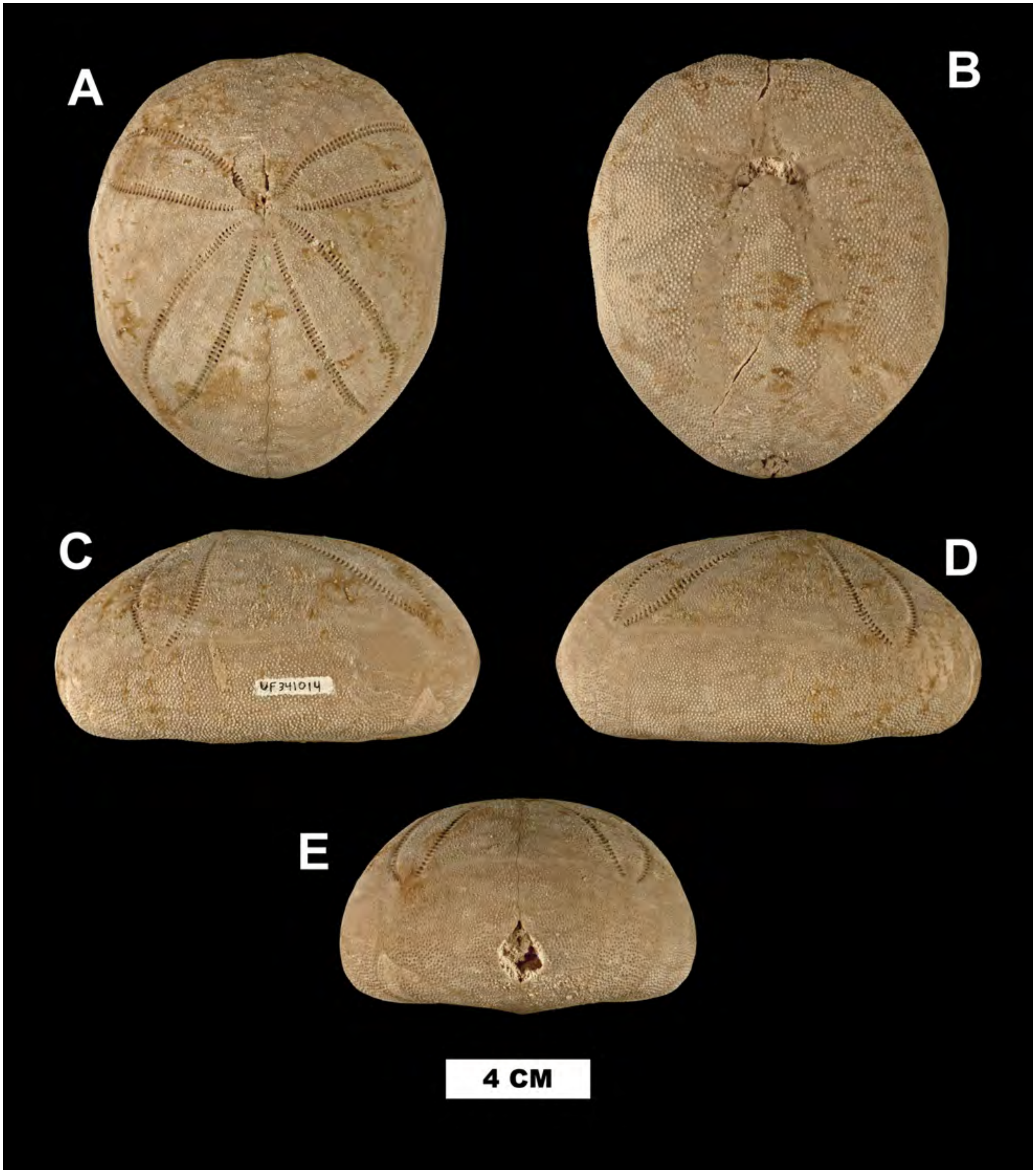


Figure 199: *Eupatagus clevei* (UF 341014) rare specimen from the Ocala Limestone with preserved test: 124 mm TL, 105 mm TW, 60.5 mm TH, Upper Eocene Ocala Limestone (precise zone within OLS is unknown), Hernando County, Florida (FM-IP HE006). A: aboral. B: oral. C: left side. D: right side. E: posterior.

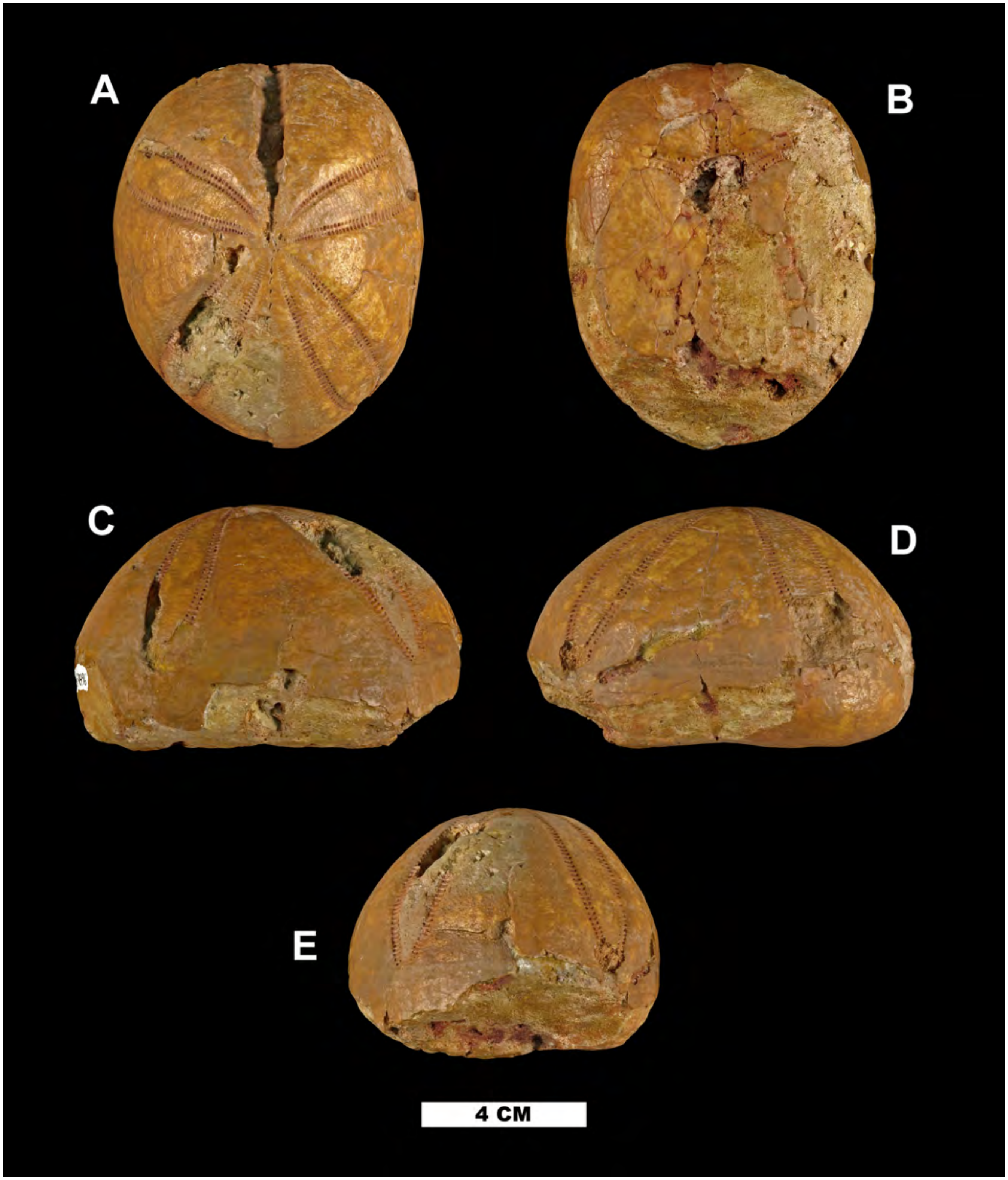


Figure 200: *Eupatagus hildae* Hawkins, in Arnold and Clark, 1927 (= *Eupatagus clevei*) (UF 4496) cast of holotype (Natural History Museum E17664), 105 mm TL, 81 mm TW, 63 mm TH, Oligocene, White Limestone. St. Hilda's School, Browns Town, Jamaica (FM-IP 2822). A: aboral. B: oral. C: left side. D: right side. E: posterior.

1949. p. 208.

Eupatagus clevei (Cotteau). Fischer, 1951. p. 83. pl. 7, figs. 1-3; txt fig. 18.

?*Eupatagus* (*Gymnopatagus*) *venturillae* Sánchez-Roig, 1951. p. 43. pl. 26, figs. 1, 2.

?*Eupatagus* (*Gymnopatagus*) *roajasi* Sánchez-Roig, 1951. p. 42. pl. 34, fig. 3.

?*Eupatagus* (*Gymnopatagus*) *zanoletti* Sánchez-Roig, 1951. p. 43. pl. 32, fig. 3.

Lajanaster guevarai Sánchez-Roig, 1951. p. 53. pl. 24, figs. 2-4.

?*Eupatagus* (*Plagiobrissus*) *herrerae* Sánchez-Roig, 1951. p. 46. pl. 25, figs. 1, 2.

?*Lajanaster venturillae* Sánchez-Roig, 1951. p. 54. pl. 25, figs. 3, 4.

?*Zanolettiaster herrerae* Sánchez-Roig, 1952c. p. 15. pl. 8, figs. 1, 2; pl. 9, fig. 4.

?*Megapatagus franciscanus* Sánchez-Roig, 1953c. p. 59. pl. 11, 2 figs.

Eupatagus clevei (Cotteau). Cooke, 1959. p. 89. pl. 41, figs. 6-8.

Eupatagus clevei (Cotteau). Cooke, 1961. pp. 26-27. pl. 10, figs. 2-5.

Eupatagus ingens Zachos, 1968. pp. 161-164.

Eupatagus clevei (Cotteau). Kier, 1974. txt. fig. 26B.

Eupatagus clevei (Cotteau). Toulmin, 1977. p. 341. pl. 66, figs. 4, 5.

Eupatagus ingens (Zachos). Zachos and Shaak, 1978. pp. 921-927.

Eupatagus clevei (Cotteau). Kier, 1984. pp. 98-100. pl. 61, figs. 3-6. pls. 62-66.

Eupatagus clevei (Cotteau) Donovan, 1993. p. 402.

Eupatagus clevei (Cotteau). Osborn et al. 2016. tbl. 2.

Occurrence.—This species is very common in sporadic concentrations along the Withlacoochee River, Cross Florida Barge Canal, Dolime Quarry (CI009), and Cemex Quarry (FM-IP CI017) south of Inglis, Citrus County, where it occurs as internal and external molds in the dolomitic lowermost portion of the OLS (formerly Inglis Formation). It occurs more rarely in the overlying limestone beds of the *Oligopygus phelani* Zone with *E. mooreanus* at these same locations. It is much rarer in the *Oligopygus wetherbyi* Zone of the upper OLS in a quarry west of Dowling Park (FM-IP LF002), Lafayette County and south of Tennille (FM-IP DI001), Taylor County.

Eupatagus clevei is widespread in the Caribbean region, including St. Bartholomew (Eocene; type locality), Panama (Eocene), Jamaica (Eocene), and Venezuela (Eocene). In Cuba, based on the synonymies and information in Kier (1984), it ranges from the Oligocene to Miocene, though the certainty of these stratigraphic designations is questionable.

Discussion.—Cotteau (1875) described *E. clevei* and *E. grandiflorus* from the Eocene of St. Bartholomew. Guppy (1882) later asserted that *E. grandiflorus* was a junior synonym of *E. clevei*, an opinion subsequent authors have largely upheld.

Zachos (1968) described *Eupatagus ingens* (Fig. 198) from the OLS of Florida. However, Kier (1984) completed an extensive review of *E. clevei* and considered *E. ingens* to be a subjective junior synonym. Subsequent workers (Carter, 1987a; Oyen, 2001) have not recognized *E. ingens* as a distinct species and neither do we, so it remains in synonymy with *E. clevei*.

Eupatagus clevei is most abundant in the lower dolomitic beds of the lower OLS near Inglis where it is preserved as internal and external molds with *P. floridanus*.

In the overlying limestone beds of the *Oligopygus phelani* Zone of the lower OLS, *E. clevei* is much rarer, but test detail is typically better preserved, as the material is not moldic (Fig. 199). In these limestone beds, *E. clevei* is associated with extremely abundant *E. mooreanus*, as well as numerous other echinoid taxa. *Eupatagus clevei* is much rarer in the upper OLS, where it is associated with the typical fauna of the *Oligopygus wetherbyi* Zone of the unit.

Eupatagus mooreanus Pilsbry, 1914
(Figs. 201-207)

Eupatagus mooreanus Pilsbry, 1914. p. 206. pl. 8.

Eupatagus floridanus (part) Clark in Clark and

Figure 201: Comparison of *Eupatagus antillarum* and *E. mooreanus*. A: *Eupatagus antillarum* holotype (specimen designated as USNM 115371 by Jackson [1922] but since redesignated USNM 207225), Eocene St. Bartholomew Limestone, St. Bartholomew (image from Smithsonian NMNH online database). B: *Eupatagus antillarum* (UF 245010), *Oligopygus phelani* Zone of lower Ocala Limestone, Citrus County, Florida (FM-IP CI012).

Twitchell, 1915. p. 176. pl. 83, figs. 1a-2b (not pl. 82, figs. 2a-d).

Maretia twitchelli Lambert in Sánchez-Roig, 1926. p. 112.

Maretia clarki Lambert in Sánchez-Roig, 1926. p. 112.

Eupatagus (*Gymnopatagus*) *mooreanus* (Pilsbry). Cooke, 1942. p. 54. pl. 1, fig. 16.

Eupatagus (*Gymnopatagus*) *mooreanus* (Pilsbry). Cooke, 1945. p. 60, fig. 6, no. 1.

Eupatagus (*Gymnopatagus*) *mooreanus* (Pilsbry). Fischer, 1951. p. 74. pls. 2, 5, 6; txt figs. 12-17.

Eupatagus (*Gymnopatagus*) *antillarum* (Cotteau). Cooke, 1959. p. 90. pl. 41, figs. 1-5 (in part, Cooke considered *E. mooreanus* a synonym of *E. antillarum*).

Eupatagus antillarum (Cotteau). Toulmin, 1977. pp. 340-341. pl. 66, figs. 1-3 (in part, Toulmin followed Cooke 1959).

Eupatagus mooreanus (Pilsbry). Buitrón and Sánchez, 1979. pp. 123-125. figs. 3, A-E.

Eupatagus cf. *antillarum* (Cotteau). Donovan and Rowe, 2000. p. 659. fig. 4 (species likely referable to *Eupatagus mooreanus*).

Eupatagus sp. cf. *E. antillarum.* (Cotteau). Donovan, 2004. fig.1, #8. p. 144 (species likely referable to *Eupatagus mooreanus*).

Eupatagus antillarum (Cotteau). Osborn et al., 2016. tbl. 2.

Occurrence.—This ubiquitous echinoid of the *Oligopygus phelani* Zone of the OLS (formerly Inglis Formation) is especially common near Inglis, in Levy and Citrus Counties. A few notable localities include the banks of the Withlacoochee River west of Inglis, especially at its mouth west of Yankeetown (type locality FM-IP LV024), as well as along the banks of the Cross Florida Barge Canal (FM-IP

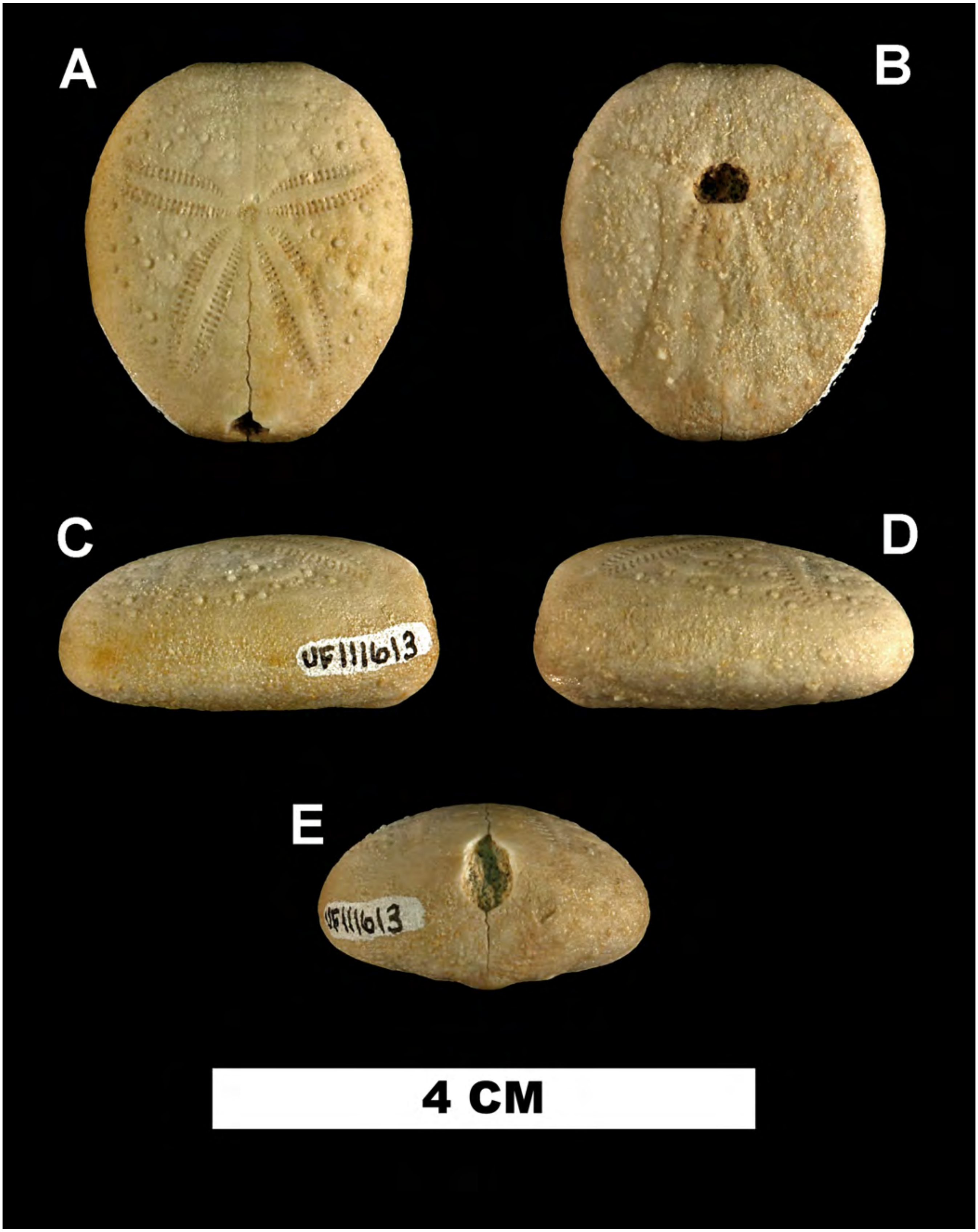


Figure 202: *Eupatagus mooreanus* (UF 111613), 27.5 mm TL, 23.5 mm TW, 12.5 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Levy County, Florida (FM-IP LV035). A: aboral. B: oral. C: left side. D: right side. E: posterior.

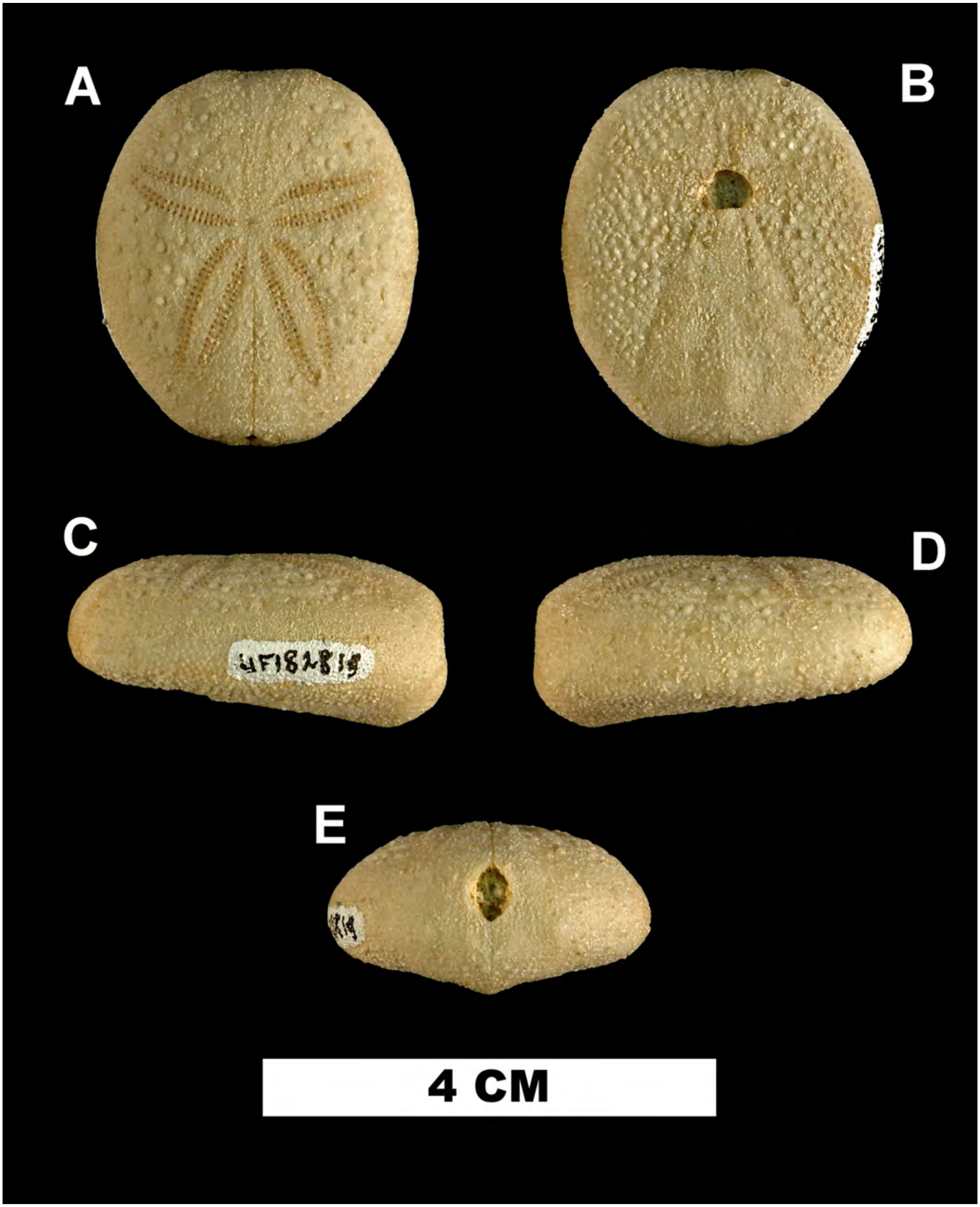


Figure 203: *Eupatagus mooreanus* (UF 182819), 34 mm TL, 29 mm TW, 14.5 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Levy County, Florida (FM-IP LV035). A: aboral. B: oral. C: left side. D: right side. E: posterior.

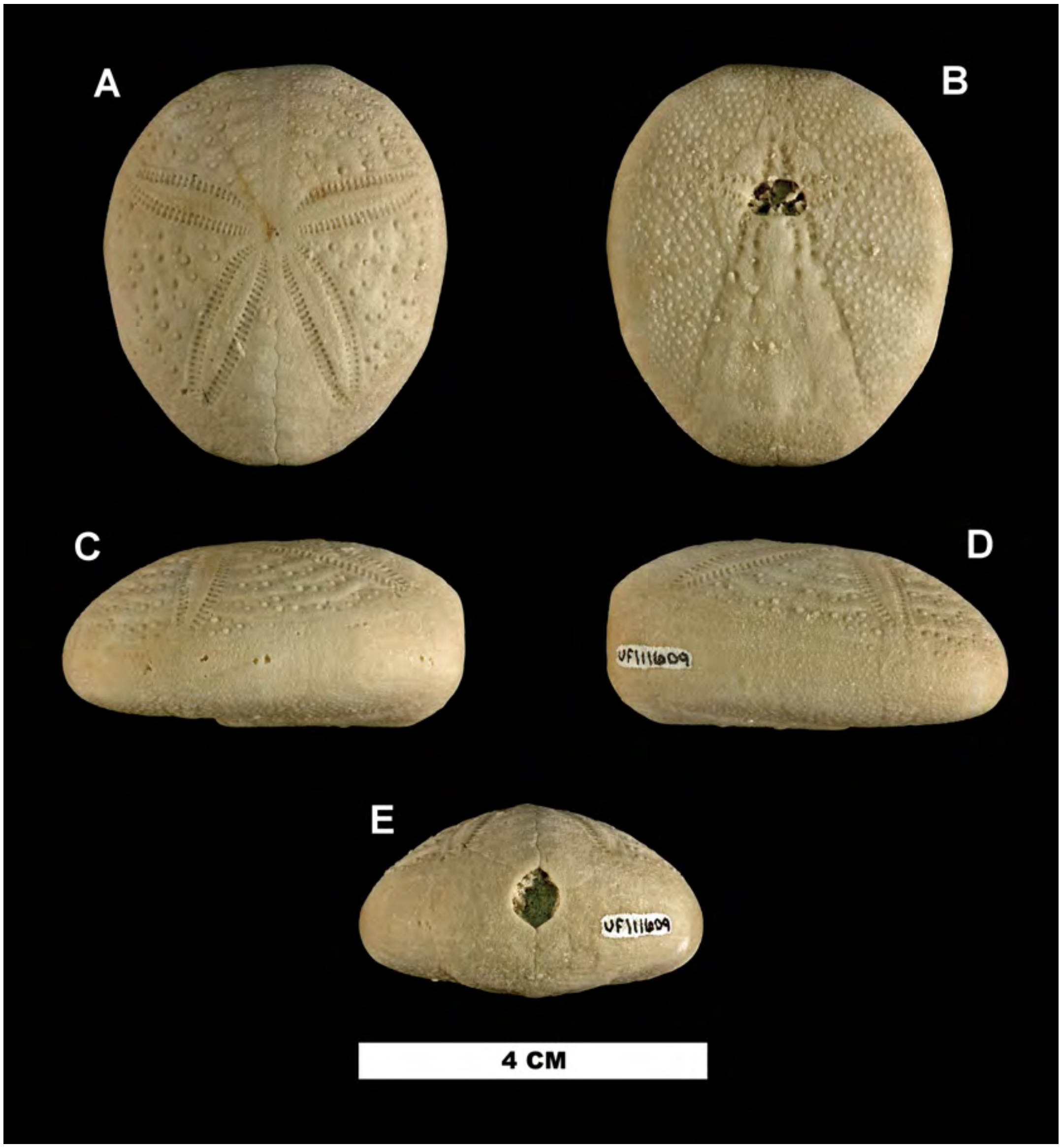


Figure 204: *Eupatagus mooreanus* (UF 111609), 44 mm TL, 38 mm TW, 21 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Levy County, Florida (FM-IP LV035). A: aboral. B: oral. C: left side. D: right side. E: posterior.

CI001). See Fischer (1951) and Cooke (1959) for additional localities.

This species also occurs in the Moodys Branch Formation in Covington and Conecuh Counties, Alabama. *Eupatagus mooreanus* also occurs in the Eocene of Jamaica (Donovan, 2004) and Mexico (Buitrón and Sánchez, 1979).

Discussion.—*Eupatagus mooreanus* is the unofficial fossil of the state of Florida (although most often erroneously called *E. antillarum*). It is ubiquitous wherever the Upper Eocene lower OLS (formerly Inglis Formation) is exposed. Fischer (1951: 74) stated that next to *Periarchus floridanus*, the robust *E. mooreanus* is the most conspicuous macrofossil in the middle portion of the "Inglis Formation" in Citrus and Levy Counties, Florida.

Pilsbry (1914) described *E. mooreanus* from specimens collected in material dredged at the mouth of the Withlacoochee River. He referred the species to the Pliocene, but this stratum is now firmly established as Upper Eocene. Pilsbry stated that the species is about the size of *E. clevei*. However, additional material of both species shows this is not always the case,

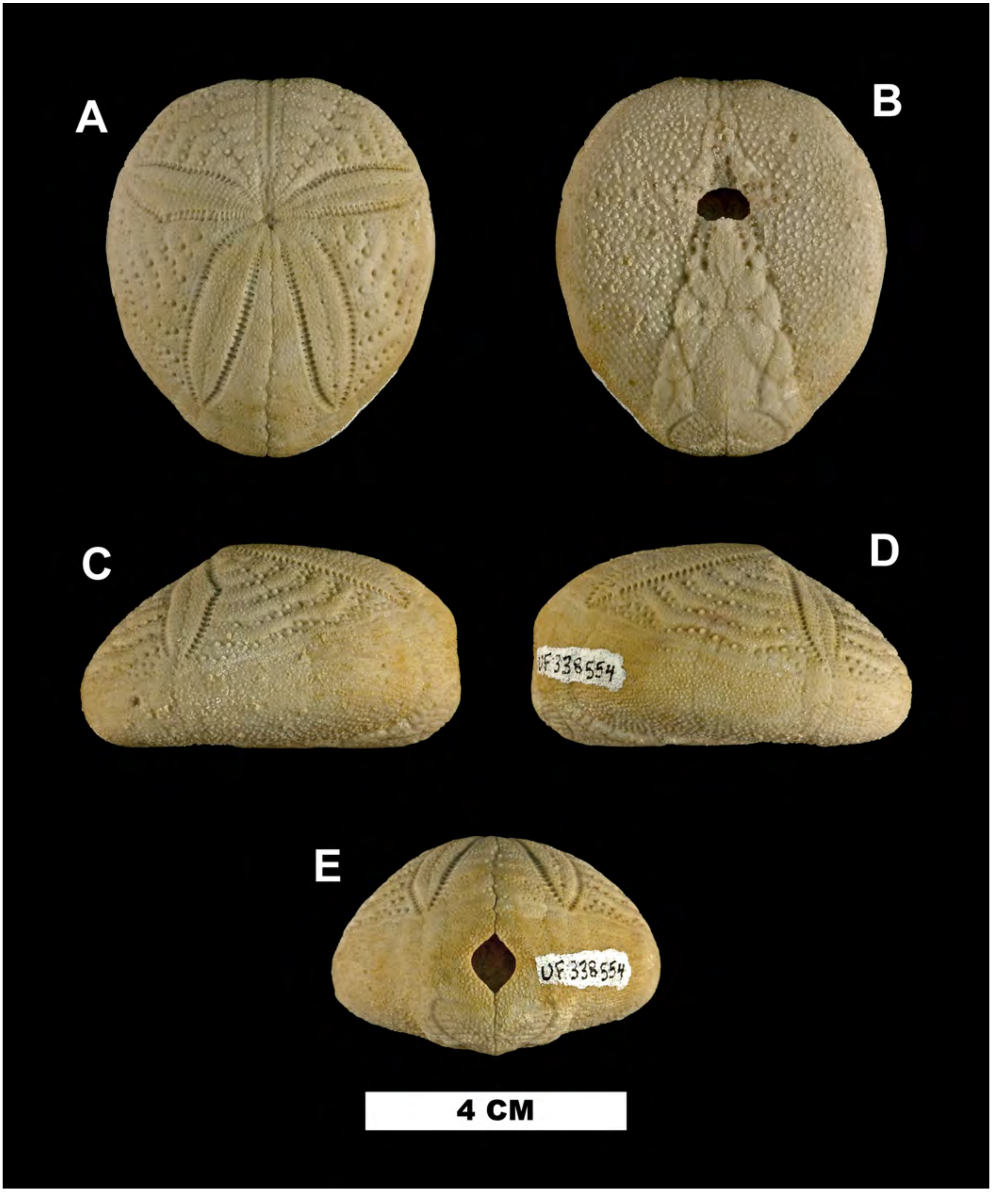


Figure 205: *Eupatagus mooreanus* (UF 338554), 59 mm TL, 51 mm TW, 32 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Citrus County, Florida (FM-IP CI012). A: aboral. B: oral. C: left side. D: right side. E: posterior.

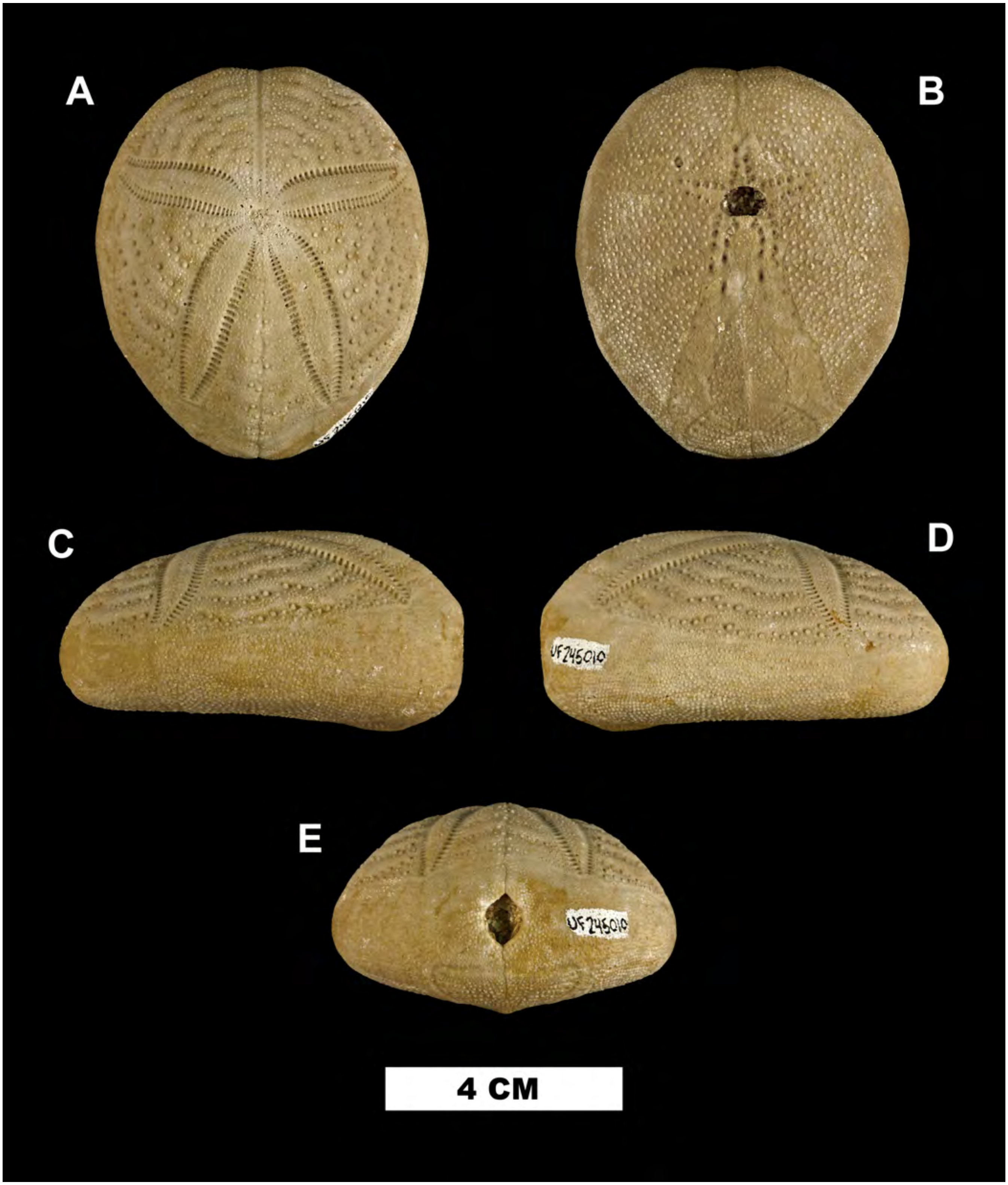


Figure 206: *Eupatagus mooreanus* (UF 245010), 68.5 mm TL, 57.5 mm TW, 33.5 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Citrus County, Florida (FM-IP CI012). A: aboral. B: oral. C: left side. D: right side. E: posterior.

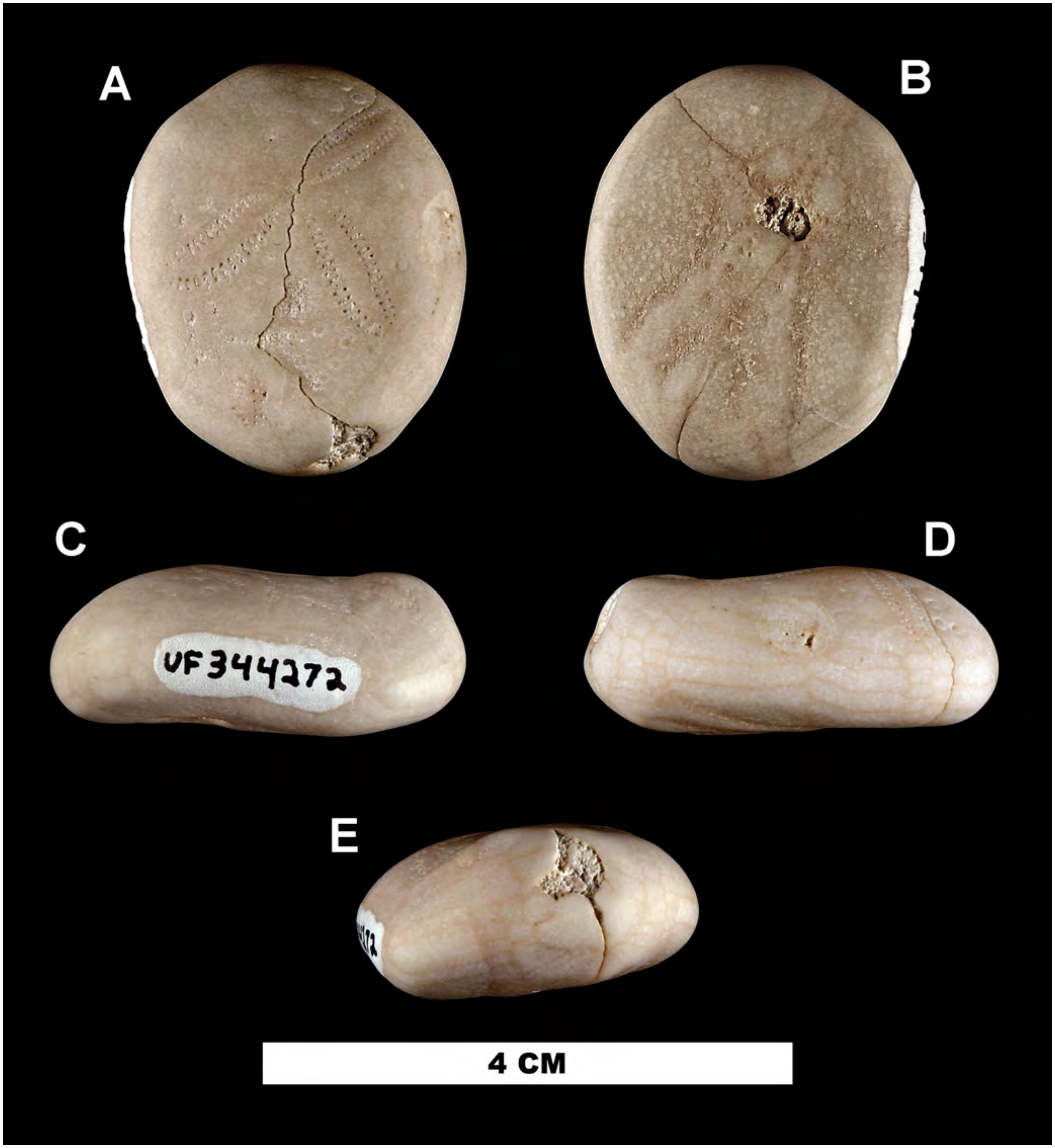


Figure 207: *Eupatagus mooreanus* (UF 344272), deformed specimen with merely three petals, 32.5 mm TL, 47 mm TW, 27 mm TH, Upper Eocene, *Oligopygus phelani* Zone, lower Ocala Limestone, Citrus County, Florida (FM-IP CI004). A: aboral. B: oral. C: left side. D: right side. E: posterior.

as *E. clevei* can attain much greater size than *E. mooreanus*.

Part of the early confusion with the species name for this taxon stems from Pilsbry (1914). Subsequently, Clark in Clark and Twitchell (1915), described *Eupatagus floridanus* from Levy County. However, of the three specimens Clark used for his description, the holotype (Clark and Twitchell, 1915: pl. 82, figs. 2a-d) from Johnson's Sink, Levy County, is an internal mold that, as pointed out by Cooke

(1942), represents a different species, having much shorter and narrower ambulacra. That specimen is likely *E. ocalanus*, although remains uncertain due to the moldic preservation of the specimen. The other two specimens of *E. floridanus* that Clark in Clark and Twitchell (1915: pl. 83, figs. 1, 2) figured are what Pilsbry described a year earlier as *E. mooreanus*.

Cooke (1942, 1959) stated that Lambert in Sánchez Roig (1926) chose the two specimens of *E. mooreanus* figured by Clark and Twitchell (1915) as the types of his *Maretia clarki* (Clark in Clark and Twitchell, 1915: pl. 83, fig. 1) and *Maretia twitchelli* (Clark in Clark and Twitchell, 1915: pl. 83, fig. 2), which Cooke (1942) then placed into synonymy with *E. mooreanus*. Mortensen (1951: 462) noted that Lambert's taxa clearly did not belong in *Maretia* but was not prepared to support the suggestion that they were different than *E. floridanus*.

Fischer (1951) completed a very thorough description of *E. mooreanus.* Cooke, via personal communication, informed Fischer that *E. mooreanus* is very closely related to, and likely identical with *E. antillarum,* from the Eocene of St. Bartholomew. However, Fischer (1951) retained the name *E. mooreanus*.

Cooke (1959) declared *E. mooreanus* a subjective junior synonym of *E. antillarum*. Cotteau's figure of the holotype of *E. antillarum* is somewhat stylized. However, the specimen was figured by Jackson (1922) and these two taxa are clearly not conspecific (Fig. 201).

Concerning *E. antillarum*, Jackson (1922) stated that the small size, ovate or subovate form, and almost perfectly transverse anterior pair of ambulacra distinguish this species from other West Indian fossil species of *Eupatagus*. Some of these same traits also serve to distinguish it from *E. mooreanus* (Fig. 201). As stated by Jackson, the anterior paired petals of *E. antillarum* are nearly straight, whereas those of *E. mooreanus* are arched anteriorly and diverge from each other at 145° per Cooke (1959).

Furthermore, the primary tubercles of *E. antillarum* are retained within the peripetalous fasciole, which does not extend outward to nearly the ambitus as viewed from above, as clearly shown in the holotype of *E. mooreanus*. The aboral surface of *E. mooreanus* is much more heavily tuberculated, with the zigzagging rows of tubercles extending nearly to the ambitus, anteriorly and laterally. The structure of the primary tubercles and the anterior petals alone serve readily to distinguish *E. mooreanus* from *E. antillarum*. We do not consider *E. mooreanus* a subjective junior synonym of *E. antillarum* and in addition, do not recognize *E. antillarum* in the Eocene faunas of the eastern United States.

Doubts concerning Cooke's (1959) synonymy of *E. mooreanus* with *E. antillarum* are not new. Kier (1984: 84), in comparing *Eupatagus alatus* from the Cuban Eocene stated: "it differs from the Late Eocene Floridian specimens that Cooke referred to *E. antillarum* (which belong to a different species, *Eupatagus mooreanus* Pilsbry) in having shorter posterior petals, a less-pointed posterior, and blunter anterior surface." The documented occurrences of *E. antillarum* in the Caribbean region need to be reconsidered, given Cooke's (1959) synonymy, because we cannot be certain whether subsequent authors were referencing the Floridian *E. antillarum* (= *Eupatagus mooreanus*) or the typical *E. antillarum* from St. Bartholomew.

For example, Donovan (1993: 402) discussed, but did not figure, a very worn specimen from the Eocene of Jamaica that he questionably attributed to *E. antillarum*. He compared it to the figures of Jackson (1922), which show *E. antillarum* from St. Bartholomew, so it is likely that Donovan was not comparing his material to the Florida *E. antillarum* (= *E. mooreanus*).

Donovan and Rowe (2000) documented *Eupatagus* cf. *E. antillarum* from the Eocene Claremont Formation of Jamaica. The angle of the petals and tuberculation of the species is more reminiscent of *E. mooreanus* than it is of *E. antillarum* (as evident in their fig. 4, #1: BMNH EE 6341). However, as Donovan (1993) noted, the specimen is damaged and incomplete.

Curiously, Donovan (2004: figs. 1, 8) also discussed and figured a specimen he tentatively referred to *E. antillarum* from the Eocene Troy

Formation of the White Limestone Group of Jamaica. However, the specimen shown is the same as that figured in Donovan and Rowe (2000: fig. 4, #1: BMNH EE 6341), from the Claremont Formation, that we concluded is *E. antillarum*.

Buitrón and Sánchez (1979: fig. 3) documented *E. mooreanus* from the Upper Eocene Tan Toyuca Formation in the northeastern portion of the state of Veracruz, Mexico. The figured specimens are clearly conspecific with *E. mooreanus*, and not *E. antillarum*.

Eupatagus mooreanus is most abundant in its type area, where it occurs in the *Oligopygus phelani* Zone of the lower OLS, in the vicinity of Inglis in Citrus and Levy Counties, where it occurs with *P. floridana, R. georgiensis, N. durhami,* and other, rarer species.

Eupatagus ocalanus Cooke, 1942
(Fig. 208)

?Eupatagus floridanus (part) Clark in Clark and Twitchell, 1915. p. 176. pl. 82, figs. 2a-d (not pl. 83, figs. 1a-c, 2a-d).

Eupatagus (*Plagiobrissus*) *ocalanus* Cooke, 1942. p. 57. pl. 6, figs. 4-8.

Eupatagus (*Gymnopatagus*) *ocalanus* (Cooke). Cooke, 1959. p. 91. pl. 42, figs. 8-12.

Eupatagus ocalanus (Cooke). Osborn et al., 2016. tbl. 2.

Occurrence.—This species occurs within the upper OLS of Florida, where it is most abundant near the top of the *Wythella eldridgei* Zone, especially north of Mayo, Lafayette County (type locality); north of Branford (FM-IP SU002), Suwannee County; south of Tennille (FM-IP DI001), Dixie County; and west of Center Hill, Sumter County (FM-IP SM010). It is much more rarely found in the *Oligopygus haldemani* Zone where it occurs in the Brooks Quarries (FM-IP JA009, FM-IP JA018, FM-IP JA027, FM-IP JA031, FM-IP JA039), northwest of Marianna, Jackson County.

Eupatagus ocalanus also occurs in the Upper Eocene of Alabama and Georgia (Cooke, 1959).

Discussion.—This species occurs with *P. dixie* at most known localities, and can be readily differentiated from the much wider poriferous zones, flattened anterior ambulacral area, and distinct zigzag arrangement of the primary tubercles in *E. ocalanus*. It is not known to occur with *E. carolinensis* Clark in Clark and Twitchell, 1915, but it could be confused with it. It is differentiated from *E. carolinensis* by its proportionately narrower and longer petals. In addition, *E. carolinensis* appears not to have attained as great a size as *E. ocalanus* (Cooke, 1942). Although *E. ocalanus* has not been documented in the *Oligopygus phelani* Zone in the lower portion of the OLS, it is readily differentiated from *E. mooreanus*, the dominant spatangoid species of the horizon, by the much less heavily tuberculated aboral surface of *E. ocalanus*.

Eupatagus dumonti n. sp.
(Figs. 209-214)

Diagnosis.—*Eupatagus* with broad (TW on average 92.9 % TL), low (TH on average 49.1% TL) test, large periproct that encompasses nearly the entire height of the vertical part of the posterior surface (periproct width on average 71% periproct height; periproct height on average 49.6% TH), and broad, long, heavily tuberculated plastron.

Description.—Description based on the holotype (UF 238275), paratypes (UF 342109, UF 342110), and non-type specimens from the Suwannee Limestone in Hernando County, Florida (FM-IP HE013, FM-IP HE038).

Test moderate in size (five specimens range 59.2 mm to 74.5 mm TL), broad (TW on average 92.9 % TL), low (TH on average 49.1% TL), widest point posterior of apical system, highest point posterior, truncated anterior margin, lacking anterior sulcus. Apical system ethmolytic, madreporic plate projects well posterior of other apical system plates, anterior edge of apical system on average 64% TL from posterior margin; 4 gonopores; posterior gonopores further apart than anterior pair. Aboral tubercles small, not prominent, randomly arranged, largely confined aboral to peripetalous fasciole, densest in anterior paired interambulacra. Ambulacrum III not petaloid, pores small, non-

Figure 208: *Eupatagus ocalanus* (UF 129328), 46.5 mm TL, 40.5 mm TW, 21 mm TH, Upper Eocene, upper portion of Ocala Limestone, Sumter County, Florida (FM-IP SM010). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Figure 209: *Eupatagus dumonti* n. sp., holotype, (UF 238275), 64 mm TL, 60 mm TW, 33 mm TH, Lower Oligocene, basal beds Suwannee Limestone, Hernando County, Florida (FM-IP HE013). A: aboral. B: oral. C: left side. D: right side. E: posterior.

conjugate. Paired petals flush, not sunken; tapered but open distally; pores conjugate, outer pore more elongate than inner; petals I and V longest, extending almost to margin, on average 42.1% TL, petals II and IV shortest, extending two-thirds distance to margin, on average 33.4% TL; petals narrow, greatest width of petal I and V on average 17.3% petal length; width of petals II and IV on average 20.9% petal length.

Peripetalous and subanal fascioles present; peripetalous fasciole thin, extending to margin anteriorly, just beyond petals I and V posteriorly, not indented aborally between petals. Subanal fasciole broadly bilobed, aboral tract passes just below lower

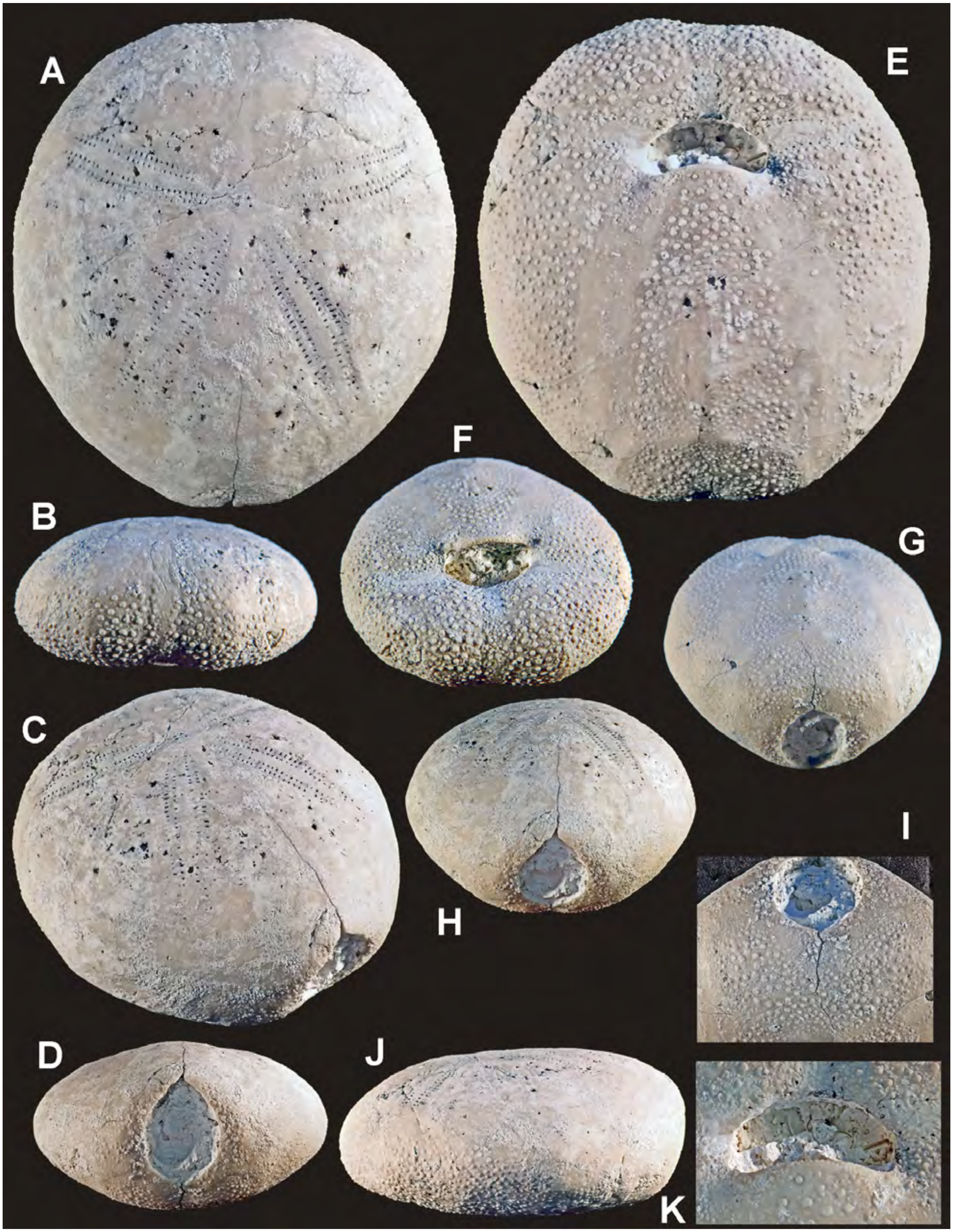


Figure 210: *Eupatagus dumonti* n. sp., paratype (UF 342110), 66 mm TL, 61 mm TW, 31 mm TH, Lower Oligocene, basal beds of the Suwannee Limestone, Hernando County, Florida (FM-IP HE038). A: aboral. B: posterior. C: oblique aboral viewpoint from posterior. D: posterior. E: oral. F: tilted oral viewpoint from anterior. G: tilted oral viewpoint from posterior. H: tilted aboral viewpoint from posterior. I: subanal fasciole. J: left side. K: peristome.

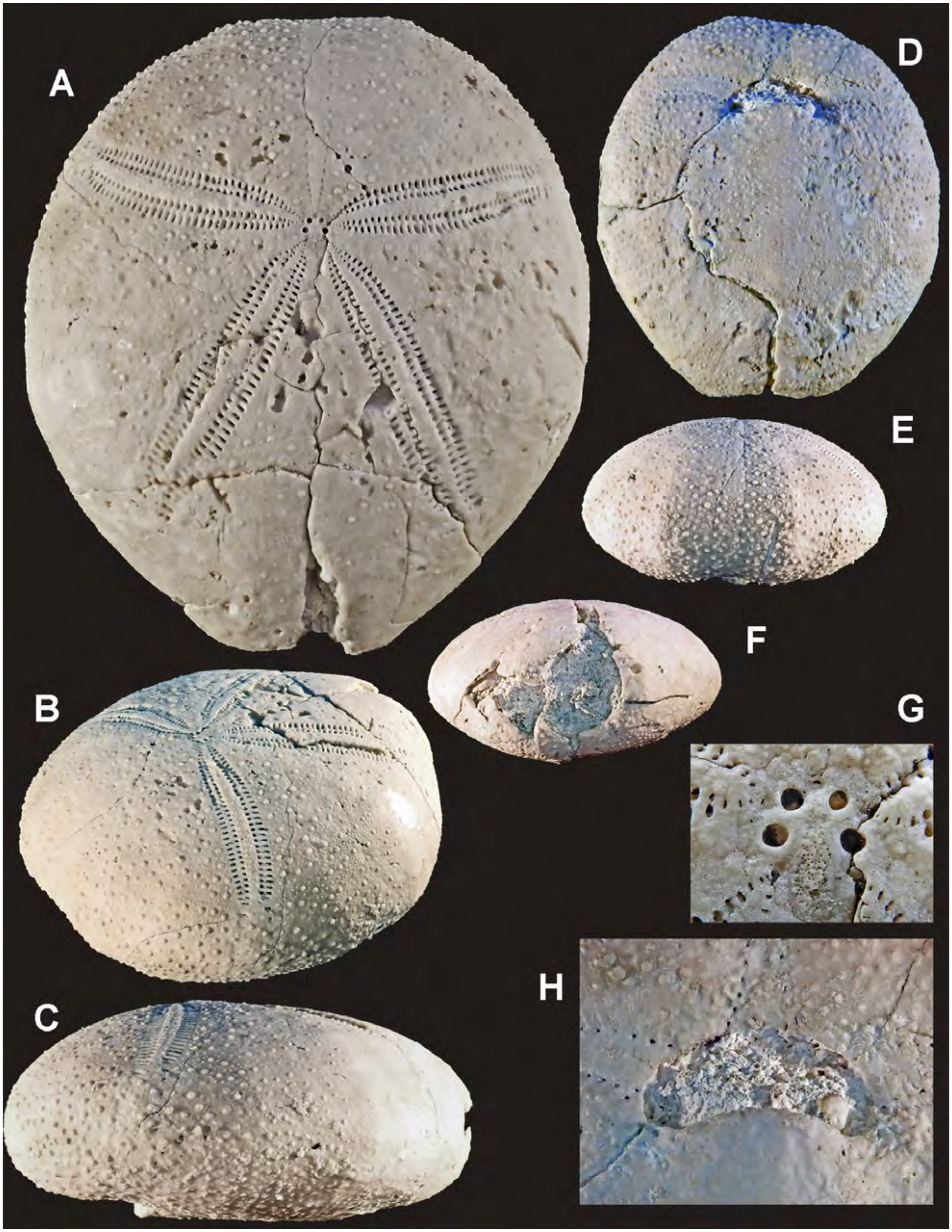


Figure 211: *Eupatagus dumonti* n. sp., paratype (UF 342109), 68 mm TL, 61.5 mm TW, 32 mm TH, Lower Oligocene, basal beds of the Suwannee Limestone, Hernando County, Florida (FM-IP HE038). A: aboral. B: oblique aboral viewpoint from anterior. C: left side. D: oral. E: anterior. F: posterior. G: apical area. H: peristome.

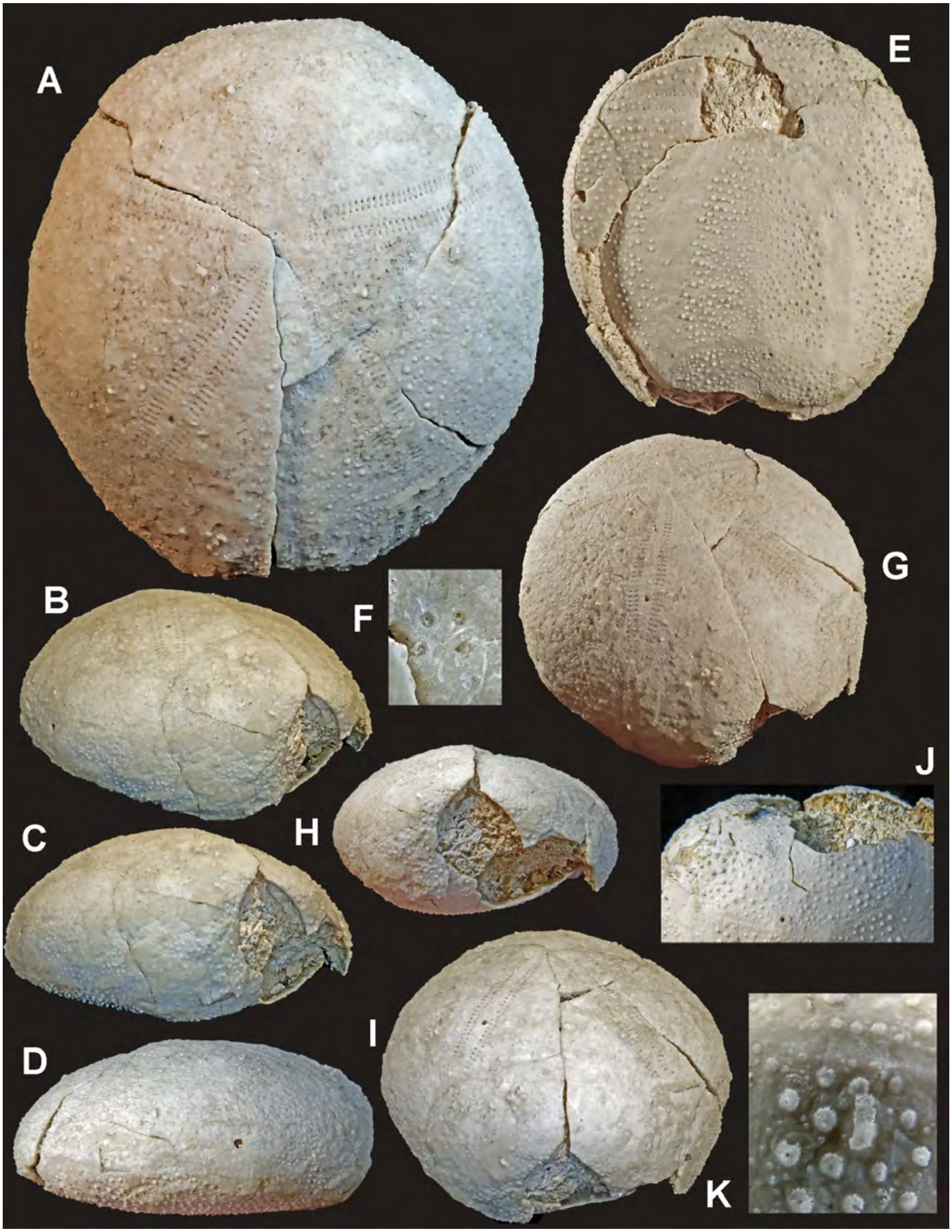


Figure 212: *Eupatagus* cf. *E. dumonti* n. sp., (UF 342108), 93 mm TL, 87 mm TW, 46 mm TH, Oligocene Bridgeboro Limestone, Duncan Church Beds, Washington County, Florida (FM-IP WG002). A: aboral. B: oblique lateral viewpoints, posterior to right. D: left side. E: oral. F: apical area. G: oblique aboral viewpoint. H: posterior. I: tilted aboral viewpoint from posterior. J: posterior portion of oral surface showing subanal fasciole. K: portion of subanal fasciole at top, tubercles within plastron below.

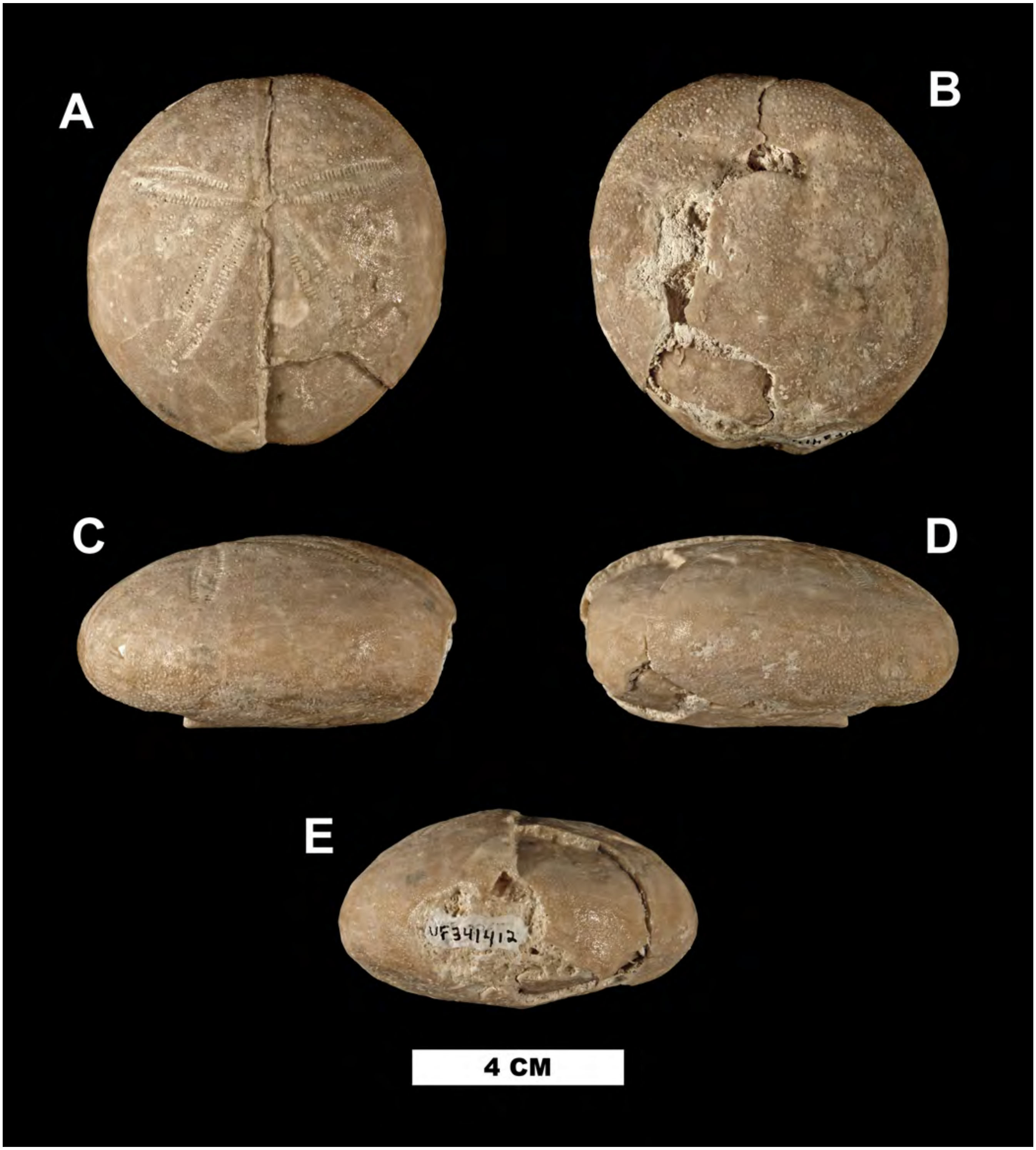


Figure 213: *Eupatagus dumonti* n. sp., paratype (UF 341412), 74.5 mm TL, 72 mm TW, 39 mm TH, Lower Oligocene, basal beds of the Suwannee Limestone, Hernando County, Florida (FM-IP HE038). A: aboral. B: oral. C: left side. D: right side. E: posterior.

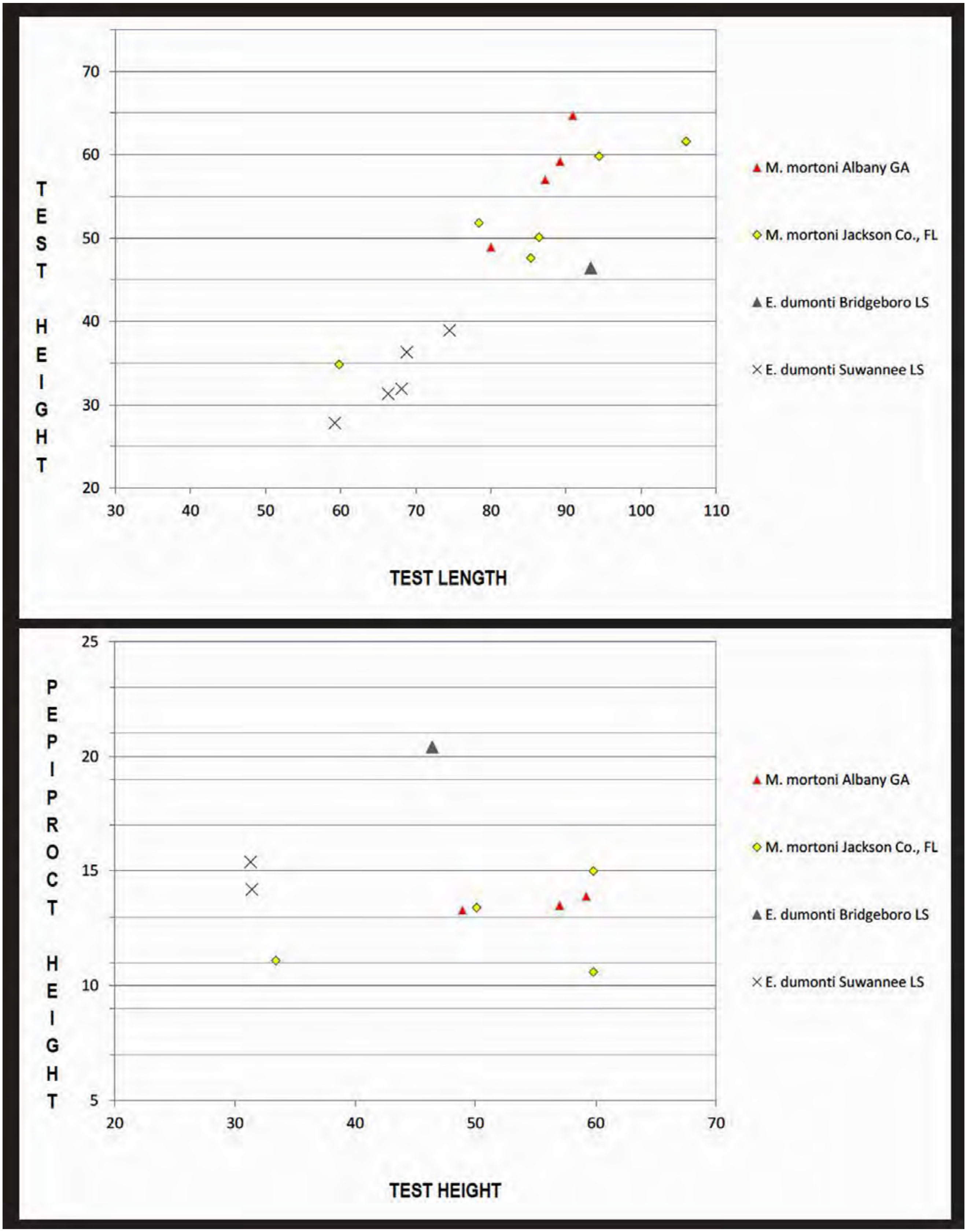


Figure 214: Top: Comparison of test height vs test length in *Eupatagus dumonti* n. sp. and *Macropneustes mortoni*. Bottom: Comparison of periproct height vs test height in *Eupatagus dumonti* n. sp. and *Macropneustes mortoni.*

edge of periproct; wider than tall, height on average 66% fasciole width; width on average 41.8% TW.

Periproct on nearly vertical to slightly overhung posterior truncation, ovate, taller than wide, periproct width on average 71% periproct height; periproct very large, height on average 49.6% TH; periproct encompasses nearly entire height of posterior. Oral surface more heavily tuberculated than aboral. Peristome anterior, distance of posterior edge (i.e., anterior edge of labrum) to posterior margin on average 68.6% TL; kidney-shaped; wider than high, peristome height on average 49% peristome width; labrum elongate, narrow; plastron fully tuberculated, long, extends anteriorly nearly to peristome (i.e., labrum); wide, greatest width posterior and on average 36.4% TW; narrows anteriorly.

Zoobank Nomenclatural Act.—2EBF3767-FC5D-4D80-A4BC-8A82F6ECF16B

Discussion.—*Eupatagus dumonti* n. sp. represents the first known occurrence of *Eupatagus* in the Oligocene of North America. The species is most found in the lowermost bed of the Suwannee Limestone, which is usually exposed below the typical floor of the Vulcan Quarry northwest of Brooksville, Hernando County, where *E. dumonti* n. sp. occurs with *Clypeaster* sp., *S. carlsoni* n. sp., and *R. gouldii*. This horizon is just above the contact with the underlying OLS, and although *E. dumonti* n. sp. is relatively common in this bed, it is typically represented by incomplete tests. The complete specimens figured (Figs. 209-211, 213) are rare.

A specimen (UF 342108) from the Oligocene Duncan Church beds of the Bridgeboro Limestone in the Florida panhandle appears to represent this species (Fig. 212). Although it is much larger than the Suwannee Limestone specimens from the type locality (93 mm TL, 87 mm TW, 46 mm TH), and the overall dimensions are slightly obscured by slight compression of the specimen, it is otherwise similar to *E. dumonti* n. sp. It has a TH 49% TL, and a periproct roughly 38% TH. We refer this specimen to *Eupatagus* cf. *E. dumonti*.

Eupatagus dumonti n. sp., has affinities with both *Macropneustes* (broad, rotund test) and *Eupatagus* (flush petals, lack of anterior notch). Fischer (1966) stated *Macropneustes* (Agassiz, 1847) differs from *Eupatagus* (Agassiz, 1847) chiefly in having depressed petals, a broad test, and distinct anterior notch.

Duncan (1889) noted the similarities of *Eupatagus* and *Macropneustes* and made *Macropneustes* a subgenus of *Eupatagus*. However, Mortensen (1951) asserted that although *Macropneustes* clearly has some relation to *Eupatagus*, it should be treated as a distinct genus. Subsequently, echinologists have continued to recognize *Macropneustes* as distinct from *Eupatagus*.

Cooke (1959) noted that *Macropneustes* shows significant variation in the depth of the ambulacral depressions, with Middle Eocene species usually having a conspicuous anterior notch and moderately depressed petals, but the Late Eocene species tend to have almost flush petals. Kier (1984) stated *Macropneustes* is difficult to distinguish from *Eupatagus*, but clarified the petals are generally narrower and that a distinct anterior ”groove” is present in *Macropneustes*. But his use of the term groove is unfortunate because this anterior sinus (to use Fischer’s word) is often merely a slight indentation in the posterior margin, as seen in *M. mortoni*, and could not be recognized as a groove. We prefer the term ”notch”, which does not connote an impression of considerable depth, and distinguishes this feature from the sinus associated with the periproct in some cassiduloids. We also reserve the term groove for the narrow depression in which hydropores occur, or for food grooves of clypeasteroids and scutelloids.

The flush petals and lack of a discernable anterior notch place this species in *Eupatagus*. We compare *Eupatagus dumonti* n. sp., to known species of both *Macropneustes* and *Eupatagus* from the eastern Americas.

In the North American faunas, *Macropneustes* is represented only by *M. mortoni* from the Upper Eocene OLS of the eastern Gulf Coast. *Eupatagus dumonti* n. sp. is similar in general morphology to *M. mortoni* but has a lower test and significantly larger periproct (Fig. 214). The average periproct height of *M. mortoni* is 26.9 % TH. The average periproct height in *E. dumonti* n. sp. is 49.6% TH (Fig. 214). In addition, on average, the TH of *M. mortoni* is 62.1% TL, whereas in *E. dumonti* n. sp. it is 49.1%.

Eupatagus dumonti n. sp. is further distinguished from *M. mortoni* by its shorter petals, which are flush and not at all depressed.

Macropneustes is sparsely represented in the fossil faunas of the Caribbean region and remainder of the eastern Americas. Kier (1984) stated that in the Cuban faunas, only the Late Eocene *Macropneustes* (*Deakia*) *armadilloensis* Sánchez-Roig, 1953b belongs to *Macropneustes*. This is the only species within the subgenus *Deakia* in the Western Hemisphere (Kier, 1984). Kier (1984) tentatively placed *Macropneustes cubensis* Cotteau, 1875 and *M. palmeri* (Sánchez-Roig, 1953b), from the Oligocene-Miocene of Cuba, within this genus. *Eupatagus dumonti* n. sp., is not at all like any of these species, which were all figured and described well by Kier (1984).

Arnold and Clark (1927, 1934) named six species of *Macropneustes* from the Eocene of Jamaica: *M. altus* Arnold and Clark, 1927; *M. augustus* Arnold and Clark, 1927; *M. parvus* Arnold and Clark, 1927; *M. dyscritus* Arnold and Clark, 1934; M. *sinuosus* Arnold and Clark, 1934, and *M. stenopetalus* Arnold and Clark, 1934. As noted by Mortensen (1951), these species are generally very poorly preserved, and as noted by Arnold and Clark (1927), their actual assignment to genus is questionable. Mortensen (1951: 451) stated: "it might perhaps have been better to leave these poor specimens undescribed." The figures of Arnold and Clark (1927, 1934) are sufficient to permit comparison with *E. dumonti* n. sp. which does not resemble any of them closely enough to warrant further consideration. However, even the most poorly preserved of these specimens shows distinctly sunken petals, among other features that distinguish them from *E. dumonti* n. sp.

Macropneustes dubius Israelsky, 1924 was described from the Miocene of the Tampico region of Mexico, but among other features, its deeply sunken petals are not at all similar to *E. dumonti* n. sp. Kew (1917) described *Macropneustes mexicanus* from the Oligocene to Miocene of Mexico, but this species has been referred to *Gillechinus* (Henderson and Fell, 1969).

Peripneustes antillarum Cotteau, 1875, was described from the Eocene of St. Bartholomew, and subsequently recorded from Cuba (Cottteau, 1897; Kier, 1980), and potentially Veracruz, México (Israelsky, 1924). This species was subsequently placed in *Macropneustes* (Guppy, 1882; Jackson, 1922), but then in *Meoma* by Chesher (1970) and Kier (1984). It is clearly distinct from *E. dumonti* n. sp.

Eupatagus is commonly found in the Eocene strata of the region, and less so in overlying Oligocene or Neogene strata of the region. Distinguishing between these myriad fossil forms is not easy. As noted by Mortensen (1951: 463) when he stated the following concerning the genus: "going over the numerous fossil species I have the impression that it must be an exceedingly difficult task to distinguish them with certainty." We try to do so below.

Eupatagus was previously represented by eight species in the fossil record of the eastern United States. All are Eocene: *E. carolinensis* Clark in Clark and Twitchell, 1915; *E. clevei*; *E. gardnerae*; *E. lawsonae* Kier, 1980; *E. mooreanus*; *E. ocalanus*; *E. texanus* Zachos in Zachos and Molineux, 2003, and *E. wilsoni* Kier, 1980. The broad test and distinctly larger periproct separate *E. dumonti* n. sp. from any of these species.

Kier (1984: 95), recognized the following Cuban species as distinct: *E. alatus* Arnold and Clark, 1927 (Middle to Late Eocene); *E. clevei* (Eocene to Oligocene); *E. cubensis* (Cotteau, 1875) (Eocene to Miocene); *E. sanchezi* (Lambert in Sánchez-Roig, 1949) (Miocene); *E. santanae* Sánchez-Roig, 1951 (Oligocene to Miocene); *E. turibacoensis* Sánchez-Roig, 1953b (Late Eocene), and *E. siboneyensis* Weisbord, 1934 (Late Eocene). These seven species are reduced from 41 species documented from the Cuban faunas that Kier (1984) examined, eight of which were unrecognizable and had to be set aside, but the remainder were placed in synonymy of the preceding seven species. Many of these were described in the works of Sánchez-Roig (1949, 1951, 1953, inter alia). Although poorly figured by the latter, the taxa recognized by Kier (1984) are not conspecific with *Eupatagus dumonti* n. sp.

Arnold and Clark (1927, 1934) and Hawkins in Arnold and Clark (1927) documented seven species of *Eupatagus* from Jamaica. All are Eocene with the exception of the Oligocene occurrence of *E. hildae* Hawkins, 1927 (= *E. clevei*), including: *E. grandiflorus* Cotteau, 1875 (= *E. clevei*); *E. alatus*, which Kier (1984) identified in the Cuban faunas; *E. attenuatus* (Arnold and Clark, 1927) which Kier (1984: 7) stated is likely synonymous with *E. alatus*; *E. longipetalus* Arnold and Clark, 1927, which Kier (1984: 7) placed in *Antillaster*; *E. defectus* Arnold and Clark, 1927; *E. hildae* Hawkins, 1927, from the Oligocene which Kier (1984) considered synonymous with *E. clevei*, and *Eupatagus* cf. *E. antillarum* (Cotteau, 1875). These Jamaican occurrences were further discussed by Dixon and Donovan (1994), Donovan (1994, 2003, 2004), and Donovan and Rowe (2000). Based on comparison with all these records, *E. dumonti* n. sp. cannot be confused with any of them.

E. clevei and *E. antillarum* are documented from their type localities in the Eocene of St. Bartholomew and elsewhere (Cotteau, 1875; Jackson, 1922; Cooke, 1959; Cooke, 1961; Kier, 1984), and Pijpers (1933) named *Brissoides aloysii* from the Eocene of Bonaire, which is clearly a *Eupatagus*. Jackson (1922) documented the occurrence of *E. depressus* Jackson, 1922, in the Oligocene of Puerto Rico, which was considered by Kier (1984) to be a synonym of *E. cubensis* (Cotteau, 1875). Jackson (1922) also named *E. elegans* and *E. vaughani*, which Kier (1984) suggested belonged to *Antillaster*. *Eupatagus dumonti* n. sp. cannot be confused with any of these species.

Some Caribbean species of *Antillaster* (Lambert, 1909) are very similar in general morphology to *E. dumonti* n. sp., such as *Eupatagus mexicanus* Jackson, 1937, from the Oligocene of Mexico. However, Kier (1984) placed *E. mexicanus* in *Antillaster* and then synonymized it with *A. vaughani* (Jackson 1922), first described from the Oligocene-Miocene of Antigua. *Antillaster* is a wide-spread genus in Cenozoic strata of the Caribbean region and northeastern South America. However, it has not been documented from North America. *Antillaster* is readily distinguished from *Macropneustes* and *Eupatagus* by the absence of fascioles, whereas *E. dumonti* n. sp. has both peripetalous and subanal fascioles.

Eupatagus dumonti n. sp., is similar to *Eupatagus longipetalus* Clark, 1927, from the Eocene of Jamaica. Although the petals and general morphology (shape and size) are similar, Kier (1984) placed this species in *Antillaster*, presumably due to the lack of discernable fascioles in the type and only known specimen.

Eupatagus dumonti n. sp. represents the first documented occurrence of *Eupatagus* in the Oligocene of North America. Including the 17 species of *Eupatagus* previously recognized in the fossil record of the eastern Americas and Caribbean region reviewed above, 15 are documented from the Eocene.

Peak of diversity of *Eupatagus* in the Eocene is not restricted to the Americas, as this seems to be true globally as well: Lambert and Thiéry (1925) listed 33 species of *Eupatagus* from the Eocene, Kier and Lawson (1978) listed an additional 27 species, and Kroh (2010) documented another 13 species from the global faunas, of which five are Eocene. Therefore, no fewer than 65 species of *Eupatagus* have been documented from Eocene strata worldwide.

Etymology.—Named in honor of Joe Dumont, collector and donor of many of the specimens used to describe this species.

Material and Occurrence.—*Eupatagus dumonti* n. sp. is represented by the holotype (UF 238275) and paratypes (UF 342109, UF 342110, UF 341412) from the type locality in the lower beds of the Suwannee Limestone in the Vulcan Quarry, west of Brooksville, Hernando County (FM-IP 6360, FM-IP HE013, FM-IP HE038). It is also represented by a single specimen UF 342108 we tentatively assign to this species from the Duncan Church beds of the Bridgeboro Limestone in the Duncan Church Quarry, south of Chipley, Washington County (FM-IP WG002).

***Eupatagus* sp. A**
(Fig. 215)

Occurrence.—Upper Eocene OLS, (occurs with *H. brooksi*), Jackson Blue Spring (FM-IP JA033), east of Marianna, Jackson County.

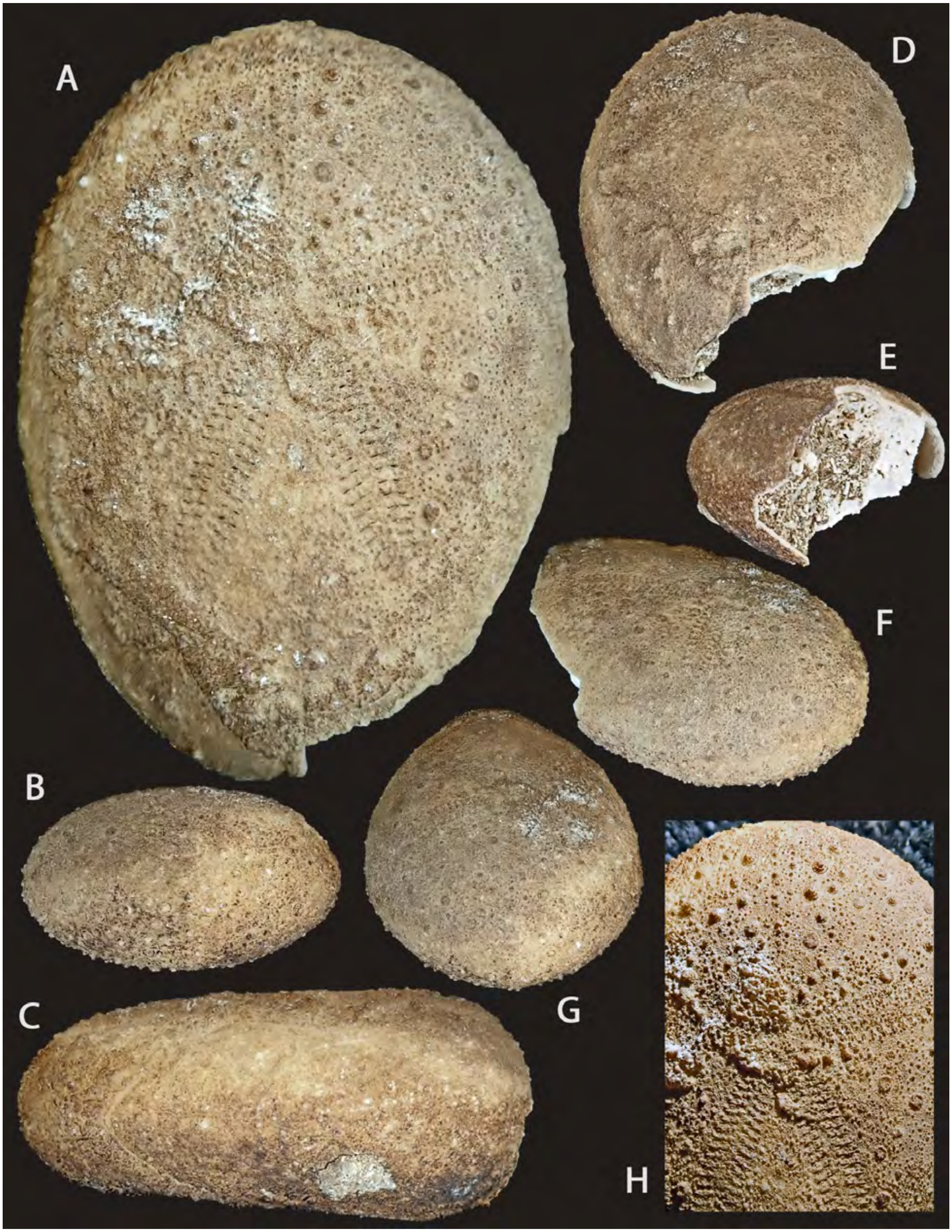


Figure 215: *Eupatagus* sp. A, (UF 341760), 22.1 mm TL, 16.3 mm TW, 9.5 mm TH (TL and TH are incomplete) Upper Eocene Ocala Limestone (*Haimea brooksi* Zone) Jackson Blue Spring (FM-IP JA033), Jackson County, Florida A: aboral. B: anterior. C: left side. D: tilted aboral viewpoint from posterior. E: posterior (largely missing). F: oblique aboral viewpoint from anterior. G: tilted aboral viewpoint from anterior. H: petaloid area with cross lighting to highlight seemingly randomly arranged, sparse, large tubercles.

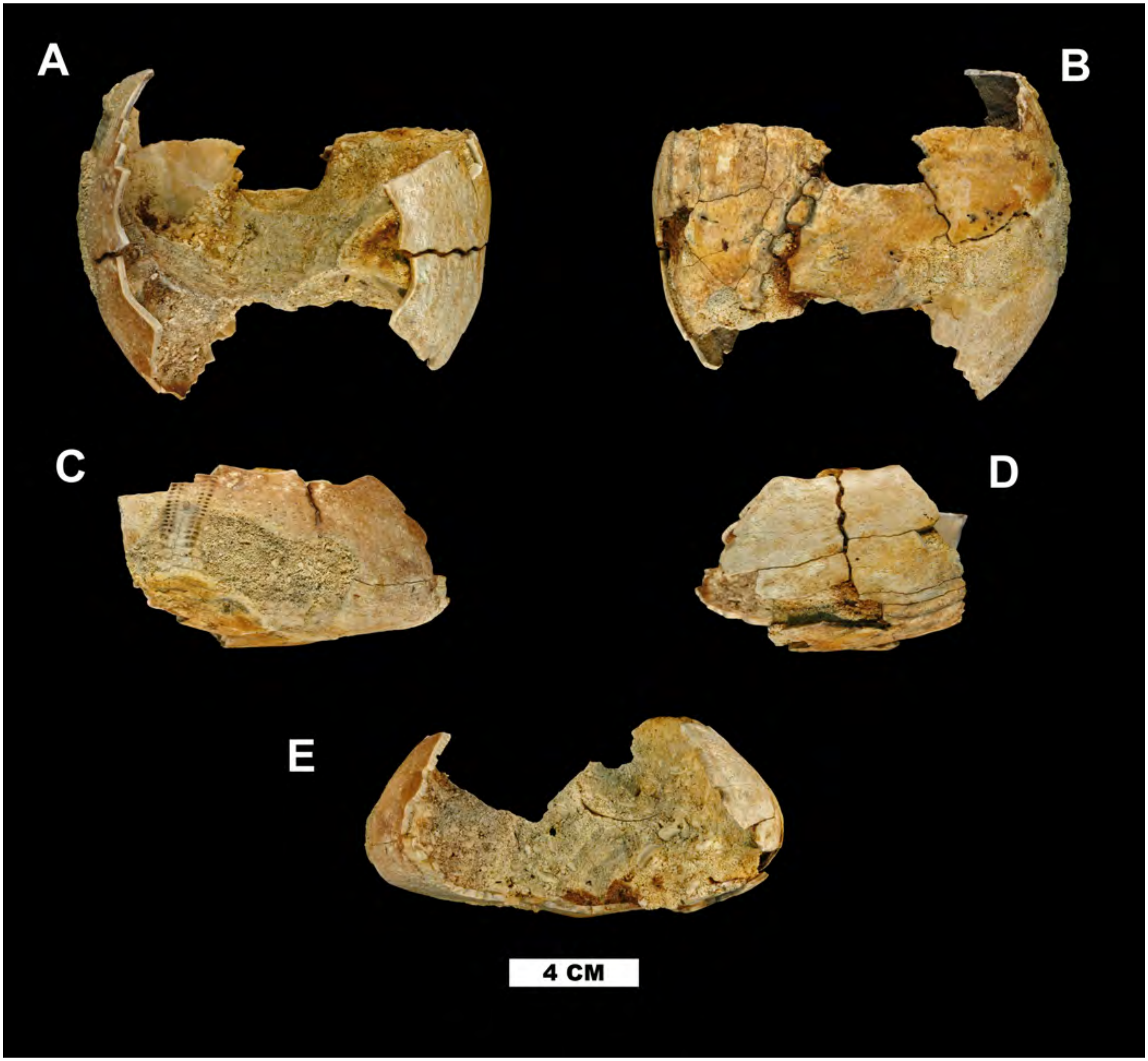


Figure 216: *Eupatagus* sp. B, (UF 344742), 108 mm TL, 137 mm TW, 59 mm TH (no dimensions are complete), Lower Oligocene Suwannee Limestone, Washington County, Florida (FM-IP WG034). A: aboral. B: oral. C: left side. D: right side. E: posterior.

Discussion.—This species is represented by a single specimen collected at Jackson Blue Spring. The incomplete specimen was associated with *H. brooksi*, *R. georgiensis,* and other species, and is the only representative of this form found within these deposits. The specimen is corroded and missing much of the posterior and oral surfaces but does show traces of a peripetalous fasciole.

This fragment (UF 341760) is small (22.1 mm TL, 16.3 mm TW, 9.5 mm TH) but TL and TH are not accurate assessments due to the missing portions of the test. The test has sparse, seemingly random, large, perforate tubercles, flush petals, and a rounded anterior margin that lacks a notch. It is not like any other spatangoid, including any documented species of *Eupatagus* from the North American or Caribbean faunas, but remains is too incomplete to describe. We document it as a taxon in *Eupatagus* facies of the Bridgeboro Limestone, which occurs near the surface in the Duncan Church Quarry (FMIP WG002) roughly 30 km northeastward. However, *R. gouldii* is not present in the Duncan Church beds of the Bridgeboro Limestone. The stratigraphic determination is therefore questionable, but its Oligocene age is certain.

None of the dimensions of this specimen is complete (108 mm TL, 137 mm TW, 59 mm TH) but enough of the test is preserved to determine that it was very large, almost undoubtedly the largest documented from the Oligocene strata of North America. The presence of a peripetalous fasciole rules out assignment to *Antillaster* (a genus also containing some very large representatives in the Eocene and Oligocene of the Caribbean region), and likely belongs in *Eupatagus*. As for *Eupatagus* sp. A, above, we leave this taxon in open nomenclature pending discovery of better specimens.

CLASSIFICATION OF SPECIES TREATED

- Class **ECHINOIDEA** Schumacher, 1817
  - Subclass **CIDAROIDEA** Smith, 1984
    - Order **CIDAROIDA** Claus, 1880
      - Family **CIDARIDAE** Gray, 1825
        - Genus ***Phyllacanthus*** Brandt, 1835
          - ***Phyllacanthus mortoni*** (Conrad, 1850)
        - Genus ***Prionocidaris*** A. Agassiz, 1863
          - ***Prionocidaris robertsi*** n. sp.
  - Subclass **EUECHINOIDEA** Bronn, 1860
    - Infraclass **AULODONTA** Jackson, 1912
      - **Aulodonta** gen. et. sp. indet.
    - Infraclass **CARINACEA** Kroh and Smith, 2010
      - Order **PHYMOSOMATOIDA** Mortensen, 1904
        - Family **PHYMOSOMATIDAE** Pomel, 1883
          - Genus ***Acanthechinus*** Duncan and Sladen, 1882
            - ***Acanthechinus dixie*** (Cooke, 1941a)
      - Order **STOMOPNEUSTOIDA** Kroh and Smith, 2010
        - Family **STOMOPNEUSTIDAE** Mortensen, 1903
          - Genus ***Phymotaxis*** Lambert and Thiéry, 1914
            - ***Phymotaxis mansfieldi*** Cooke, 1941a
      - Order **CAMARODONTA** Jackson, 1912
        - ”Triplacidiids” temporary family (Kroh and Mooi, 2022)
          - Genus ***Gagaria*** Duncan, 1889
            - ***Gagaria mossomi*** (Cooke, 1941a)
        - Family **TRIGONOCIDARIDAE** Mortensen, 1903
          - Genus ***Brochopleurus*** Fourtau, 1920
            - ***Brochopleurus pretiosus*** (Clark, 1915)
        - Family **TOXOPNEUSTIDAE** Troschel, 1872
          - Genus ***Lytechinus*** A. Agassiz, 1863
            - ***Lytechinus floralanus*** (Cooke, 1941a)
            - **Euechinoidea** gen. et. sp. indet.
    - Infraclass **IRREGULARIA** Latreille, 1825
      - Subterclass **NEOGNATHOSTOMATA** Smith, 1981
        - Order **ECHINONEOIDA** H.L. Clark, 1925

- Family **ECHINONEIDAE** Agassiz and Desor, 1847
  - Genus ***Amblypygus*** L. Agassiz, 1840
    - ***Amblypygus americanus*** Michelin, 1856
- Superorder **LUMINACEA** Mongiardino Koch, Thompson, Hiley, McCowin, Armstrong, Coppard, Aguilera, Bronstein, Kroh, Mooi, & Rouse, 2022
  - Order **CLYPEASTEROIDA** A. Agassiz, 1872
    - Family **OLIGOPYGIDAE** Duncan, 1889
      - Genus ***Haimea*** Michelin, 1851
        - ***Haimea brooksi*** Osborn et al., 2016
      - Genus ***Oligopygus*** de Loriol, 1887
        - ***Oligopygus haldemani*** (Conrad, 1850)
        - ***Oligopygus phelani*** Kier, 1967
        - ***Oligopygus rotundus*** Cooke, 1942
        - ***Oligopygus wetherbyi*** de Loriol, 1887
    - Suborder **CLYPEASTERINA** L. Agassiz, 1835
      - Family **CLYPEASTERIDAE** L. Agassiz, 1835
        - Genus ***Clypeaster*** Lamarck, 1801
          - ***Clypeaster cotteaui*** Egozcue in Cotteau, 1897
          - ***Clypeaster marinanus*** Jackson, 1937
          - ***Clypeaster oxybaphon*** Jackson, 1922
          - ***Clypeaster rogersi*** (Morton, 1834)
          - ***Clypeaster* sp. A**
          - ***Clypeaster* sp. B**
          - ***Clypeaster* sp. C**
  - Order **ECHINOLAMPADACEA** Mongiardino Koch et al., 2018
    - Suborder **CASSIDULOIDA** Agassiz and Desor, 1847
      - Family **EURHODIIDAE** Souto et al., 2019
        - Genus ***Eurhodia*** Haime in d'Archiac and Haime, 1853
          - ***Eurhodia patelliformis*** (Bouvé, 1851)
      - Family CASSIDULIDAE L. Agassiz and Desor, 1847
        - Genus ***Rhyncholampas*** A. Agassiz, 1869
          - ***Rhyncholampas conradi*** (Conrad, 1850)
          - ***Rhyncholampas ericsoni*** (Fischer, 1951)
          - ***Rhyncholampas fontis*** (Cooke, 1942)
          - ***Rhyncholampas georgiensis*** (Twitchell, 1915)
          - ***Rhyncholampas gouldii*** (Bouvé, 1846)
          - ***Rhyncholampas trojanus*** (Cooke, 1942)
          - ***Rhyncholampas mariannaensis*** n. sp.
          - ***Rhyncholampas bao*** n. sp.
    - Suborder **ECHINOLAMPADOIDA** Kroh and Smith, 2010
      - Family **ECHINOLAMPADIDAE** Gray, 1851
        - Genus ***Echinolampas*** Gray, 1825
          - ***Echinolampas aldrichi*** Twitchell, 1915
          - ***Echinolampas tanypetalis*** Harper and Shaak, 1974
    - Suborder **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 macneili*** Cooke, 1959
  - Genus ***Fibularia*** Lamarck, 1816
    - ***Fibularia vaughani*** (Twitchell, 1915)
- Family **NEOLAGANIDAE** Durham, 1954
  - Genus ***Neolaganum*** Durham, 1954
    - ***Neolaganum archerensis*** (Twitchell, 1915)
    - ***Neolaganum dalli*** (Twitchell, 1915)
    - ***Neolaganum durhami*** Cooke, 1959
  - Genus ***Durhamella*** Kier, 1968
    - ***Durhamella ocalana*** (Cooke, 1942)
    - ***Durhamella floridana*** (Twitchell, 1915)
    - ***Durhamella tetrapora*** n. sp.
  - Genus ***Weisbordella*** Durham, 1954
    - ***Weisbordella cubae*** (Weisbord, 1934)
    - ***Weisbordella johnsoni*** (Twitchell, 1915)
    - ***Weisbordella inglisensis*** n. sp.
    - ***Weisbordella libum*** n. sp.
  - Genus ***Wythella*** Durham, 1954
    - ***Wythella eldridgei*** (Twitchell, 1915)
- Family **SCUTELLINIDAE** Pomel, 1888 (Scutelliformes stem group)
  - Genus ***Porpitella*** Pomel, 1883
    - ***Porpitella micra*** H. L. Clark, 1937
- Infraorder **SCUTELLIFORMES** Haeckel, 1896
  - Family **PROTOSCUTELLIDAE** Durham, 1955
    - Genus ***Periarchus*** Conrad, 1866
      - ***Periarchus floridanus*** Fischer, 1951
      - ***Periarchus quinquefarius*** (Say, 1825)
  - Genus ***Protoscutella*** Stefanini, 1924
      - ***Protoscutella pentagonium*** Cooke, 1942
- Subterclass **ATELOSTOMATA** von Zittel, 1879
  - Order **SPATANGOIDA** L. Agassiz, 1840
    - Suborder **MICRASTERINA** Fischer, 1966 *incertae sedis*
      - Genus ***Gillechinus*** Fell, 1964
        - ***Gillechinus alabamensis*** (Cooke, 1942)
    - Suborder **PALEOPLEUSTINA** Markov and Solovjev, 2001
      - Family **SCHIZASTERIDAE** Lambert, 1905
        - Genus ***Ova*** Gray, 1825
          - ***Ova beckeri*** (Cooke, 1942)
          - ***Ova ocalanus*** (Cooke, 1942)
        - Genus ***Schizaster*** L. Agassiz, 1836
          - ***Schizaster americanus*** Clark, 1915
          - ***Schizaster armiger*** Clark, 1915
          - ***Schizaster carlsoni*** n. sp.
      - Family **PRENASTERIDAE** Lambert, 1905

Genus ***Agassizia*** Valenciennes, 1846
  Agassizia mossomi Cooke, 1942
Genus ***Prenaster*** Desor, 1853
  cf. ***Prenaster*** sp.
Suborder **BRISSIDINA** Kroh and Smith, 2010
Family **BRISSIDAE** Gray, 1855
Genus ***Brissopsis*** L. Agassiz, 1840
  Brissopsis steinhatchee Cooke, 1942
  cf. ***Brissopsis*** sp.
Genus ***Brissus*** Gray, 1825
  Brissus bridgeboroensis Carter, 1987b
  Brissus jonesi n. sp.
Genus ***Plagiobrissus*** Pomel, 1883
  Plagiobrissus curvus (Cooke, 1942)
  Plagiobrissus dixie (Cooke, 1942)
  Plagiobrissus cassadyi n. sp.
Superfamily **SPATANGOIDEA** Gray, 1825
Family **MACROPNEUSTIDAE** Lambert, 1905
Genus ***Macropneustes*** L. Agassiz, in Agassiz and Desor, 1847
  Macropneustes mortoni (Conrad, 1850)
Family **EUPATAGIDAE** Lambert, 1905
Genus ***Eupatagus*** L. Agassiz, in Agassiz and Desor, 1847
  Eupatagus clevei (Cotteau, 1875)
  Eupatagus mooreanus Pilsbry, 1914
  Eupatagus ocalanus Cooke, 1942
  Eupatagus dumonti n. sp.
  ***Eupatagus* sp. A**
  ***Eupatagus* sp. B**

CONCLUSIONS

This work documents occurrences of all echinoids currently known from Florida's Paleogene strata. Our work is based on decades of extensive collecting, thorough examination of the FM-IP collections, the collections of regional institutions, and the collections of numerous regional avocational collectors. These collectors have contributed much through their diligence, careful documentation, and willingness to share important specimens.

Despite intense efforts of professional paleontologists and avocational collectors alike, there undoubtedly remain large numbers of undocumented echinoid species in Florida. It is hoped that a monographic treatment such as this will inspire and aid those who will have further interest in the echinoids of these remarkable fossil-bearing strata spanning crucial time intervals in the evolutionary history of the Echinoidea. The present work is not intended to be the final word, but a progress report for a better understanding of the evolution and diversity of these animals within the sedimentary sequences of Florida.

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LOCALITY APPENDIX

FM-IP FLORIDA LOCALITIES

2409

Levy County, 1.0 mi. west of US19 along Cross Florida Barge Canal, Upper Eocene lower OLS.

2432

Alachua County, 5.0 mi. southwest of Gainesville at Gainesville Limestone Pit on Archer Road, Upper Eocene OLS.

2434

Alachua County, Upper Eocene OLS.

2613

Alachua County, in and around Archer, Upper Eocene OLS.

3142

Levy County, 4.0 mi. north of Williston at Johnsons Sink on southwest end of Johnson's Lake, Upper Eocene OLS.

3573

Polk County, Lake Wales from well at 200 ft. depth, Middle Eocene Avon Park Formation.

5649

Taylor County, Upper Eocene upper OLS.

6340

Hernando County, Lower Oligocene Suwannee Limestone.

6341

Citrus County, Upper Eocene lower OLS.

6360

Hernando County, Upper Eocene OLS.

AL002 (FT. CLARK QUARRY)

Alachua County, quarry southwest of Gainesville on Ft. Clark Church Road (29.631667°, -82.440807°)

(WGS84), Upper Eocene OLS.

AL004 (DICKERSON LIMEROCK MINES (HAILE COMPLEX)

Alachua County, 5.0 mi. northeast of Newberry (29.678299°, -82.568823°) (WGS84), Upper Eocene OLS.

AL030 (OLD SANTE FE RIVER BRIDGE 01)

Alachua County, 1.0 mi. north of High Springs along riverbank just west of US441 bridge over Sante Fe River (29.851999°, -82.611524°) (WGS84), Lower Oligocene Suwannee Limestone.

CI001 (INGLIS 01A)

Citrus County, 1.5 mi. southwest of Inglis along Florida Cross State Barge Canal (29.007775°, -82.688094°) (WGS84), Upper Eocene lower OLS.

CI003 (FLORIDA BARGE CANAL, NORTH BANK)

Citrus County, 1.0 mi. south of Inglis along north bank of Florida Cross State Barge Canal, east of US98 bridge (29.014996°, -82.658378°) (WGS84), Upper Eocene lower OLS.

CI004 (FLORIDA CROSS STATE CANAL 02)

Citrus County, approximately 6.0 mi. west of Inglis, spoil banks on an island approximately 2.0 mi. offshore from the west end of Florida Cross State Barge Canal (28.981799°, -82.765421°) (WGS84), Upper Eocene lower OLS.

CI009 (DOLIME QUARRY 01)

Citrus County, 2.5 km south of Inglis; southeast side of Florida Cross State Barge Canal at US19/98 Bridge (29.010862°, -82.653961°) (WGS84), Upper Eocene lower OLS.

CI010 (MAPLE SUGAR CAVE)

Citrus County, about 10 mi. south of Lecanto in cave (28.7017°, -82.4629°) (NAD27), Upper Eocene lower OLS.

CI012 (FLORIDA CROSS STATE CANAL 03)

Citrus County, approximately 2.5 mi. southwest of Inglis on spoil pile approximately 2 mi. west of US19 Bridge (29.0060870°, -82.6940940°) (WGS84), Upper Eocene lower OLS.

CI014 (RED LEVEL DOLOMITE MINE)

Citrus County, Red Level Quarry complex on west side of US19/US98 (28.965858°, -82.640819°) (NAD27), Upper Eocene lower OLS.

CI015 (FLORIDA CROSS STATE CANAL 04)

Citrus County, approximately 1.5 mi. southwest of Inglis, 1.25 mi. southwest of US19 Bridge on north bank of canal (29.009092°, -82.683842°) (WGS84), Upper Eocene lower OLS.

CI017 (INDEPENDENT AGGREGATES 01)

Citrus County, quarry approximately 2 mi. southwest of Inglis (29.014478°, -82.702498°) (WGS84), Upper Eocene lower OLS.

CI020 (FLORIDA CROSS STATE CANAL 06)

Citrus County, 3.6 mi. southwest of Inglis, Florida Cross State Barge Canal 3.5 mi. west of US19 (29.001074°, -82.715253°) (WGS84), Upper Eocene lower OLS.

CI021 (FLORIDA CROSS STATE CANAL 07)

Citrus County, 4.6 mi. west southwest of Inglis along Barge Canal (28.9956°, -82.7353°) (NAD27), Upper Eocene lower OLS.

CI022 (FLORIDA CROSS STATE CANAL 08)

Citrus County, southwest of Inglis along Barge Canal (29.0055°, -82.6918°) (NAD27), Upper Eocene lower OLS.

CI024 (FLORIDA CROSS STATE CANAL 10)

Citrus County, 3-4 mi. west southwest of Barge Canal in Gulf of Mexico (28.9726°, -82.7922°) (NAD27), Upper Eocene lower OLS.

CI038 (INGLIS 05)

Citrus County, 4.23 mi. west southwest of Inglis, U.S.E.D. Well on south side of the Florida Cross State Barge Canal (28.997472°, -82.727882°) (WGS84), Upper Eocene lower OLS.

CI052 (CRACKERTOWN 03)

Citrus County, south side of Crackertown on south bank of the Withlacoochee River, 0.25 mi. up and down river from Faris Landing (29.032574°, -82.688149°) (WGS84), Upper Eocene lower OLS.

CR013 (BELLE MEADE 01)

Collier County, about 3 mi. northwest of Golden Gate (26.2443°, -81.6827°) (NAD27), Middle Eocene Avon Park Formation.

DI001 (STEINHATCHEE 02)

Dixie County, near Tennille at quarry east of Steinhatchee River (29.769017°, -83.317604°) (WGS84), Upper Eocene OLS.

DI013 (STEINHATCHEE 05)

Dixie County, near Tennille at quarry east of Steinhatchee River (29.769017°, -83.317604) (WGS84), Upper Eocene upper OLS.

HE006 (RIDGE MANOR 01)

Hernndo County, Ridge Manor in limerock quarry northeast of corner of US301 and SR50 (28.519215°, -82.160042°) (NAD27), Upper Eocene OLS.

HE007 (BROOKSVILLE ROCK QUARRY 01)

Hernando County, northwest of Brooksville at Cargil Vulcan Quarry, 4.25 mi. south of county line and 2.0 mi. southwest of US98 (28.6316°, -82.4806°) (NAD27), Lower Oligocene Suwannee Limestone.

HE012 (BROOKSVILLE ROCK QUARRY 02)

Hernando County, 9.01 mi. northwest of Brooksville at Cargil Vulcan Quarry, mine 2.05 mi. south southeast of intersection of SR589 and US98 (28.6562260°, -82.4851720°) (NAD27), Lower Oligocene Suwannee Limestone.

HE013 (BROOKSVILLE ROCK QUARRY [GENERAL 01])

Hernando County, Brooksville Rock Company Quarry 4.0 mi. south of county line and 1.5 mi. southeast of US98 (28.636318°, -82.476333°) (NAD27), Lower Oligocene Suwannee Limestone.

HE019 (BROOKSVILLE ROCK QUARRY 06)

Hernando County, Brooksville Rock Quarry 1.57 mi. northeast of the intersection of SR589 and Centralia Road (28.629629°, -82.474583°) (NAD27), Lower Oligocene Suwannee Limestone.

HE026 (BROOKSVILLE ROCK QUARRY 12)

Hernando County, 9.0 mi. northwest of Brooksville at Cargil Vulcan Quarry, pit 2.09 mi. south southeast of intersection of SR589 and US98 (28.65453°, -82.483983°) (NAD27), Lower Oligocene Suwannee Limestone.

HE028 (BROOKSVILLE ROCK QUARRY 14)

Hernando County, Brooksville Rock Quarry 1.33 mi. northeast of the intersection of SR589 and Centralia Road (28.628452°, -82.478524°) (NAD27), Lower Oligocene Suwannee Limestone.

HE034 (BROOKSVILLE ROCK QUARRY 17)

Hernando County, Brooksville Rock Quarry 1.72 mi. northeast of the intersection of SR589 and Centralia Road (28.630768°, -82.472073°) (WGS84), Lower Oligocene Suwannee Limestone.

HE038 (BROOKSVILLE ROCK QUARRY 20)

Hernando County, Brooksville Rock Quarry 1.5 mi. northeast of the intersection of SR589 and Centralia Road (28.629297°, -82.475314°) (WGS84), Lower Oligocene Suwannee Limestone.

JA009 (MARJAX PIT)

Jackson County, 3.38 mi. northwest of Marianna, 1.5 mi. northwest of the junction of US90 and SR73 (30.801477°, -85.274942°) (WGS84), Upper Eocene upper OLS.

JA010 (DRY CREEK 01)

Jackson County, 2.5 mi. southwest of Oakdale at Dry Creek (30.673458°, -85.207758°) (WGS84), Lower Oligocene Marianna Limestone.

JA013 (MARJAX PIT A)

Jackson County, 3.38 mi. northwest of Marianna (30.801477°, -85.274942°) (WGS84), Lower Oligocene Marianna Limestone.

JA014 (OAKDALE 01)

Jackson County, quarry north of Altha (30.639833°, -85.173137°) (WGS84), Lower Oligocene Marianna Limestone.

JA018 (MARIANNA LIME PRODUCTS)

Jackson County, quarry northwest of Marianna (30.807°, -85.2606°) (NAD27), Upper Eocene upper OLS.

JA019 (MARIANNA LIME PRODUCTS 01)

Jackson County, quarry northwest of Marianna (30.807°, -85.2606°) (NAD27), Lower Oligocene Marianna Limestone.

JA020 (MARIANNA LIME PRODUCTS 02)

Jackson County, quarry northwest of Marianna (30.807°, -85.2606°) (NAD27), *ex situ*, Upper Eocene upper OLS, Upper Eocene to Lower Oligocene Bumpnose Limestone, and Lower Oligocene Marianna Limestone.

JA021 (MARIANNA LIME PRODUCTS 03)

Jackson County, quarry northwest of Marianna (30.807°, -85.2606°) (NAD27), Upper Eocene to Lower Oligocene Bumpnose Limestone.

JA025 (MARIANNA LIME PRODUCTS 05)

Jackson County, quarry northwest of Marianna (30.8052°, -85.2634°) (NAD27), Upper Eocene to Lower Oligocene Bumpnose Limestone.

JA026 (MARIANNA LIME PRODUCTS 06)

Jackson County, quarry northwest of Marianna (30.8052°, -85.2634°) (NAD27), Lower Oligocene Marianna Limestone.

JA027 (MARIANNA LIME PRODUCTS 07)

Jackson County, quarry northwest of Marianna (30.8052°, -85.2634°) (NAD27), Upper Eocene upper OLS.

JA029 (MARIANNA LIME PRODUCTS 09)

Jackson County, quarry northwest of Marianna (30.8068°, -85.2567°) (NAD27), Lower Oligocene Marianna Limestone.

JA030 (MARIANNA LIME PRODUCTS 10)

Jackson County, quarry northwest of Marianna (30.8068°, -85.2567°) (NAD27), Upper Eocene to Lower Oligocene Bumpnose Limestone.

JA031 (MARIANNA LIME PRODUCTS 11)

Jackson County, quarry northwest of Marianna (30.8068°, -85.2567°) (NAD27), Upper Eocene upper OLS.

JA033 (JACKSON BLUE SPRING 01)

Jackson County, 5.8 km east northeast of Marianna at head of Merritt's Millpond (30.7903°, -85.1402°) (NAD27), Upper Eocene OLS.

JA039 (MARIANNA LIME PRODUCTS 13)

Jackson County, northwest of Marianna (30.811°, -85.2689°) (NAD27), Upper Eocene upper OLS.

JA084 (MARIANNA 12 [TYPE MARIANNA LIMESTONE])

Jackson County, about 1 mi. east of Marianna (30.773°, -85.2165°) (NAD27), Lower Oligocene Marianna Limestone.

JA085 (CHIPOLA 29)

Jackson County, east side of Marianna along Chipola River between US90 Bridge and SR166 Bridge (30.784072°, -85.213872°) (WGS84), Upper Eocene upper OLS.

JA086 (SILLS PIT 06)

Jackson County, approximately 7.0 mi. north northeast of Cottondale, east of Union Road and northwest of Waddell's Millpond (30.88°, -85.3489°) (WGS84), Upper Eocene upper OLS.

LF001 (DELL LIMEROCK MINE)

Lafayette County, 4.5 mi. northwest of Mayo (30.0894°, -83.2345°) (NAD27), Upper Eocene upper OLS.

LF002 (MILL CREEK QUARRY 01)

Lafayette County, 2.0 mi. west of Dowling Park at quarry complex (30.2529°, -83.2578°) (NAD27), Upper Eocene OLS.

LF010 (MILL CREEK QUARRY 03)

Lafayette County, 2.0 mi. west of Dowling Park at quarry complex (30.2529°, -83.2578°) (NAD27), Lower Oligocene Suwannacoochee Dolostone.

LF015 (DOWLING PARK 04)

Lafayette County, 1.04 mi. west of Dwling Park at quarry just west of Suwannee River (30.244454°, -83.253597°) (WGS84), Upper Eocene upper OLS.

LF023 (SUWANNEE RIVER 12)

Lafayette County, 0.75 mi. west of Dowling Park on west bank of Suwannee River (30.245852°, -83.249011°)

(WGS84), Upper Eocene upper OLS.

LV004 (GULF HAMMOCK QUARRY 01)

Levy County, 1.0 mi. southeast of Gulf Hammock (29.237046°, -82.700545°) (NAD27), Middle Eocene Avon Park Formation.

LV005 (DEVIL'S DEN)

Levy County, 2.0 mi. north and 1.0 mi. west of Williston (29.407548°, -82.47642°) (WGS84), Upper Eocene OLS.

LV014 (GULF HAMMOCK 02)

Levy County, quarry 2.4 mi. south of Gulf Hammock (29.21619°, -82.703966°) (WGS84). Upper Eocene lower OLS.

LV016 (INGLIS 02 [COTYPE LOCALITY INGLIS MEMBER])

Levy County, quarry 1.0 mi. west of Inglis north of SR40 (29.037226°, -82.681656°) (WGS84), Upper Eocene lower OLS.

LV021 (INGLIS 03 [COTYPE LOCALITY INGLIS MEMBER])

Levy County, 0.125 mi. south of Inglis at Florida Power Corporation Plant, north bank of the Withlacoochee (29.0308°, -82.6817°) (NAD27), Upper Eocene lower OLS.

LV024 (WITHLACOOCHEE BAY 01)

Levy County, dredged from the mouth of the Withlacoochee River (29.00131°, -82.759994°) (WGS84), Upper Eocene lower OLS.

LV035 (WITHLACOOCHEE BAY 02)

Levy County, approximately 2.5 mi. southwest of Yankeetown, first and second spoil islands west of boat ramp at end of SR40 (29.001221°, -82.766074°) (WGS84), Upper Eocene lower OLS.

LV039 (GULF HAMMOCK QUARRY 04)

Levy County, 2.25 mi. southeast of Gulf Hammock, 1.16 mi. northeast of SR19 (29.238256°, -82.692481°) (NAD27), Middle Eocene Avon Park Formation.

LV101 (WITHLACOOCHEE RIVER 09)

Levy County, southeast of Crackertown, dredging along the Withlacoochee River between Inglis and Crackertown (29.030179°, -82.678837°) (WGS84), Upper Eocene lower OLS.

LV104 (WITHLACOOCHEE RIVER 07)

Levy County, east of Yankeetown, dredging on both sides of the Withlacoochee River between Inglis and Yankeetown (29.032912°, -82.694589°) (WGS84), Upper Eocene lower OLS.

LV106 (WITHLACOOCHEE RIVER 11)

Levy County, 1.46 mi. west of Inglis, dredging on north bank of the Withlacoochee River 1.0 mi. below Power Plant at Inglis (29.03273°, -82.692578°) (WGS84), Upper Eocene lower OLS.

LV114 (ROYAL ROAD PIT 01)

Levy County, 6.15 mi. south of Otter Creek, pit 0.57 mi. south of the intersection of Royal Road and Buck Island Road (29.235935°, -82.778488°) (WGS84), Upper Eocene lower OLS.

MR018 (BRIAR CAVE)

Marion County, 3.5 mi. southwest of Ocala, Upper Eocene OLS.

OK005 (FRED GANNON ROCKY BAYOU STATE PARK 01)

Okaloosa County, 0.96 mi. northwest of Seminole, well core in Fred Gannon Rocky Bayou State Park (30.4912247°, -86.4194612°) (WGS84), Upper Eocene OLS.

PA002 (MORRELL PIT 06)

Pasco County, limerock mine approximately 2.5 mi. northeast of Branchborough (28.286469°, -82.066235°) (WGS84), Lower Oligocene Suwannee Limestone.

PO017 (TERRAMAR 01 [WEST COAST MINE])

Polk County, limerock mine approximately 6 mi. northwest of Socrum (28.232729°, -82.098447°) (NAD27), Lower Oligocene Suwannee Limestone.

PO050 (PALMETTO PHOSPHATE COMPANY 02)

Polk County, phosphate mine 2.63 mi. west northwest of Ft. Meade (27.761748°, -81.843375°) (WGS84), Middle Eocene Avon Park Formation.

SM010 (CEMEX CENTER HILL QUARRY 01)

Sumter County, 1.63 mi. northwest of Center Hill (28.6641°, -82.01397°) (WGS84), Upper Eocene OLS.

SU002 (O'BRIEN QUARRY)

Suwannee County, 1.0 mi. northwest of O'Brien at quarry off SR349 (30.047505°, -82.952708°) (WGS84), Upper Eocene upper OLS and Lower Oligocene Suwannee Limestone.

SU003 (BRANFORD 01A)

Suwannee County, Denali Quarry north of Branford (30.0041°, -82.9388°) (NAD27), Upper Eocene upper OLS.

SU004 (WATERMELON PIT 01)

Suwannee County, 10.0 mi. northeast of Branford along SR247, near Suwannee/Columbia County line (30.047505°, -82.952708°) (WGS84), Upper Eocene upper OLS.

TA001 (CABBAGE GROVE 01)

Taylor County, road metal pit approximately 3 mi. west of Cabbage Grove (30.208337°, -83.920824°) (WGS84), Lower Oligocene Suwannee Limestone.

TA004 (TENNILLE 01 [LIMEROCK INDUSTRIES INC.])

Taylor County, southwest of Tennille (29.776211°, -83.330453°) (WGS84), Upper Eocene upper OLS.

VO001 (BLUE SPRINGS 01)

Volusia County, approximately 2.5 mi. west of Orange City (28.947472°, -81.339528°) (WGS84), Middle Eocene Avon Park Formation.

WG002 (DUNCAN CHURCH 01)

Washington County, 4.5 mi. north of Wausau (30.705215°, -85.590275°) (WGS84), Lower Oligocene Bridgeboro Limestone, Duncan Church beds.

WG033 (DUNCAN CHURCH 02)

Washington County, quarry 4.5 mi. north of Wausau (30.705215°, -85.590275°) (WGS84), Lower Oligocene Marianna Limestone.

WG034 (EBRO BLUE SPRING 01)

Washington County, 5.0 mi. north northeast of Ebro (30.5134°, -85.84652°) (WGS84), Lower Oligocene

Suwannee Limestone.

FM-IP LOCALITIES OUTSIDE OF FLORIDA

2822

Jamaica, St. Ann Parish, Browns Town at St. Hilda's School, Upper Oligocene Moneague Formation.

ZA023 (STOVALL QUARRY 01)

Alabama, Covington County, approximately 7.5 mi. northeast of Florala northwest of SR54 (31.035°, -86.2315°) (NAD27), Lower Oligocene Florala Limestone.

ZA026 (PERDUE HILL)

Alabama, Monroe County, Perdue Hill, Claiborne Lime Plant Pit, Eocene.

ZA145 (CONECUH RIVER 08)

Alabama, Covington County, 5.51 mi. west southwest of Andalusia (31.279206°, -86.569924°) (WGS84), Upper Eocene Moodys Branch Formation.

ZA147 (BROOKLYN QUARRY 01)

Alabama, Conecuh County, 3.0 mi. south southeast of Brooklyn (31.248186°, -86.723239) (WGS84), Lower Oligocene Marianna Limestone.

ZA181 (BROOKLYN 01)

Alabama, Conecuh County, 1.68 mi. southeast of Brooklyn (31.246556°, -86.747938°) (WGS84), Lower Oligocene Marianna Limestone.

ZA192 (TOMBIGBEE RIVER 02)

Alabama, Washington County, 1.94 mi. northeast of St. Stephens, bluff on the west bank of the Tombigbee River northwest of Cowans Bluff (31.557915°, -88.028804°) (WGS84), Lower Oligocene Marianna Limestone.

ZN039 (LANIER PIT 01)

North Carolina, Pender County, 17.5 km northwest of Holly Ridge, Lanier Pit 1.1 km south southwest of intersection of SR50 and Lee Road, just west of Williams Road (34.6268°, -77.6763°) (NAD27), Middle Eocene Castle Hayne Formation.

ZN125 (TRENT RIVER 02)

North Carolina, Jones County, 0.75 mi. east of Trenton, west bank of Trent River at boat ramp (35.062529°, -77.341431°) (WGS84), Middle Eocene Castle Hayne Formation.

ZN126 (MARTIN MARIETTA RICHLAND QUARRY 01)

North Carolina, Onslow County, northwest of Jacksonville, quarry northwest of intersection of Union Chapel Church Road and Duffy Field Road (34.841991°, -77.542205°) (WGS84), Middle Eocene Castle Hayne Formation.

ZZ104 (SMITH COUNTY LIME PLANT 02)

Mississippi, Smith County, 1.92 mi. southeast of Sylvarena, Smith County Lime Plant at the end of CR18-8 (31.988756°, -89.361082°) (WGS84), Lower Oligocene Marianna Limestone.