

**Late Paleozoic ophiuroid biodiversity based on a diverse fauna from the
Indian Springs Shale Member of the Big Clifty Formation, Sulphur,
Indiana, USA**

**A Thesis Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville**

Nicholas Scott Smith

December 2020

Copyright © 2020 by Nicholas Scott Smith
All rights reserved.

ACKNOWLEDGEMENTS

I would like to thank the following people and societies for their help and guidance with this project. Without them, this would not be possible.

First, I would like to thank my advisor, Colin D. Sumrall, for giving me the opportunity to work on such a fascinating and challenging project, pushing me to my limits, and providing me with the support and confidence I needed to complete this project. I am truly thankful for the foundation we have laid to continue this project for years to come.

I would like to graciously thank the additional members of committee: Stephanie Drumheller, Ben Thuy, and Benjamin Auerbach. Thank you for your feedback and guidance during this process.

I would like to thank the many wonderful people that helped me along the way in different capacities. My lab mates for their continued support and, of course, my two wonderful office mates and close friends, Maggie Limbeck and Kristan Watkins. Thank you for always providing me with a shoulder to cry on, listening to my daily rants, and always giving me that extra piece of advice I needed to keep going. Additionally, many thanks to Maggie for your late night Zoom and FaceTime sessions to help me with edits and composing important emails.

I would like to thank my two undergraduate rock stars Colby Sain and Julie Coulombe. Thank you for your hard work and persistence through this project. You both helped this project make leaps and bounds with the many hours you put in picking and

organizing skeletal elements. Additionally, your awesome presentations at national conferences truly put a spotlight on this project. You both rock!

I would like to thank the department for their support during my project and with the continued support through these trying times. Thank you to the wonderful office staff, Angie, Melody, Teresa, and Diane, for the many fires you have helped me extinguish and always there to answer my endless questions.

This project was funded by several small research grants: Richard K. Bambach Paleontological Society Student Research Grant, Southeastern Geological Society of America Student Research Grant, Cincinnati Dry Dredgers Paleontological Research Award, University of Tennessee Graduate Student Senate Professional Development Award, and University of Tennessee Center for Global Engagement Global Catalyst International Travel Grant. Additionally, my work on this thesis was funded by an EPS Departmental GTA.

ABSTRACT

Ophiuroids (brittle stars and basket stars) are a diverse echinoderm group (i.e. star fish, sea urchins, and sea lilies) found in almost all marine environments and often major components of seafloor communities. Originating in the early to middle Devonian, the group quickly diversified and is today the most species rich echinoderm clade.

Unfortunately, our knowledge of their diversity and evolutionary pathways during the Late Paleozoic has been understudied leaving a large gap in our understanding of their true biodiversity. This can be attributed to study methods and a poor understanding of Paleozoic ophiuroid skeletal morphology. Ophiuroid skeletons are composed of thousands of individual calcite ossicles which easily disarticulate shortly after death, but individual ossicles can be found in high numbers in washed sediment. Taxonomic studies of Paleozoic ophiuroids have historically been focused on morphologies of the central-disk, with sparse attention being paid to the intricate morphology of the skeletal elements of the arm. Recent studies of Mesozoic and Cenozoic ophiuroids, however, have focused on the morphologies of skeletal elements of the arm called lateral arm plates which bear spine articulations. These plates are morphologically distinctive, numerous, and have proven to be diagnostic for taxonomic assignment. Here, we use similar methods established with studies on Mesozoic and Cenozoic ophiuroids to describe a Late Mississippian ophiuroid fauna from the Indian Springs Shale Member of the Big Clifty Formation in Sulphur, Indiana utilizing lateral arm plates collected from washed sediment. The goal of this study is to establish a framework for describing Paleozoic ophiuroids to fill in the gap of our knowledge of Late Paleozoic ophiuroid biodiversity.

We find that this single locality has higher taxonomic diversity than previously described for Mississippian global diversity and has higher diversity than the most diverse locality known during this time period utilizing wholly articulated ophiuroid skeletons. In all, eleven taxa are described, with five new species and one new genus described, and four taxa with unknown affinities. Utilizing these methods, we can continue to investigate Late Paleozoic localities to get a better understanding of true Late Paleozoic ophiuroid biodiversity.

TABLE OF CONTENTS

INTRODUCTION	1
Part I: Paleozoic ophiuroids	3
Ophiuroid morphology.....	3
Ophiuroid origins and relationships.....	4
Part II: Taphonomy of ophiuroids.....	5
CHAPTER I A diverse brittle star (OPHIUROIDEA: ECHINODERMATA) fauna from the Indian Springs Shale Member of the Big Clifty Formation, Sulphur, Indiana, USA, and its implications for Late Paleozoic brittle star biodiversity	7
Abstract	8
Introduction.....	9
Defining species based solely on LAP morphologies.....	12
Locality and Geologic Setting	13
Materials and methods	14
Repositories and institutional abbreviations	15
Discussion and implications	15
Systematic paleontology	17
Acknowledgements.....	51
References.....	52
Appendix.....	61
CONCLUSION.....	69
VITA	70

LIST OF FIGURES

Figure 1. Ophiuroid body and arm morphology	62
Figure 2. Images of the biostratigraphic ranges of Late Paleozoic and Early Mesozoic ophiuroids	63
Figure 3. Lateral arm plates of ophiuroids SULOPH001 – SULOPH003 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN	64
Figure 4. Lateral arm plates of ophiuroids SULOPH005 – SULOPH009 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN	65
Figure 5. Lateral arm plates of ophiuroids SULOPH010 – SULOPH012 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN	66
Figure 6. Lateral arm plates of ophiuroids SULOPH013 – SULOPH017 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN	67
Figure 7. Lateral arm plates of ophiuroids SULOPH018 – SULOPH021 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN	68

INTRODUCTION

The echinoderm clade Ophiuroidea (brittle stars, snake stars, and basket stars, Fig. 1.A. – 1.B.)¹ has a long and rich fossil history, but it still remains largely understudied, especially during the Late Paleozoic. This can be attributed to a lack of investigation, small specimen size, and poor understanding of the group's microscale morphology, as well as the use of different study methods in Paleozoic and post-Paleozoic taxa. Because of this, the study of Paleozoic brittle stars has been lacking as researchers have often focused on rare, wholly articulated skeletons.

Brittle stars, like all echinoderms, have skeletons composed of thousands of calcite ossicles that completely disarticulate shortly after death (Brett et al., 1997; Kerr and Twitchett, 2003). Studies of Mesozoic and Cenozoic brittle star taxonomy rely heavily on documenting morphologically rich skeletal elements called lateral arm plates (LAPs) that extend along the sides of the arms and bear spine articulations (Fig. 1.C. and 1.D.). While those study methods have shown promise toward brittle star taxonomic studies, similar methods have not been utilized with Paleozoic brittle star skeletal elements where taxonomy has dominantly relied on morphologies of the central disk (Fig. 1.A. – 1.B.).

By utilizing established methods that focus on the microscale anatomy of LAPs, attempts can be made to improve our understanding of Late Paleozoic brittle star biodiversity. Here, these methods are used to examine a brittle star fauna collected from washed and sieved sediment from a late Mississippian locality in Sulphur, Indiana, USA,

¹ All images can be found in the Appendix.

and explore the implications it has for Late Paleozoic brittle star biodiversity. This study documents a previously unknown high-level diversity both at the species and higher clade level, including numerous range extensions and describing one new genus and five new species.

Part I: Paleozoic ophiuroids

Ophiuroid morphology

Studies of Mesozoic and Cenozoic ophiuroids have relied heavily on data from disarticulated arm ossicles as they are morphologically distinctive, common in the fossil record, and have phylogenetically important features (Martynov, 2010a; Martynov, 2010b; Thuy and Stöhr, 2011; Stöhr et al., 2012; O’Hara et al., 2014). Ophiuroid arms are constructed of repeated segments of five, distinctive, interlocking plates (Fig. 1.C.) that allow for increased flexibility and movement. The main core of the arm (the vertebral ossicle or vertebra) is constructed from a pair of fused ambulacral plates in modern genera, and either fused or unfused ambulacral plates arranged as paired biserial or alternate biserial patterns in more archetypical genera (Spencer and Wright, 1966; Stöhr et al., 2012). Each arm segment has an associated, but undiagnostic dorsal and ventral arm plate that close off the ambulacral system and coelomic cavity. Connected to the sides of each segment are morphologically distinct ossicles called lateral arm plates (LAPs) that bear articulation points for spines along the distal margin (Fig. 1.C.), and indentations for the podial canal and ampilae basins on the interior surface (Spencer and Wright, 1966). Spine morphology among ophiuroids is variable in both size and angle of

protrusion (i.e. lay flat against the arm or protrude out away from the arm), and in some cases can be absent entirely (i.e. encrinasterids).

General ophiuroid body morphology consists of a central disk that holds the visceral mass that is clearly demarcated from the five arms that meet with the disk on its lateral sides (Fig. 1.A. – 1.B.). The central disk is composed of many non-descript plates on its dorsal side with the mouth located on the ventral side. Morphology of the plates constructing the oral surface can be quite distinctive and data-rich (Stöhr et al., 2012) but, these plates are far less numerous, and, consequently, difficult to find compared to the many arm ossicles that are present, and difficult to associate with the LAPs in mixed faunas.

Lateral arm plate morphology (Fig. 1.C. – 1.D.) is complex and can differ greatly across taxa. Generally, there is a main plate body, a vertebral articulation structure, and spine articulations. Each of these structures can have additional complexity and differing morphologies both as independent structures as well as how these structures are incorporated into the gross arm morphology. ‘Archaic’ taxa often have groove spines that line the ventral margins of the lateral arm plates (Fig. 1.D.). These groove spines protect the podia and are lost in modern-type taxa with the transition to lateral arm plates that completely enclose the vertebrae and podia.

Ophiuroid origins and relationships

Asterozoan origination is heavily debated amongst researchers with two main hypotheses: a crinoid ancestry based on presumed homologies or arm arrangement, and an edrioasteroid ancestry that has been less favored because of ambulacral construction

(Spencer, 1951; Shackleton, 2005; Blake, 2013; Jell, 2014; Blake and Guensberg, 2015).

Current molecular phylogenies place Asterozoa (the larger group containing both Asterozoa and Ophiurozoa) closer to echinoids and holothuroids than crinoids (Christensen et al., 2015). Ophiurozoa is believed to have diverged from the Somasteroidea during the Early Ordovician with the appearance of the stenuroids (Stenurida). Somasteroids are recognized by the presence of a series of rod-like ossicles that extend laterally from each ambulacral ossicle (called virgals). Stenurida show a similar metapinnular structure (laterals that show strong transverse alignment with the ambulacrals) to Somasteroidea, but are morphologically distinct in comparison (Spencer and Wright, 1966; Blake, 2013).

Stenurida possess the typical arm structure of ophiuroids, however, common fusion of the ambulacrals into vertebrae occurs with the appearance of Oegophiurida during the Middle to Late Ordovician. All other Paleozoic ophiuroids fall into separate clades, Phrynophiurida and Ophiurida, both with fully developed vertebrae. These clades appeared by the Devonian and have persisted to the Recent. It is presumed they diverged from Oegophiurida, however, their detailed evolutionary history is not well constrained (Spencer and Wright, 1966), and is further confounded by the large gap in the biostratigraphic record of ophiuroids during the Late Paleozoic.

Part II: Taphonomy of ophiuroids

The Ophiuroid body is composed of a large central disk and thin, fragile arms (Fig. 1.A. – 1.B.). Their skeletons are composed of thousands of weakly sutured mesodermal calcite ossicles bound together by the organism's soft tissues. Because of

this, previous work on echinoderm taphonomy has categorized ophiuroids with other weakly articulated forms such as asteroids and edrioasteroids (Brett et al., 1997; Kerr and Twitchett, 2003). In most cases, complete disarticulation of ophiuroids occurs within one to two weeks after death, therefore, discovering completely articulated skeletons is rare. Without rapid burial, the skeleton disarticulates into isolated ossicles that become a component of bioclastic sediment in the area.

Recognizing the distinctiveness of disarticulated ossicles, more recent studies of Mesozoic and Cenozoic ophiuroids focus on arm ossicles (primarily the lateral arm plates), providing a more comprehensive taxonomic and ecologic understanding than could be achieved using only articulated material (i.e. Thuy and Stöhr, 2011; Stöhr et al., 2012; O'Hara et al., 2014; Thuy, 2015; Thuy and Stöhr, 2016; Stöhr et al., 2016; O'Hara et al., 2017; Thuy et al., 2017; Thuy and Stöhr, 2018). These studies have identified numerous morphologic features of lateral arm plates (Thuy and Stöhr, 2011; Stöhr et al., 2012; O'Hara et al., 2014) that aid in identification of taxa and phylogenetic inference. Translating this methodology to Paleozoic taxa has been problematic as most ophiuroid higher level diversity goes extinct by the end of the Permian (Thuy et al., 2017; Hunter and McNamara, 2018) and there is no prior detailed morphological framework for understanding these elements in strictly Paleozoic clades.

CHAPTER I

A DIVERSE BRITTLE STAR (OPHIUROIDEA:

ECHINODERMATA) FAUNA FROM THE INDIAN SPRINGS

SHALE MEMBER OF THE BIG CLIFTY FORMATION, SULPHUR,

INDIANA, USA, AND ITS IMPLICATIONS FOR LATE PALEOZOIC

BRITTLE STAR BIODIVERSITY

A version of this chapter will be published by Nicholas S. Smith, Colin D. Sumrall, and Ben Thuy:

Smith, Nicholas S., Thuy, Ben., and Sumrall, Colin D. (in prep). A diverse brittle star (Ophiuroidea: Echinodermata) fauna from the Indian Springs Shale Member of the Big Clifty Formation, Sulphur, Indiana, USA, and its implications for Late Paleozoic brittle star biodiversity. *Journal of Paleontology*.

My major contributions to this paper include: (1) evaluating and describing lateral arm plate morphologies; (2) writing the manuscript; (3) creating figures and photographs; (4) interpreting data; (5) making submissions and revisions. Colin D. Sumrall and Ben Thuy, both co-authors, assisted with the manuscript interpretations, descriptions, figures, and editing. Submission will be made once both co-authors make final agreements on descriptions and interpretations of the data.

Abstract

Ophiuroids (brittle stars) are some of the most diverse echinoderms with a rich evolutionary history. Today they can be found in almost all marine environments and in the past were often major components of marine seafloor communities. Unfortunately, shortly after they die, they break apart into thousands of individual skeletal elements making the discovery of whole, articulated skeletons rare. Past paleontological studies, especially those in the Paleozoic, have based taxonomic descriptions on whole skeleton morphology while overlooking disarticulated material, causing a large gap in our knowledge of Paleozoic ophiuroids. Recent studies of Mesozoic and Cenozoic ophiuroids, however, have examined the fine morphological details of ophiuroid arm plates and have documented them to show useful characters for taxonomic assignment. Here, we use similar methods for examining disarticulated ophiuroids to describe a Late Mississippian (Serpukhovian) ophiuroid fauna based solely on microfossils sieved from sediment collected in Sulphur, Indiana, USA. We find that the ophiuroid fauna has a greater diversity than that presently known globally for this time, and more diverse than the highest known faunal diversity from the Mississippian. There are eleven total taxa

with one new genus and five new species. This finding extends the known stratigraphic ranges of three clades into the Late Mississippian. We conclude that it is necessary to take into account the microfossil record of ophiuroids as it gives us a better understanding of the true diversity of evolutionarily important organisms.

Introduction

Ophiuroids, commonly referred to as brittle stars (Fig. 1.A.), are a significant component of the modern (and ancient) seafloor communities. They are extremely diverse and occupy most marine ecosystems from the tropics to the poles and the tidal zones to the deep trenches (Stöhr, 2012; Stöhr et al., 2012). With approximately 2,100 species (O'Hara et al., 2016), they are the most species rich class of echinoderms and at times are among the most numerous faunal elements within marine ecosystems (Gage and Tyler, 1991; Aronson et al., 2007). However, despite their evolutionary and ecological importance, their evolutionary history and diversity patterns have remained largely understudied (Stöhr 2012; O'Hara et al., 2016; Thuy and Stöhr, 2016).

The Late Paleozoic (Mississippian – end Permian) fossil record of ophiuroids is poorly documented globally (Fig. 2.B.). Previous published reports of late Mississippian ophiuroids include some nine genera across multiple basins, but several localities in the North American mid-continent alone have as many as ten to eleven making them among the most diverse in the Paleozoic (Chen and McNamara, 2005). At these localities specimens can be abundant but typically overlooked. The poor documentation of this diversity results from three factors 1) study methods, 2) small specimen size, and 3) poor understanding of arm plate morphologies among Paleozoic taxa.

Unlike Paleozoic ophiuroid taxonomy, which relies heavily on the morphology of fully articulated central-disks (a rarity in echinoderm preservation), recent Mesozoic and Cenozoic work is based on arm plate morphologies of disarticulated material. As a result, Paleozoic ophiuroid diversity has been poorly documented globally except for a few notable Lagerstätten (Jell, 1997; Glass, 2006) and, as such, our current understanding of diversity patterns has remained nearly unchanged for the past 30 years (Sprinkle, 1980; Hunter and McNamara, 2018).

The vast majority of late Mississippian taxa are very small making the discovery of articulated specimens rare. Whole ophiuroid skeletons during this time period are often 2 – 3 cm in diameter and individual skeletal pieces range from 125 – 250 microns in length and width. This, coupled with the inherent taphonomic fragility of these taxa (Brett et al., 1997; Kerr and Twitchett, 2003), makes their preservation and discovery unlikely except in the most ideal conditions. Even under ideal conditions, whole specimens of these taxa may be overlooked because of their small size.

Recognition of elements is further complicated by a lack of precise and detailed analysis of these elements in previous studies. Because studies of Paleozoic ophiuroid taxonomy has not focused on the fine details of the arm morphologies, these features are largely understudied (Thuy and Stöhr, 2016). Thuy and Stöhr (2011) detailed the morphologies of the ophiuroid lateral arm plates and how they can be used for the assignment of genera and species, however, this study focused solely on Mesozoic and Cenozoic taxa. Most ophiuroid high-level diversity went extinct by the Permian-Triassic boundary (Thuy et al., 2017; Hunter and McNamara, 2018); and, as a result, there was no

morphological framework for understanding these elements in strictly Paleozoic clades prior to this study.

New data from the Upper Mississippian (Chesterian) Indian Springs Shale Member of the Big Clifty Formation of Crawford Co., Indiana, USA, documents a rich and diverse fauna of fossil brittle stars collected as isolated ossicles in washed sediment residues. However, articulated ophiuroid skeletons have yet to be collected from this locality. Analysis of the collected ossicles show surprisingly high taxonomic diversity, higher than known global ophiuroid diversity from the Mississippian (Spencer and Wright, 1966; Sprinkle, 1980; Hunter and McNamara, 2018), indicating a large sampling bias. Within these isolated ossicles, ophiuroid arm plates, specifically the vertebrae (ossicles that core the arm) and especially lateral arm plates (plates that hold spine articulations and protect the core of the arm) have enough morphological features to determine specific and generic assignments.

Herein, we describe the ophiuroid faunal composition of the Indian Springs Shale Member, which is represented by eleven different taxa, five of them newly described. These taxa include two furcasterids *Furcaster wardi* sp.nov., and *Furcaster crispisulcans* sp.nov., two modern-type taxa *Aganaster monoceros* sp. nov., and *Sulphaster solus* gen. and sp. nov., one protasterid (possibly *Strataster*), one cheiroptasterid (possibly *Vandelloaster*), a stenuroid (*Umerophiura daki* sp. nov.), and four taxa with unknown affinities. This taxonomic richness is higher than previously described global diversity for the Mississippian (Spencer and Wright, 1966; Sprinkle, 1980, Chen and McNamara, 2005; Hunter and McNamara, 2018), and higher than the most diverse known locality for

the entire Mississippian (Crawfordsville, IN, Jell, 1997). These results extend the stratigraphic ranges of several ophiuroid taxa to the end of the Mississippian (furcasterids, cheiropterasterids, and stenuroids; Fig. 2.B.), some known for the first time in post-Devonian rocks. Furthermore, the presence of two modern-type ophiuroids, both newly described, shows that the complex early history of today's modern clade started much earlier than previously thought and is still poorly understood.

Defining species based solely on LAP morphologies

Biodiversity studies rely heavily on detailed morphological descriptions and taxonomic assignments of organisms. In most cases, study organisms are fully articulated and can be studied with ease. Challenges occur when morphological descriptions and taxonomic assignments are based on disarticulated skeletal elements, as in ophiuroids, where a clear understanding of species definitions is absent. Taxonomic studies of ophiuroids based solely on disarticulated skeletal elements was first proposed by Hess (1962) and subsequent studies began to highlight the complications of using lateral arm plates as a means for taxonomic assignment. First, ophiuroid arms grow from their distal end toward the central disk, with distal most plates being less developed, longer, and having variability in within plate morphologies (Stöhr, 2005). Second, ontogenetic variation among individuals of a species can cause issues when assigning taxonomic descriptions. As aforementioned, juvenile ophiuroids will have less arm segments with differing morphologies seen in adults. Third, some ophiuroids have differing lateral arm plate morphologies based on which side of the arm is being examined. For example, the modern ophiuroid *Ophiotrix* sp. has lateral arm plates that alternate from dorsal to ventral

projection of the spine articulations down the arm. Nevertheless, taxonomic studies based solely on disarticulated lateral arm plates have shown promising results (i.e. Jagt, 2000; Boczarowski, 2001; Štorc and Žižt, 2008; Thuy and Stöhr, 2011).

Thuy and Stöhr (2011) introduced the first systematic study on the morphological diversity of disarticulated lateral arm plates and their significance in the use of taxonomic assignment. This study addressed arm plate morphology changes by examining variation according to position along the arm, as well as changes resulting from ontogeny, size-independent intraspecific variability, and intraspecific variability with regards to geographic separation. They found that ophiuroid adult proximal-most lateral arm plates show the most variability and morphologically distinct features. Based on the results of this study, it is suggested that taxonomic descriptions and assignments be based solely on one proximal-most adult lateral arm plate which is to be designated as the species holotype. Representatives from the median and distal parts of the arms should be described as paratypes as to include variation along the arm. Furthermore, a suite of lateral arm plates specific to that species should be acquired as to ensure the most adult, proximal lateral arm plate has been chosen for taxonomic description and assignment.

Locality and Geologic Setting

Samples used in this study were collected from a several meters thick, light-gray, fossiliferous shale that is interbedded with hard limestone layers, referred to as the Indian Springs Shale Member of the Big Clifty Formation (Horowitz et al., 1979; Kelly, 1984; Nelson et al., 2002). Indian Springs Member specifically includes a lower mudstone layer and an upper marine shale and limestone layer (Shaver et al., 1986; Horowitz and Kelly,

1987) and contacts the overlying Haney Limestone by a locally minor disconformity (Nelson et al., 2002). The shale was collected from exposures in southeastern Indiana at the intersection of Interstate 64 and Main Street in Crawford County, Sulphur, Indiana (38°14'33" N; 86°28'09" W).

The locality is Upper Mississippian (Chesterian) and represents a tidally influenced, shallow water ramp with clastic sediment influx from deltas to the east-northeast (Klein, 1977; Nelson et al., 2002). The shale is fossil rich and includes brachiopods, echinoderms, bryozoans, and fish teeth (Smith and Sumrall, 2019). Echinoderms (mostly identified from disarticulated ossicles) are diverse and abundant, including crinoids (in particular *Pterotocrinus*), blastoids (*Pentremites*), edrioasteroids, echinoids, ophiuroids, and holothuroids (Shaver et al., 1986; Jell, 1997; Nelson et al., 2002; Smith and Sumrall, 2019).

Materials and methods

The ophiuroid material described in this paper was hand-picked from washed, sieved residues of bulk sediment samples. Micropaleontological samples were processed by immersing shale residues overnight in a 3 percent hydrogen peroxide and water bath to disaggregate the shale and separate individual skeletal elements. Sediment was washed to remove the clay fraction and the process was repeated until the sediment residue consisted of only bioclasts. The cleaned sediment was sieved down to 125µm and hand-picked using a dissection microscope and a wet paintbrush. Sieved ossicles were cleaned using a needle under high magnification, as needed, and a sonic water bath. Cleaned

ossicles were mounted on aluminum stubs and coated with silver for scanning electron microscopy.

Lateral arm plates were compared to publications for the purpose of identification. Material here is described following the terminology and procedures of Thuy and Stöhr (2011) and, when possible, identifications were made to species level. In most cases, vertebrae were collected with LAPs, but not described herein.

Repositories and institutional abbreviations

Lateral arm plates were assigned specimen numbers SULOPH001 – SULOPH021. The specimens will be repositied in the, MMNH, McClung Museum of Natural History and Culture, Knoxville, Tennessee, USA.

Discussion and implications

In total, seven brittle star species have been described solely based on the morphologies of lateral arm plates, with four additional brittle star types remaining poorly documented. These taxa included two previously unknown furcasterid species (*Furcaster wardi* and *Furcaster crispisulcans*), one undetermined protasterid species (possibly *Strataster*), one undetermined cheiropterasterid species (possibly *Vandellooaster*), a previously unknown aganasterid species (*Aganaster monoceros* sp. nov.), one previously unknown modern-type genus and species (*Sulphaster* gen. nov., *Sulphaster solus* sp. nov.), one previously unknown stenuroid species (*Umerophiura daki* sp. nov.), and four undetermined species. This expanded the biostratigraphic record of furcasterids, cheiropterasterids, and stenuroids into the Late Mississippian, as well as increased the known global taxa in the Late Mississippian from three to ten taxa (Fig.

2.B.). Furthermore, ossicles in the sediment were mainly of furcasterids, suggesting them to be the dominant brittle star taxa in this environment. It must be noted that while there were four undetermined species, they are morphologically distinctive enough to be considered separate taxa and until more specimens are available for analysis, will remain in open nomenclature.

Originally thought to have gone extinct at the end of the Devonian (Blake, 2013; Blake and Guensburg, 2015), the presence of an ‘archaic’ stenuroid species in the fauna shows that this early brittle star lineage survived much longer than previously thought and extending their stratigraphic range to the end of the Mississippian. Additionally, while the presence of an aganasterid (*A. monoceros* sp. nov.) is not new for this time period, the addition of this species in tandem with another previously unknown modern-type taxon suggests that the early evolution of the modern ophiuroid clades is much more dynamic and happened much earlier than previously hypothesized (Hunter and McNamara, 2018).

The Late Paleozoic has long been considered to be a crucial time in the evolution of Ophiuroidea with the origin of extant clades and demise of the ancestral clades (Thuy et al., 2017; Hunter and McNamara, 2018). However, the known ophiuroid fossil record is sparse and largely incomplete from the Mississippian to the Triassic (Sprinkle, 1980; Thuy et al., 2017; Hunter and McNamara, 2018), causing difficulties with timing constraints, modalities, and dynamics of these evolutionary changes. Therefore, a detailed analysis of the intricate morphologies of Late Paleozoic ophiuroids is imperative for the

understanding of the dynamics of this clade during such an evolutionarily complex and important time in the clade's history.

The large knowledge gap of Late Paleozoic brittle stars can be remedied by studying the fine details of brittle star arm plates collected at important time intervals in Earth's history during the Late Paleozoic. Utilizing similar methodology to expand our knowledge of previously described fully articulated skeletons where these details were lacking from previous studies will greatly aid in the description and reconciliation of brittle star arm plates discovered in future studies. While the Late Paleozoic has considerable amount of work left to be done to better our understanding of brittle star biodiversity, we suggest that it will also be worthwhile to expand these methods into earlier time periods. It is evident that to get a complete picture of brittle star paleobiodiversity, particular attention must be paid to the dissociated skeletal elements throughout the brittle star record.

Systematic paleontology

Phylum **Echinodermata** Klein, 1734

Subphylum **Asterozoa** Zittel, 1895

Class **Ophiuroidea** Gray, 1840

Order: **Oegophiurida** Matsumoto, 1915

Suborder: **Lysophiurina** Gregory, 1896

Family: **Protasteridae** Miller, 1889

Genus ident.

Protasterid species A

Figure 3.1 – 3.5

Figured specimen 1: Specimen SULOPH001 (Fig. 3.1 – 3.2) is a proximal right lateral arm plate.

Diagnosis. — Bulky trapezoidal-shaped lateral arm plate with three spine articulations close to the distal edge, projecting laterally from the outer surface. Exterior surface covered in fine to coarse tuberculation. Inner surface with belt buckle-shaped vertebral articulation.

Description. — Description based on proximal lateral arm plate (Fig. 3.1 – 3.3), lateral arm plate slightly longer than high with rounded trapezoidal outline, highest distally, tapering towards the proximal edge; dorsal edge straight; ventral edge oblique and convex, devoid of incisions or protuberances; distal edge weakly convex; proximal edge convex; view down the proximal-distal axis shows domed shape, flat on the inner side of the proximal axis, convex on the inner side of the distal axis, and convex on the outer surface, gives the appearance of a cupped glove; view down dorso-ventral axis shows elongate surface, rounded on the edge and increasing in height toward the midline of the plate; outer surface (Fig. 3.1) with a two-fold ornamentation, consisting of a fine tuberculation covering the entire surface and a much coarser tuberculation composed of large, irregular, smooth knobs covering the center of the outer surface in a vertical band between the proximal edge of the plate and the row of spine articulations; proximal edge of lateral arm plate covered by fine tuberculation and showing three round, poorly defined but prominent knobs, one at the dorso-proximal tip of the plate, one in the center of the proximal edge and a third one close to the ventro-proximal tip of the plate; three

large spine articulations sunken into the outer surface in a vertical, slightly oblique row approximately 50 microns from the distal edge of the lateral arm plate; size of spine articulations and distance between spine articulations increasing towards the ventral edge (i.e. ventralmost spine articulation largest); every spine articulation composed of a single, large opening encompassed by two comma-shaped, vertical lobes (Fig. 3.3). Interior surface of lateral arm plate (Fig. 3.2) with a large, well-defined peg with raised margins shaped like a belt buckle, and a weakly depressed center; peg distally bordered by a deep vertical depression (podial basin) dorsally enclosed by the dorsal edge of the lateral arm plate and ventrally open; ventral edge of lateral arm plate around opening of central depression lined by small, inconspicuous groove spine articulations consisting of weakly raised cones with a tiny central opening; distal edge of the lateral arm plate smooth and slightly pinnacled, devoid of spurs.

Figured specimen (SULOPH002): Right median lateral arm plate (Fig 3.4), slightly longer than high, with rounded rectangular outline; ventral edge less strongly oblique than SULOPH001; outer surface ornamentation as in SULOPH001; three spurs on proximal edge but the central one closer to the dorsal one; three spine articulations as in SULOPH001 but without size gradient; inner side as in SULOPH001, axial views same as in SULOPH001.

Figured specimen (SULOPH003): Right distal lateral arm plate (Fig. 3.5), approximately 1.5 times longer than high; dorsal edge weakly concave; distal edge convex; ventral edge weakly convex but not oblique; proximal edge concave and oblique, with only central and ventral spurs visible; outer surface ornamentation as in

SULOPH001 but with groove spine articulations poorly visible, axial views same as in SULOPH001.

Remarks. — This species is characterized by its flat, quadratic main plate body, spine articulations composed of small depressions in a vertical line just before the distal margin, and a double-knobbed vertebral articulation on the inner surface that resembles a belt buckle. These are characters most commonly seen in protasterid ophiuroids (i.e. *Protaster*, *Strataster*, etc.). They are often square-shaped, articulate to the vertebrae on the proximal side of the inner surface, and extend slightly outward from the vertebrae (often appear imbricated) but never fully enclosing the vertebrae. The spine articulations are often simple, small depressions in a vertical row just offset from the distal margin. Due to these similarities we assign this specimen to the protasterids. A good candidate for this specimen is the protasterid *Strataster ohioensis* of the Lower Mississippian in northern Ohio (Kessling and Le Vasseur, 1971). LAPs of *S. ohioensis* show the same robust square shape, simple spine articulations in a vertical row. An equal candidate is the protasterid genus *Drepanaster* gen. (i.e. *Drepanaster wrighti*, Middle Devonian, Ontario, Kesling, 1970) with its similar square shaped main body and vertical spine articulations just offset from the distal edge. In both these cases the spine articulations superficially appear to be along a distally directed ridge, however, the preservation of these specimens is poor. Without further analysis we cannot confidently assign a species to this specimen but can be assigned to the protasterids based on the aforementioned characters.

Family **Cheiropterasteridae** Spencer, 1934

Genus *Vandelooaster* Jell, 1997

Vandellooaster sp. ident.

Figure 3.6 – 3.8

Figured specimen 2: Specimen SULOPH004 (Fig. 3.6 – 3.7) is a proximal left lateral arm plate.

Diagnosis. — Spatula shaped lateral arm plate with broad distal main plate body and short, thick proximal vertebral articulation. Distal edge undulating with up to four small spine articulations directly on distal edge. Covered in fine stereom on outer and inner surface. Small spur on ventral edge of vertebral articulation.

Description. — Descriptions based on proximal lateral plate SULOPH004 (Fig. 3.6 – 3.8), wider than high, general “spatula-like” outline, lateral arm plate highest distally, tapering slightly proximally for two thirds of the plate length; proximal third of plate significantly longer than high and has general peg-like shape; distal edge undulating with slight convexity overall; dorsal edge strongly convex proximally, slightly raising to concave edge distally; proximal edges come together at proximal-most edge to form peg-like articulation structure with vertebrae; articulation peg is slightly closer to the dorsal edge of the lateral arm plate; main plate body superficially rounded and thick, in dorso-ventral axial views with rounded edge that slightly increases in height toward plate center, rounded ridge encircles center of the main body plate; distal axial view similar to dorso-ventral view but with a rounded ridge along the ventro-distal margin; proximal axial view with rounded, conical appearance that expands toward the plate midline, diminishing toward the plate midline when it meets the main plate body; outer surface (Fig. 3.6) ornamentation consisting of fine tuberculation; peg-like articulation structure

strongly convex on all edges except where it connects with distal two thirds of the lateral arm plate; outer surface consisting of a very fine tuberculation covering the entire surface, devoid of patterns, with slightly more coarse tuberculation along the ventral edge of the flattened “paddle-like” main body of the plate; slightly raised ridge present, starting at the dorso-distal edge and curving along the middle of the plate to the ventro-distal edge; approximately three to four small, inconspicuous spine articulations directly along the distal edge of the plate, slightly protruding away from the plate as part of the distal edge undulation, and following the curvature of the distal plate edge; all spine articulations of equal size, median spine articulations closer together than outer spine articulations; every spine articulation composed of a small, round opening, even with the outer surface of the plate (Fig. 3.8). Interior side of the lateral arm plate (Fig. 3.7) bears a thick ridge along the ventral edge of the distal half of the plate; proximal peg bordered by a deep depression in the center of the main body of the plate, closed on the ventral, distal, and dorsal edges by a slight raise in the surface of the plate, proximal edge of the depression opens to a flat even surface with the rest of the plate; small spur consisting of two vertical, ellipsoid, dome-like ridges of equal height and width along the ventral edge of the peg where the peg meets the main body of the plate.

Remarks. — This specimen is characterized by its paddle-like main body, spine articulations on a ridge like extension of the main plate body along the ventro-distal margin, spine articulations composed of simple round openings, and a conical vertebral articulation off the proximal edge of the main plate body. It most closely resembles the LAPs of the Carboniferous cheiropterasterid *Vandeloaster plicatilis* (Jell, 1997). The

LAPs described here and those of *V. plicatilis* both show a flat paddle-like main plate body, spine articulations along a ridge like extension from the ventro-distal margin, and an elongate conical vertebral articulation. Specimens of *V. plicatilis* viewed both at the National Museum of Natural History (USNM 467196) and those figured by Jell (1997) show poor preservation of LAP features that make further comparisons difficult. As the general main plate body and spine articulation structures appear similar, and due to geographic and temporal proximity, we suggest *Vandelloaster* as the most viable generic assignment, however, further analysis must be completed before a species identification can be determined.

Suborder **Zeugophiurina** Matsumoto, 1929

Family **Furcasteridae** Stürtz, 1900

Genus *Furcaster* Stürtz, 1900

Furcaster wardi sp. nov.

Figures 1.D, 4.1 – 4.4

Holotype: Holotype specimen SULOPH005 (Fig. 4.1 – 4.2) is a proximal right lateral arm plate.

Etymology. — This species named in honor of Gabe Ward who provided valuable specimens that helped with the description of this specimen.

Diagnosis. — Scythe-shaped lateral arm plate with coarse to fine tuberculation covering the outer surface. Clearly defined fine tuberculation on proximal edge where adjacent lateral arm plate overlaps. Undulating distal edge with up to nine large, deep, rectangular spine articulations composed of a comma-shaped lobe, each lobe constantly vertical.

Distal margin below spine articulations with small ledge leading to spine articulations. Inner surface with coarse to fine tuberculation. Large knob-like vertebral articulation protruding off the ventral edge. Two large deep groove spines on ventral margin, composed of a deep v-shaped proximal depression and a deep rounded distal depression.

Description. — Description based on proximal lateral arm plate holotype SULOPH005 (Fig. 4.1 – 4.3); plate significantly higher than wide; scythe-shaped outline, concave proximally, widest at the base and decreasing in size dorsally, distal margin convex and rounded; proximal edge concave with spurs on a slightly raised surface that start at the proximal edge and move distally approximately one third of the way to the middle of the plate; ventral edge slightly convex on the ventro-distal edge with prominent convexity on the ventro-proximal edge; plate body is broadly convex if viewed axially on the proximal and distal sides; outer surface (Fig. 4.1) with two-fold ornamentation, consisting of slightly coarse tuberculation composed of small, irregular pores covering from the middle to distal edge with very weak striations, pores are oriented distally; proximal edge of lateral arm plate covered by fine tuberculation consistent with articulation surface with the adjoining lateral arm plate, slightly beveled, creating a short oblique plane to the main plate body; presence of a slightly depressed area on the ventro-proximal edge with finely meshed tuberculation; small, inconspicuous spurs consisting of small equally shaped and sized ridges present along the proximal edge approximately half way between the ventral margin and the dorsal tip of the main body plate; up to nine large spine articulations sunken into the outer surface along the distal edge of the lateral arm plate, consistent with the curvature of the distal edge; size of spine articulations and distance between them

equal along the margin; every spine articulation composed of a single, large, rectangular opening encompassed by one comma-shaped vertical lobe on the inner edge of the plate (Fig. 4.3), inner vertical lobe thick and prominent, size and shape consistent with all spine articulations; slight, less prominent ridge bordering the outer side of the spine articulations where they meet the outer surface of the spine articulations, constituting edge of outer plate surface; spine articulations ornamented by the slightly coarser tuberculation present on the outer surface of the lateral arm plate; small, round nerve opening with a raised edge present on the margin of the inner vertical lobe. Interior surface of lateral arm plate (Fig. 4.2) with a large protruding vertebral articulation peg on the ventro-proximal edge, protruding slightly past the proximal edge of the plate, dorsal and ventral edge slightly convex, proximal edge undulating with three, slightly prominent knobs, distal edge tapering into the main body of the lateral arm plate; inner surface also with two-fold ornamentation, consisting of a coarse tuberculation composed of large to small smooth pores with a weak striation pattern along the proximal edge, mesh size largest in the middle, decreasing in size proximally and distally, projecting dorso-proximally on the dorsal side of the vertebral articulation peg and ventro-distally on the ventral side of the vertebral articulation peg; finer, smooth tuberculation along the distal edge; two inconspicuous spurs consisting of larger dorsal ridge and smaller ventral ridge with a slightly deep canal running between them on the ventro-distal edge of the lateral arm plate (Fig. 4.2), consistent with articulation surface of the adjoining lateral arm plate; slight depression (podial basin) on the ventral edge of the lateral arm plate, bordered proximally and dorsally by the vertebral articulation peg, open on the ventral and distal

edge; ventral edge of lateral arm plate around opening of central depression lined by two large groove spine articulations consisting of one large v-shaped, notch-like depression on the proximal side of the ventral margin, and a large, deep rounded depression level with the ventral margin on the distal side of the margin, only visible from inner side of the lateral arm plate; possible nerve opening present on the distal edge of the vertebral articulation peg where it meets the dorsal spur, consisting of a small round opening projecting ventro-proximally.

Paratype (SULOPH006): Left distal lateral arm plate (Fig. 4.4), twice as high as it is wide, with a rounded triangular outline; dorsal edge as in holotype; ventral edge oblique, projecting ventro-proximally; distal edge slightly oblique; proximal edge slightly oblique; flat and oblique when viewed axially from the distal and proximal side; outer surface ornamentation similar to holotype, less defined, smoother in the dorsal third of the lateral arm plate; up to five spine articulations similar to holotype, but less depressed into edge of lateral arm plate; ventral edge with two large groove spines (Fig 4.4), even with plate surface, composed of large circular openings, distalmost groove spine largest; inner surface of lateral arm plate with ornamentation same as in holotype; prominent peg-like protrusion on the ventral edge, smaller and projecting more ventrally than peg in holotype, with slight sinusoidal tip.

Remarks. — This species is characterized by its scythe-shaped main plate body, large and deep rectangular spine articulations with lobed musculature openings, and vertebral articulation peg on the ventral margin. This LAP most closely resembles *Furcaster aequoreus* from the Devonian of Poland (Boczarowski, 2001). Due to this, we assign this

LAP to the genus *Furcaster* which shares the following apomorphies with this genus: spine articulations composed of oval depressions, bladed to triangular shaped main body plate that reduces in height and width down the arm away from the central disk, a vertebral articular protrusion on the inner surface near or off the ventro-proximal margin, and a distinctive tuberculation composed of small circular openings that project toward the distal edge of the main body plate. This species differs from *F. aequoreus* by the presence of a more prominent edge extension on the distal margin, more pronounced undulations that penetrate deeper into the main body of the plate surrounding the spine articulations, and a shorter vertebral articulation with 3 main knobs that extends ventralwards as opposed to directly outwards from the main plate as seen in *F. aequoreus*. *Furcaster cataphractus*, also from the Devonian of Poland, differs from *F. wardi* sp. nov. by the presence of a more robust triangular and squat main plate body shape, and absence of a ventral vertebral articulation. Furthermore, while the proximal plates in Boczarowski (2001) show the similar scythe-shaped main plate body, distal plates illustrated possess a more rounded triangular shape as those of *F. crispisulcans* sp. nov. Here, we illustrate that distal plates retain the dorsally elongate main plate body. It differs from *F. crispisulcans* sp. nov. by its scythe-shaped main plate body, rectangular-shaped spine articulation depressions, spine articulations with vertical lobes absent of obliqueness, and presence of a ventral vertebral articulation. Since there are no other similar specimens and due to the temporal and geographic gaps of the specimens described here, we describe this as a new species.

Furcaster crispisulcans sp. nov.

Figure 4.5 – 4.10

Holotype. — Holotype specimen SULOPH007 (Fig. 4.5 – 4.6) is a proximal right lateral arm plate.

Etymology. — The species name *crispisulcans* is Latin for wavy, referring to the undulating distal margin.

Diagnosis. — Robust, triangular lateral arm plate with distal edge higher than proximal edge. Outer surface with coarse to fine tuberculation. Undulating distal edge with up to six large, deep, rounded spine articulations sunk into the distal edge composed of a comma-shaped lobe on the inner edge, each one vertical but at an oblique angle. Distal margin composed of a two-tiered ledge just below spine articulations. Inner surface with coarse tuberculation changing to fine tuberculation on the edges of the plate. Vertebral articulation composed of two large knobs. Two medium-sized groove spines on ventral margin, composed of a v-shaped distal depression and a rounded proximal depression.

Description. — Description based on holotype specimen SULOPH007 (Fig. 4.5 – 4.8); plate higher than wide; of rounded triangular outline; plate highest distally, tapering towards the proximal edge; distal edge convex; dorsal edge long and slightly sinusoidal, convex at dorso-distalmost point of plate with short straight edge meeting convex edge approximately half way between the distal and proximal edge, strongly oblique on proximal side, final third of dorsal edge concave; proximal edge short and sharply convex; ventral edge slightly sinusoidal with a convex edge on the ventro-proximal side, slightly oblique, concave edge along the final two thirds of the ventral edge; plate body is

moderately convex if viewed axially on the proximal and distal sides; plate body is rounded and oblique when viewed axially from the dorsal side; plate body convex when viewed axially from the ventral side; outer surface (Fig. 4.5) with two-fold ornamentation, consisting of coarse tuberculation covering two-thirds of the plate from the spine articulations to the proximal edge, final third of plate on the proximal margin covered by finer tuberculation consistent with articulation surface of overlapping lateral arm plate, facet scar surface cuts into the main plate body adradially and creates a plane that is oblique to the outer surface of the plate; coarse tuberculation changes to finer tuberculation on dorsal and ventral edges; distal margin constructed of two, tiered ledges that go from the dorsal to ventral edges, both ledges consist of fine tuberculation devoid of incisions or protruding parts; outer surface shows wavy, undulating pattern around spine articulations with sharp, rounded, prominent edges; slightly raised and prominent sinusoidal ridge with up to six spine articulations sunken into the outer surface in a vertical, slightly oblique row approximately 50 microns from the distal edge of the lateral arm plate, just above tiered distal margin; sunken spine articulation penetration into plate increases from distal edge to the third spine articulation which is the most penetrated into the plate, the rest of the sunken spine articulations decrease penetration into the plate ventrally; size and distance between spine articulations is equal; each spine articulation (Fig. 4.7 – 4.8) composed of a single, large, rounded opening encompassed by one comma-shaped, vertical lobe on the inner edge that is sunken into a concave depression some approximately 50 microns from the top tiered margin of the distal edge of the plate, inner vertical lobe thick and prominent, reducing in size and length ventrally; slight, less

prominent ridge bordering the outer side of the spine articulations where the spine articulations meet the outer surface, constituting margin of outer plate surface; small, round nerve opening with a raised edge just on the margin of the inner vertical lobe. Interior side of lateral arm plate (Fig. 4.6) with large, well-defined vertebral articulation with two prominent domes, distal-most dome larger than proximal dome; peg distally bordered by shallow, broad depression (podial basin) in the ventral-most half of the inner side of the plate, dorsally enclosed by the dorsal half of the lateral arm plate and ventrally closed; coarse tuberculation present in the center of the depression, radiating outwards and slightly decreasing in size towards the distal edge of the plate; fine tuberculation composed of small pores line the distal margin consistent with articulation surface for adjoining lateral arm plate; ventral margin of lateral arm plate directly below central depression lined by two medium-sized groove spines composed of a slightly v-shaped, notch-like depression on the distal side of the margin and a rounded depression that is flush with the ventral edge on the proximal side of the margin, only visible from inner side of the lateral arm plate (Fig. 4.6); small, circular nerve opening on the ventral edge of the largest dome on the peg, approximately 100 microns from the ventral edge of the plate.

Paratype (SULOPH008): Right median lateral arm plate (Fig. 4.9); plate is twice as wide as it is high, general rounded ellipsoid outline with triangular proximal margins; dorsal margin mostly straight, with a short concave edge leading to an oblique edge on the proximal third of the dorsal margin; ventral margin oblique on the proximal third of the edge, weakly convex on the middle third, slightly oblique on the distal third; distal

margin convex; proximal edge short, convex; slightly domed when viewed axially on all sides, flat on the inner side and increasing in height toward the plate center on the outer surface; outer surface ornamentation same as in holotype, except ornamentation remains constant size over entire surface; undulations approximately 100 to 150 microns from distal margin as in holotype; distal edge with thin lip approximately 100 to 150 microns from spine articulations, similar to holotype, but not tiered; three spine articulations, composed same as in holotype; size and distance between spine articulations equal. Interior side of lateral arm plate with thick, spade-shaped elevated ridge extending to the middle half of the lateral arm plate from the proximal edge; ridge bordered on the distal edge by a small depression (podial basin), closed on all sides; inner surface ornamentation with fine, almost smooth stereom, slightly fine, irregular tuberculation around the proximal ridge; distal edge devoid of spurs and protrusions.

Paratype specimen (SULOPH009): Right distal lateral arm plate (Fig. 4.10); plate slightly wider than high, with general rectangular outline, tapering proximally to a triangular proximal edge; dorsal edge weakly convex with a slightly straight middle on the distal half, oblique on the proximal half; ventral margin very weakly concave on the distal half, oblique on the proximal edge; distal margin trapezoidal, oblique on the dorso-distal half of the edge, straight on the ventro-distal edge; proximal edge convex; plate body square like when viewed axially on dorsal, ventral, distal, and proximal side, increasing in height toward the plate center; plate body appears three dimensionally trapezoidal when viewed down the inner surface axis; outer surface ornamentation as in holotype, except reduced in size proximally, starting slightly on the proximal side of the

plate midline; thin tapered lip on the distal edge, just below the spine articulations as in the holotype, except not tiered; ventro-proximal edge with two, slightly inconspicuous, raised knobs; undulations approximately 50 to 75 microns from distal edge as in holotype, except decreasing in size ventrally; four spine articulations similar to holotype, except without size and distance gradient, ventralmost spine articulation depression without vertical inner lobe as seen in holotype. Interior side of lateral arm plate with large peg-like knob on the proximal edge, of rounded triangular outline, widest in the middle, tapering in size proximally and distally, dorsal edge straight; large, elevated, rounded, and rectangular block-like protrusion on the distal edge; inner surface ornamentation three-fold, consisting of coarse tuberculation on the distal half of the inner surface, composed of large, irregular knobs, smooth stereom on the ventral half, and fine tuberculation covering the proximal and distal protrusions.

Remarks. — *Furcaster crispisulcans* sp. nov. is characterized by its rounded triangular main plate body, deep rounded spine articulation depressions with lobed musculature openings that also possess some obliqueness, and a double-knobbed vertebral articulation on the ventro-proximal edge of the inner surface. This specimen most closely resembles more distal specimens of both *Furcaster cataphractus* and *F. aequiroeus* from the Devonian of Poland as described by Boczarowski (2001). Due to this, we assign this LAP to the genus *Furcaster* which shares the following apomorphies with this genus: spine articulations composed of oval depressions, bladed to triangular shaped main body plate that reduces in height and width down the arm away from the central disk, a vertebral articular protrusion on the inner surface near or off the ventro-proximal margin, and a

distinctive tuberculation composed of small circular openings that project toward the distal edge of the main body plate. Since there were no complete specimens to compare changes in morphology through the progression of the arm, it is possible that the two species from the Devonian of Poland could be interchangeable. *Furcaster crispisulcans* differs from both *F. cataphractus* and *F. aequiroeus* by the presence of a more dominant and elongate tiered ridge along the distal margin, deeper and more pronounced undulations surrounding the spine articulations, absence of a curl to the ventral edge, less pronounced groove spines, more pronounced roundness to the proximal edge, and the presence of a double-knobbed vertebral articulation on the ventro-distal tip of the inner surface. Additionally, proximal plates of *F. crispisulcans* possess the rounded triangular main plate body while distal plates become more elongate and rounded unlike the proximal and distal plates described in Boczarowski (2001) which show a more pointed triangular proximal plate. This specimen also differs from *F. wardi* sp. nov. by possessing a robust, rounded and triangular main plate body, rounded spine articulation depressions with musculature openings that have lobes which possess obliqueness, and a vertebral articulation that is incorporated into the inner surface instead of an extension of the main plate. Since there are no other specimens that resemble this species and due to the temporal and geographic gaps of the Devonian specimens, we describe this as a new species.

Order **Stenurida** Spencer, 1951

Suborder **Parophiurina** Jaekel, 1923

Family **Palaeuridae** Spencer, 1951

Genus *Umerophiura* Boczarowski, 2001

Umerophiura daki sp. nov.

Figure 5.1 – 5.5

Holotype. — Holotype specimen SULOPH010 (Fig 5.1-5.2) is a proximal left lateral arm plate.

Etymology. — This species is named in honor of my doxie Dak which provided comfort during the writing of this manuscript.

Diagnosis. — Racquet-shaped lateral arm plate with glove-like main body and short rounded peg-like vertebral articulation. Outer surface smooth, devoid of ornamentation. Inner surface mostly smooth with slightly coarse tuberculation along distal margin. Distal edge with spiny, triangle-shaped protrusions and lined underneath by medium-sized spine articulations composed of shallow depressions. Inner surface with large deep podial basin.

Description. — Description based on holotype specimen SULOPH010 (Fig. 5.1 – 5.2); plate slightly wider than high, with “racquet-like” outline; main body of plate shaped like a glove, slightly convex, elliptical with long axis extending from dorso-proximal to dorso-ventral; a peg-like structure extends from the ventro-proximal margin of the plate body; dorsal edge sinusoidal with a short convex edge on the proximal third of the ventral edge, long concave edge in the middle, strongly convex edge on the distal third of the ventral edge; proximal edge short, widely convex, slightly oblique; distal edge long, widely convex; ventral edge sinusoidal, convex on the dorso-proximal edge, oblique and concave in the middle, short convex edge on the dorso-distal edge; plate body convex

when viewed axially from the dorsal, ventral, and distal sides; articulation peg cylindrical in shape when viewed axially, with a slight constriction as it enters the main plate body; outer surface (Fig. 5.1) ornamentation smooth, devoid of tuberculation; proximal half with rounded peg; distal half with a rounded ovoid-like main plate body; ventro-proximal margin with tapered lip that extends from the dorsal edge of the connection between the proximal peg and distal main body, tapering toward the inner surface at a ventro-proximal direction, creating an oblique plane that cuts into main plate body; distal edge with slightly oblique lip that tapers ventrally, ventral margin of distal lip lined with up to nine rounded triangular protrusions, protrusions in the middle largest, decreasing in size dorsally and ventrally; spine articulations line the distal edge just below the triangular protrusions, composed of medium-sized depressions, further details not preserved. Inner side of the lateral arm plate (Fig. 5.2) broadly concave with a large, central depression (podial basin) that encompasses most of the entirety of the inner part of the main plate body; depression closed on the distal edge by a thick ridge covered weakly in coarse tuberculation; proximal and dorsal edge closed by a short, thick ridge; ventral edge open by small concave tentacle opening; inner surface ornamentation two-fold, consisting of a primary finely meshed stereom on the peg and in the depression; thick distal ridge with coarse tuberculation, composed of irregular, medium sized knobs.

Paratype (SULOPH011): Left median/distal lateral arm plate (Fig. 5.3 – 5.5); plate broadly convex, slightly wider than high, highest on the distal edge, of general cuneate outline; dorsal edge concave; ventral edge slightly convex; distal edge convex; proximal edge convex; proximal third of the lateral arm plate thin and peg-like; distal two-thirds of

the lateral arm plate (main body) wide, triangular with rounded edges; plate body convex when viewed axially; articulation peg cylindrical when viewed axially; outer surface ornamentation (Fig. 5.3) two-fold, consisting of a slightly coarse tuberculation on the proximal third peg-like surface, composed of medium-sized, irregular pores, distal two-thirds of the lateral arm plate covered with a smooth, finely meshed stereom; distal edge undulating as in holotype; up to six spine articulations (Fig. 5.5) sunken into and lining the distal edge, just below the undulating edge, in a slightly oblique row, projecting ventro-proximally; every spine articulation composed of a large, deep circular opening, decreasing in size ventrally, second spine articulation from the dorsal edge larger than all of the other spine articulations; space between spine articulations equal. Inner side of the lateral arm plate (Fig. 5.4) with large, deep depression covering entire distal two-thirds of the lateral arm plate, bordered dorsally, ventrally, and distally by a large, thick convex ridge circling the distal edge, open proximally; thick distal ridge with thin, short ridges extending distally from the edge of the central depression and moving down the midline of the distal undulating protrusions; small, inconspicuous concave tentacle opening on the ventro-proximal edge of the depression; distal peg with a small canal down the midline, extending from the central depression to the proximal edge of the peg, most likely a podial canal; inner surface ornamentation consisting of coarse tuberculation, composed of medium-sized irregular knobs, decreasing in size toward the proximal edge of the peg.

Remarks. — The lateral arm plates of *Umerophiura daki* sp. nov. are characterized by their broad glove-shaped main plate body, proximal rounded peg-like vertebral articulation, distal edge lined with triangular protrusions, and a depression on the inner

surface leading to a prominent incision for the podial basin and opening. This species most closely resembles other isolated LAPs of *Umerophiura* sp. from the Devonian of Poland (Boczarowski, 2001) and share the following apomorphies: “raquet-shaped” main body plate with prominent club like articulation peg protruding from the proximal margin, wedge-shaped protrusions aligning the distal margin, smooth surface stereo, and a large central podial depression that encompasses a majority of the inner surface of the main body plate. Due to this, we assign this specimen to the genus *Umerophiura*.

Umerophiura daki differs from *Umerophiura opipara* by having a glove-like main plate and rounded peg-like proximal vertebral articulation. *Umerophiura umera* shows the most similarity but, there are difference in the concavity of the main plate body, obliqueness of the peg from the main plate body, and more prominence and roundness to the proximal articulation peg. Since there are no other similar described species and because of the temporal separation of these species, we describe this as a new species.

Suborder **Ophiurina** Müller and Troschel, 1840

Family unknown

Genus *Aganaster* Miller and Gurley, 1891

Aganaster monoceros sp. nov.

Figure 5.6 – 5.9 and Figure 6.1 – 6.3

Holotype. — Holotype SULOPH012 (Fig. 5.6 – 5.7) specimen is a proximal right lateral arm plate.

Etymology. — The species name *monoceros* is Latin for giraffe, referring to the appearance of the associated vertebra of the lateral arm plate which looks like the head of a giraffe in dorsal profile.

Diagnosis. — Robust, quadratic lateral arm plate with fine stereom and distinct trabecular intersections and weak vertical rows. Distal edge with two grouped spine articulations on the ventro-distal tip composed of large muscle openings and a small, inconspicuous nerve opening. Inner surface smooth, with a large, thick central ridge that serves as a vertebral articulation. Large tentacle notch present on the distal edge of the ventral margin.

Description. — Description based on holotype SULOPH012 (Fig. 5.6 – 5.9); plate robust, approximately as high as long, with rounded quadratic outline, with weakly convex dorsal and ventral edges; distal edge weakly convex with an angular projection close to the ventro-distal tip; proximal edge irregularly concave; plate body shaped like a vertically bisected barrel when viewed axially, with dorsal and ventral margins more medial than the protuberant horizontal midline; outer surface (Fig. 5.6) covered by finely meshed stereom with trabecular intersections merged into very small, uniform tubercles, arranged into weak vertical rows; proximal edge formed by narrow beveled articulation facet with poorly defined band of more coarsely meshed stereom with a weak horizontal striation and devoid of spurs; two equal-sized articulations grouped near the ventro-distal tip of the lateral arm plate, sunken into the distal edge and distally bordered by the angular projection of the distal edge; spine articulations (Fig. 5.8 – 5.9) composed of a large muscle opening proximally bordered by finely meshed stereom and distally

bordered by a well-defined, irregular, prominent vertical ridge followed by a depression including a small, inconspicuous nerve opening. Interior side of the lateral arm plate (Fig. 5.7) with thick dorsal and ventral edges and with single, large, prominent, well-defined, ridge-shaped vertebral articulation in the center, reaching from the dorsal to ventral margins; ventral edge of the lateral arm plate distally incised by a large tentacle notch; distal edge of lateral arm plate smooth, pinnacled distally, devoid of spurs.

Paratype (SULPOPH013): left median lateral arm plate (Fig. 6.1); plate similar to holotype in general outline; outer surface with slightly smaller tubercles arranged in more clearly developed vertical rows; spine articulations as in holotype but poorly preserved. Inner side of lateral arm plate as in holotype but better preserved, showing weak vertical furrow distally bordering vertebral articulation ridge; tentacle notch distally bordered by a thickened ventro-distal tip of the plate; axial view same as in holotype.

Paratype (SULOPOH014): right median lateral arm plate (Fig. 6.2); plate as long as high, quadratic in outline, with nearly straight dorsal and ventral edges, weakly convex distal edge with very weak projection near the ventro-distal tip of the plate; proximal edge evenly concave and lined by band of more coarsely meshed stereom as in holotype but slightly more sharply defined; outer surface ornamentation as in holotype; two spine articulations near ventro-distal tip of lateral arm plate as in holotype, but with additional third spine articulation similar to the two ventral ones in the dorsal half of the distal edge. Inner side with vertebral articulation ridge as in holotype but with uniformly thickened ventral plate edge not incised by a tentacle notch; small perforation corresponding to

tentacle opening between ventral tip of vertebral articulation tip and ventro-distal tip of lateral arm plate; axial view same as in holotype.

Paratype (SULOPH015): right distal lateral arm plate (Fig. 6.3); plate almost 1.5 times as long as high, with rectangular outline, straight dorsal and ventral edges; distal edge uniformly convex; proximal edge concave, lined by band of more coarsely meshed stereom as in holotype; outer surface ornamentation similar to that of holotype; two spine articulations grouped in ventral half of distal edge, with much larger and more prominent vertical ridges than those of holotype. Vertebral articulation on inner side as in holotype, but shorter and rounded triangular rather than ridge shaped; ventral edge uniformly thickened, not incised by tentacle notch; small perforation between ventral tip of vertebral articulation and ventro-distal tip of lateral arm plate, corresponding to tentacle opening; axial view same as in holotype.

Remarks. — *Aganaster monoceros* sp. nov. is characterized by a quadratic, non-bulging plate body that encloses the entire vertebra, distinctive finely meshed stereom with trabecular intersections forming weak vertical rows, two spine articulations composed of large muscle openings and a round nerve opening on the ventral distal tip, large central vertebral articulation ridge on the inner side, and a large tentacle notch on the ventral edge of the inner side of the plate. This species most closely resembles the lateral arm plates of *Aganaster jagiellonicus* (Thuy et al., 2015). *Aganaster monoceros* differs from the type species *Aganaster gregarious* by having a thicker main body plate that is non-bulging, smaller amount of spine articulations, and the lack of an elevated ridge on the distal margin holding the spine articulations. It differs from *A. jagiellonicus* by the

presence of two, very small spine articulation on the proximal plates instead of three and the absence of in-plate tentacle pores in distal most plates. Additionally, *A. cingulatus* (Easton, 1943), *A. ? fujiaensis* (Liao and Wang, 2002), and *A. huaanensis* (Wu, 1982), although poorly known due to poor preservation, do not share similarities with this specimen. Because of its base similarities with species in the genus *Aganaster* (i.e. half-barrel shape, spine articulations composed of shallow muscle depressions along the distal margin, between-plate tentacle openings, and enclosing of the vertebrae) we assign this LAP to the *Aganaster*, however, since there are currently no described species completely matching this specimen we assign it to a new species.

Order unknown

Family unknown

Genus *Sulphaster* gen. nov.

Type species. — *Sulphaster solus* sp. nov. from the Late Mississippian (Surpokhovian) Indian Springs Shale Member, Big Clifty Formation, Sulphur, Indiana, USA

Diagnosis. — Same as *Sulphaster solus* sp. nov., by monotypy.

Description. — Same as *Sulphaster solus* sp. nov., by monotypy.

Etymology. — This genus named in honor of Sulphur, Indiana, the type locality for this genus.

Species *Sulphaster solus* gen. and sp. nov.

Figure 6.4 – 6.8

Holotype. — Holotype SULOPH016 (Fig. 6.4 – 6.5) specimen is a proximal left lateral arm plate.

Etymology. — The species name *solus* is Latin for alone, referring to the single spine articulation that shows modern-type affinities.

Diagnosis. — Generally quadratic lateral arm plate, robust rectangular main plate body and pennate vertebral articulation on the proximal margin with vertical constriction between main plate and vertebral articulation, constriction stronger on the dorsal edge. Outer surface covered with coarse tuberculation and fine tuberculation on the proximal and distal margins where adjacent plates overlap. Four prominent and well-defined spine articulations in a vertical row on a slightly bulged area of the distal margin of the plate. Spine articulations increase in size dorsally, with dorsalmost spine articulation largest and composed of one small comma-shaped lobe, other spine articulations composed of small round openings. Distal edge with a distinctive lip. Inner surface with fine stereom except on ridge encircling the large central podial basin and tentacle notch.

Description. — Description based on holotype SULOPH016 (Fig. 6.4 – 6.8); plate slightly wider than high, rounded quadratic outline with a slight constriction close to the proximal edge; lateral arm plate highest distally, tapering towards the proximal edge, thickening in the last third of the plate toward the proximal edge; dorsal edge sinusoidal with long, convex edge on the distalmost side, becoming concave at the middle, and again convex near the proximal margin; ventral edge weakly sinusoidal with short, concave edge close to the distalmost edge, long, convex edge on the distalmost side, slight concave edge on the proximal side of the middle of the plate, short (shorter than dorsal edge) convex edge on the proximalmost side; distal edge slightly sinusoidal with convex edge on the dorsalmost half and concave edge on the ventralmost half; proximal

edge pennate and oblique with the dorsalmost edge higher than it is wide, long and slightly convex with the widest point at the dorso-proximal edge, ventralmost edge wider than it is high, widest point at the ventro-proximal edge, tipped with a small convex edge; sharp and concave edge splits the two pennate edges approximately midway on the proximal edge; flat edge that tapers slightly up toward the domed inner portion of the plate present on the distal edge of the plate; slight constriction between the pennate proximal edge and the rectangular main body of the lateral arm plate, constriction most prominent on the dorsal edge; plate body convex, bulging on the outer surface when viewed axially on the distal side, obliquely convex when viewed axially from the dorsal and ventral sides, and slightly convex with a constriction when viewed axially from the proximal side; outer surface (Fig. 6.4) ornamentation uniform, consisting of coarse, irregular tuberculation, weakly striated vertically, flat distal edge loses the striations; four spine articulations (Fig. 6.6 – 6.7) raised above outer surface in a vertical, slightly oblique row approximately 50 to 75 microns (ventralmost almost to 100 microns) from the distal edge, just above the slightly raised flat edge; size of spine articulations increases dorsally (i.e. dorsalmost spine articulation largest) and distance between spine articulations is greatest between the dorsalmost and ventralmost spine articulations with the median most spine articulations, median most spine articulations are slightly separated from each other; dorsalmost spine articulation slightly more pinnacled than the other articulations, making it higher above the lateral arm plate surface, composed of a single, large opening encompassed by one comma-shaped, vertical lobe on the upper side of the spine articulation; other spine articulations composed of single, large round openings slightly

depressed in the outer surface of the plate. Interior side of the lateral arm plate (Fig. 6.5) with a large, thick ridge starting at the ventro-distal edge and follows the edge of the lateral arm plate ending just short of the dorso-proximal edge of the lateral arm plate; large, deep depression (podial basin) in the center of the lateral arm plate, encompassing most of the inner side of the plate, closed distally and dorsally by thick ridge, closed proximally by beginning of the vertebral articulation structure, large opening on the ventral side about as wide as the lateral arm plate corresponding to tentacle opening; vertebral articulation composed of two vertical, large and thick ridges on the proxo-ventral and proxo-dorsal edges of the inner side of the lateral arm plate, with slight and inconspicuous central ridge connecting the two ridges; proximal edge of the inner surface of the lateral arm plate smooth and highly pinnacled approximately 50 microns into the plate; distal edge slightly rough, devoid of spurs.

Paratype (SULOPH017): Left median/distal lateral arm plate (Fig. 6.8); plate slightly wider than high, general outline same as in holotype, except with more convex distal edge, and proximal edge sinusoidal, undulating starting with a convex ventro-proximal edge and ending with a concave dorso-proximal edge; outer surface ornamentation as in holotype, except uniform over entire surface; proximal edge with thin protruding ridge just below spine articulations as in holotype, except more convex; four spine articulations on the proximal edge just above protruding ridge, all spine articulations as in holotype, except dorsal most spine articulation largest, slightly decreasing in size ventrally, distance between spine articulations equal; inner side with thick, convex ridge lining the inner side of the dorsal edge, starting at the dorso-proximal tip and ending at the

beginning of the distal edge; proximal two thirds with a large, deep, slightly oblique and concave channel, closed dorsally by the convex ridge, ventrally by the ventral edge of the lateral arm plate, open proximally, and bordered distally by a round, large depression (podial basin); depression with concave tentacle notch on the ventro-distal edge; inner surface ornamentation consisting of fine tuberculation covering entire surface, consisting of small irregular knobs; distal edge devoid of spurs or protrusions; axial views same as in holotype but less of a bulge and constriction.

Remarks. — *Sulphaster solus* gen. and sp. nov. is characterized by a rounded quadratic main plate body that bulges on the distal edge with a pennate proximal edge that connects to the adjoining plate, complete enclosing of the vertebrae, at least four spine articulations that protrude from the outer surface surrounded by a thick rim, dorsalmost spine articulation showing similarities to modern ophiuroids by the presence of a lobed muscular attachment, a large internal podial basin, a large ventral podial opening, lack of a prominent internal vertebral articulation surface, and absence of groove spines. This lateral arm plate shows some similarities to those of *Chattaster locus* from the Devonian of Poland (Boczarowski, 2001) with its distal bulge, and roughly tube-like appearance, protruding spine articulations, and ventral tentacle opening. It differs mainly in the presence of spine articulations on the distal plates that are similar to those on the proximal plates, absence of a strongly pennate proximal edge, larger and more robust main plate body, ventral concavity of distal plates, and absence of a protrusion or ridge on the inner side of the plate. Since no other lateral arm plates seem to be compatible, a lack of strong evidence connecting *Chattaster locus* to this lateral arm plate, and the

presence of strongly modern-type ophiuroid affinities we describe this as a new genus and species.

Ophiuroidea *incertae sedis*

Lateral arm plate type 1

Figure 7.1 – 7.2

Description. — Description based on proximal lateral arm plate SULOPH018 (Fig. 7.1 – 7.2); plate robust, approximately wide as high, of rounded rectangular outline; center of lateral arm plate thicker than dorsal and ventral sides; distal edge long, convex; proximal edge with straight edge in the middle half of the lateral arm plate, concave edges on the dorsal and ventral quarters of the ventral edge; plate body convex, appearance almost like a turtle shell when viewed axially on the distal and proximal sides, concave increasing in height to the plate center when viewed axially from the dorsal and ventral sides; outer surface ornamentation consisting of a fine tuberculation covering the entire surface composed of small, irregular knobs; two spine articulations, one on the dorsal edge and one on the ventral edge, even with the surface of the lateral arm plate, composed of a large, irregular, rounded depression, entire spine articulation covered in the same fine tuberculation as on the surface of the lateral arm plate; size of the spine articulations approximately the same; all edges devoid of spurs and protrusions. Inner side of plate with two vertical ridges in the middle of the plate, slightly elevated, closest to the dorsal edge, separated by a narrow, shallow valley; distal edge with a slight depression, bordered proximally by a concave ridge, open distally, ventrally, and dorsally; inner surface ornamentation consisting of coarse tuberculation covering the entire inner

surface, composed of medium-sized, irregular knobs; distal edge devoid of knobs and protrusions

Remarks. — This specimen is characterized by a robust, rectangular main body with fine tuberculation covering the outer surface, thicker main body along the central midline of the plate, up to two large spine articulations of the same size, an inner side with two vertical ridges in the middle of the plate that are slightly elevated, distal edge with slight depression, and inner surface covered in coarse tuberculation composed of medium-sized, irregular knobs. There is currently not enough data and comparable specimens to reconcile this specimen; therefore, we place this specimen in open nomenclature.

Lateral arm plate type 2

Figure 7.3 – 7.4

Description. — Description based on left proximal lateral arm plate SULOPH019 (Fig. 7.3 – 7.4); plate twice as wide as it is high, with rounded elongated ellipsoid to bean-shape; dorsal edge convex; ventral edge convex on distal two thirds of lateral arm plate, slightly concave at the beginning of the proximal third of the edge, with last third of the ventral edge convex; distal edge convex; proximal edge convex; plate body cylindrical when viewed axially on the distal side, when viewed axially on the proximal side plate body is domed on the inner surface and oblique, increasing in height toward the plate center on the outer surface; outer surface with a two-fold ornamentation consisting of a fine tuberculation with a weak radiating pattern from the center of the proximal third of the lateral arm plate which it covers, cutting into the main plate body creating an oblique plane, consistent with an articulation surface for an adjoining lateral arm plate, and a

much coarser tuberculation composed of large, irregular, smooth knobs with a weak vertical striation covering the distal two thirds of the plate; small inconspicuous round opening at the center of the proximal third of the lateral arm plate; outer surface devoid of spurs, incisions, protrusions, and spine articulations. Interior surface of lateral arm plate covered in large tuberculation present on outer surface, decreasing in size toward the distal and proximal edge; two large spine articulations slightly depressed on the distal edge of the inner surface in a vertical row; both spine articulations composed of a large depressed opening , devoid of ridges; shape of spine articulations and size of spine articulations equal; all edges devoid of spurs and protrusions.

Remarks. — This specimen is characterized by a rounded shape of the main body plate with the appearance of a grain of rice, weak radiating pattern in the tuberculation on the proximal outer surface, large and coarse tuberculation covering the remainder of the main plate body, and two large spine articulations on the interior side of the distal margin. There is currently not enough data and comparable specimens to reconcile this specimen; therefore, we place this specimen in open nomenclature.

Lateral arm plate type 3

Figure 7.5 – 7.7

Description. — Description based on left lateral arm plate SULOPH020 (Fig. 7.5); plate approximately twice as high as it is wide, with rounded, half-ellipsoid outline; lateral arm plate highest down the midline of the plate; dorsal edge convex; ventral edge convex, devoid of incisions or protruding parts; distal edge mostly convex, short straight edge on the middle of the distal edge; proximal edge straight; plate body appears as squashed,

rounded and “bean-like” when viewed axially; outer surface covered in slightly coarse tuberculation composed of medium-sized irregular knobs, decreasing in size toward the edges of the lateral arm plate on all sides; distal edge with undulating outer surface, separate from the physical edge of the lateral arm plate by a slight extended edge; undulating edge probably a part of the spine articulation morphology, however, the spine articulations are not visible at this time; proximal edge with a small spur on the ventral third of the edge, composed of two small, oblique domes; medium-sized slit-like opening present approximately half way between the spur and the distal edge of the lateral arm plate. Inner side of plate with two large, round knobs on the middle of the distal edge, knobs separated slightly by a small, shallow indentation; inner surface ornamentation two-fold, consisting of fine tuberculation in the dorso-distal half and coarser tuberculation in the ventro-proximal half, composed of large, irregular pores; distal edge with slight undulation as seen on the outer surface; large depression covering most of the entire inner surface, bordered dorsally, ventrally, and distally by a thick, concave ridge, open on the proximal edge.

Remarks. — This specimen is characterized by a rounded ellipsoid shape of the main body plate, undulating distal edge (as in *Furcaster wardi* sp. nov. and *Furcaster crispisulcans* sp. nov.), rounded pennate-like spur on the proximal edge, and outer surface ornamentation composed of medium-sized, irregular tuberculation covering the main body plate and decreasing in size toward the edges of the main body plate. This specimen does share some similar affinities with *Furcaster wardi* sp. nov. and *Furcaster crispisulcans* sp. nov., namely the undulating surface and stereom pattern. It is possible

that this specimen is a furcasterid but, more investigation of the spine articulations must be completed. Because of this, we place this specimen in open nomenclature.

Lateral arm plate type 4

Figure 7.8 – 7.9

Description. — Description based on left lateral arm plate SULOPH021 (Fig. 7.7 – 7.9); plate approximately twice as high as it is wide, robust, rounded half-ellipsoid outline; dorsal edge sinusoidal, distal two-thirds long, convex, small concave edge connecting to short convex edge; ventral edge convex; distal edge long, convex two-thirds of the edge from the dorsal to ventral edge, ventral third of the distal edge slightly oblique; proximal edge long, concave with short convex edges on the ventral and dorsal tips; plate body appears as a thick moon-shaped crescent when viewed axially; outer surface ornamentation uniform, entire surface covered in fine tuberculation composed of very small knobs, slight horizontal striation pattern; four spine articulations even with the outer surface in a vertical, slightly oblique row, down the middle of a distal elevated ridge; ridge holding spine articulations bulge around the second spine articulation from the dorsal edge; first spine articulation from the dorsal edge slightly larger than the third and fourth spine articulation, second spine articulation significantly larger than all other spine articulations; third and fourth spine articulation from the dorsal edge smallest in size, but both of equal size to each other; distance between spine articulations decreases ventrally; first, third, and fourth spine articulation from the dorsal edge with a slightly depressed opening, second spine articulation from the dorsal edge with a large, deep depression; each spine articulation surrounded by a slight rimmed edge, slightly ovoid in

shape. Interior side of the lateral arm plate with long, elevated, convex ridge from the dorsal tip to the ventro-distal tip, elevated ridge holding spine articulations approximately 100 microns off to the distal side of this internal ridge; inner surface covered with same fine tuberculation as outer surface; ventral edge triangular, thinner than inner part of the plate; all edges devoid of spurs and protrusions.

Remarks. — This specimen is characterized by a large, rounded ellipsoid main body plate, ornamentation consisting of fine tuberculation composed of small knobs with a slight horizontal striation, and four spine articulations composed of clearly defined circular openings, all at a vertical angle along a ridge protruding from the ventral edge. There is currently not enough data and comparable specimens to reconcile this specimen; therefore, we place this specimen in open nomenclature.

Acknowledgements

The authors would like to thank University of Tennessee undergraduates Colby Sain and Julie Coulombe for their work on picking and organizing skeletal material, and graduate student Maggie Limbeck for help with illustrations. This project was funded by several small grants from The Paleontological Society, Cincinnati Dry Dredgers, Southeastern Geological Society of America, University of Tennessee Graduate Student Senate, and University of Tennessee Center for Global Engagement.

References

- Aronson, R. B., Thatje, S., Clarke, A., Peck, L. S., Blake, D. B., Wilga, C. D. & Seibel, B. A., 2007, Climate change and invasibility of the Antarctic benthos: Annual Review of Ecology, Evolution, and Systematics, 38, p. 129–154.
- Blake, D.B., 2013, Early Asterozoan (Echinodermata) diversification: a paleontologic quandary: Journal of Paleontology, v. 87, p. 353-372.
- Blake, D.B., and Guensberg, T.E., 2015, The class Somasteroidea (Echinodermata, Asterozoa): morphology and occurrence: Journal of Paleontology, v. 89(3), p. 465-486.
- Boczarowski, A., 2001, Isolated sclerites of Devonian non-pelmatozoan echinoderms: Palaeontologia Polonica, 59, p. 1–219.
- Brett, C.E., Moffat, H.A., and Taylor, W.L., 1997, Echinoderm Taphonomy, Taphofacies, and Lagerstätten: Paleontological Society Papers, v. 3, p. 147–190.
- Bruguière J.G., 1791, Tableau encyclopédique et méthodique des trois règnes de la nature, Vol. 7, L'helminthologie. Paris, France: Charles–Joseph Panckoucke.
- Chen, Z.Q., and McNamara, K.J., 2005, End-Permian extinction and subsequent recovery of the Ophiuroidea (Echinodermata): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 236, p. 321–344, doi:10.1016/j.palaeo.2005.11.014.
- Christensen A.B., Herman J.L., Elphick M.R., Kober K.M., Janies D., et al., 2015, Phylogeny of Echinoderm Hemoglobins. PLOS ONE 10(8):e0129668. <https://doi.org/10.1371/journal.pone.0129668>.
- Easton, W.H., 1943, The fauna of the Pitkin Formation of Arkansas: Journal of Paleontology, 17 (2): p. 125–154.

- Gage, J.D. and Tyler, P.A., 1991, Deep Sea Biology: A Natural History of Organisms at the Deep-Sea Floor: Cambridge University Press, Cambridge.
- Glass, A., 2006, The brittle star fauna of the Hunsrück Slate and a phylogeny of the Paleozoic Ophiuroidea. Unpublished Ph.D. thesis, University of Illinois, Urbana, Ill., 610 pp. [= *Dissertation Abstracts International* 67(11B), 6270].
- Gray, J.E., 1840, A synopsis of the genera and species of the class Hypostoma (Asterias Linn.): *Annals and Magazine of Natural History*, 6: p. 275–290.
- Gregory, J. W., 1896, The classification of the Palaeozoic echinoderms of the group Ophiuroidea: *Proceedings of the Zoological Society of London*, p. 1028-1044.
- Hess, H., 1962, Mikropaläontologische Untersuchungen an Ophiuren I: Einleitung. *Eclogae Geologicae Helvetiae*, 55/2, p. 595–608.
- Hunter, A.W., and McNamara, K.J., 2018, Prolonged co-existence of ‘archaic’ and ‘modern’ palaeozoic ophiuroids - Evidence from the early Permian, southern Carnarvon basin, western Australia: *Journal of Systematic Palaeontology*, v. 16, p. 891–907, doi:10.1080/14772019.2017.1353549.
- Jaekel, O.M.J., 1923, Zur morphogenie der Asterozoa: *Palaeontologische Zeitschrift*, 5:344–350.
- Jell, P.A., 1997, Early Carboniferous Ophiuroids from Crawfordsville, Indiana: *Journal of Paleontology*, v. 71, p. 306–316, doi:10.1017/s0022336000039214.
- Jell, P.A., 2014, A Tremadocian asterozoan from Tasmania and a late Llandovery edrioasteroid from Victoria. *Alcheringa: An Australasian Journal of Palaeontology*, doi, p. 1080/03115518.2014.911642.

- Horowitz, A.S., and Kelly, S.M., 1987, The Chesterian section near Sulphur, Indiana: Boulder, Colorado, Geological Society of America, Centennial Field Guide, North-Central Section, p. 387-390.
- Horowitz, A.S., Mamet, B.L., Neves, R. Potter, R.E. and Rexroad, C.B., 1979, Carboniferous paleontological zonation and inter-continental correlation of the Fowler No. 1 Traders core, Scott County, Tennessee, U.S.A.: *Southeastern Geology*, v. 20, p. 205-228.
- Jagt, J.W.M., 2000, Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium – Part 3: Ophiuroids. With a chapter on Early Maastrichtian ophiuroids from Rügen (northeast Germany) and Møn (Denmark) by Manfred Kutscher & John W. M. Jagt. *Scripta Geologica*, p. 121, 1–179.
- Kelly, S.M., 1984, Paleocology and paleontology of the Indian Springs Shale Member, Big Clifty Formation (middle Chesterian) in south-central Indiana [Ph.D. thesis]: Bloomington, Indiana University, p. xix – 343.
- Kerr, T. J. V. and Twitchett, R. J., 2004, Experimental decay and disarticulation of *Ophiura texturata*: implications for the fossil record of ophiuroids: Echinoderm: Munchen: Proceedings of the 11th International Echinoderm Conference, 6-10 October 2003, Munich, Germany, p. 439–446.
- Kesling, R.V., 1970, *Drepanaster wrighti*, a new species of brittle–star from the Middle Devonian Arkona shale of Ontario: Contributions from the Museum of Paleontology, The University of Michigan, 23, p. 73–79

- Kesling, R. V. and Le Vasseur, D., 1971, *Strataster ohioensis*: A new early Mississippian brittle-star, and the paleoecology of its community: Contributions from the Museum of Paleontology, University of Michigan, 23, p. 305–341, pls 1–13.
- Klein, J. T., 1734, *Naturlis dispositio echinodermatum: Accessit lucubrationum de aculeis echinorum marinarum, cum spicilegio de belemnitis. Tab. I-XXXV. Gedani.*
- Klein, G. deV., 1977, *Clastic tidal facies: Champaign, Illinois, Continuing Education Publication Company*, p. 149.
- Liao, Z.T. and Wang, X.J., 2002, Fossil ophiuroids from Tongziyan Formation (Middle Permian) in Longyan, Fujian: *Acta Palaeontologica Sinica*, 41 (3): p. 396–402.
- Martynov, A., 2010a, Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae: *Zootaxa*, 2697, p. 1–154.
- Martynov, A., 2010b, Structure of the arm spine articulation ridges as a basis for taxonomy of Ophiuroidea (a preliminary report): In: Harris, L., Böttger, S.A., Walker, C.W. & Lesser, M.P. (Eds.), *Echinoderms: Durham. Proceedings of the 12th International Echinoderm Conference, Durham, New Hampshire, USA, 7-11 August 2006*. CRC Press, Taylor & Francis, Boca Raton, London, New York, Leiden, p. 233–239.
- Matsumoto, H., 1915, A new classification of the Ophiuroidea: with descriptions of new genera and species: *Proceedings of the Academy of Natural Sciences of Philadelphia*, 67: p. 43–92.

- Matsumoto, H., 1929, Outline of the classification of the Echinodermata: Science Reports of the Tokyo Imperial University, 2nd ser. (Geology), 13 (2): p. 27–33.
- Miller, S.A., 1889, North American Geology and Palaeontology for the use of Amateurs, Students, and Scientists: Press of Western Methodist Book Concern, Cincinnati, Ohio, p. 664.
- Miller, S.A. and Gurley, W.F.E., 1891, Description of some new genera and species of Echinodermata from the Coal Measures and Subcarboniferous rocks of Indiana, Missouri, and Iowa: In: W.F.E Gurley (ed.), Indiana Department of Geology and Natural Resources, Danville, Illinois, 16th Annual Report, p. 327–373.
- Müller, J. and Troschel, F.H., 1840, Über die Gattungen der Ophiuren: Archiv für Naturgeschichte, 6: 327–330.
- Nelson, W. J., Smith, L. B., Tregworgy, J. D., Keith, B. D., & Furer, L. C., 2002, Sequence Stratigraphy of the Lower Chesterian (Mississippian) Strata of the Illinois Basin: Illinois State Geological Survey, Bulletin 107.
- O’Hara, T.D., Hugall, A.F., Thuy, B., and Moussalli, A., 2014, Phylogenomic Resolution of the Class Ophiuroidea Unlocks a Global Microfossil Record: Current Biology, v. 24, p. 1874–1879, doi:10.1016/j.cub.2014.06.060.
- O’Hara, T.D., Hugall, A.F., Thuy, B., Stöhr, S., and Martynov, A. V., 2016, Restructuring higher taxonomy using broad-scale phylogenomics: The living Ophiuroidea: Molecular Phylogenetics and Evolution, v. 107, p. 415–430, doi:10.1016/j.ympev.2016.12.006.
- Shaver, R. H., Ault, C. H., Burger, A. M., Carr, D. D., Droste, J. B., Eggert, D. L., Gray,

- H. H., Harper, D. , Hasenmueller, N. R., Hasenmueller, W. A., Horowitz, A. S., Hutchison, H. C., Keith, B. , Keller, S. J., Patton, J. B., Rexroad, C. B., Wier, C. E., 1986, Compendium of Paleozoic rock-unit stratigraphy in Indiana—a revision: Indiana Geological Survey Bulletin 59, p. 203, 2 fig., 2 pl.
- Shackleton, J.D. 2005. Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *Journal of Systematic Palaeontology*, v. 3, p. 29-114.
- Smith, N.S., and Sumrall, C.D., 2019, A Comparison of Brittle Star (Ophiuroidea: Echinodermata) Biodiversity from the Upper Mississippian (Chesterian) Big Clifty Fm. in Sulphur, IN and Glen Dean Fm. in Hopkinsville, KY: *Abstracts with Programs*, Geological Society of America, Boulder, CO: Geological Society of America (GSA) Southeastern Section Meeting, Charleston, SC.
- Spencer, W. K., 1934, The British Palaeozoic Asterozoa: Palaeontographical Society of London Monograph, Pt. 9 (for 1933), p. 437–494.
- Spencer, W.K., 1951, Early Palaeozoic starfish: *Philosophical Transactions of the Royal Society, London, Ser. B*, 235: p. 87-129.
- Spencer, W.K., Wright, C.W., 1966, Asterozoans. In: Moore, R.C. (Ed.): *Treatise on Invertebrate Paleontology. Part U. Echinodermata. 3. Asterozoa-Echinozoa*. Geological Society of America and University of Kansas Press, Kansas, p. U4–U107.
- Sprinkle, J., 1980, An overview of the fossil record, in T.W. Broadhead and J.A. Waters (eds.): *Echinoderms, Notes for a Short Course*: University of Tennessee, Department of Geological Sciences, Studies in Geology, 3, p. 15-26.

- Stöhr, S. (2005) Who's who among baby brittle stars (Echinodermata: Ophiuroidea): postmetamorphic development of some North Atlantic forms. *Zoological Journal of the Linnean Society*, 143, 543–576.
- Stöhr, S., 2012, Ophiuroid (Echinodermata) systematics—where do we come from, where do we stand and where should we go?: *Zoosymposia*, 7(1), p. 147–162.
<https://doi.org/10.11646/zoosymposia.7.1.14>.
- Stöhr, S., O'Hara, T.D., and Thuy, B., 2012, Global Diversity of Brittle Stars (Echinodermata: Ophiuroidea): PLoS ONE, v. 7, doi:10.1371/journal.pone.0031940.
- Stöhr, S. and Thuy, B., 2016, Bridging the gap between now and then: a morphological tree of brittlestars: *Systematikdagarna*, doi:10.13140/RG.2.2.29249.97121.
- Štorc, R. & Žítt, J., 2008, Late Turonian ophiuroids (Echinodermata) from the Bohemian Cretaceous Basin, Czech Republic. *Bulletin of Geosciences*, 83(2), 123–140.
- Stürtz, B., 1900, Ein weiter Beitrag zur Kenntnis palaeozoischer Asteroiden: *Verhandlungen des naturhistorischen vereins der preussischen Rheinlande und Westfalens*, 56: p. 176-240.
- Thuy, B., 2015, Unravelling the origin of the euryalid brittle stars: A preliminary report: *Progress in Echinoderm Palaeobiology*, p. 185–188.
- Thuy, B., Kutscher, M., and Plachno, B.J., 2015, A new brittle star from the early Carboniferous of Poland and its implications on Paleozoic modern-type ophiuroid systematics: *Acta Palaeontologica Polonica*, v. 60, p. 923–929,
doi:10.4202/app.00093.2014.
- Thuy, B., and Stöhr, S., 2011, Lateral arm plate morphology in brittle stars

(Echinodermata: Ophiuroidea): New perspectives for ophiuroid micropalaeontology and classification: *Zootaxa*, v. 47, p. 1–47.

Thuy, B., and Stöhr, S., 2016, A new morphological phylogeny of the Ophiuroidea (Echinodermata) accords with molecular evidence and renders microfossils accessible for cladistics: *PLoS ONE*, v. 11, p. 1–26, doi:10.1371/journal.pone.0156140.

Thuy, B., and Stöhr, S., 2018, Unravelling the origin of the basket stars and their allies (Echinodermata, Ophiuroidea, Euryalida): *Scientific Reports*, v. 8, p. 1–14, doi:10.1038/s41598-018-26877-5.

Thuy, B., Hagdorn, H., and Gale, A.S., 2017, Paleozoic echinoderm hangovers: Waking up in the Triassic: *Geology*, v. 45, p. 531–534, doi:10.1130/G38909.1.

Wu, Q., 1980, First discovery of an upper Permian ophiuroid in Fujian: *Acta Palaeontologica Sinica* 19 (1): 61–62.

Zittel, von K.A., 1895, *Grundzüge der Palaeontologie (Palaeozoologie)*: R. Oldenbourg, München & Leipzig, p. 971.

Appendix

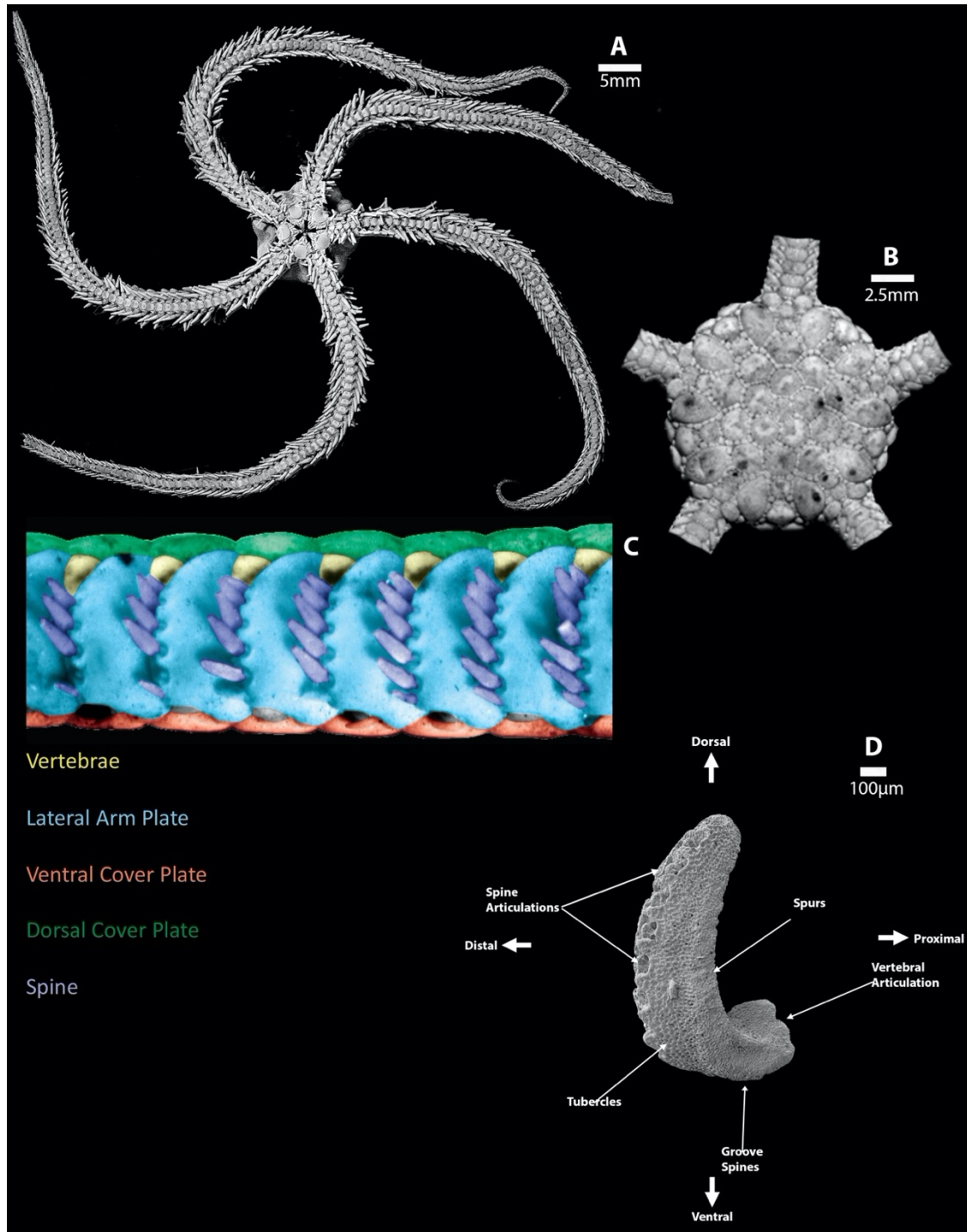
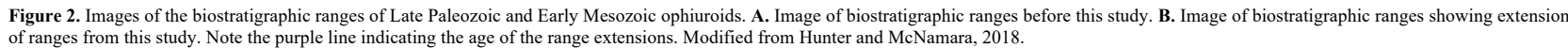


Figure 1. Ophiuroid body and arm morphology. **A.** Photograph of whole specimen of the ophiuroid *Ophiotrix* sp. in ventral view. **B.** Photograph of the central disk of the ophiuroid *Ophiura* sp. in dorsal view. **C.** Detail of the arm morphology of the ophiuroid *Ophiura* sp. **D.** Morphology of the holotype specimen of SULOPH005, *Furcaster wardi* sp. nov., right lateral arm plate from the proximal part of the arm in external view.



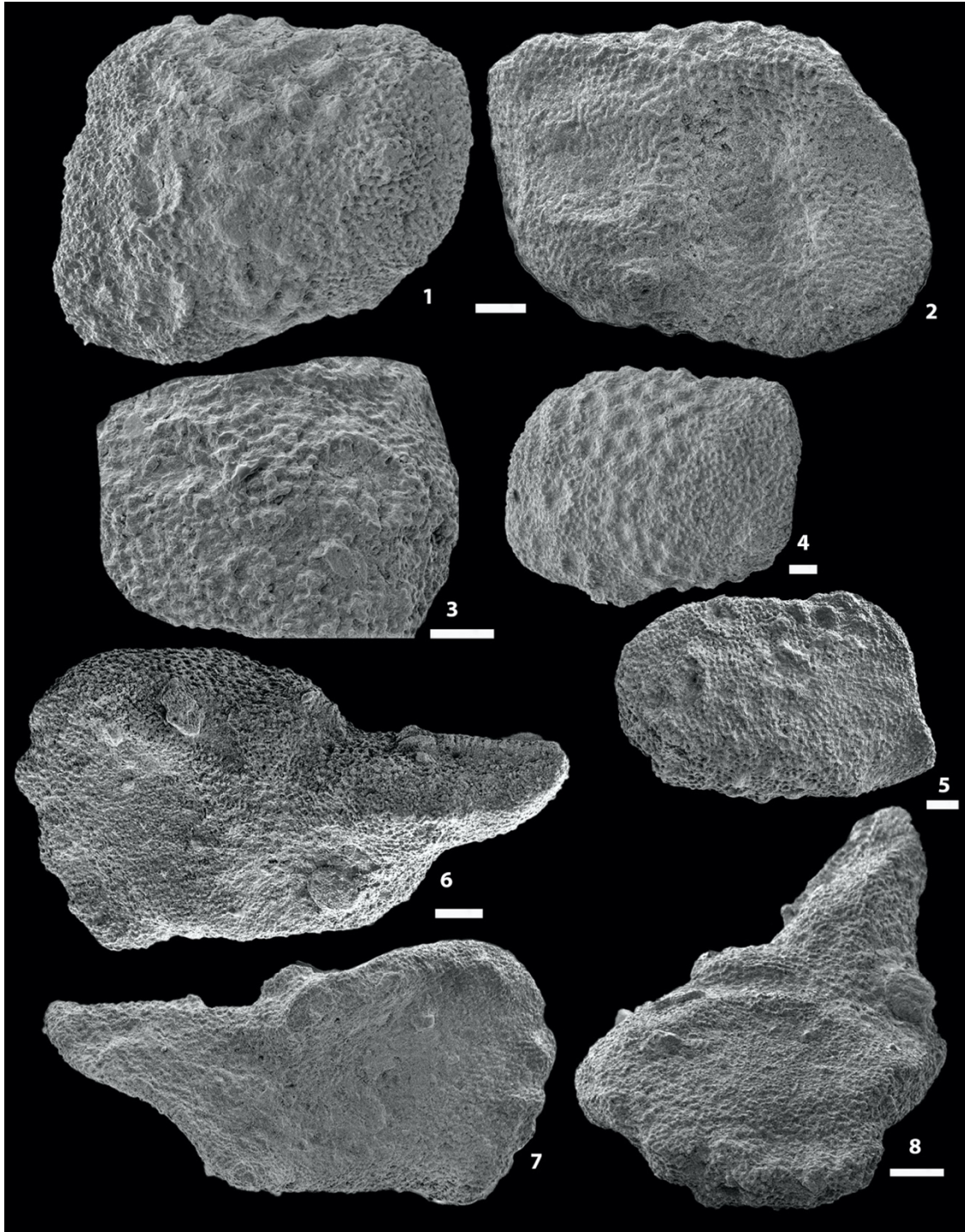


Figure 3. Lateral arm plates of ophiuroids SULOPH001 – SULOPH003 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN. **1-5.** protasterid species A **1-3.** Specimen SULOPH001, right lateral arm plate from the proximal part of the arm in (1) external view, (2) internal view, and (3) detail of spine articulations. **4.** Specimen SULOPH002, right lateral arm plate from the median part of the arm in external view. **5.** Specimen SULOPH003, right lateral arm plate from the distal part of the arm in external view. **6-8.** *Vandeloaster* sp. ident., specimen SULOPH004, left lateral arm plate from the proximal part of the arm in (6) external view, (7) internal view, and (8) distal horizontal view with detail of spine articulations. Scale bars represent 100µm.

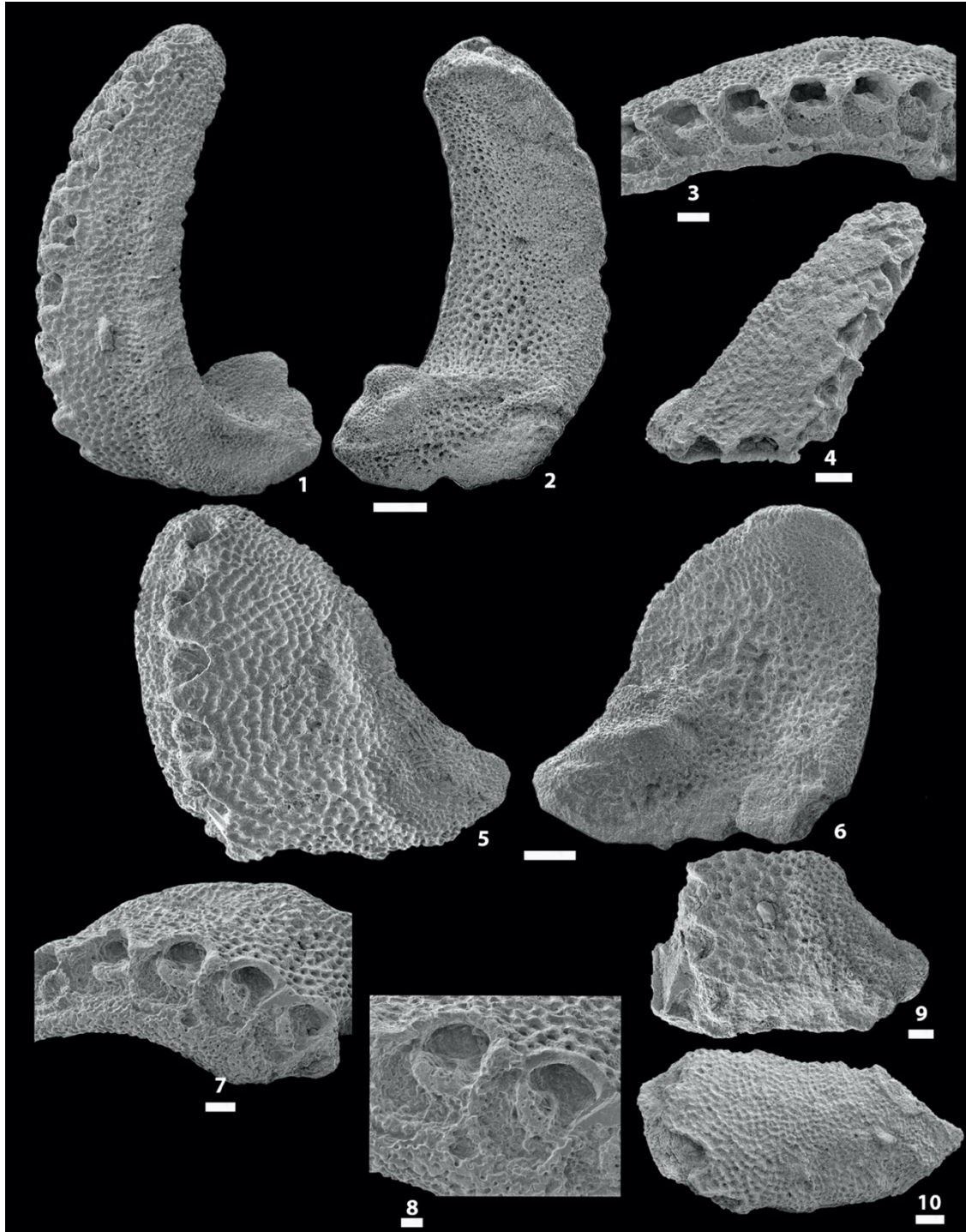


Figure 4. Lateral arm plates of ophiuroids SULOPH005 – SULOPH009 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN. **1-4.** *Furcaster wardi* sp. nov. **1-3.** Holotype specimen of SULOPH005, right lateral arm plate from the proximal part of the arm in (1) external view, (2) internal view, and (3) detail of spine articulations. **4.** Paratype specimen SULOPH006, left lateral arm plate from the distal part of the arm in external view. **5-10.** *Furcaster crispisulcans* sp. nov. **5-8.** Holotype specimen SULOPH007, right lateral arm plate from the proximal part of the arm in (5) external view, (6) internal view, and (7-8) detail of spine articulations. **9.** Paratype specimen, SULOPH008, right lateral arm plate from the median part of the arm in external view. **10.** Paratype specimen SULOPH009, right lateral arm plate from the distal part of the arm in external view. Scale bars represent 100µm.

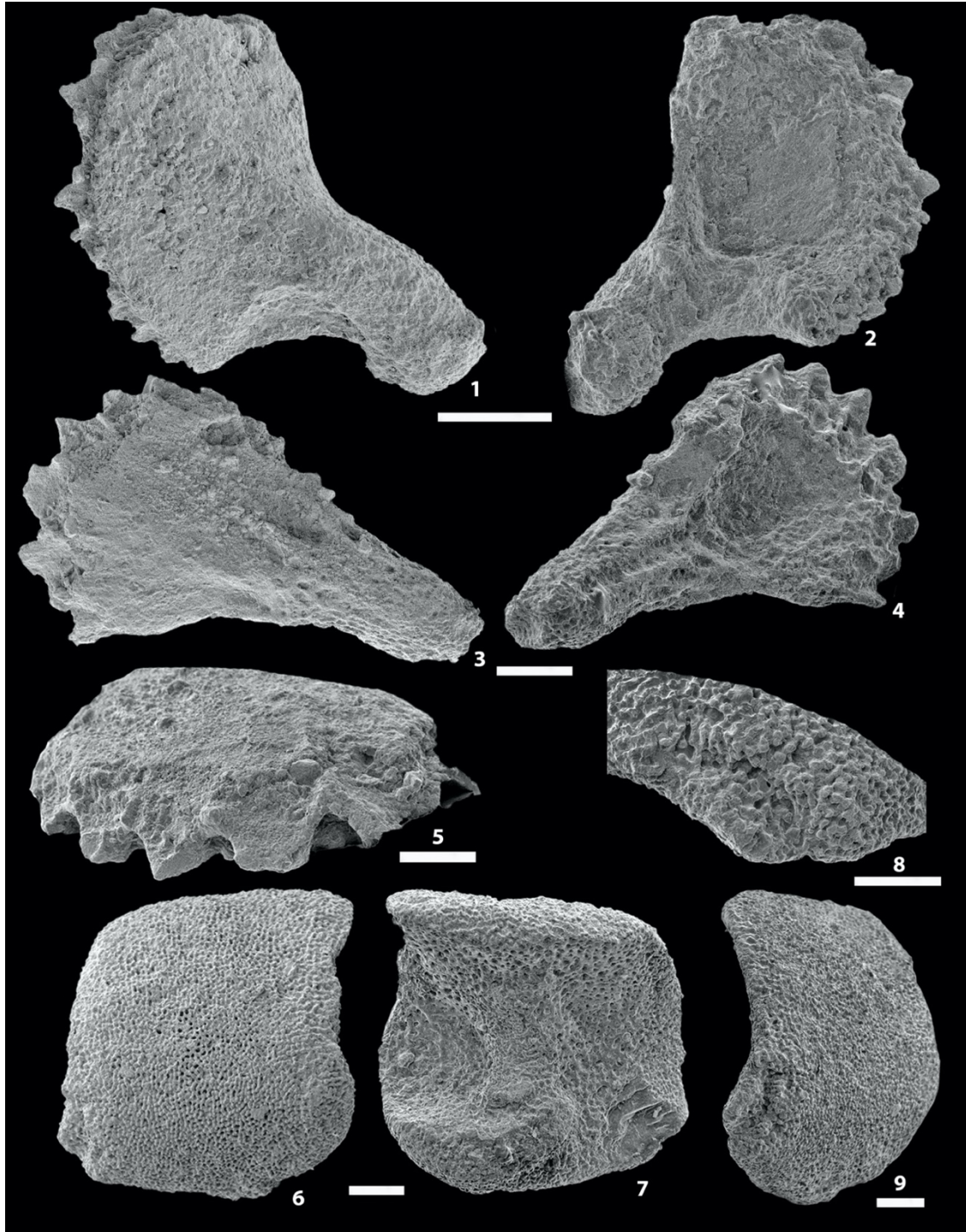


Figure 5. Lateral arm plates of ophiuroids SULOPH010 – SULOPH012 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN. **1-5.** *Umerophiura daki* sp. nov. **1-2.** Holotype specimen SULOPH010, right lateral arm plate from the proximal part of the arm in (1) external view and (2) internal view. **3-5.** Paratype specimen SULOPH011, right lateral arm plate from the median/distal part of the arm in (3) external view, (4) internal view, and (5) detail of spine articulations. **6-9.** *Aganaster monoceros* sp. nov., holotype specimen SULOPH012, right lateral arm plate from the proximal part of the arm in (6) external view, (7) internal view, (8) detail of spine articulations, and (9) in distal lateral view. Scale bars represent 100µm.

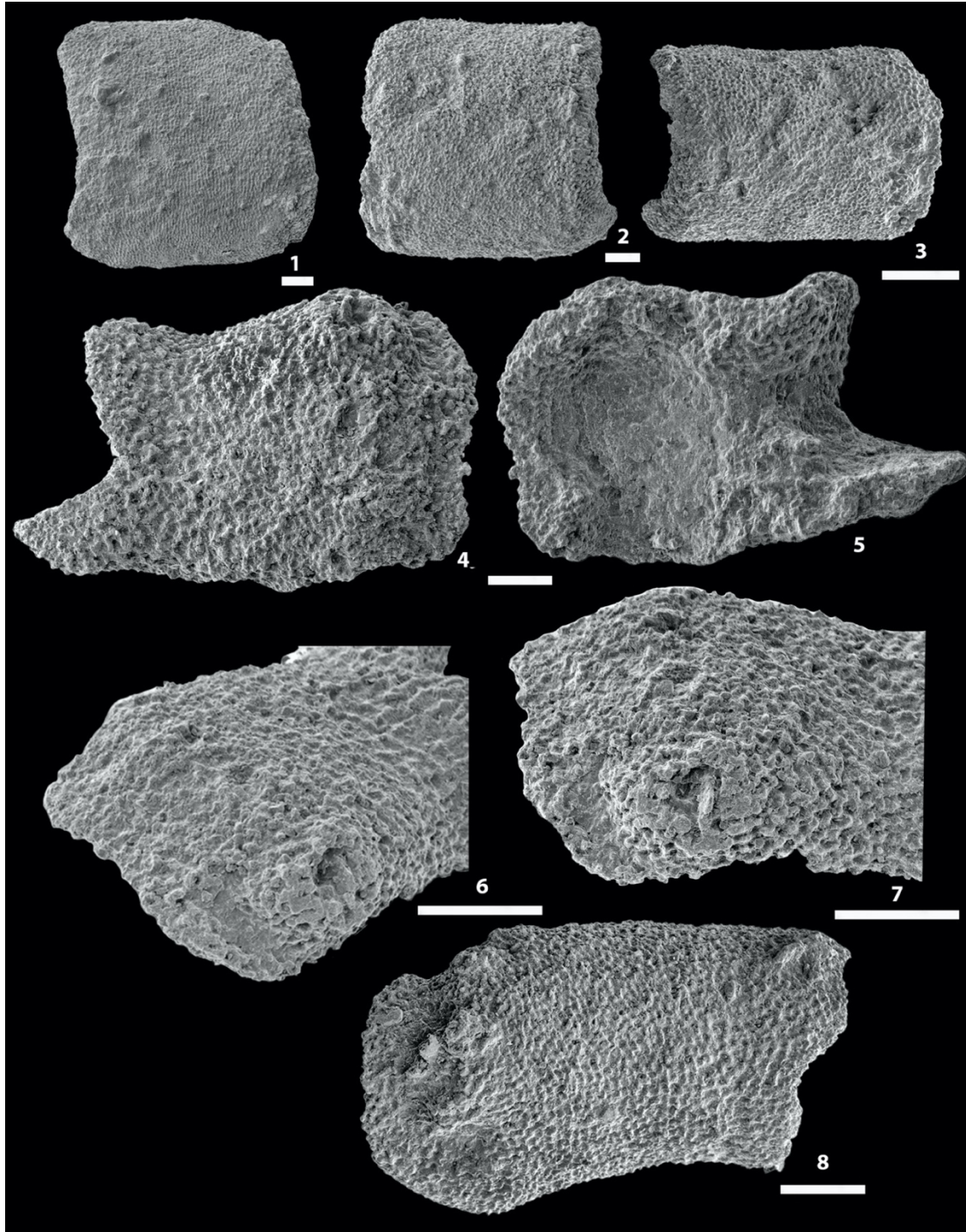


Figure 6. Lateral arm plates of ophiuroids SULOPH013 – SULOPH017 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN. **1-3.** *Aganaster monoceros* sp. nov. **1.** Paratype specimen SULOPH013, left lateral arm plate from the median part of the arm in external view. **2.** Paratype specimen SULOPH014, right lateral arm plate from the median/distal part of the arm in external view. **3.** Paratype specimen SULOPH014, right lateral arm plate from the distal part of the arm in external view. **4-8.** *Sulphaster solus* gen. nov. and sp. nov. **4-7.** Holotype specimen SULOPH016, right lateral arm plate from the proximal part of the arm in (4) external view, (5) internal view, (6) distal lateral view with detail of spine articulations, and (7) external view with detail of spine articulations. **8.** Paratype specimen SULOPH017, left lateral arm plate from the median/distal part of the arm in external view. Scale bars represent 100µm.

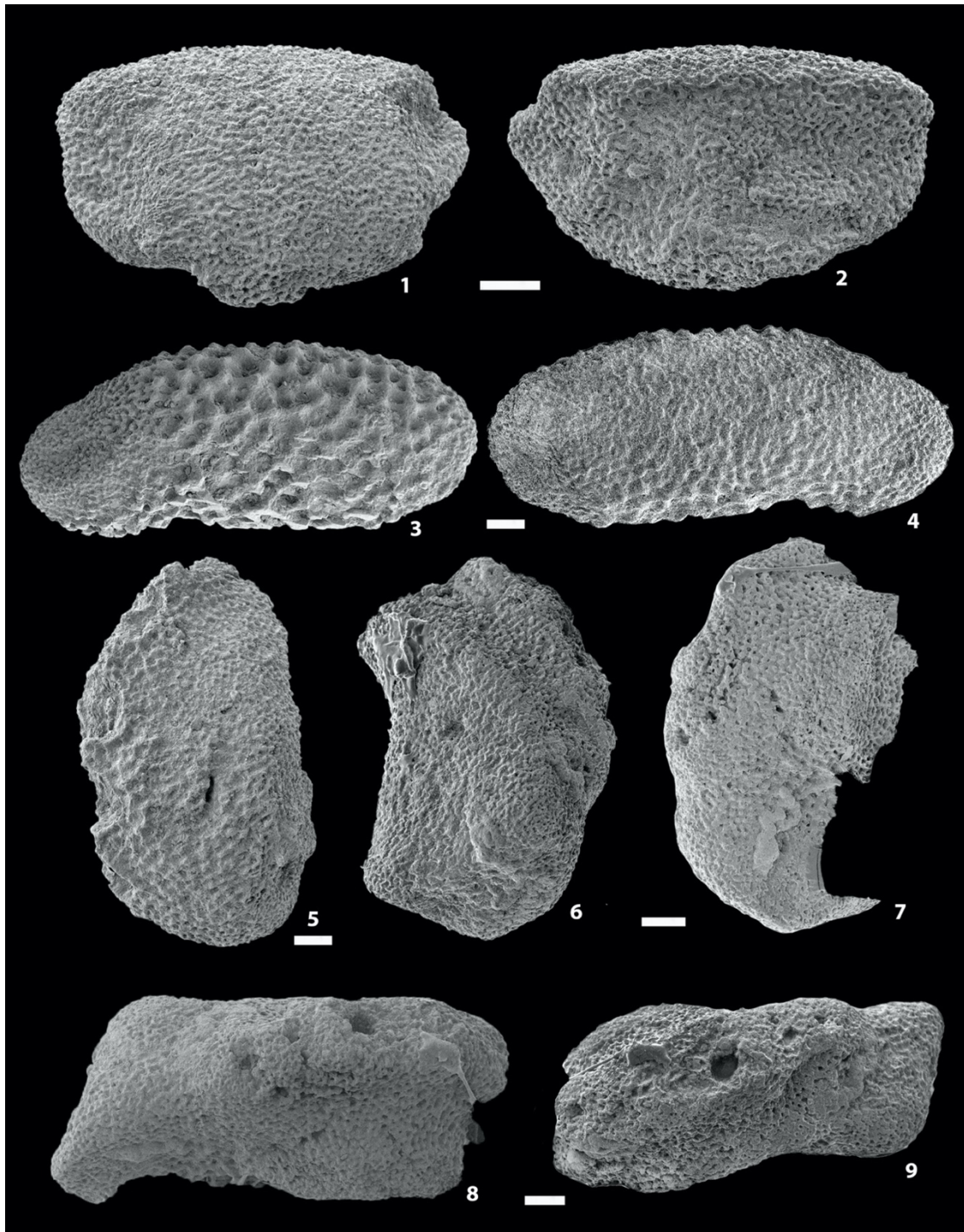


Figure 7. Lateral arm plates of ophiuroids SULOPH018 – SULOPH021 from the Indian Springs Shale Mb. of the Big Clifty Fm., Sulphur, IN. **1-2.** Lateral arm plate incertae sedis type 1, SULOPH018, in (1) external view and (2) internal view. **3-4.** Lateral arm plate incertae sedis type 2, SULOPH019, in (1) external view and (2) internal view. **5.** Lateral arm plate incertae sedis type 3, SULOPH020, in external view. **6-9.** Lateral arm plate incertae sedis type 4, SULOPH021, in (6) external view, (7) internal view, and (8-9) detail of spine articulations. Scale bars represent 100µm.

CONCLUSION

Reliance on the traditional paleontological method of describing wholly articulated skeletons has diminished our understanding of Late Paleozoic brittle star biodiversity. Methods established with studies on Mesozoic and Cenozoic brittle stars describing morphologically rich microscale skeletal elements called lateral arm plates have shown promise toward a more complete understanding of these historically important animals. These skeletal elements can be assigned to genera and species which can be utilized to help fill in missing gaps within their evolutionary history, used to expand our knowledge of time periods where fully articulated skeletons have been previously found, and used in future paleobiogeographic, evolutionary history, and paleoecological studies of brittle stars. In the future, it is imperative that scientists studying these organisms pay attention to the microscale detail in order to get the full picture both ecologically and morphologically. By studying the fine details of brittle star arm morphologies, we can expand our knowledge of Late Paleozoic brittle star biodiversity and provide a truer picture of brittle star biodiversity.

VITA

Nick Smith was born in Rome, Georgia in 1987. He received his B.S. in geology with a minor in geography and biology from the University of West Georgia in May 2018.

While at the University of Tennessee, Nick worked under the guidance of Dr. Colin Sumrall examining Late Paleozoic brittle star biodiversity. His research has been funded by numerous internal and external grants and has been presented at multiple national scientific meetings. Nick is graduating with a Master of Science in geology in December 2020 and will be staying at the University of Tennessee to pursue his Ph.D. in geology.