

Paleoecology and taxonomy of *Schoenaster carterensis*, a new encrinasterid ophiuroid species from the Upper Mississippian (Chesterian) Slade Formation of northeastern Kentucky, USA

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Abstract.—*Schoenaster carterensis* new species, is an asteroid-like ophiuroid (Echinodermata) from Upper Mississippian (Chesterian) shallow-water carbonates in the Ramey Creek Member of the Slade Formation in northeastern Kentucky. First described in the 1860s from Lower and Middle Mississippian rocks, *Schoenaster* Meek and Worthen, 1860 is not a well-known fossil genus, but the 39 specimens in this collection permitted further definition of the genus and extended its range by ca. 17 Ma into Late Mississippian (Chesterian) time. The number of specimens also permitted differentiation of growth stages based on average arm length and showed that arm length, disk perimeter, and disk area are interrelated in statistically significant ways. Although replaced by chert, the specimens are nearly intact due to rapid burial as rare constituents in habitat communities distributed among four once-contiguous habitats, including shoal, shoal margin, transitional, and basinal. Most of the ophiuroids were concentrated on firm grounds or hardgrounds in shoal and transitional environments, concentrations that probably reflect substratum stability and the ability to support the ophiuroid's generalist feeding strategy. Many fossil ophiuroid species are known from only a few specimens, severely limiting interpretations about their detailed taxonomy, individual variation, and ecology. In contrast, the greater number of specimens and extensive knowledge of geologic occurrence in this study permitted detailed interpretations regarding the taxonomic, intraspecific, and ecologic attributes of this species, which might be useful in the study of other fossil ophiuroids.

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Introduction

At more than 2,000 species, ophiuroids constitute the largest extant echinoderm class (O'Hara et al., 2014; Stöhr et al., 2017). In the fossil record, however, ophiuroids are relatively uncommon fossils, because they are weakly articulated, Type 1 echinoderms (Brett et al., 1997) that rapidly disaggregated into hundreds of plates upon death. Moreover, because most of these plates are the hydrodynamic equivalents of sand, they are widely transported or further comminuted. Fossil ophiuroids first appear in the Lower Ordovician rocks of Europe (Thoral, 1935; Spencer, 1951), and perhaps > 100 fossil genera are known, mostly from individual specimens. Here, we report a new Late Mississippian ophiuroid species from limestones of the Ramey Creek Member of the Slade Formation (Etnensohn et al., 1984) in northeastern Kentucky, USA (Figs. 1–3), which extends the range of the genus. Although generally poorly preserved because of silicification, 39 individuals were collected, and from all of these individuals, it has been possible to piece together the most important parts of the organism's external morphology. With so many specimens, it has been possible to distinguish probable ophiuroid life stages and demonstrate relationships between average arm length, disk

perimeter, and disk area. What makes the occurrence unique is the fact that the species was a part of four apparently contiguous, echinoderm-rich communities, which might be related to various environmental parameters. As a result, several environmental and ecological conditions are suggested that likely contributed to the species' presence.

Geologic setting

Thirty-nine ophiuroid specimens were collected by F.R. Etnensohn in the early 1970s from the former Olive Hill Ken-Mor Quarry locality, now known as the Valley Stone Quarry, in Carter County, Kentucky (Fig. 1); the quarry is now infilled and inaccessible. Samples from the Valley Stone Quarry include five different echinoderm classes along with several other invertebrate and vertebrate (class Chondrichthyes) phyla collected on 136 slabs. Chondrichthyan fossils include isolated teeth and dermal plates, which do not reflect entire organisms and could not be tallied in the same way as other fossil individuals.

The ophiuroids are included on 18 slabs along with several loose specimens. Most of the specimens are silicified and not well preserved, but preservation is good enough to measure disk and arm dimensions. In a few partially silicified specimens,

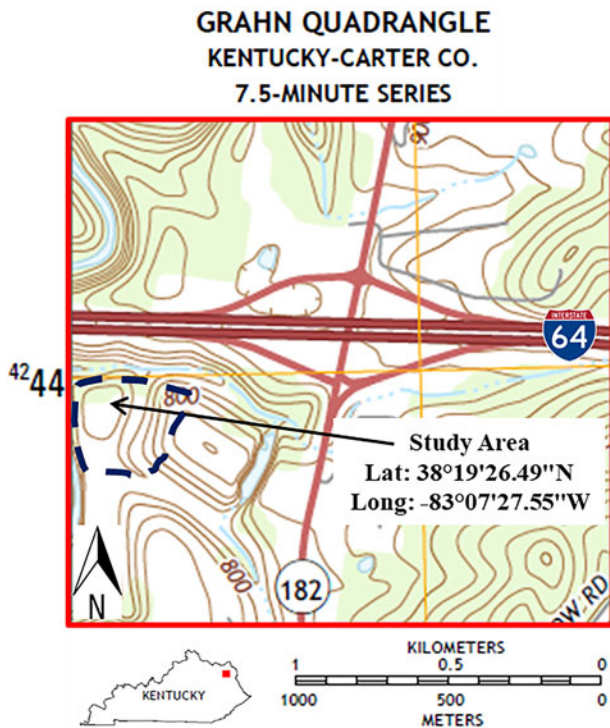


Figure 1. Location map of the Valley Stone Quarry in Carter County, Kentucky. The dashed area represents the approximate quarried area (0.17 km²) from which the 39 ophiuroid specimens were collected. Map after USGS (2016).

preservation is sufficient to discern specific plate morphology. Sixteen of the specimens are preserved in ventral (oral) aspect and 23 in dorsal (aboral) aspect.

Overall, echinoderm-bearing rocks in the quarry were probably present across several facies in an area > 0.2 km² (0.1 mi²) (Fig. 1). The specimens come from the Ramey Creek Member of the Slade Formation, which is an upper Middle (upper Osagean–Meramecian) to Upper (middle Chesterian) Mississippian (Viséan–Lower Serpukhovian), shallow-water carbonate unit, 55–65 m thick (Ettensohn et al., 1984; Ettensohn, 2009), deposited on the western margin of the Appalachian Basin, in what is today the Cumberland Escarpment outcrop belt in northeastern Kentucky (Fig. 2). The Ramey Creek Member occurs in the upper part of the Slade Formation (Fig. 3) and represents a shallow, open-marine setting on an eastward-dipping ramp in a late early to middle Chesterian (Gasperian–Hombergian; early Serpukhovian) transgressive sequence (Ettensohn, 1981; Ettensohn et al., 2004) at ca. 328 Ma (Davydov et al., 2012). In this setting, deposition is interpreted to have occurred across an array of tide- and wave-influenced shoals and intervening basins, with modern analogs in the Persian Gulf (e.g., Kassler, 1973). Skeletal sands were deposited on the shoals, whereas calcareous mud and silt, as well as argillaceous muds, predominated in the deeper intervening basins (Ettensohn, 1975, 1977, 1986). Argillaceous calcarenites and nodular calcilutites with interbedded shales and mudstones represent basinal deposition below wave and tidal influence, whereas well-washed, cross-bedded, skeletal calcarenites represent deposition on shoals near wave base or in storm-generated backflow currents from

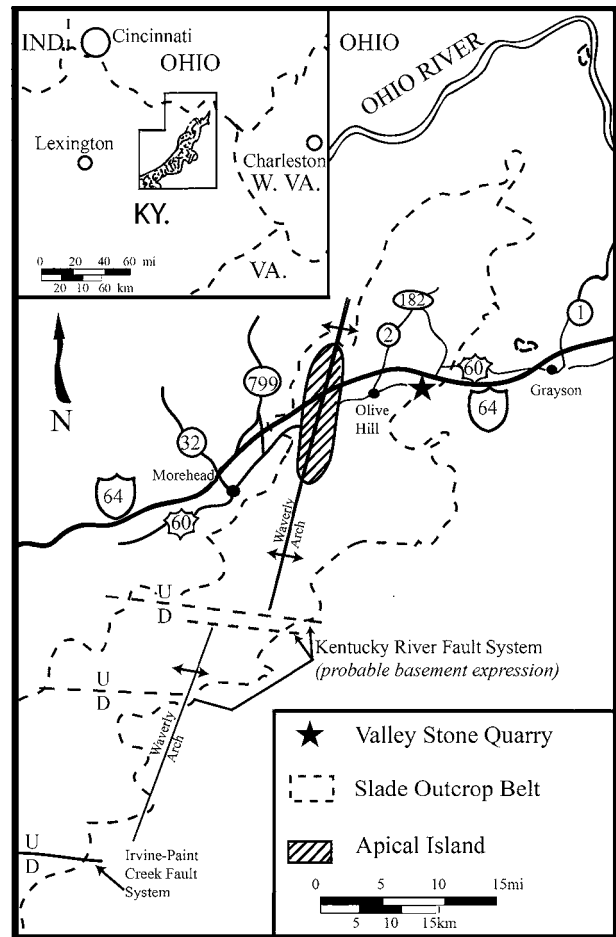


Figure 2. Map showing the Mississippian outcrop belt along the Cumberland Escarpment in northeastern Kentucky. The Valley Stone Quarry (black star) is located on the northern uplifted block of the Kentucky River Fault System (adapted from Ettensohn, 1986).

the shoals (Fig. 4). The lithofacies and features noted here are very similar to those storm-related lithofacies described by Aigner (1982) as proximal (shoals) and distal (basinal) tempestites in the Triassic, shallow-marine, upper Muschelkalk carbonates of Germany. Moreover, the area was present in a major storm belt during Mississippian time (Marsaglia and Klein, 1983).

At the Valley Stone Quarry locality, the Ramey Creek Member is 4.7 m thick and exhibits four lithofacies that reflect distinct depositional environments (Fig. 4). The coarse-grained calcarenite lithofacies represents shoal environments; the coarse-grained argillaceous calcarenites represent shoal-margin environments; the fine-grained calcarenites and interbedded calcilutites reflect transition areas into the basins; and the argillaceous calcilutite and shale lithofacies reflect the deeper basinal environments (Fig. 4) (Harris and Ettensohn, 2017; Harris, 2018). Although these lithofacies typically occur in vertical sequence, based on Walther's Law, at any one time and place, these facies represented laterally juxtaposed environments (e.g., Boggs, 2006) as shown in Figure 4. Ophiuroid fossils occur across all lithofacies (Fig. 5).

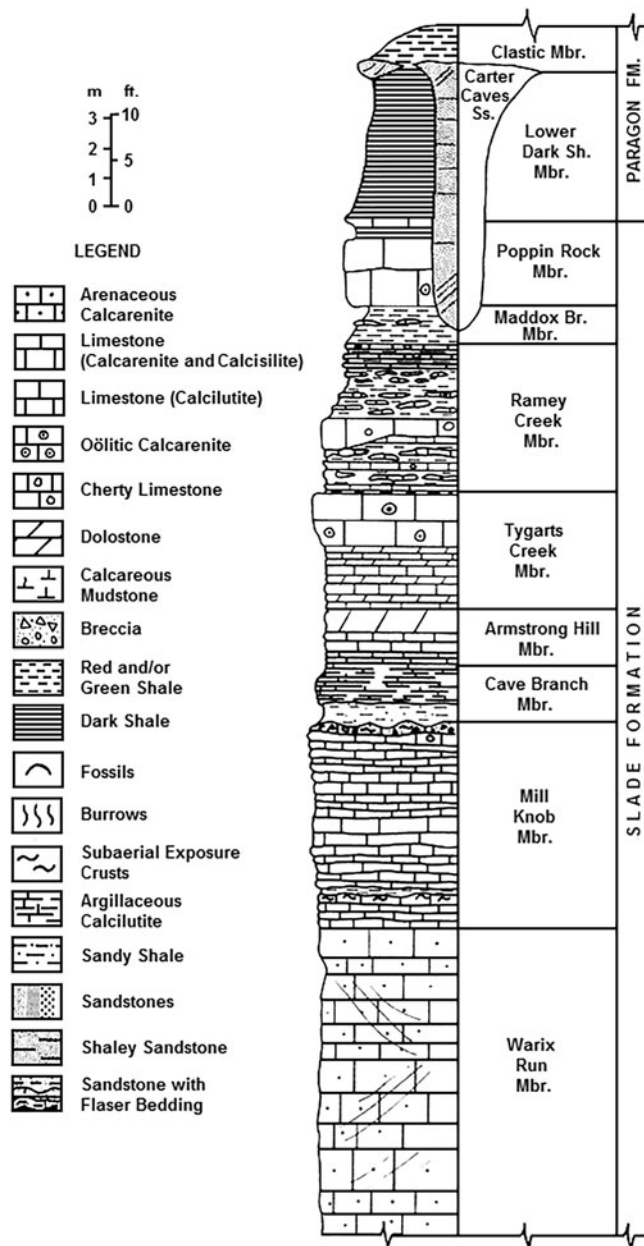


Figure 3. Detailed stratigraphic section from the Valley Stone Quarry, Carter County, Kentucky study area. The Ramey Creek Member is the focus of this study. The thick calcarenite bed in the middle of the member represents a shallow-water shoal in the midst of deeper, basinal environments (see Fig. 4) (adapted from Lierman et al., 2011).

Materials and methods

Specimens were collected from loose quarry debris over a number of years, and many occur in large slabs. Slab lithologies were identified and placed into the appropriate Ramey Creek Member lithofacies, which were interpreted to represent four different, shallow, open-marine depositional environments based on lithology, fossils, and sedimentary features (Harris, 2018). The ophiuroids and all associated fauna were identified to genus or species level and tallied by lithofacies; slab areas and specimen tallies, which totaled 1,894 specimens, were used to calculate ordinal measures of abundance and community density (Harris,

2018). Important ophiuroid specimens were photographed using standard procedures, University of Kentucky numbers were assigned, and measurements of arm lengths and disk margins were made. These dimensional parameters were then statistically analyzed for significance, using F- and t-tests in Minitab Statistical Software 18 (Minitab, Inc., 2018). Minitab was also used to calculate means, standard deviations, confidence intervals, Pearson's r and r^2 , and regression lines in determining the relationships between average arm length, disk area, and disk perimeter (see Franzblau, 1958; Triola, 2018); Microsoft Excel was used to generate the pie chart (Fig. 5). Data and assumptions used for F- and t-tests are presented in Tables 1–5, and the terminology is based largely on Spencer and Wright (1966).

Abbreviations.—Amb (plural Ambb) = ambulacral; L (plural LL) = lateral; L_F = height of 'boot toe' (Fig. 6); L_L = height of 'boot leg' (Fig. 6); MAP (plural MAPP) = mouth-angle plate; M (plural MM) = marginal plate; W_{DF} = width of 'distal fitting' (Fig. 6); W_F = length of 'boot foot' (Fig. 6); W_T = length of 'boot toe' (Fig. 6).

Repository and institutional abbreviations.—USNM S = Springer Collection, National Museum of Natural History (United States National Museum), Washington, DC; UK = Department of Earth & Environmental Sciences, University of Kentucky, Lexington. Of the 39 collected specimens, 10 were used in this study (UK 116000–116009).

Systematic paleontology

Phylum Echinodermata Bruguière, 1791
 Class Ophiuroidea Gray, 1840
 Order Oegophiurida Matsumoto, 1915
 Suborder Lysophiurina Gregory, 1897
 Family Encrinasteridae Schuchert, 1914
 Genus *Schoenaster* Meek and Worthen, 1860

- 1860 *Palasterina* (*Schoenaster*) Meek and Worthen, p. 449.
 1866a *Schoenaster*; Meek and Worthen, p. 277.
 1915 *Schoenaster*; Schuchert, p. 202.
 1930 *Encrinaster* Haeckel, 1866; Spencer, p. 418 (partim).
 1942 unidentifiable asterozoan genus; Kirk, pl. 1, fig. 2.
 ?1943 *Schoenaster*?; Easton, p. 137.
 ?1966 *Euzonosoma* Spencer, 1930; Spencer and Wright, p. U86 (partim).
 1988 unidentifiable asterozoan genus; Chesnut and Ettensohn, p. 68, pl. 12, figs. 8, 9.

Type species.—*Palasterina* (*Schoenaster*) *fimbriata* Meek and Worthen, 1860 from the Mississippian St. Louis Limestone of St. Clair County, Illinois.

Diagnosis.—Individuals with stout, convex arms that taper uniformly to acute points; arms never petaloid. Margins of disk between rays concave with poorly organized plating. Ambb alternate and are L- or boot-shaped in ventral aspect with elongate 'boot leg' parallel to arm axis. LL (= adambulacrals) subventral with broad ventral faces,

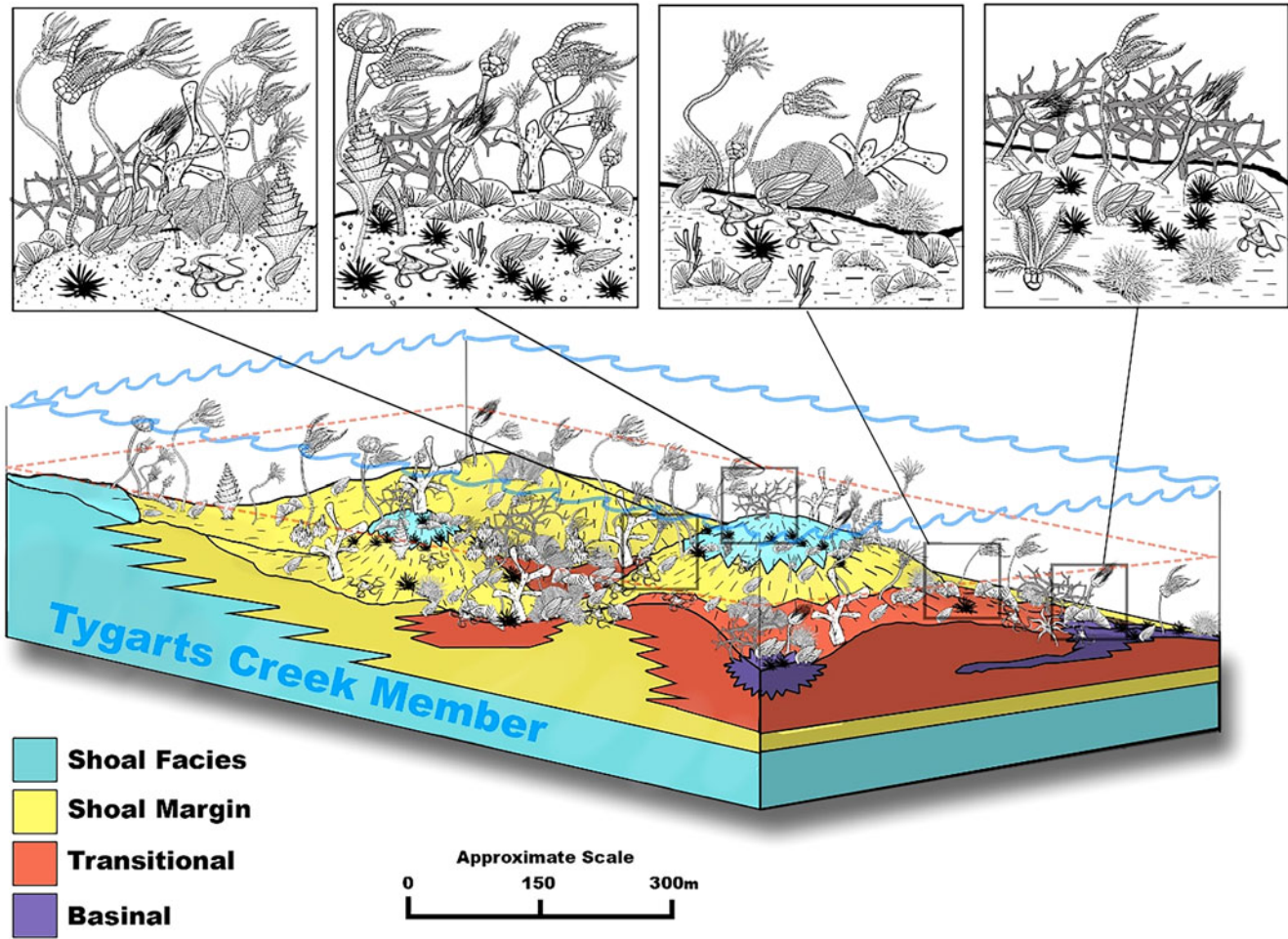


Figure 4. Schematic reconstruction of the interpreted, shallow, open-marine, Ramey Creek environmental continuum that developed seaward of the Tygarts Creek sandbelt, based on lithologies at the Valley Stone Quarry (Fig. 3). Blue wavy line at top reflects sea level; the red dashed line reflects approximate normal wave base. Different colors represent different interpreted depositional environments for each lithofacies. Inset figures at the top show likely organism communities for each environment. Organism rank and abundance in the inset figures reflect species frequency of Harris (2018). Diagram in lower panel emphasizes organisms at a larger scale than the environments in which they lived.

rectangular with adradial termination near Ambb, arranged with long axes directed obliquely outward, giving twisted-rope appearance after which the genus was named (Latin, *schoenus* = rope; Greek, *aster* = star; Meek and Worthen, 1860). Mouth frame robust. First and second pairs of Ambb do not overlap; dorsal lateral channelway on LL absent.

Occurrence.—Early–middle Late Mississippian (Kinderhookian–middle Chester [Hombergian]; Tournaisian–early Serpukhovian). If the single arm specimen of Easton (1943) belongs in the genus *Schoenaster*, then the generic range is extended to late Chesterian (Elviran; late Serpukhovian) time.

Remarks.—As originally designated, Meek and Worthen (1860) placed their specimens in the asteroid genus *Palasterina* M’Coy, 1851, but the LL in their specimens were oriented obliquely to the Ambb, which differs from the perpendicular orientation of the Ambb in *Palasterina*. Hence, Meek and Worthen (1860) created the subgenus *Schoenaster* to accommodate this difference. However, by 1866, Meek and Worthen (1866a) thought that this difference and a few others were substantial enough to separate it as a distinct genus under the name *Schoenaster*. Although Schuchert (1915) recognized the genus and several species, Spencer (1930) thought that the genus was unrecognizable and placed some *Schoenaster* species in *Encrinaster* Haeckel, 1866, and others in *Euzonosoma* Spencer, 1930, based on the presence of ventral-surface spines and arm shape, respectively (Spencer and Wright, 1966).

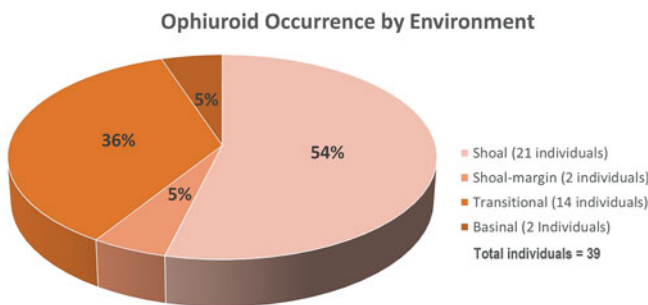


Figure 5. Percentage occurrence of ophiroids by depositional environments in the Ramey Creek Member of the Slade Formation at the Valley Stone Quarry. See Table 1 for the number of ophiroids by life stage in each environment, and Table 6 for the total number of tallied fossil specimens per environment.

Table 1. Arm-length ranges and classes, number of individuals (N) per class, and numbers of individuals per class per depositional environment for 38 specimens of *Schoenaster carterensis* n. sp. In one additional specimen, only the disk was preserved, so arm data were unavailable.

Average arm-length range (cm)	Arm-length class	N	Shoal	Shoal-margin	Transitional	Basinal
0.05–1.55	Class 1	22	8	1	13	0
1.55–3.05	Class 2	12	9	0	1	2
3.05–4.55	Class 3	3	2	1	0	0
4.55–6.05	Class 4	1	1	0	0	0

Jell (1997) resurrected the genus based on the absence of petaloid arms and assigned it to the Encrinasteridae. Harper and Morris (1978), Jell (1997), and Blake et al. (2017) provided additional information on the history of the family Encrinasteridae and the genus *Schoenaster*. *Schoenaster* is currently placed in the suborder Lysophiurina based on alternating Ambb on either side of the perradial suture at the ambulacral midline (Figs. 6, 7.1–7.3, 7.5), and in the family Encrinasteridae based on the presence of wide, robust, transversely elongate, subventral LL (which are oriented obliquely on either side of the arm such that the LL give the appearance of a twisted rope; Fig. 7.1–7.3), transversely grooved ambulacrals, and ambulacrals that join interradial lateral surfaces of MAPP (Fig. 7.4) (Spencer and Wright, 1966; Jell, 1997; Shackleton, 2005).

Compared with the type species, *Schoenaster fimbriatus*, specimens assigned to the genus in this study have the same dorsally convex, acutely tapering arms that are approximately equal in length to the diameter of the disk (Fig. 8.1, 8.2, 8.5, 8.6). Most importantly, however, the LL are adradially expanded and oriented obliquely to the ‘boot-shaped’ Ambb (Fig. 7.3), giving the typical rope-like appearance, and comprise the sides of the

arms beyond the disk. As in the type species, the MM form a concave margin but are poorly organized and irregular in shape (Figs. 7.1, 7.2, 8.3). In contrast to the type species, specimens in this study have stouter plates and lack evidence of spines, although the absence of spines could reflect preservational conditions.

The truly defining characteristic of this genus is the obliquely oriented LL, which give a rope-like appearance, as was best noted by Schuchert (1915, pl. 19, fig. 7c, d) and Jell (1997, fig. 3). In other encrinasterid ophiuroids, the LL are oriented nearly perpendicular to the Ambb (e.g., Spencer and Wright, 1966, fig. 74). Inasmuch as all the currently known *Schoenaster* species show this character—if nothing else—the authors think that all currently known species are congeneric.

Kirk (1942) illustrated an asterozoan specimen from a slab on which he identified the crinoid *Ampelocrinus bernhardinae* Kirk, 1942 (USNM S-4402B), but never identified the specimen. Chesnut and Etnsohn (1988) also noted the same specimen as an unidentifiable asterozoan. However, Chesnut and Etnsohn (1988) also described a similar specimen as an unidentifiable ophiuroid (UK 115583). Subsequent examination of both specimens shows that they have the same distally tapering arms and obliquely oriented LL that show the twisted-rope appearance characteristic of *Schoenaster*. Hence, the authors conclude that all of the unidentifiable asterozoan specimens illustrated by Kirk (1942) and Chesnut and Etnsohn (1988) belong to the genus *Schoenaster*. In the Chesnut and Etnsohn (1988) specimens, the internal disk plates, however, are so disorganized that it is impossible to identify the species. Easton (1943) doubtfully identified part of one arm from the Pitkin Formation of Arkansas as an arm from the ‘asteroid’ *Schoenaster*. Although the arm tapers distally and shows a similar twisted-rope arrangement of the LL characteristic of *Schoenaster*, all of the disk and other arms are missing. Easton (1943) suggested

Table 2. One-way analysis of variance (ANOVA): average arm length by class in *Schoenaster carterensis* n. sp. The ANOVA, generated by Minitab, was used for tests of hypotheses for analysis in this study. α = alpha (level of significance); Adj MS = adjusted mean squares; Adj SS = adjusted sum of squares; CI = confidence interval; DF = degrees of freedom; F-value = test statistic used to determine whether to reject null hypothesis; P-value = probability of obtaining a test statistic at least as extreme as the F-value ($P \leq \alpha$ indicates that null hypothesis is rejected in favor of the alternative hypothesis); N = sample size; Std Dev = standard deviation; * = sample size not large enough to calculate StDev.

Method					
Null hypothesis (H_0)	All means are equal				
Alternative hypothesis (H_a)	Not all means are equal				
Significance level	$\alpha = 0.05$				
Equal variances were assumed for the analysis.					
ANOVA					
Source	DF	Adj SS	Adj MS	F-Value	P-Value
Factor	3	39.894	13.2979	79.56	0.000
Error	34	5.683	0.1671		
Total	37	45.577			
Average arm length class	N	Mean	Std Dev	95% CI**	
Class 1	22	0.9853	0.3668	(0.8082, 1.1624)	
Class 2	12	2.0980	0.5060	(1.858, 2.338)	
Class 3	3	3.3667	0.1528	(2.8870, 3.8464)	
Class 4	1	6.0000	*	(5.169, 6.831)	

**Confidence-Interval (CI) Interpretations:

- 95% confident that population mean for Class 1 arm length is between 0.8082 cm and 1.1624 cm.
- 95% confident that the population mean for Class 2 arm length is between 1.858 cm and 2.338 cm.
- 95% confident that the population mean for Class 3 arm length is between 2.8870 cm and 3.8464 cm.
- 95% confident that the population mean for Class 4 arm length is between 5.169 cm and 6.831 cm.

Conclusion: $P \leq \alpha$, therefore, null hypothesis is rejected in favor of the alternative hypothesis, and sufficient evidence is present to support the claim that not all the population means are equal.

Table 3. Two-sample t-test and CI: Mean Class 1 and Class 2 arm lengths. DF = degrees of freedom; N = sample size; P-value = probability of obtaining test statistics at least as extreme as the t-value; Pooled Std Dev = weighted average of StDev of each class; SE Mean = standard error of the mean; Std Dev = standard deviation; t-value = test statistic used to determine whether to reject the null hypothesis.

Method				
μ_1 = Class 1 mean arm length				
μ_2 = Class 2 mean arm length				
Null hypothesis (H_0)	$\mu_1 - \mu_2 = 0$			
Alternative hypothesis (H_a)	$\mu_1 - \mu_2 < 0$			
Mean arm length	N	Mean	Std Dev	SE Mean
Class 1	22	0.985	0.367	0.078
Class 2	12	2.098	0.506	0.150
Estimation for Difference				
Difference	Pooled Std Dev			
-1.113	0.420			
t-value	DF	P-value		
-7.39	32	0.000		

Conclusion: $P \leq \alpha$, therefore, the null hypothesis is rejected in favor of the alternative hypothesis, and it can be concluded that there is sufficient evidence to support the claim that the population mean arm length of Class 1 is less than the population mean arm length of Class 2.

Table 4. Two-sample t-test and CI: Mean Class 2 and Class 3 arm lengths. See Table 3 for abbreviations.

Method				
μ_1 = Class 2 mean arm length				
μ_2 = Class 3 mean arm length				
Null hypothesis (H_0)	$\mu_1 - \mu_2 = 0$			
Alternative hypothesis (H_a)	$\mu_1 - \mu_2 < 0$			
Sample	N	Mean	Std Dev	SE Mean
Class 2 mean arm length	12	2.098	0.506	0.150
Class 3 mean arm length	3	3.367	0.153	0.088
Estimation for Difference				
Difference	Pooled Std Dev			
-1.268	0.469			
t-value	DF	P-value		
-4.19	13	0.001		

Conclusion: $P \leq \alpha$, therefore, the null hypothesis is rejected in favor of the alternative hypothesis, and it can be concluded that there is sufficient evidence to support the claim that the population mean arm length of Class 2 is less than the population mean arm length of Class 3.

that the specimen resembles *S. montanus* Raymond, 1912, which is discussed below; we questionably suggest that the specimen might reside in the genus *Schoenaster*. Similarly, Schuchert (1915) noted the occurrence of a small specimen that he questionably referred to the genus *Schoenaster*, indicating that it was most likely related to *S. wachsmuthi* Meek and Worthen, 1866b. The specimen has never been illustrated or described.

Table 5. Linear correlation coefficients (r), coefficients of determination (r^2), and correlation interpretations (Franzblau, 1958) for relationships noted in leftmost column.

Linear correlation	r	r^2	Pearson's r interpretation
Disc area (cm^2) to average arm length (cm)	0.649	0.421	Marked degree of correlation
Disc perimeter (cm) to average arm length (cm)	0.656	0.430	Marked degree of correlation
Disc area (cm^2) to disc perimeter (cm)	0.965	0.931	High correlation

The combination of long, distally tapering arms and concave disk margins readily differentiate *Schoenaster* from other encrinasterid ophiuroids (Jell, 1997). In particular, the genus can be differentiated from both *Encrinaster* and *Euzonosoma*, with which Spencer (1930) and Spencer and Wright (1966) synonymized it, based on its lack of petaloid arms and a well-developed, concave ambital framework, apparent lack of spines on ventral surface, and straight-sided blocky ambulacrals (see Shackleton, 2005). The first pair of Ambb also does not override the second pair as in the encrinasterid genera *Euzonosoma*, *Encrinaster*, and *Mastigactis* Spencer, 1930 (see Blake et al., 2017). The encrinasterid *Ophiocantabria* Blake, Zamora, and García-Alcalde, 2015, in contrast, has a comparatively larger disk with fewer, better-developed MM, Ambb that are more rectangular than boot-shaped, and stouter pustulose plates throughout. *Marginura* Haude, 1999, a Devonian encrinasterid, has a smaller disk composed of tiny polygonal plates and irregularly polygonal LL with club-shaped abradial expansions (see Jell and Theron, 1999; Glass, 2006a). At least some members of the encrinasterid genera *Encrinaster*, *Ophiocantabria*, and *Crepidiosoma* Spencer, 1930, also each display a prominent longitudinal channelway on the dorsal surface of LL (Schöndorf, 1910; Blake et al., 2015, 2017), which is lacking in *Schoenaster* (Fig. 7.6). Ventral-surface spines can also be a distinguishing trait of *Schoenaster*, but their presence or absence probably depends on the preservational state of specimens.

Schoenaster carterensis new species Figures 7–9

Type specimens.—Holotype, UK 116000; 9 paratypes, UK 116001–116009.

Diagnosis.—Thick, stout, L-shaped Ambb in proximal parts of ventral arm surfaces, becoming irregularly rectangular distally. Ambital margins concave with poorly to moderately developed, wider-than-high MM. Dorsal surface of irregular, pustulose plates with raised, carinal ridge along midline of each ray, terminating in irregular boss above mouth frame on dorsal disk.

Occurrence.—Ramey Creek Member of the Slade Formation, Upper Mississippian (middle Chesterian, Hombergian; Serpukhovian, Pendleian), Kentucky, USA (38°19'26.49"N, -83°07'27.55"W) (Figs. 1–3).

Description.—Small to large, pentagonal individuals (Figs. 7.2, 8.1–8.5). Dorsal surface covered with mm-sized, tumid, pustulose, polygonal plates (Fig. 8.3, 8.5–8.6). Arms tapering uniformly to acute points (Fig. 8.1, 8.2, 8.4); in some specimens, arms folding back on themselves (Figs. 7.6, 8.4).

Table 6. Relative frequency (RF) as a percentage of ophiuroids and accompanying fauna in each of the four Ramey Creek environments. SA = species abundance. The numbers in parentheses are the numbers of species per taxon. abs = absent; C = common, 10% < x ≤ 30%; D = dominant, > 50%; F = frequent, 30% < x ≤ 50%; O = occasional, 5% < x ≤ 10%; R = rare, 1% < x ≤ 5%; S = sporadic, ≤ 1% (abundance descriptors from Harris, 2018); — = not applicable.

Phylum	Class	Order	Species Abundance & Relative Frequency by Environment							
			Shoal		Shoal Margin		Transitional		Basinal	
			RF	SA	RF	SA	RF	SA	RF	SA
Porifera	Demospongiae (1)		18.7%	C	4.3%	R	4.2%	R	13.9%	C
Cnidaria	Anthozoa (1)		0.1%	S	abs	—	abs	—	abs	—
	Scyphozoa? (2)		1.0%	S	3.5%	R	4.7%	R	1.3%	R
Mollusca	Pelecypoda (1)		0.1%	S	abs	—	abs	—	0.6%	S
Annelida?	Polychaeta? (1)		0.3%	S	abs	—	abs	—	abs	—
Brachiopoda	Articulata (11)		33.7%	F	67.2%	D	35.3%	F	35.2%	F
	Inarticulata (2)		0.4%	S	0.5%	S	1.6%	R	abs	—
Bryozoa	Stenolaemata (9)	Cryptostomida (1)	1.8%	R	1.1%	R	abs	—	5.2%	O
		Cystoporida (1)	abs	—	abs	—	abs	—	0.2%	S
		Fenestrata (6)	4.0%	R	4.6%	R	11.1%	C	3.7%	R
		Trepostomatida (1)	0.3%	S	abs	—	abs	—	0.2%	S
Echinodermata	Edrioasteroidea (2)		0.8%	S	abs	—	abs	—	0.2%	S
		Blastoidea (1)	4.0%	R	2.2%	R	1.1%	R	9.3%	O
		Echinoidea (1)	0.1%	S	abs	—	7.4%	O	7.2%	O
		Ophiuroidea (1)	2.9%	R	0.5%	S	7.4%	O	0.4%	S
	Crinoidea (18)	Camerata (3)	0.6%	S	0.3%	S	1.6%	R	0.2%	S
		Eucladida (14)	29.9%	C	15.9%	C	25.8%	C	22.0%	C
	Flexibilia (1)	1.1%	R	abs	—	abs	—	0.6%	S	
Individual fossils per environment			723		376		185		610	

but such flexibility could be a taphonomic overprint related to softening with onset of tissue decay; length of arms beyond the disk reflects approximately two-thirds of total arm length (Fig. 8.1–8.3) and ranges from 0.2–6.0 cm, averaging 1.7 cm. In well-preserved specimens, a carinal ridge, one-to-two-plates wide, extends along the midline of each ray and terminates in a prominent boss above the mouth frame on the dorsal surface (Fig. 8.5). Disk pentagonal and concave at ambitus (Figs. 7.1, 7.2, 8.1–8.5) with a perimeter that ranges from 0.5–6.5 cm, averaging 2.6 cm; sides range from 0.1–1.3 cm in length, averaging 0.6 cm. MM poorly to moderately differentiated (Figs. 7.1, 7.2, 8.3) and terminating against L series at approximately one-third the total arm length (Figs. 7.1, 7.2, 8.1); 8–14 MM per ambital side; MM polygonal, taller than wide, in line with each other, and smaller than inner disk plates with which they imbricate. Ambb and LL plates stout, robust (Fig. 7.3), changing shape along length of the arm; Ambb forming a biserial row with plates on either side of the perradial suture alternating by up to half of an Amb length (Figs. 6, 7.1–7.3); perradial suture straight or gently undulatory (Figs. 6, 7.2–7.5); 5–7 Ambb in disk on ventral surface. In ventral aspect, Ambb are L-, boot-, or stocking-shaped with an elongate boot leg (L_L , Fig. 6) parallel to the arm axis, slightly longer than wide in medial parts of the arm and concave on the distal and abradial margins (Figs. 6, 7.2, 7.3). Using the terminology of Glass and Blake (2004), Glass (2006b, c), and Hunter et al. (2016) (Fig. 6), in the proximal arm, W_F is wider than L_F ; L_L is relatively long; top or proximal part of ‘boot’ is rounded to blocky; W_{DF} is smaller than W_F ; central leg widening, forming a curved ‘ankle’ area that joins a blocky or rounded toe; distal end of W_{DF} slightly concave; width of central ‘leg’ narrowing slightly distally; W_T is slightly shorter than W_{DF} ; the abradial edge of ‘toe’ is generally curved; W_T is approximately one-third of W_F (Figs. 6.1, 6.2, 7.3); the ‘lace

area’ is concave and continues toward the rounded or blocky ‘toe’ (Fig. 6.2). Distally, Ambb become irregularly rectangular and elongate in a distal-proximal direction such that L_L is nearly four times longer than W_F (Figs. 6.3, 7.6); distal Ambb are rounded and protuberant at both ends, but the proximal end is slightly larger (Fig. 6.3) and expands proximally to become the ‘toe of the boot.’ In dorsal aspect, proximal Ambb are very elongate, perpendicular to the perradial suture (Fig. 7.4), and shaped like ‘hourglasses’ that bifurcate into two ‘prongs’ on the abradial ends (Figs. 7.4–7.6, 9); relationships between MAPP and proximal Ambb (Figs. 7.4, 9) suggest that if the animal were to break or lose a MAP, the most proximal ‘prong’ on the next most proximal Amb will elongate and move proximally to become a new MAP (Figs. 7.4, 9); any MAP, along with a MAP from an adjacent ray, forms an interray pair of the mouth frame (Figs. 7.2, 7.4, 8.1, 8.3, 9). LL subventral (Fig. 8.6), robust with broad ventral faces, and rectangular with pointed adradial terminations (Fig. 7.3, 7.6, 7.7) that apparently imbricate across Ambb; LL arranged with their long axes directed obliquely outward (Fig. 7.1, 7.3); distally, LL become elongate-oval to ‘apostrophe-shaped’ (Fig. 7.6, yellow arrow); proximally, LL become smaller and more irregularly shaped, appearing to merge with interradial disk plates (Figs. 7.1, 7.2, 7.4, 9). L-shape of the Ambb can be difficult to observe, because adjacent LL articulate with Ambb at the internal angle of the ‘L’ (Fig. 7.3). LL apparently functioned to close and protect components along the ambulacral midline, because all stages of open and closed ambulacral grooves are apparent (Fig. 7.1–7.3). Podial gap shared equally by adjacent Ambb and LL (Fig. 7.3, 7.6). Mouth frame formed from adjacent MAPP that join interradially (Figs. 7.2, 7.4, 8.1, 8.3, 9). Spines (Fig. 8.4) and pustules (Fig. 7.3) can be present on the ventral surface but recognizing them depends upon preservational state.

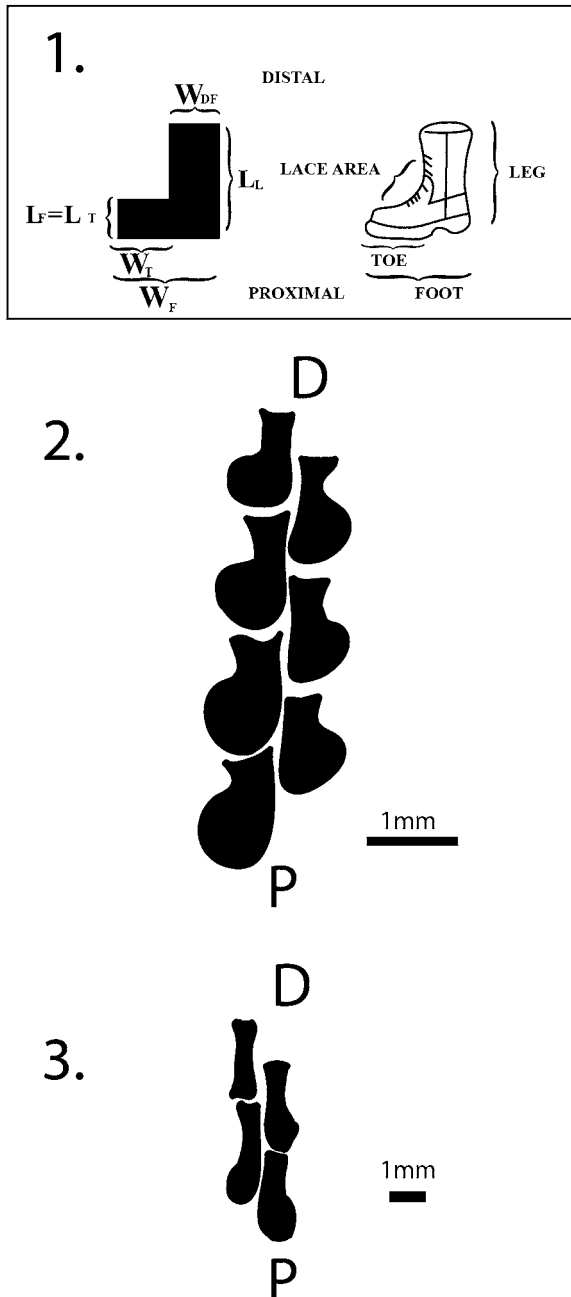


Figure 6. Terminology and dimensional measurements for the Ambb of *Schoenaster carterensis* n. sp.: (1) terminology for ‘boot-shaped,’ *Schoenaster* Ambb compared to parts of a ‘boot’ (adapted from Glass and Blake, 2004); (2) sketch showing outline of proximal Ambb along a perradial suture in ventral view of *S. carterensis* n. sp. (see Fig. 7.3); (3) sketch in ventral view showing outline of distalmost, elongated Ambb from *S. carterensis* n. sp. (see Fig. 7.6).

Etymology.—The specific name *carterensis* comes from Carter County, Kentucky, where the specimens were found.

Remarks.—This new species differs from the Meramecian (St. Louis) type, *Schoenaster fimbriatus*, which has very small delicate Ambb and less elongate squat LL, in its stout, thicker, almost rectangular Ambb and more elongate LL. In the type species, the ‘leg’ of the ‘boot’ is more constricted near its top to form a more defined, rounded podial basin than that present in

S. carterensis n. sp. (Fig. 7.3). The new species also apparently lacks the ventral spines that characterize *S. fimbriatus*. The new species differs from the Osagean (Burlington) species, *S. wachsmuthi*, in that the latter has more ovoid and less oblique LL. Finally, the new species differs from the Kinderhookian species, *S. legrandensis* Miller and Gurley, 1888, in that the latter has nearly straight, narrow arms and oblong LL with rounded ends. Raymond (1912) collected *S. montanus* from the Madison Limestone of southwestern Montana, which means that it could be Kinderhookian through Meramecian in age (Ballard et al., 1983). This species is known from one poorly preserved specimen but appears to differ from the new species in the presence of rounded LL and small arms. The genus *Schoenaster* was previously known only from Lower and Middle Mississippian (Kinderhookian–Meramecian) rocks, but the new occurrence described herein extends its range into the Upper Mississippian (Chesterian) section.

Although most *Schoenaster* species apparently have more delicate laterals than the species described here, *S. carterensis* n. sp. appears somewhat similar to the asteroid-like encrinasterid species *Ophiocantabria elegans* Blake, Zamora, and García-Alcalde, 2015. The new species is also asteroid-like and has laterals and ambulacra that are very similar to those of *O. elegans*. The latter differs, however, in having petaloid arms, a more developed ambital framework, and a more complex mouth framework.

In this *Schoenaster* species, moreover, it seems almost certain that MAPP develop through elongation of proximal parts of the most proximal ambulacral plate in adjacent arm rays (Fig. 9).

Statistical comparison of dimensional parameters

Because ophiuroid fossils are generally rare, most descriptions are based on one or very few specimens. In this study, however, 39 specimens of *Schoenaster carterensis* n. sp. were available. Although detailed preservation is generally poor in most of these specimens, the original lengths and shapes of the arms and disks can still be measured, making it possible to interpret size classes and discern relationships between the arms and disks (Harris et al., 2019) (Fig. 10). Also, because arm length relative to disk size and the sharp demarcation of disk and arms were significant factors in the original separation of ophiuroids from asteroids (Forbes, 1841), the number of available specimens allows for a detailed statistical examination of these relationships.

Size classes.—The collection includes specimens of various disk and arm sizes, which, in both cases, range from relatively small to large. Although in some ophiuroid species, observations suggest that the animals increase in size with age (e.g., Zeleny, 1903), little to no work deals with the specific relationships between ophiuroid arm length and age. Nonetheless, the specimens in the studied collection show a positive correlation between arm length and disk perimeter/disk area (Fig. 10.1–10.3), suggesting that as the ophiuroids grew in size (larger disk perimeters and disk areas), their arms lengthened proportionately.

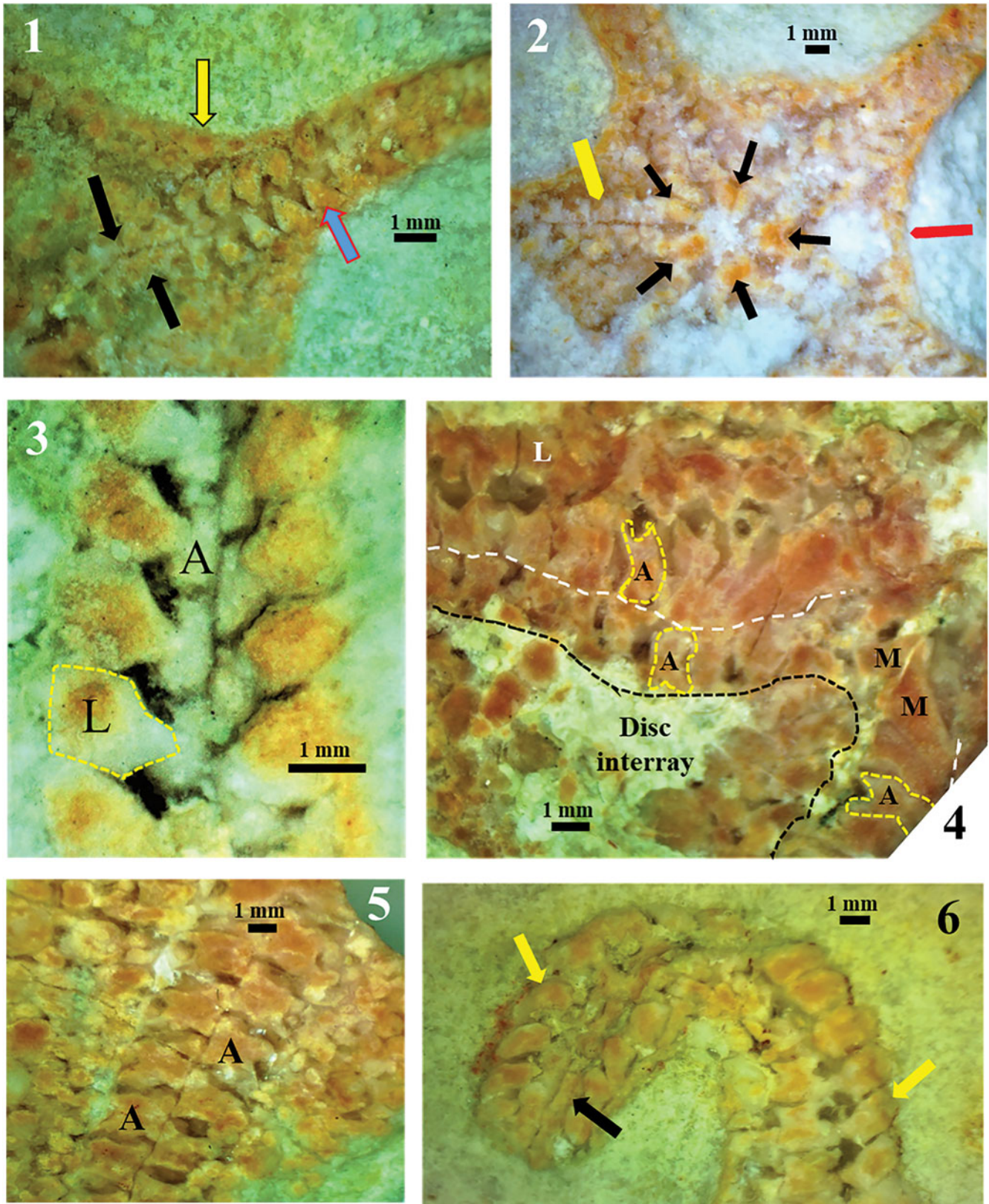


Figure 7. Magnified views of *Schoenaster carterensis* n. sp. photographed in alcohol: (1–2) holotype, UK 116000: (1) parts of arm and disk in ventral aspect showing LL (blue arrow), termination of ambital framework plate against LL (yellow arrow), and stout, L-shaped Ambb on both sides of perradial suture (black arrows); LL on lower side of arm become smaller proximally and merge with disk plates; (2) central disk in ventral aspect showing five pairs of MAPP (black arrows), L- or ‘boot-shaped’ Ambb (yellow arrow), and ambital framework plates (red); (3–6) paratypes: (3) highly magnified view (UK 116002; distal at top) of a partial arm showing alternating Ambb (A) on either side of the perradial suture and LL on either side of ambulacral groove (one labelled L and outlined with yellow dashes); L- or ‘boot-shaped’ nature of Ambb is not apparent because of articulating LL overlying Ambb; dark areas are podial gaps shared with adjacent Ambb and LL; small pustules can be present on LL; red-brown to orange areas are silicified whereas white areas are still calcite; (4) magnified view (UK 116004; proximal at right) of an interray area in dorsal aspect showing Ambb from adjacent rays meeting in interray area to form MAPP; perradial sutures from adjacent arms labelled with white dashes; a few Ambb (A) outlined with yellow dashes; note that Ambb elongate proximally and show prong-shaped extensions abradially; the most proximal ‘prong’ on the most proximal Amb elongates proximally to form a MAP (M); two MAPP from adjacent rays are shown coming together to form one of the five, two-plate parts of the mouth frame (see Figs. 7.2, 8.1, 8.3); LL (L) at the top become smaller proximally and join small, irregular disk plates in the interray; (5) Ambb (A) in dorsal aspect (UK 116003) near beginning of the disk, showing ‘hourglass-like’ or chain-link shapes with abradial ‘prongs’; (6) magnified view (UK 116003; dorsal at right, ventral at left) of a folded arm; dorsal view to the right shows a normally shaped L (yellow arrow) and adjacent Ambb with ‘prongs’; ventral view to the left shows distalmost elongate Ambb (black arrow) and rounded distal LL (yellow arrow).

Hence, arm length is used to divide specimens into four arbitrary size classes, generally assuming that the longer the arm, the older the individual (Harris et al., 2019). Specimens were separated into groups of similar arm lengths by inspection, which resulted in four groupings. The specimen arm lengths ranged from 0.05–6.05 cm, a range that was divided into four even parts of 1.5 cm each, reflecting the initial groupings. These groups were subsequently assigned to classes (1–4; Table 1). To check the validity of arm-size classes, a one-way analysis of variance (ANOVA using F-test statistic) was performed (Table 2). At the level of significance of $\alpha=0.05$, the test showed a significant difference in average arm lengths, and therefore, it was concluded that those values come from populations having at least one mean different from all others (Table 2).

Using a level of significance of $\alpha=0.05$, t-tests were then performed on the average arm lengths between successive arm-size classes, and these tests showed that each class has a statistically smaller arm length than the next following class (Tables 3, 4). Testing was not done for Class 4 because this class contained only one individual.

Disk-arm relationships.—Disk-arm relationships were subsequently determined for the 38 specimens (one specimen lacked the disk) in the studied collection. Arm length in this study was assumed to be the length of the arm beyond the disk, and using this dimension, relationships between arm length, disk perimeter, and disk area were calculated (Table 5). Disk sides were measured from the points where any two arms intersected the disk, and the values were averaged to get an average disk side for each individual. These values were then inserted into the geometric formulae for the perimeter and area of a pentagon. We initially began by attempting to correlate arm length with perimeter by arm-size classes, but a sufficient number of specimens (22) for meaningful correlation was only available for Class 1. By using the entire population of individuals, however, sufficient numbers were available to get meaningful correlations (Table 5). In comparing average arm length with disk perimeter (Fig. 10.1), the linear correlation coefficient (Pearson’s r ; Franzblau, 1958; Triola, 2018) was 0.656, indicating a marked degree of correlation between average arm length and disk perimeter. In fact, the coefficient of determination (r^2) is 0.430, meaning that ~43% of the variation in disk perimeter can be explained by the linear

relationship between average arm length and disk perimeter. Similarly, in comparing average arm length with disk area (Fig. 10.2), $r=0.649$, again indicating a marked correlation, and $r^2=0.421$, meaning that ~42% of the variation in disk area can be explained by the linear relationship between average arm length and disk area. As expected, comparison of disk perimeter with disk area (Fig. 10.3) showed an r value of 0.965, indicating a high level of correlation. Similarly, the related r^2 value of 0.931 means that 93% of the variation in disk area can be explained by the linear relationship between perimeter and disk area, as would be expected mathematically in a pentagon. Hence, the high value for r^2 indicates that one variable effectively controls the other. Glass (2006a) provided the only other morphometric data on encrinasterid ophiuroids based on large population sizes.

Preservation

Fossil ophiuroids in this study are preserved nearly intact with 64 other species (Table 6) along stylolitic bedding planes in cross-bedded skeletal calcarenites (Fig. 11.1) or on former hardground surfaces covered by calcilutites and shales (Fig. 11.2). Brachiopods, sponges, and crinoids are the most abundant associated fauna (Fig. 11; Table 6). Entire crinoid crowns, blastoid thecae, and echinoid tests occur intact, except that crinoids are typically ripped apart from their stems (Fig. 11), and delicate brachioles are absent from the blastoids. Entire size-class assemblages, from small to very large individuals (immature to sexually mature?), are present for crinoids and ophiuroids (Table 1), and on a few of the slabs, crinoids and ophiuroids lay on top of each other. Brachiopods are typically articulated but crushed; all sponges are also intact but crushed.

The modern taphonomy of ophiuroids provides mixed results about ophiuroid preservation. Meyer (1971) indicated that ophiuroids completely disaggregate in 5–6 days (e.g., Meyer, 1971), whereas Allison (1990) reported that disarticulation only began after 11–48 days, and Brett et al. (1997) suggested that disarticulation could occur in a space of one day to two weeks. In contrast, Lewis (1986, 1987), as well as Glass and Blake (2004), suggested that disarticulation rates varied among different species and for different environments. All of the above disaggregation rates are probably accurate for respective species and environments and provide generalizations that necessitate relatively rapid burial for high-quality ophiuroid preservation. Clearly, the specimens studied herein are all

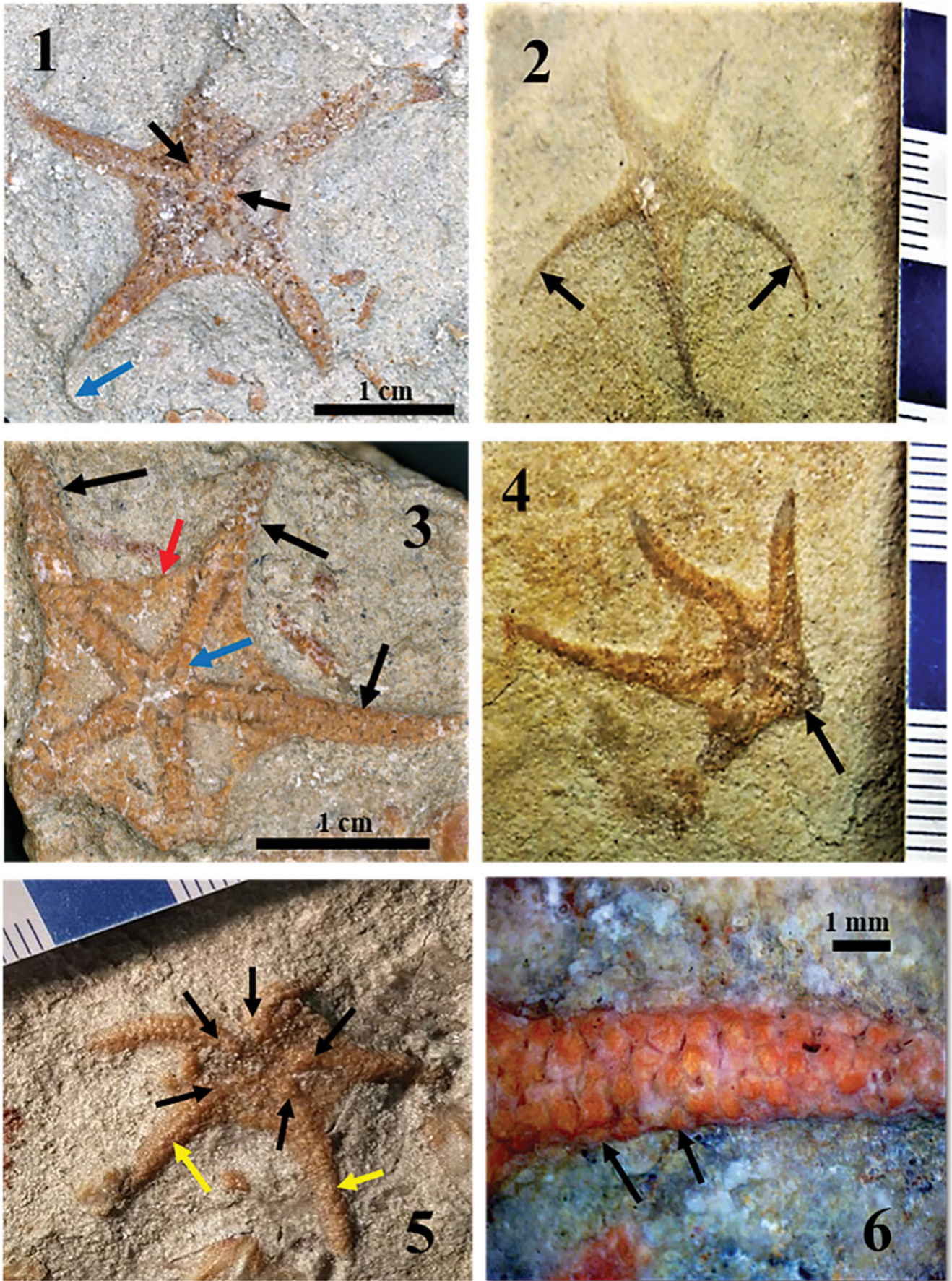


Figure 8. *Schoenaster carterensis* n. sp., paratypes: (1) ventral aspect (UK 116001) showing pentagonal disk with concave margins, tapering arms (blue arrow), and mouth-angle plates (black arrows); (2) entire ophiuroid in dorsal aspect (UK 116008) showing the tapering arms (black arrows); (3) disk with partial arms in dorsal aspect (UK 116005) showing small pustulose plates on dorsal surface of arms (black arrows), star-shaped mouth frame (blue arrow), and ambital framework plates (red arrow); (4) entire ophiuroid in dorsal aspect (UK 116009) showing arm folded under the disk (black arrow); submillimeter-sized spines can project from the sides of the arms; (5) entire ophiuroid in dorsal aspect (UK 116006) showing bosses (black arrows) and carinal ridges on arms (yellow arrows); (6) partial arm in dorsal aspect (UK 116005) photographed in alcohol showing small polygonal plates that comprise dorsal arm surface and subventral parts of a few lateral plates (black arrows). Scale (2, 4, 5) in mm and cm.

articulated, lack evidence of predation or disruption by bioturbation, and show no evidence of attempted escape. Hence, all that can be said about the specimens, as weakly articulated, Type 1 echinoderms (Brett et al., 1997), is that their detailed preservation indicates rapid burial alive or immediately postmortem. Other sedimentological indicators already mentioned also allude to rapid burial related to storms. Hence, it is suggested that the community assemblages were ripped up and transported for short distances during storms before burial by migrating sands on the shoals or by mud fallout in the deeper basinal areas. Hence, these assemblages are burial assemblages (taphocoenoses) that might not reflect original community composition. Nonetheless, study of modern transported assemblages suggests that such assemblages can still provide strong signals of original community composition and environmental dynamics (Kidwell and Flessa, 1996; Kidwell, 2001). Although it is clear that differences in the preservability of depositional settings, different organism hard-part construction, and the possibility of unpreserved benthic plants and animals might influence final assemblage composition (e.g., Arkle and Miller, 2018), species tallies (Table 6) are used to provide at least some indication of how the ophiuroids might have fit into respective community structures.

In a final stage of preservation, all fossils were partially or completely replaced with red chert (Figs. 7, 8, 11), which could reflect early diagenetic remobilization of silica from the many demosponges (e.g., Fig. 11.1) in all of the assemblages. Sources of opaline silica and organic matter on which the silica can nucleate are necessary for silicification (Müller, 1979; Butts and Briggs, 2011; Butts, 2014). The spongy, nonpervasive type of silicification (Butts and Briggs, 2011) that prevails in these echinoderms (Fig. 7.3) could reflect the limited distribution of remnant organic matter in the echinoderm stereom.

Paleoecology

Presently, ophiuroids are most common in coastal or littoral marine environments, but live at all depths on all sediment types, and as a group can be euryhaline, eurythermal, and eurybathic (e.g., Hyman, 1955; Fechter, 1972). Ophiuroids also exhibit a negative response to light and are positively stereotrophic, seeking cover under various surfaces (e.g., Hyman, 1955).

The specimens in this study are interpreted to have lived in a series of subtropical, shallow, open-marine environments (Fig. 4) that occurred at ~20°S latitude (Boucot et al., 2013) on the former Laurussian continent (Euramerica) before its collision with Gondwana in Pennsylvanian time. Lithologies, sedimentary structures, and fossils in the Ramey Creek Member suggest a network of shoals and intervening basinal areas (Ettensohn, 1975, 1977, 1980, 1981) (Fig. 4) interpreted to have ranged in depth from approximately normal wave base (10 m) on

the shoals to ~40 m in the basinal areas, based on modern analogs in the Persian Gulf (Kassler, 1973; Purser and Evans, 1973). The occurrence of ophiuroids from this study in all lithofacies suggests that they were present in all Ramey Creek environments (Fig. 4) across all depths.

Despite its presence in all Ramey Creek environments, at 0.4–7.4% of the Ramey Creek fauna, the occurrence of *Schoenaster carterensis* n. sp. was only sporadic to rare (Table 6). The greatest number of ophiuroid specimens (20 individuals @ 54%; Table 1; Fig. 5) are present in the interpreted shoal lithofacies (Fig. 4; light blue), where articulate brachiopods, eucladid crinoids, and demosponges comprised ~81% of the 39 species in the fauna (see Fig. 11.1). Total faunal density for the shoal environments was ~997 individuals/m² (Harris, 2018; Harris et al., 2018). In particular, the articulate brachiopod *Anthracospirifer leidy* (Norwood and Pratton, 1855), the demosponge *Belemnospongia fascicularis* (Ulrich, 1890), and the eucladid crinoid *Pentaramicrinus bimagniramus* Burdick and Strimple, 1973 were the most abundant individuals on the shoals (Fig. 11.1), comprising ~51% of the shoal fauna (Harris, 2018). Moreover, based on arm length, most of the ophiuroids were smaller, perhaps younger, individuals (Table 1).

Shoal-margin and basinal lithofacies (Fig. 4; yellow and purple, respectively), with totals of 29 and 49 species, respectively, produced only two ophiuroid specimens each (Table 1), comprising 5% each of the total ophiuroid count (Fig. 5) and 0.5% or less of the faunas from the two lithofacies (Table 6). In both settings, the articulate brachiopods, especially *Composita subquadrata* (Hall, 1858) and *Anthracospirifer leidy*, the demosponge *Belemnospongia fascicularis*, the eucladid crinoid *Pentaramicrinus bimagniramus* and the blastoid *Pentremites elegans* Lyon, 1860, were the most abundant associated faunal elements, comprising ~80–89% of the fauna at densities of 419 individuals/m² and 1024 individual/m², respectively.

The transitional lithofacies or depositional environment (Fig. 4; orange-brown), with 21 different species, represents a transition from shoal-margin to basinal environments. This environment, with a faunal density of 320 individuals/m², produced the second greatest number of ophiuroid specimens (14 individuals or 36%; Table 1; Fig. 5), most of which were probably younger individuals (based on arm length; Table 1). Many of the ophiuroids in this environment occurred on hardgrounds (Fig. 11.2). Ophiuroids attained the greatest percentage of the fauna in this environment (7.4%; Table 6), wherein articulate brachiopods, fenestrate bryozoans, and eucladid crinoids composed nearly 72% of the remaining individuals (Table 6). In particular, the brachiopods, *Anthracospirifer leidy* and *Composita subquadrata*, and the crinoid *Pentaramicrinus bimagniramus* were the three most abundant species, together comprising 47% of the fauna (Harris, 2018; Harris et al., 2018).

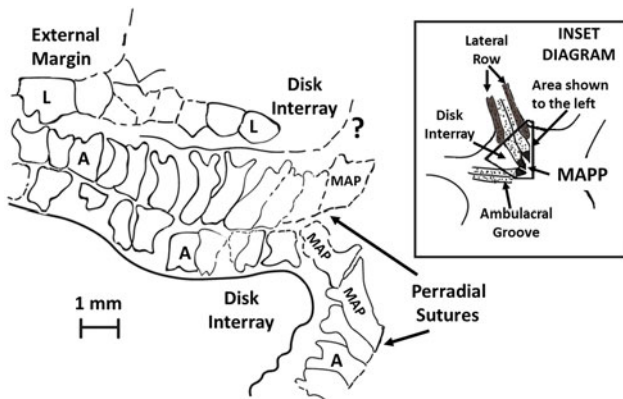


Figure 9. Sketch in dorsal view showing the organization and shape of Ambb (A) and MAPP along perradial sutures in adjacent arms (see Fig. 7.4). Inset diagram shows the approximate location of the sketch relative to the five arms of *Schoenaster carterensis* n. sp. In dorsal view, Ambb (A) bifurcate abradially into two ‘prongs.’ The arrangement of plates in the sketch and figure suggest that as MAPP are lost, the most proximal ‘prong’ on the next-most proximal Amb elongates to become a MAP. The sketch also shows how MAPP from adjacent rays form an interrayer pair of the mouth frame. At top, LL (L) are shown decreasing in size and merging with disk-interrayer plates. Sketch shows that several plates are slightly out-of-normal position. Dashed lines indicate uncertainty about plate boundaries.

Discussion

Schoenaster carterensis n. sp. is recognized based largely on the shape and size of its lateral and ambulacral plates, and its geographic occurrence is typical of most *Schoenaster* species. Based on its current distribution in the United States (Schuchert, 1915), *Schoenaster* was a tropical to subtropical species apparently restricted to south-central Laurussia. With the exception of a species from Montana, all other species come from southern parts of Laurussia where illustrated species appear to show a progressive increase in the thickness and sturdiness of their ambulacral with time. This apparent trend could culminate in the Chesterian form *S. carterensis* n. sp. and could reflect the decreasing depths and higher energies present on this part of Laurussia in later Mississippian time due to regional uplift related to the concurrence of Ouachita and Neocadian far-field forces (Ettensohn, 1993; Zeng et al., 2013).

In contrast to most other fossil ophiuroid species, sufficient specimens of the new species are available that it has been possible to divide the specimens into statistically significant classes based on arm length as well as on the relationships between arm length, disk area, and perimeter. As indicated in Table 1, across all environments, the number of specimens in Class 1, with the smallest arm lengths, is nearly 1.5 times greater than the number of specimens in all the other arm-length classes. Moreover, if specimens in Classes 1 and 2 are grouped together, their numbers are nearly nine times greater in abundance than specimens in Classes 3 and 4. Assuming that specimens with smaller arms represent younger individuals, this distribution of interpreted arm-length classes would give a right- or positive-skewed size-frequency distribution that is typical of some marine invertebrates and probably reflects the interaction of high natality and juvenile mortality rates (Fagerstrom, 1964), or simply the result of a spatfall event. The abundance of individuals with smaller arms and disks could merely reflect

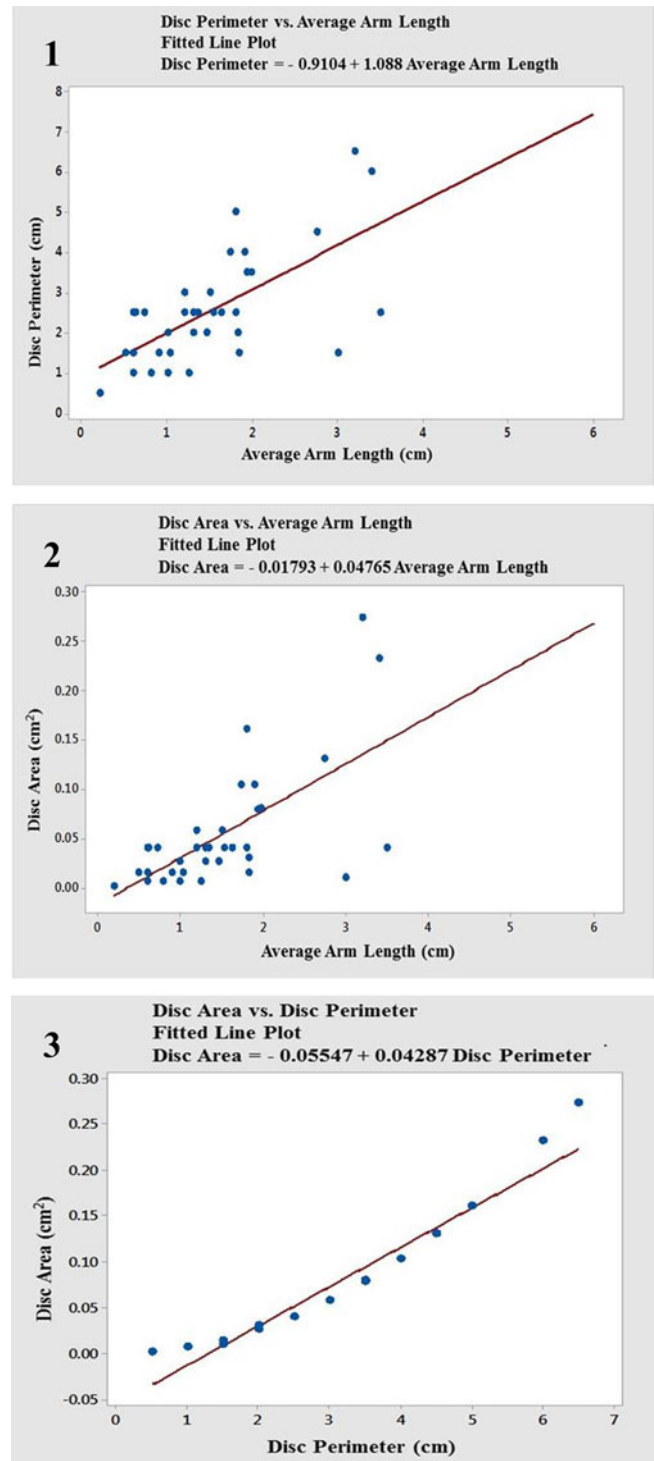


Figure 10. Graphs showing linear correlations in *Schoenaster carterensis* n. sp. between: (1) average arm length and disk area; (2) average arm length and disk perimeter; (3) disk perimeter and disk area. One specimen lacks arms and another lacks the disk; these specimens were not used for analysis.

the fact that early death is typical of most animals, and that the ophiuroids in these communities represent small but relatively normal populations.

Sufficient specimens are also available to demonstrate both dorsal (Figs. 7.4–7.6, 8.2–8.6) and ventral (Figs. 7.1–7.3, 7.6, 8.1) aspects of the species, but perhaps more importantly, to



Figure 11. Large-scale views of typical bedding surfaces from the two major ophiuroid-bearing lithofacies (see Fig. 5); all ophiuroids are *Schoenaster carterensis* n. sp.: (1) stylolitic surface of bed, which might have represented a former firm ground, from the coarse-grained calcarenite lithofacies (shoal environment; see Fig. 4), showing nature of fossil preservation; preservation of all fossils in red chert; (2) hardground surface from the fine-grained calcarenite and interbedded calcilitite lithofacies (transitional environment; see Fig. 4), showing nature of fossil preservation; most fossils preserved in red chert; holes on surface are corrosion hollows partially infilled with shale. Blue arrows = juvenile specimens of *Pentaramicrinus binagniramus* Burdick and Strimple, 1973; orange arrow = brachiopod *Anthracospirifer leidyi* (Norwood and Pratton, 1855); red arrows = ophiuroid *Schoenaster carterensis* n. sp. (specimen at upper red arrow hidden in shadows is paratype UK 116009); yellow arrows = poorly preserved and unidentified edrioasteroids encrusting surface; C = crinoid *Cymbiocrinus grandis* Kirk, 1944; CM = crinoid molds; O = ophiuroid *Schoenaster carterensis* n. sp. in dorsal aspect (paratype UK 116007); S = sponge *Belemnospongia fascicularis* (Ulrich, 1890); T = crinoid *Taxocrinus whitfieldi* (Hall, 1858).

show how the ambulacral and lateral plates change along the length of the arm.

As already noted, the 39 ophiuroid specimens were found across four lithofacies in the Ramey Creek Member (Figs. 4, 5), which have been interpreted to represent distinct depositional environments or habitat communities (Fig. 4) in the sense of Newell et al. (1959). Such communities reflect assemblages of organisms that probably had similar responses to certain physical parameters in their environments (e.g., Johnson, 1964; Patzkowsky and Holland, 2012). Although two articulate brachiopods (*Anthracospirifer leidyi* and *Composita subquadrata*), a sponge (*B. fascicularis*), and a crinoid (*Pentaramicrinus bimagniramus*) predominated in each environment (see Table 6), overall diversity in the shoal, transitional, and basinal communities was high (Simpson's Index of Diversity = 0.9; the closer the index is to 1.0, the higher the diversity; Simpson, 1949). In the shoal-margin community, however, diversity was only somewhat high at 0.7 (Harris, 2018; Harris et al., 2018). Despite the relatively high diversities of Ramey Creek communities, the ophiuroid *Schoenaster carterensis* n. sp. was apparently not a common member of the communities (see Table 6), although its relative abundance might merely reflect taphonomic factors unique to the different Ramey Creek environments.

The Ramey Creek environments with the highest numbers of ophiuroids were the shoal and transitional environments (Figs. 4, 5) with 21 and 14 individuals, respectively, and the ophiuroids' increased numbers there might reflect the fact that in both environments, the substrata were firm to hard. The shoal environments apparently developed in high-energy conditions near or within normal wave base (Fig. 4) that facilitated carbonate lithification (Fursich, 1979). The presence of sessile suspension feeders and absence of burrowing or bore holes on these surfaces (Fig. 11.1) suggests that substrata were firm but were never exposed long enough to become full hardgrounds. During storms, organisms such as brachiopods, sponges, crinoids, and ophiuroids that lived on the shoals (Fig. 11.1) were ripped up, transported short distances, and then buried rapidly below migrating sand dunes. The shoal-margin environments exhibited lower diversity and very few ophiuroids; these environments were probably not very stable, because even normal wave processes would have continually sent fans of sand and skeletal debris down the gentle slopes. The transitional and basinal environments both exhibit high diversity and, although still within the storm wave base, were far enough removed from the shoals that these environments were not continually inundated by lobes of moving sand. Removed from most inundating sands, most transitional surfaces exhibit fixosessile suspension feeders such as edrioasteroids (Fig. 11.2) and corrosion pits, indicating that the surfaces were exposed long enough to become fully cemented, colonized, and eroded (Fursich, 1979), but trace fossils on these surfaces are absent. The stable hard surfaces, perhaps coated with various algae and organic debris, apparently attracted ophiuroids. In contrast, the more distal basinal environments apparently collected carbonate and argillaceous muds, which at the time were not compacted sufficiently to form firm grounds or hardgrounds (see Fursich, 1979). Many of the fossils found here, however, are very well preserved, having been completely engulfed in mud, suggesting that at times, mud fallout was intense. The rarity of ophiuroids

in this environment (Fig. 5; Table 6) could reflect these soft bottoms or the fact that the bottoms did not support their feeding strategy, although soft bottoms in other Paleozoic settings do not seem to have precluded ophiuroids (e.g., Glass and Blake, 2002, 2004; Glass, 2006a, b, c). More likely, however, the rarity of ophiuroids in the basinal setting might reflect taphonomic factors. Being Type 1 echinoderms (Brett et al., 1997), preservation of these ophiuroids would have required rapid burial by thick storm deposits, and the rarity of ophiuroids there might merely reflect the rarity of storm-generated deposits in such settings. Hence, it was only during the largest of storm events that the basinal muds were stirred sufficiently to bury and preserve the ophiuroids intact. Otherwise, the ophiuroids disarticulated rapidly and entered the fossil record piecemeal.

These ophiuroids were apparently parts of tiered feeding communities (sensu Bottjer and Ausich, 1986), in which brachiopods, sponges, and ophiuroids occupied the surface tier, bryozoans and a few blastoids occupied a midlevel tier, and crinoids occupied the highest tier (Fig. 4). With the exception of the ophiuroids, nearly all of the other organisms were suspension feeders, but ophiuroid occurrences like this are typical (e.g., Twitchett et al., 2005). Unlike modern ophiuroids with relatively small disks and long, slender, lightly constructed, serpentine arms capable of moving in all directions, *Schoenaster carterensis* n. sp. had a relatively large disk and ventrally flat, triangular, sturdily constructed arms with many small polygonal plates (Fig. 8) that would have limited their motion. These were asteroid-like arms that could move in a vertical plane (Figs. 7.6, 8.4), but probably lacked much lateral movement and certainly could not coil. Dean (1999) and Blake et al. (2015) suggested that arms like this indicate feeding generalists that probably concentrated on surficial detritus feeding and chance carnivory. Such arms were also probably not conducive to suspension feeding or to burrowing (Dean, 1999). Fechter (1972) indicated that modern ophiuroids are commonly associated with sponges, and the abundant, small, spherical demosponges (< 2 cm in diameter) in some Ramey Creek environments (Table 6) might have provided feeding opportunities. In fact, sponge spicules from the same Mississippian species (*Belemnospongia fascicularis*) have been found in the stomach area of the asteroid *Emphereaster missouriensis* Blake and Elliott, 2003, suggesting that sponges might have been common food sources for asteroids and ophiuroids (Elliott, 2008). Hence, the joint occurrence of sponges and ophiuroids in the various Ramey Creek environments (Figs. 4, 11.1) might have been more than coincidental. Overall, however, *Schoenaster carterensis* n. sp. seems to have been the most important detritus feeder in the Ramey Creek environments, although in the transitional and basinal environments (Fig. 4), the similarly feeding echinoid, *Archaeocidaris megastylus* (Shumard, 1858), was also present.

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