

A NEW SPECIES OF *PROTOSCUTELLA* (ECHINOIDEA, CLYPEASTEROIDA, PROTOSCUTELLIDAE) FROM THE MIDDLE EOCENE (LUTETIAN) SANTEE LIMESTONE IN BERKELEY COUNTY, SOUTH CAROLINA

¹ADAM S. OSBORN, RICH MOOI² AND ³CHARLES N. CIAMPAGLIO

¹1500 Lakeshore Drive, Camden, SC 29020 <macropneustes@netzero.com>

²Department of Invertebrate Zoology & Geology, California Academy of Sciences,
55 Music Concourse Drive, San Francisco, CA 94118 <rmooi@calacademy.org>

³Earth and Environmental Sciences, Wright State University – Lake Campus,
7600 Lake Campus Drive, Celina, OH 45822 <chuck.ciampaglio@wright.edu>

ABSTRACT

A new species of protoscutellid clypeasteroid sand dollar, *Protoscutella palmeri* n. sp., is described and discussed. Specimens were collected from a quarry near Jamestown, Berkeley County, South Carolina in which the mid-Eocene Santee Limestone is exposed. The new species occurs below the strata containing *Protoscutella mississippiensis mississippiensis* (Twitchell), which can be collected in the same quarry. The new *Protoscutella* is distinguished by a greatly widened (alate) test, yielding a width to length ratio much higher than that found in the subpentagonal to slightly elongated test of its congeners. Also unique among *Protoscutella*, the periproct of *P. palmeri* n. sp. is consistently and strongly supramarginal throughout ontogeny. Material was preserved well enough to present details of the oral plate pattern, and analysis of this pattern in several specimens reveals that there is some variation among individuals in terms of the disjunction of the interambulacral plate columns, but that there is consistency in the plate counts to the periproct. Protoscutellid sand dollars are important index fossils in the middle and upper Eocene of the Carolinas. *Protoscutella palmeri* n. sp. is no exception, being stratigraphically one of the earliest members of the family Protoscutellidae, and the earliest in the Carolinas.

INTRODUCTION

The genus *Protoscutella* Stefanini, 1924,

presently includes six nominal taxa of relatively flat, discoidal, scutelliform (*sensu* Kroh and Smith, 2010) clypeasteroids belonging to a group colloquially referred to as sand dollars. Five species and one subspecies of *Protoscutella* have been described, including: *P. plana* (Conrad, 1865), *P. conradi* (Cotteau, 1891), *P. mississippiensis mississippiensis* (Twitchell in Clark and Twitchell, 1915), *P. tuomeyi* (Twitchell in Clark and Twitchell, 1915), *P. pentagonium* (Cooke, 1942), and the subspecies *P. mississippiensis rosehillensis* (Kier, 1980).

Protoscutella Stefanini, 1924, *Periarchus* Conrad, 1866, and *Mortonella* Pomel, 1883 are presently placed within the Protoscutellidae Durham, 1955. This clade, restricted to the Eocene of North America, is characterized by the presence of a fifth gonopore in the posterior interambulacrum. This feature has been characterized as a synapomorphy for the Protoscutellidae (Mooi 1987). All viable out-groups to the Protoscutellidae, notably other, possibly earlier Eocene forms, have four gonopores. Present views of the phylogenetic relationships within the Clypeasteroida strongly support the idea that a fifth gonopore has been derived independently in a small number of very distantly related clades, including protoscutellids.

Protoscutella is restricted to the middle Eocene of the Gulf Coast and Atlantic Coastal Plain of the southeastern United States, ranging as far west as Texas and as far north as North Carolina (Figure 1). Although phylogenetic relationships of taxa within the genus *Protoscutella* remain obscure, Durham (1955) and Mooi (1989) distinguished the genus from the other

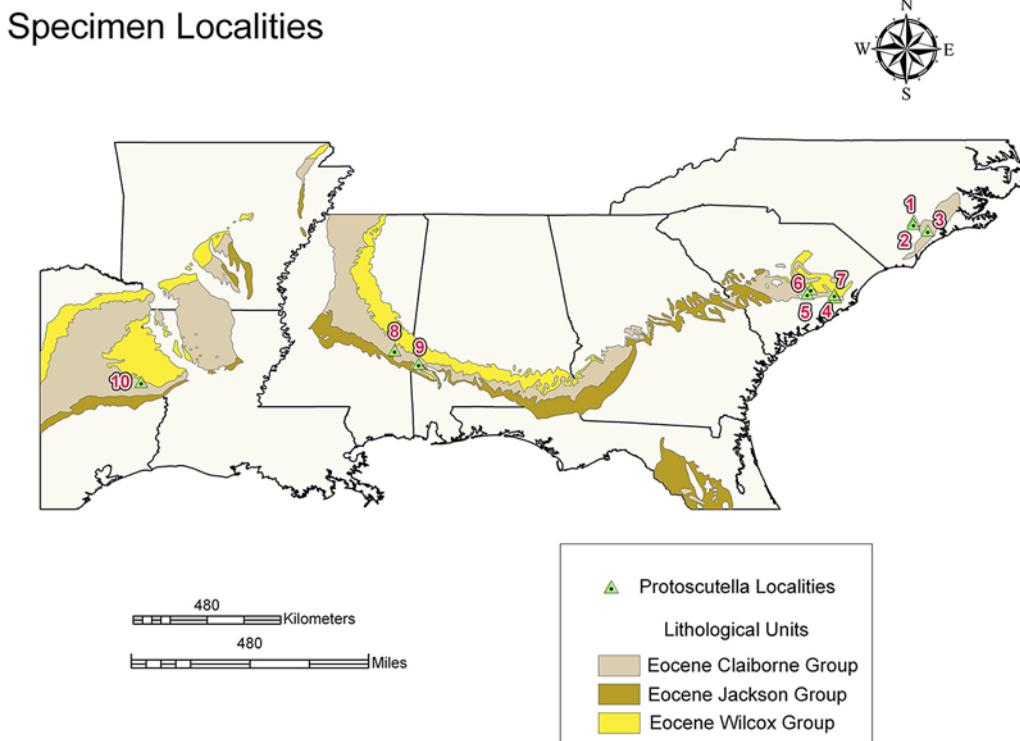


Figure 1. Outcrop zone of Eocene age strata in the Southeastern United States, with *Protoscutella* collecting localities mentioned within text annotated: 1) Well's Quarry, Rose Hill, Duplin Co., NC; 2) Fussel's Quarry, Rose Hill, Duplin Co., NC; 3) East Coast Quarry, Maple Hill, Pender Co., NC; 4) Martin Marietta Jamestown Quarry, *Protoscutella palmeri* n. sp., type locality, Jamestown, Berkeley Co., SC; 5) Wilson's Landing, Berkeley Co., SC.; 6) Martin Marietta, Orangeburg County Quarry, located directly across County Line Road from the now inactive Berkeley County Quarry, near Cross, Berkeley Co., SC; 7) Georgetown Quarry, now inactive, Georgetown Co., SC; 8) Type area of the type species of *Protoscutella*, *P. mississippiensis mississippiensis* (Twitchell), Chickasawhay River, Enterprise, Clarke Co., MS; 9) Valley of Souwilpa Creek, Choctaw Co., AL; 10) San Augustine, San Augustine Co., TX.

members of the Protoscutellidae, *Periarchus* and *Mortonella*, by its variably, but often discontinuous oral interambulacrum and straight, unbranched food grooves. Kier (1980) indicated that an interrupted posterior interambulacrum cannot be considered a unique feature of *Protoscutella*, as specimens of *Protoscutella conradi* (Cotteau, 1891) from Georgetown County, South Carolina, and Fussel's Quarry near Rose Hill, Duplin County, North Carolina (Figure 1) included specimens with a continuous posterior interambulacrum. Furthermore, Kier (1980) studied specimens that he identified as *Protoscutella plana* (Conrad, 1865) from

Maple Hill, Pender County, South Carolina (Figure 1) with a continuous posterior interambulacrum. However, recent examination of Kier's material suggests Kier (1980) was incorrect in assigning the name *Protoscutella plana* to this material. Plate maps and other features of these specimens strongly suggest that these are actually members of the genus *Periarchus*.

Periproct position has been the key, and sometimes sole, feature used to distinguish the six nominal *Protoscutella* taxa accepted to date (Cooke 1959). Mooi (1989) tried to distinguish *Protoscutella* from *Periarchus* by its just submarginal periproct. Although the periproct is

NEW SPECIES OF PROTOSCUTELLA

positioned closer to the margin in *Protoscutella* than in either *Periarchus* or *Mortonella*, a just submarginal periproct is not a consistent trait in the genus. In many specimens identified as *Protoscutella conradi* and *P. plana*, the periproct is far enough anterior to be considered firmly on the oral surface, and not at all associated with the posterior margin. This condition also applies to *P. pentagonium* and *P. tuomeyi*. *Protoscutella mississippiensis mississippiensis*, the type species of the genus, has a periproct that ranges from just submarginal, to slightly supramarginal. In juvenile specimens of *P. mississippiensis rosehillensis*, the periproct is typically situated directly on the margin or just supramarginally. Finally, in the new species described here, *P. palmeri* n. sp., the periproct remains strongly supramarginal throughout growth (see below).

Although there is clearly some value to periproct position as a systematic feature in *Protoscutella*, there is considerable variation among populations presently assigned to either *Protoscutella conradi* or *P. plana*. Even early results from a complete re-examination of all members of the genus, taking into account oral plate architecture and other characters, show that the commonly used, present nomenclature is widely divergent from the original descriptions and morphology of the types. It would appear that no one has consulted the types (actually lectotypes) of *P. plana* and *P. conradi* since their images were shown in Clark and Twitchell (1915), and this has caused much confusion in the nomenclature of the group. For example, as suggested above, it became apparent during our comparative analysis for *P. palmeri* n. sp. that Kier (1980) did not have the true *P. plana* in hand when he described and figured material he ascribed to that species, further underscoring the need for a complete revision of the genus, if not the entire family. Our access to type material of all the relevant species is resulting in a major revision of *Protoscutella* -- ongoing work that informs the present paper, but which will be published elsewhere.

GEOLOGIC SETTING

The specimens of *Protoscutella palmeri* n. sp. described herein were collected from the basal bryozoan biomicrudite, "lithozone 1a" of Banks (1977), of the mid-Eocene Santee Limestone within the Martin Marietta Quarry, southeast of Jamestown, Berkeley County, South Carolina (Figure 1). This horizon is equivalent to the Warley Hill Marl of the mid-Eocene Santee Limestone, residing in NP zone 15 in the Martin Marietta Quarry. Here, the new species occurs below its congener *P. mississippiensis mississippiensis*, from which it is easily distinguished (see below). We have found no specimens of *P. palmeri* n. sp., or any records of this distinct form, outside of the Jamestown Quarry where strata of equivalent age are mined in Berkeley, Dorchester, and Orangeburg Counties, South Carolina. The addition of *P. palmeri* n. sp., along with a new species of *Salenia* currently being studied by the authors, increases the number of echinoid species recorded from the Santee Limestone to 17 (Kier 1980, Powell and Baum 1982).

The horizon in which the *P. palmeri* n. sp. is found consists of a dense, pale gray, indurated bryozoan biomicrudite. Banks (1977) designated the *Cubitostrea lisbonensis* biozone as extending to the base of the Santee Limestone to include strata formerly referred to the Warley Hill Marl. This designation places *P. palmeri* n. sp. within the biozone of the oyster *C. lisbonensis* (Banks 1977, Baum et al. 1980), though specimens of *C. lisbonensis* were not collected from this horizon within this quarry. *Protoscutella palmeri* n. sp. occurs with a sparse echinoid assemblage consisting of rare, elongate specimens of *Santeelampus oviformis* (Conrad), *Cidaris pratti* (Clark) and an undescribed species of the genus *Salenia*. The authors are currently studying specimens of this elongate variant of *S. oviformis* (Conrad), as well as specimens of the genus *Salenia*. The latter represents the first occurrence of *Salenia* in the Eocene of North America. Other invertebrates are present, including abundant crab remains, the nautiloid *Aturia*, and a rich fauna of bryozoans

Table 1: Measurements of *Protoscutella palmeri* n. sp. All measurements are in millimeters.
 * denotes approximation based on reconstruction, dash means measurement was not made due to matrix or damage. L = length (mm), W = width (mm).

Specimen	L	W	L as % of W	Petaloid			Peristome	Periproct	Periproct to posterior margin	# Pores in one column of petaloid I	# Pores in one column of petaloid II	# Pores in one column of petaloid III
				I L	II L	III L				W	W	
Holotype UF 213520	39.3	55*	140	10.1	9.6	10.6	2.5	1.5	2.5	48	47	48
Paratype UF 213521	29.1	34.4	118	7.4	—	7.4	2.3	1.4	1.8	—	—	36
Paratype UF 213522	38.5	—	—	—	—	—	2.7	—	—	—	—	—
Paratype UF 213523	26.8	33.6	125	—	—	—	2.0	1.0	1.8	—	—	—
Paratype UF 213524	28.9	34.9	121	—	—	—	—	1.2	1.8	—	—	—
Paratype UF 213525	20.6	22.8	111	—	—	—	1.6	—	—	—	—	—
Paratype ASG 72081	29.0	37.6	130	—	—	—	1.9	—	—	—	—	—
Paratype ASG 72082	33.9	43.9	129	—	—	—	1.8	—	—	—	—	—
B. Palmer Collection	29.3	39.1	133	7.5	7.4	7.7	—	1.4	1.9	35	—	—
A. Osborn Collection	51.5	81.6	158	—	—	—	3.7	—	—	—	—	—

and small bivalves.

The *in situ* fossiliferous deposit is not directly accessible because the quarry is water-filled. Mining operations consist of dredging limestone from beneath the water and blocks of this horizon are brought up from the deepest portions of the quarry along the quarry perimeter. Excavations containing blocks of the *P. palmeri*-bearing basal Santee Limestone horizon also contain sediment from an underlying zone of glauconitic limestone with a rich fossil vertebrate fauna. This fauna was discussed by Cicimurri and Knight (2009), and based on the vertebrate and invertebrate fauna of this unit, they speculated that this horizon represents an unnamed lower Eocene, Ypresian deposit which unconformably underlies the Santee Limestone in the Jamestown Quarry.

The presence of this material mixed in the dredges with the basal Santee Limestone blocks, which contain the remains of *P. palmeri* n. sp., helps secure the placement of this sand dollar within the stratigraphic succession of this quarry. A less indurated horizon of limestone

with a rich mollusk and crab fauna overlies the zone containing *P. palmeri* n. sp. This horizon harbors the two characteristic echinoid species of the *Cubitostrea lisbonensis* biozone, *Santeelampas oviformis* and *P. mississippiensis*, as well as *Eurhodia baumi* (Kier). In turn, this horizon is overlain by lithozone II of the Santee Limestone (Banks 1977), and the *Cubitostrea sellaeformis* (Conrad) biozone of the Santee Limestone (Baum et al., 1980), which contains the aforementioned echinoids *Cidaris pratti* and *P. conradi*, as well as *Eurhodia rugosa rugosa* (Ravenel), *Eurhodia holmesi* (Twitchell), and *Linthia hanoverensis* (Kellum).

Cooke and MacNeil (1952) erected the Warley Hill Marl to include glauconitic sands containing the oyster *Cubitostrea lisbonensis*. However, Banks (1977) included this unit within the Santee Limestone, as the lithofacies of both were similar. Baum et al. (1980) proposed the abandonment of the term Warley Hill Marl in favor of the *Cubitostrea lisbonensis* and overlying *Cubitostrea sellaeformis* biozones of the Santee Limestone. Geisler et al. (2005) pro-

NEW SPECIES OF PROTOSCUTELLA

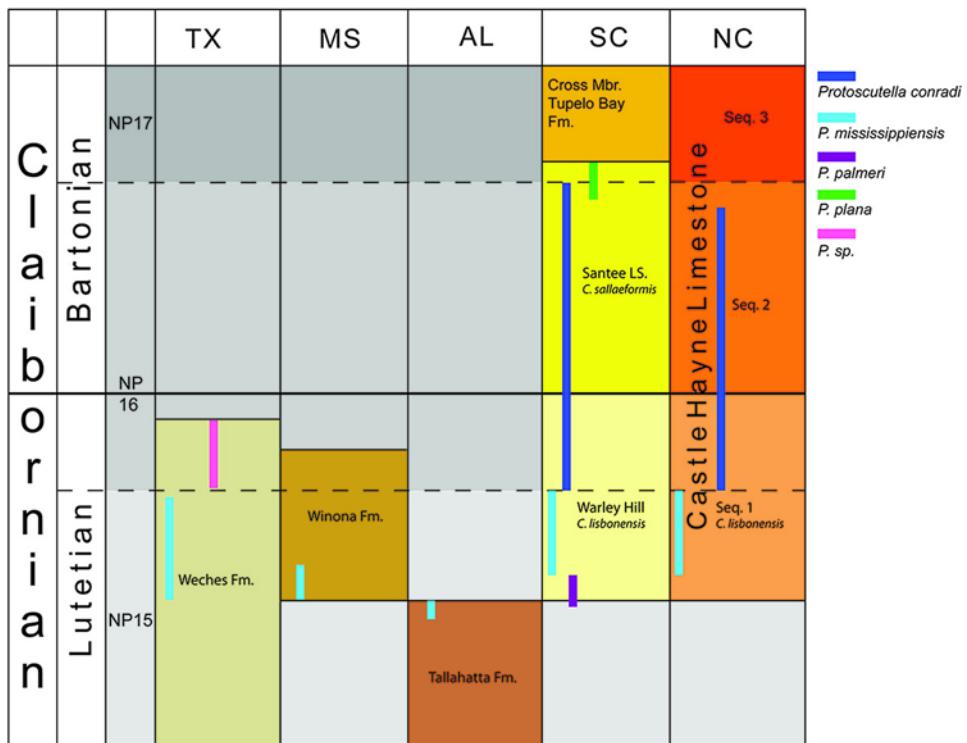


Figure 2. Generalized correlation chart of significant *Protoscutella*-bearing units displaying distribution of *Protoscutella* species. Correlation and *Protoscutella* distribution follows Baum and Vail (1988), Geisler et al. (2005), Toulmin (1977), Zachos and Molinaux (2003), and Zullo and Harris (1987). Note that the *P. palmeri*-bearing NP15 limestone in the Jamestown Quarry is herein treated as the basal Santee Limestone, age equivalent of the Warley Hill Formation. Precise placement of *P. palmeri* within the unit is uncertain. Additionally, examination of type material of both *P. conradi* and *P. tuomeyi* undermines the designation of *P. conradi* for specimens documented from the Weches Formation of Texas by Zachos and Molinaux (2003). We here designate these specimens as *Protoscutella* sp., pending further study. Furthermore, new data from field work that will soon be reported upon has uncovered *P. conradi* occurring *in situ* with *P. plana* in the lower bed of their distribution in Orangeburg Co., SC. This observation is also reflected in the chart.

posed restricting the name Santee Limestone to the strata of NP 16 age underlying the Tupelo Bay Formation, and reviving the Warley Hill Formation to occupy the portion of the Santee Limestone that resides beneath zone NP16. If the redesignations proposed by Geisler et al. (2005) are accepted, the basal limestone containing *P. palmeri* n. sp. in the NP 15 zone would be “technically” designated as the Warley Hill Formation, though it is lithologically more similar to the overlying limestone of the *Cubitostrea sellaeformis* zone than the typical glauconitic sandy marl of the Warley Hill For-

mation.

The original type locality of the Santee Limestone at Eutaw Springs, Orangeburg County, South Carolina now lies beneath the waters of Lake Marion, created in the 1940s after the damming of the Santee River. Although Geisler et al. (2005) suggested Eutaw Springs should still be recognized as the type area for the Santee Limestone, as other outcrops of the Santee Limestone can be viewed in the area, the formation is best viewed in South Carolina within a series of quarries in Berkeley, Dorchester, and Orangeburg Counties. Within these

quarries the Santee Limestone is overlain by an upper-middle Eocene age bryozoan-brachiopod-bivalve biomicrite formerly referred to as the Cross Member of the Santee Limestone (Ward et al. 1979). Geisler et al. (2005) proposed the name “Tupelo Bay Formation” for the strata that were formerly included within the Cross Member of the Santee Limestone, and proposed limestone from depths 189.4 to 90.9 feet of the USGS Pregnall Core (Edwards et al. 1997), Dorchester County, South Carolina, as the type section for the Tupelo Bay Formation.

The Santee Limestone was deposited in open, warm, clear waters of normal marine salinity, free of terrigenous sediment and similar to current-day subtropical to tropical environments (Banks 1977). Gardner (1957) proposed a maximum depth of 50 m for the *Cubitostrea lisbonensis* zone, while Banks (1977) surmised the limestones were deposited on a sublittoral, offshore open shelf, in waters less than 100 m deep.

To summarize, at the Jamestown Quarry, Berkeley Co., South Carolina (Figure 1), the Santee Limestone consists of a lower portion (Warley Hill Formation equivalent), that contains *Protoscutella palmeri* n. sp. This lower portion lies beneath a limestone horizon containing species characteristic of the *Cubitostrea lisbonensis* biozone of NP zone 15. The unit is underlain by an Ypressian age, unnamed, vertebrate-rich, glauconitic deposit (Cicimurri and Knight, 2009).

SYSTEMATIC PALEONTOLOGY

Figured specimens are deposited with the Invertebrate Paleontology Division, Florida Museum of Natural History at the University of Florida (UF), and at the California Academy of Sciences, San Francisco (CASG). The classification follows Kroh and Smith (2010).

Class ECHINOIDEA Leske, 1778

Order CLYPEASTEROIDA L. Agassiz, 1835

Suborder SCUTELLINA Haeckel, 1896

Family PROTOSCUTELLIDAE Durham, 1955

Type genus *Protoscutella* Stefanini, 1924

Type species *Protoscutella mississippiensis mississippiensis* (Twitchell in Clark and Twitchell, 1915)

Protoscutella palmeri new species
(Figures 3 - 5)

Diagnosis: Test significantly expanded laterally (alate, *sensu* Mooi et al., 2000), much more so than in any other species of *Protoscutella*. Test width increases significantly in proportion to the test length as the specimens increase in size so that the test has a distinct triangular shape as the test widens through the posterior paired interambulacra. Periproct conspicuously supramarginal in both small and large specimens. First plates to contact the periproct moving distally from the peristome are the a7 and b7 plates, as identified using the Lovénian system (Lovén, 1874).

Description: Test medium to large, largest specimen with complete margin (not in type series): L = 51.5 mm; W = 81.6 mm; width being 158% of length, smallest specimen: L = 20.6 mm; W = 22.8 mm; width being 111% of length (table 1). Outline subpentagonal in juvenile specimens, becoming progressively laterally elongate with increasing size (Figures 3 and 4). Mature specimens distinctly triangular, widest points occurring at intersection of line drawn orthogonally to anterior-posterior axis through posterior paired interambulacra (Figure 4), about half-way between apical system and posterior margin of test. Margin thin, posterior margin with distinct anal notch and slight indentations where ambulacra 1 and 5 form the ambitus, indentations more pronounced with increased size (Figures 3 and 4).

Aboral surface slightly tumid, highest at apical system. Apical system central with five genital pores and large central madreporite containing scattered hydropores not associated with grooves *sensu* Mooi (1989) (Figure 5).

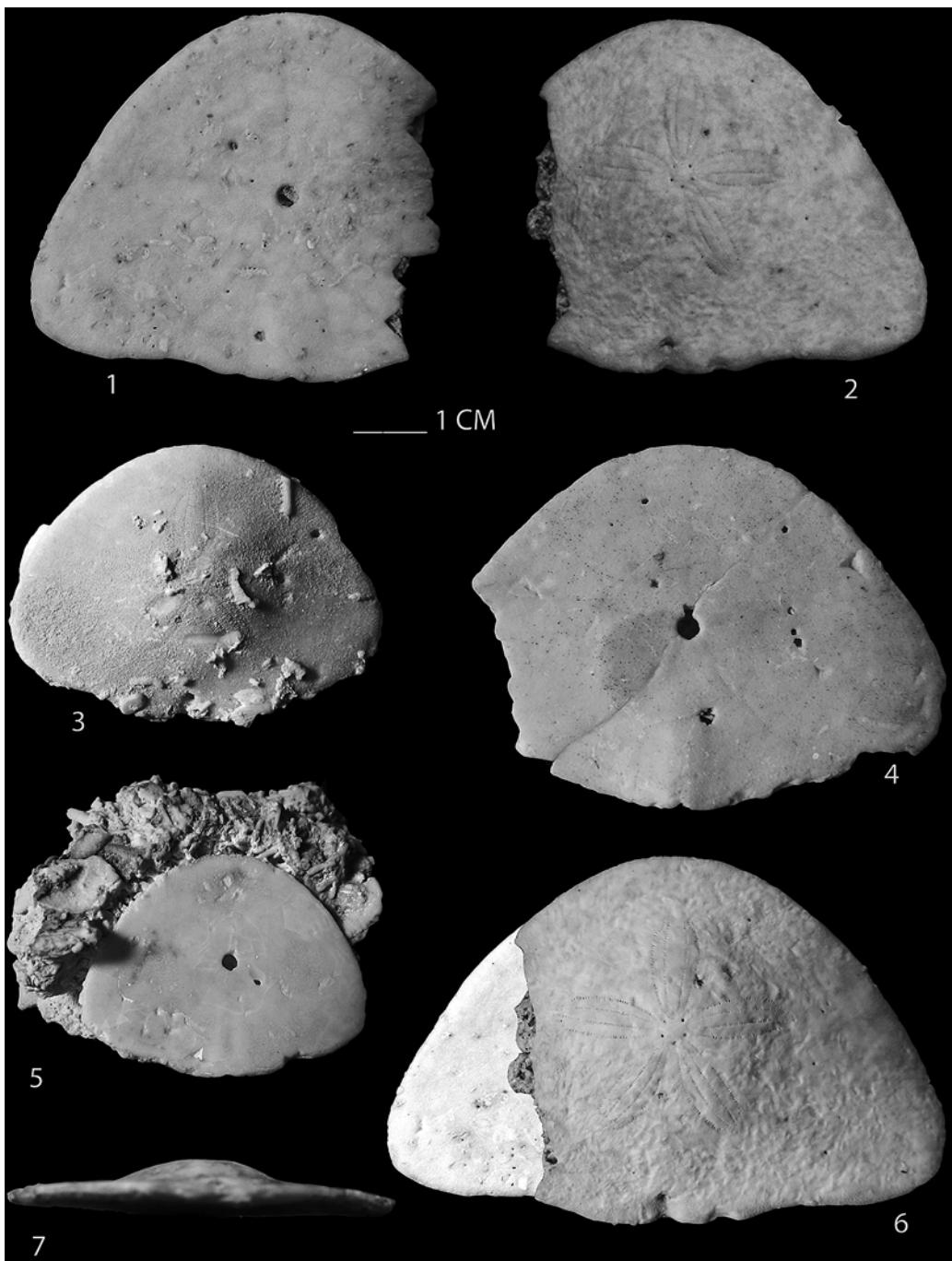


Figure 3. *Protoscutella palmeri*, n. sp., Santee Limestone, Jamestown Quarry, Jamestown, Berkeley County, South Carolina. Anterior unpaired ambulacrum (ambulacrum III) at top of each image. 1: Holotype, UF 213520, oral surface. 2: Holotype, UF 213520, aboral surface. 3: Paratype, UF 213521, aboral surface. 4: Paratype, UF 213522, oral surface. 5: Paratype, UF 213523, oral surface. 6: Holotype, UF 213520, aboral surface with reconstructed left side. 7: Paratype, UF 213524, left lateral view.

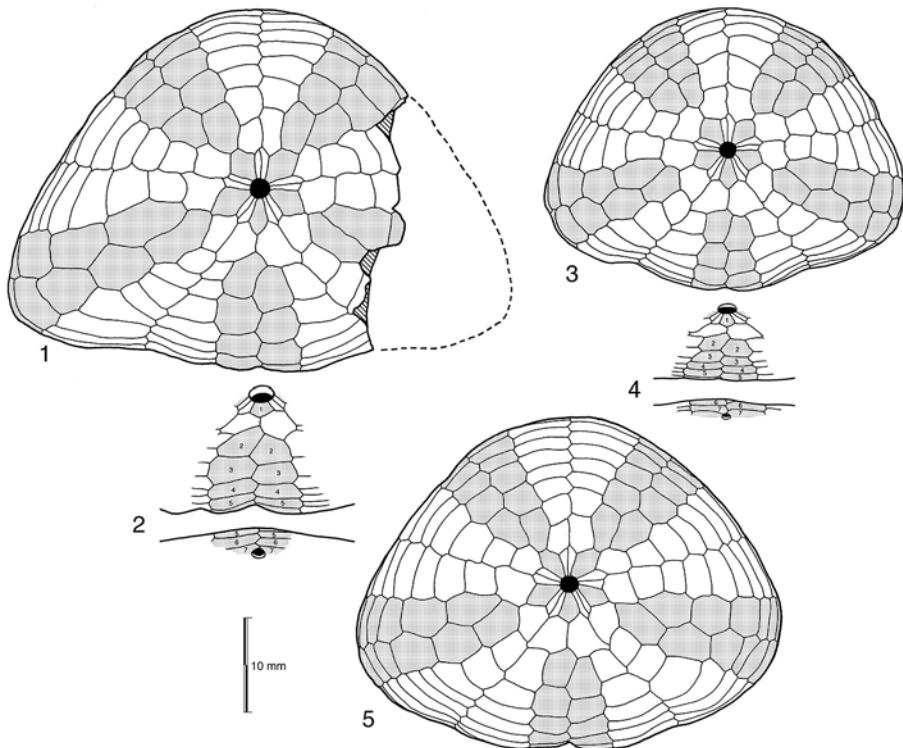


Figure 4. Plate maps of the oral surface and periproct positions for *Protoscutella palmeri* n. sp. Interambulacral plates are shaded, peristome and periproct are filled in black, damaged areas cross-hatched. Plates in the posterior interambulacrum numbered according to the Lovénian system. Anterior unpaired ambulacrum (ambulacrum III) towards top of each image. All images to same scale. 1: Holotype, UF 213520, oral surface with reconstructed left side. 2: Holotype, UF 213520, 2 successive, oblique views at increasing angles around the ambitus showing plating up to the aboral periproct. 3: Paratype, CASG 72081, oral surface. 4: Paratype, CASG 72081, 2 successive, oblique views at increasing angles around the ambitus showing plating up to the aboral periproct. 5: Paratype, CASG 72082, oral surface

Petaloids lanceolate, headed by small but distinct ocular plate containing an ocular pore (Figure 5). Petaloids slightly closed distally with 2 or 3 trailing podia (*sensu* Mooi 1989). Distal plates of petaloid do not typically appear to be occluded from contact with adjacent interambulacral plates in most cases (Figure 5), but this occlusion does seem to occur in only one or two instances in one of the paratypes (UF 213521). Petaloids approximately same length, equal to 25–26% of test length (Figures 3, 5; Table 1). Petaloid in ambulacrum III extends on average 60% distance from apex to margin, but in ambulacra I, II, IV, V, petaloids extend on av-

erage 50% of distance from apical system to corresponding ambitus. Pore pair counts (not counting the trailing podia) for a single column of respiratory pores in ambulacra I, II, and III are shown in Table 1 for specimens in which the aboral surface is visible. Accessory pores present in interporiferous zone of petaloids, scattered in plates distal to petaloids and approaching the ambitus. Interambulacra are zig-zag biserial all the way to apical system (Figure 5). Aboral spine tubercles small, densely packed as typical for most scutellines, differentiated into primary and miliary (*sensu* Mooi 1986).

NEW SPECIES OF PROTOSCUTELLA

Periproct strongly supramarginal, ovate, slightly longer than wide, diameter equal to 3.8 - 4.9% test length, positioned in slight groove on aboral surface on average 6% of test length from posterior margin. Oral surface flat with slightly raised (keeled) region extending from posterior marginal notch towards peristome, becoming flush with oral surface about 1/3 of distance from margin to peristome. Pressure drainage channels (*sensu* Mooi 1989) absent. Peristome central, 6.3-7.9% of test length. Basicoronal plates star-shaped, interambulacral plates much larger than ambulacral, almost twice as long (Figure 4). In holotype and two paratypes for which complete oral surface plate maps were obtained, paired interambulacra (interambulacra 1, 2, 3, and 4) were variably disjunct (Figure 4). However, posterior interambulacrum (interambulacrum 5) always disjunct, with first post-basicoronal widely separated from corresponding basicoronal. Main branch of food grooves extending to distal part of second post-basicoronal in each oral ambulacrum. Distal to this point are faint traces of bifurcation barely detectable in some ambulacra of some specimens where absence of tubercles and slight elongation of podial pores delineate short, simple branch onto each column of more distal interambulacral plates. Apparent extension of main branch of groove to ambitus seen in Figure 3 is result of artifact or preparation. Center of unbranched part of food groove occupied by sharply defined keel flanked by food groove podial pores. Proximal portion of keel slightly swollen where it passes over sphaeridial chamber, in which single, glassy sphaeridium is present in well-preserved specimens. Keel produced into small point directed into peristome, with buccal podial pores flanking this point just inside peristome relative to point. Little or no differentiation of tubercles into ambulacral versus interambulacral locomotor fields. Tubercles only slightly larger than those on aboral surface.

Internal peripheral buttressing and pillars well-developed, but not thickened or heavy. Lantern supports consist of single auricles, one per interambulacral basicoronal. Lantern structure unknown.

Material: Holotype UF 213520, and paratypes: UF 213521 - 213525, CASG 72081 - 72083, all collected from the Santee Limestone, Jamestown Quarry, Berkeley County, South Carolina. Measurements for examined specimens are given in Table 1.

Etymology: This species is named in honor of Bill Palmer, collector of many of the studied specimens.

Occurrence: *Protoscutella palmeri* n. sp. has not been documented outside of Berkeley County, South Carolina where it is found in the basal horizon of the mid-Eocene Santee Limestone in the Martin Marietta Quarry, Jamestown, South Carolina (Figures 1 and 2).

Discussion: *Protoscutella palmeri* n. sp. is most similar to *Protoscutella mississippiensis mississippiensis* (Twitchell), but is readily differentiated by its greatly exaggerated width to length ratio and the consistently aboral position of its periproct. The smallest measured specimen has a width to length ratio of 111%, whereas the largest studied specimen has a width to length ratio of 158% (Table 1).

Kier (1980) stated that specimens of *P. mississippiensis mississippiensis* from the Winona Formation at the type locality near Enterprise, Mississippi have a width that is on average 103.7% of the test length, and specimens of *P. mississippiensis mississippiensis* from Wilson's Landing, near Eadytown, Berkeley County, South Carolina, have a width on average 107% of test length. However, specimens of *P. mississippiensis mississippiensis* from the Santee Limestone within the Jamestown quarry above the occurrence of *P. palmeri* n. sp. have a width that is on average only 99% of test length. *P. mississippiensis rosehillensis* from the type locality near Rose Hill, Duplin County, North Carolina, have a width on average 100.4% of test length. Zachos and Molineaux (2003) stated that large specimens of *P. mississippiensis mississippiensis* from the Weches Formation of Texas have widths that range from 110-125% test length, but it appears that the very highest width to length ratios of this population are not common or typical, nor does it result in the alate, or slight triangular outline of the test seen in even the smallest known *P. palmeri* n. sp.

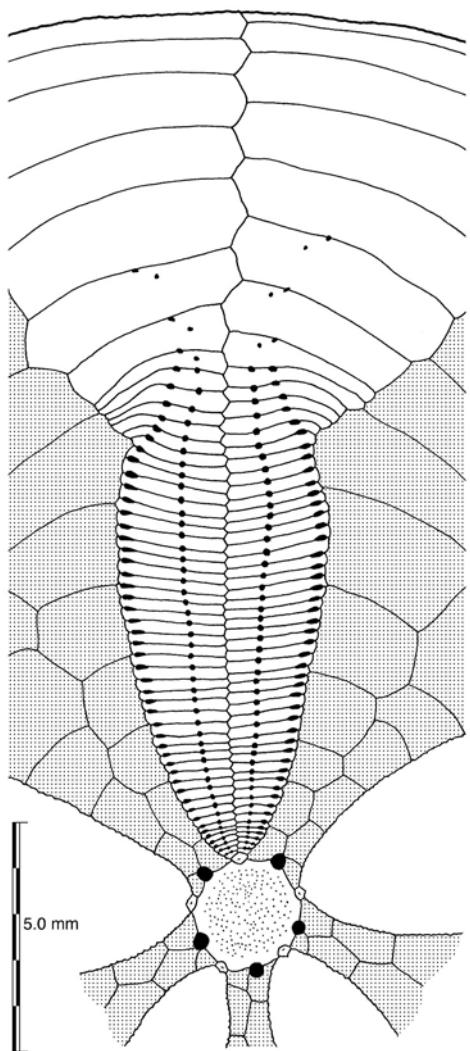


Figure 5. Plate map and pore patterns of the apical region and ambulacrum III for *Protoscutella palmeri* n. sp., Holotype, UF 213520. Interambulacral plates are shaded, pores are filled in black, details of ambulacral plating in interambulacra 1, 2, 4, and 5 omitted, accessory pores in interporiferous zone and distal ambulacral plates present, but not shown.

The width to length ratio of the test of *P. palmeri* n. sp. increases significantly as the specimens increase in size (Table 1, Figures 3 and 4). The point of greatest width of *P. palmeri* n. sp. is significantly more posterior than in other species of *Protoscutella*. Juvenile specimens

of *P. palmeri* n. sp. have a point of greatest width that is adjacent to, or just posterior of the apical system, which is similar to other species of *Protoscutella* which typically have a point of greatest width that is central or just posterior of center. However, as individuals of *P. palmeri* n. sp. increase in size, the point of greatest width progressively becomes more posterior, eventually to become situated more than 50% of the distance from the apical system to the posterior margin. The effect of this is to produce a very distinctive triangular outline in the largest individuals (Figures 3, 4).

Protoscutella palmeri n. sp. is also readily differentiated from all other protoscutellid species by the consistently aboral position of its periproct. All other Protoscutellidae have submarginal or distinctly oral periprocts with the exception of *P. mississippiensis*, in which the periproct is variably placed, ranging from marginal to just barely supramarginal. Specimens from the Winona Formation in the type area of Enterprise, Mississippi and from the Weches Formation in Texas have a periproct that is just submarginal in large specimens, and marginal in small specimens. *P. mississippiensis mississippiensis* from Wilson's Landing, South Carolina and specimens of the subspecies *P. mississippiensis rosehillensis* from North Carolina have a periproct that is just supramarginal in small specimens, but it becomes more marginal in larger individuals (Kier 1980). The periproct placement of *P. palmeri* n. sp. is most similar to, though distinctly different from, the marginal to just supramarginal periproct of the Tallahatta Formation population of *P. mississippiensis mississippiensis*, in the valley of Souwilpa Creek, Choctaw County, Alabama. However, three of eight examined specimens of the Souwilpa Creek population had marginal periprocts. Of the five specimens with just supramarginal periprocts, the distance of the periproct above the margin is on average merely 1.8% of test length. In *P. palmeri* n. sp., the periproct is at a distance of 6.1 - 6.6% of test length above the posterior margin. The periproct on specimens in the Tallahatta Formation is situated in an anal notch, and though the periproct is visible from above, the periproct is also clearly

NEW SPECIES OF PROTOSCUTELLA

visible when viewing the test from the posterior margin. The periproct of *P. palmeri* n. sp., being positioned further from the margin on the aboral surface, is not typically visible from a marginal aspect.

Data from plate maps across all taxa of protoscutellids (personal observation) suggest that the degree to which the interambulacra are disjunct from the basicoronals on the oral surface is a key taxonomic feature. However, *P. palmeri* n. sp. is somewhat enigmatic in this regard due to the variation seen in the three specimens for which these data are available. In all specimens, the posterior, unpaired interambulacrum (interambulacrum 5) is disjunct, which is a feature seen in a variety of other *Protoscutella* species, including *P. mississippiensis*, some specimens of *P. conradi*, the type and only known specimen of *P. pentagonium*, and all specimens that can be assigned unambiguously to *P. plana*. In two of the *P. palmeri* n. sp., the anterior paired interambulacra (interambulacra 2 and 3) are continuous by contact between the basicoronals with only one of the two corresponding post-basicoronals (Figure 4). The posterior paired interambulacra (interambulacra 1 and 4) are disjunct in all specimens, except for slight contact by one of the post-basicoronals in the holotype (Figure 4). In almost all *Protoscutella* species for which preliminary data exist, the larger the specimen, the more likely that some disjunction will occur. However, in *P. palmeri*, the smallest of the specimens examined for oral plate mapping shows the highest degree of disjunction, furthermore in all five of the interambulacra. The significance of this variation has yet to be related to phylogenetic, ontogenetic, or environmental factors, or to phenotypic plasticity that might influence disjunction in other species of *Protoscutella*. It is likely that additional data from other specimens of the new species will shed light on these questions, particularly if complete surveys of plate patterns can be made for all valid taxa in the family.

The apparent succession of species of *Protoscutella* has been given great importance because the members of the genus are regarded as important index fossils for the middle Eocene faunal zones of the Carolinas (Kier 1980, Zullo

and Harris 1987). As suggested by Zachos (2009), the relative stratigraphic positions of protoscutellid taxa from *P. mississippiensis* to *P. conradi* (to *P. plana* in South Carolina), followed by *Periarchus lyelli*, is consistent throughout their range without regard to sediment type. The specimens are found within clastics in the Gulf Coastal Plain and carbonates in North and South Carolina. With the addition of *P. palmeri* n. sp. to the genus, the sequence of taxa in South Carolina is now modified to include *P. palmeri* n. sp. as the earliest species for the region (Figure 2).

The earliest protoscutellids known from the Gulf Coast region belong to a population of *P. mississippiensis* occurring with *Cubitostrea perplicata* (Dall), at the top of the Tallahatta Formation in the valley of Souwilpa Creek, Choctaw County, Alabama (Figure 1). It is likely that this occurrence of *P. mississippiensis* predates that of *P. palmeri* n. sp. Banks (1977) used the biostratigraphic correlation of Toulmin (1969) and the presence of *Cubitostrea lisbonensis* (Harris) to correlate lithozone 1 of the Santee Limestone (equivalent of the Warley Hill Marl of Cooke and MacNeil [1952]) with the middle Eocene, lower Lisbon Formation of Alabama. This correlation suggests that *P. mississippiensis* (Twitchell) from the *C. perplicata* (Dall) zone in the upper Tallahatta Formation, just below the contact with the Lisbon Formation, is older than the population of *P. palmeri* n. sp. discussed within this paper, making the Tallahatta sand dollars the oldest documented population of *Protoscutella* (Figure 2). However, at Enterprise, Mississippi (Figure 1), near the type locality of *P. mississippiensis*, both *C. lisbonensis* and *C. perplicata* occur in the Winona Formation with *P. mississippiensis* (Dockery 1980). It can be concluded that using oyster biozonation to correlate these strata is imperfect (Zullo and Harris 1987). It is also notable that *C. lisbonensis*, which is known to occur with *P. mississippiensis* above *P. palmeri* n. sp. in the Santee Limestone, does not appear in the basal limestone bed with *P. palmeri* n. sp. in the Jamestown, South Carolina quarry. Therefore, the horizon containing *P. palmeri* n. sp. within the Jamestown Quarry could reside beneath the

Cubitostrea lisbonensis horizon, and its relationship to the population of *P. mississippiensis* at the top of the Tallahatta Formation would then be in question. The Eocene stratigraphy of South Carolina has been a topic of much debate amongst regional geologists, and until a consensus is reached, the authors are unable to make a determination on the aforementioned correlations. The relationship between the ages of these two populations remains an area for further study, though the relative positions of the Protoscutellidae in the Carolinas is now clear, from oldest to youngest: *P. palmeri* n. sp., *P. mississippiensis*, *P. conradi*, *P. plana*, and *Periarchus* (Figure 2).

The extreme widening of the test in *P. palmeri* n. sp. is reminiscent of eoscutellids, but it is premature to suggest through outgroup comparison that this feature of *P. palmeri* must be plesiomorphic for protoscutellids in general. This is not to say that the Eoscutellidae should not be considered a candidate outgroup for analysis of cladistic relationships within the Protoscutellidae, especially given the fact that both taxa evolved in the Eocene and are most likely to turn out to be basal to the rest of the scutelliforms (contrary to Kroh and Smith 2010). *Protoscutella palmeri* n. sp. is better regarded as providing evidence that specialized forms existed among the protoscutellids very early in the radiation of the group, and that widening of the test was an independent derivation of a mechanism to enhance feeding efficiency as suggested by Mooi et al. (2000).

Phylogenetic placement of *P. palmeri* n. sp. and its relationship to the stratigraphic occurrences of all species in the genus will provide significant understanding of the pattern of evolution and origins of novel traits among the Eocene clypeasteroids. Revisions of the taxonomy of these taxa, along with better understanding of their cladistic relationships could also lead to reinterpretations of the stratigraphy in North and South Carolina of strata for which protoscutellids are indicators and indices for correlation. Already, the unusual features of taxa such as *P. palmeri* n. sp. are posing questions that challenge previous understanding of these correlations, many of which are already not well

understood.

ACKNOWLEDGEMENTS

We thank Bill Palmer for his specimen contributions, and comments concerning the geology and fauna of the Santee limestone in Berkeley County, South Carolina. His experience and knowledge gained from innumerable hours spent collecting the Santee Limestone were critical in the development of this manuscript. We also thank Dave Cicimurri for his insight on the stratigraphy of the Santee Limestone, and Adam Armstrong for providing a specimen of *Protoscutella palmeri* n. sp., for study and deposit as a paratype. The authors also wish to thank Vic Wright for preparing many of the paratypes from their ridiculously stubborn matrix. The authors are also indebted to the Martin Marietta Corporation, and their quarry managers who graciously allowed the collection of fossils from their quarries. We extend special appreciation to Mr. Handsome Major, of the Jamestown Quarry, for without his cooperation, *Protoscutella palmeri* n. sp. would remain undocumented. We are also indebted to Don Clements of Rocky Point, North Carolina, for providing specimens of North Carolina Protoscutellids for study from his extensive collection. We thank George Phillips, Lou Zachos and Roger Portell for their thorough and constructive reviews which greatly improved this manuscript.

REFERENCES CITED

- Agassiz, L. 1835. Prodrome d'une monographie des Radiaires ou Echinodermes. *Memoires de la Société des Sciences Naturelles de Neuchatel*, 1: 168-199.
- Banks, R.S. 1977. Stratigraphy of the Eocene Santee Limestone in three quarries of the coastal plain of South Carolina. *Geologic Notes, South Carolina Geological Survey*, 21(3): 1-149.
- Baum, G.R., Collins, J.S., Jones, R.M., Madlinger, B.A., and Powell, R.J. 1980. Correlation of the Eocene strata of the Carolinas. *South Carolina Geology*, 24(1): 19-27.
- Baum, G.R., and Vail, P.R. 1988. Sequence stratigraphic concepts applied to Paleogene outcrops, Gulf and Atlantic Basins. Pp. 309-327 in: *Sea-Level Changes—an Integrated Approach*, SEPM Special Publication No. 42.
- Cicimurri, D.J., and Knight, J.L. 2009. New record of an

NEW SPECIES OF PROTOSCUTELLA

- extinct fish, *Fisherichthys folmeri* Weems (Osteichthyes), from the lower Eocene of Berkeley County, South Carolina, USA. *PaleoBios*, 29(1): 24-28.
- Clark, W.R., and Twitchell, M.W. 1915. The Mesozoic and Cenozoic Echinodermata of the United States. *United States Geological Survey Monograph* 54, 341p.
- Conrad, T.A. 1865. Descriptions of new species of Echinidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 17: 75.
- Conrad, T.A. 1866. Check list of the invertebrate fossils of North America: Eocene and Oligocene. *Smithsonian Miscellaneous Collections*, 7(200): 1-41.
- Cooke, C.W. 1942. Cenozoic irregular echinoids of the eastern United States. *Journal of Paleontology*, 16(1): 1-62.
- Cooke, C.W. 1959. Cenozoic echinoids of eastern United States. *United States Geological Survey Professional Papers*, 321: 1-106.
- Cooke, C.W., and MacNeil, F.S. 1952. Tertiary stratigraphy of South Carolina. *United States Geological Survey Professional Papers*, 243-B: 1-29.
- Cotteau, G.H. 1891. *Sismondia conradi*. In: Cotteau, G. H. 1889-1894. Terrain Tertiaire, Tome II. Échinides Éocènes. Familles des Cassidulidées (pars), Conoclypéidées, Clypéasteroidées, Scutellidées, Scutellinidées, Fibularidées et les Échinides réguliers. Paléontologie Française ou description des fossiles de la France continuée par une réunion de paléontologues sous la direction d'un comité spécial, 1re Série. - Animaux Invertébrés G Masson, Paris, 789 pp.
- Dockery, D.T. III. 1980. The invertebrate macropaleontology of the Clark County, Mississippi Area. *Mississippi Department of Natural Resources Bureau of Geology Bulletins*, 72: 1-387.
- Durham, J.W. 1955. Classification of clypeasteroid echinoids. *University of California Publications in Geological Sciences*, 31: 73-198.
- Edwards, L.E., Bybell, L.M., Gohn, G.S., and Frederiksen, N.O. 1997. Paleontology and physical stratigraphy of the USGS-Pregnall no. 1 core (DOR-208), Dorchester County, South Carolina. *United States Geological Survey Open File Reports*, 97-145: 1-35.
- Gardner, J. 1957. Little Stave Creek, Alabama-Paleontological Study. *Geological Society of America Memoirs*, 67: 573-588.
- Geisler, J.H., Sanders, A.E., and Zhe-Xi Luo. 2005. A new protocetid whale (Cetacea: Archaeoceti) from the late middle Eocene of South Carolina. *American Museum Novitates*, 3480: 1-65.
- Haeckel, E.H.P.A. 1896. Systematische phylogenie Entwurf eines natürlichen Systema der Organismen auf Grund ihrer Stammesgeschichte. Th. II. *Systematische Phylogenie der Wirbellosen Thiere (Invertebrata)*, Berlin. 720 p.
- Kier, P.M. 1980. The echinoids of the middle Eocene Warley Hill Formation, Santee Limestone and Castle Hayne Limestone of North and South Carolina. *Smithsonian Contributions to Paleobiology*, 39: 1-102.
- Kroh, A. and Smith, A.B. 2010. The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8(2): 147-212.
- Leske, N. G. 1778. Additamenta ad Jacobi Theodori Klein naturalem dispositionem Echinodermatum et lucubratiunculam de aculeis echinorum marinorum. Lipsiae, Leipzig, 278 pp.
- Lovén, S. 1874. Études sur les échinoïdées. *Kongliga Svenska Vetenskaps Akademiens Handlingar*, 11: 1-91.
- Mooi, R. 1986. Structure and function of clypeasteroid milky spines (Echinodermata, Echinoides). *Zoomorphology*, 106: 212-223.
- Mooi, R. 1987. A cladistic analysis of the sand dollars (Clypeasteroida: Scutellina) and the interpretation of heterochronic phenomena. University of Toronto, Canada Ph.D. Thesis, 204 pp.
- Mooi, R. 1989. Living and fossil genera of the Clypeasteroidea (Echinoidea: Echinodermata). An illustrated key and annotated checklist. *Smithsonian Contributions to Zoology*, 488: 1-51.
- Mooi, R., Martínez, S., and Parma, S.G. 2000. Phylogenetic systematics of Tertiary monophorasterid sand dollars (Clypeasteroida: Echinoidea) from South America. *Journal of Paleontology*, 74(2): 263-281.
- Pomel, A. 1883. Classification méthodique et genera des Échinides vivantes et fossiles. Thèses présentées à la Faculté des Sciences de Paris pour obtenir le Grade de Docteur des Sciences Naturelles 503, Adolphe Jourdan, Alger, 131 pp.
- Powell, R.J., and Baum, G.R. 1982. Eocene biostratigraphy of South Carolina and its relationship to Gulf Coastal Plain zonations and global changes of coastal onlap. *Geological Society of America Bulletins*, 93: 1099-1108.
- Stefanini, G. 1924. Relations between American and European Tertiary echinoid faunas. *Geological Society of America Bulletins*, 35(4): 827-846.
- Toulmin, L.D. 1969. Paleocene and Eocene guide fossils of the eastern Gulf Coast Region. *Transactions Gulf Coast Association of Geological Society*, 19: 465-487.
- Toulmin, L.D. 1977. Stratigraphic distribution of Paleocene and Eocene fossils in the Eastern Gulf Coast region. *Geological Survey of Alabama Monographs*, 13: 1-602.
- Ward, L.W., Blackwelder, B.W., Gohn, G.S., and Poore, R.Z. 1979. Stratigraphic revision of Eocene, Oligocene and lower Miocene formations of South Carolina. *Geologic Notes, South Carolina Geological Survey*, 23: 2-23.
- Zachos, L. G. 2009. The sand dollar *Periarchus lyelli* (Echinoidea: Clypeasteroida: Scutelliformes) in the Caddell Formation (Upper Eocene) of Texas. *Texas Journal of Science*. V. 61. p. 181-186.
- Zachos, L.G., and Molineux, A. 2003. Eocene echinoids of Texas. *Journal of Paleontology*, 77(3): 491-508.
- Zullo, V.A., and Harris, W.B. 1987. Sequence stratigraphy, biostratigraphy and correlation of Eocene through lower Miocene strata in North Carolina. *Cushman Foundation for Foramaniferal Research, Special Publications*, 24: 197-213.